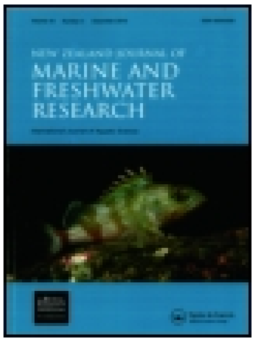

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Common bivalve larvae from New Zealand: Leptonacea

J. D. Booth

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Common bivalve larvae from New Zealand: Leptonacea

J. D. BOOTH*

Marine Laboratory, Department of Zoology, Victoria University of Wellington, Wellington, New Zealand

The late stage larvae of three erycinid bivalves (Mollusca: Pelecypoda: Leptonacea) taken from the brood chamber of the adult are described (*Kellia cycladiformis, Lasaea rubra hinemoa,* and *L. maoria*), and the provisionally identified late stage larva of the erycinid *Arthritica bifurca* taken from the plankton is described. Also, the D-shaped larvae of the erycinid bivalves *Kellia cycladiformis, Borniola reniformis, Arthritica crassiformis,* and *A. bifurca* taken from the parent brood chamber are described. The seasonal occurrence of each late stage larva in the plankton at the Bay of Islands (35° 15′S, 174° 10′E), Wellington Harbour (41° 16′S, 174° 51′E), and Raumati Beach (40° 56′S, 174° 58′E), New Zealand is described. Aspects of the reproductive cycles of *Lasaea rubra hinemoa* and *Arthritica bifurca* are presented.

INTRODUCTION

This is the third paper in a series (Booth 1977, 1979) on the common bivalve larvae recovered from plankton samples taken at the Bay of Islands, Wellington Harbour, and Raumati Beach, New Zealand during 1970–72 (Booth 1972). The paper deals with the larvae of six leptonacean (= erycinacean) species: Family Erycinidae — *Kellia cycladiformis* (Deshayes), *Lasaea rubra hinemoa* Finlay, *L. maoria* (Powell), *Borniola reniformis* (Suter), *Arthritica crassiformis* Powell, and *A. bifurca* (Webster).

The late stage pelagic veligers (veliconchae) and pediveligers of *Kellia cycladiformis* and *Arthritica bifurca* are described (but, for *A. bifurca,* the description and identification remain only provisional) and the seasonal occurrences of both species of larvae in the plankton are outlined. Other larvae described are the D-shaped larvae of *Kellia cycladiformis, Borniola reniformis, Arthritica crassiformis,* and *A. bifurca,* and the late stage larvae and postlarvae of *Lasaea rubra hinemoa* and *L. maoria.* Also presented are aspects of the reproductive cycle of *L. rubra hinemoa* and *Arthritica bifurca.*

All these species incubate their larvae to some extent. Where descriptions are based on larvae removed from the parent brood chamber, the larval identifications are positive (*Kellia cycladiformis, Lasaea rubra hinemoa,* and *L. maoria* late stage larvae; *Kellia cycladiformis Borniola reniformis, Arthritica crassiformis,* and *A. bifurca* D-shaped larvae), but identification of larvae collected from the plankton must remain tentative until the species have been grown in the laboratory (*A. bifurca* late stage larva).

No New Zealand leptonacean larvae have hitherto been described, although several overseas species have received attention. Jorgensen (1946) and Rees (1950) noted, in particular, that the hinge lacked a true provinculum, although the straight edge of the hinge of larger larvae may appear rough or corrugated, thereby giving the impression of feebly developed teeth. Chanley & Chanley (1970) emphasised the difficulties in identifying pelagic erycinacean (= leptonacean) larvae, and summarised the usual larval features of this group; long hinge line, umbo appears late in development and remains low and rounded; larvae more laterally compressed, paler, and attain a larger pelagic size than most other bivalve larvae.

The incubatory habit within the genus *Kellia* is well known (Lebour 1938, Howard 1953, Oldfield 1964), with the larvae being released at a small size (60–120 μm) in *K. suborbicularis* and *K. laperousi.* In the genus *Lasaea,* the free veliger stage has been suppressed; the young are liberated as miniature adults (Oldfield 1955, 1964). Ponder (1967) recognised the incubatory habit of *Borniola reniformis,* with the small veligers closely resembling "those of *Kellia (suborbicularis)*." The incubation of *Arthritica crassiformis* larvae to a length of at least 109 μm has been documented by Ponder (1965), and Wear (1966) pointed out the incubation of *A. bifurca* larvae "at least to the shelled prodissoconch stage."

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*Present address: *Fisheries Research Division, Ministry of Agriculture and Fisheries, P.O. Box 19062, Wellington, New Zealand*
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Although bivalves of the superfamily Leptonacea are well represented in New Zealand (Ponder 1971), and are numerically the commonest bivalves on the shore (Morton & Miller 1968), there is relatively little information on the distribution and ecology of the adults. *Kellia cycladiformis* (= *Marikellia rotunda*) is widespread throughout New Zealand (F. M. Climo, National Museum, Wellington, pers. comm.), mainly inhabits intertidal rock crevices (Morton & Miller 1968), and reaches at least 18 mm in length. *Lasaea rubra hinemoa* is a small bivalve (up to 4.6 mm in length) occurring throughout New Zealand, but is most abundant towards the south (Ponder 1971). It usually occurs in crevices or amongst barnacles or mussels in moist, low light conditions, and most commonly near low tide. *Lasaea maoria* is a bivalve of similar size and lives only in moist, dark conditions, and occurs as far south as Cook Strait (Ponder 1971). *Borniola reniformis* is also a small bivalve (up to 7 mm in length), "moderately common . . . at low tide in clean, coastal situations" throughout New Zealand and to a depth of at least 190 m (Ponder 1967). *Arthritica crassiformis* (up to 5.4 mm in length) occurs commensally with the rock-boring bivalve *Barnea* (= *Anchomasa*) *similis*, at least throughout the North Island (Ponder 1965, Morton 1973). *Arthritica bifurca*, a bivalve of similar size, occurs free-living in mud or muddy sand, though probably not deeper than 190 m (Ponder 1965), and also in association with the tubeworm *Pectinaria australis* according to Wear (1966). Observations made in Bay of Islands estuaries (Table 2, also Booth 1972) suggest that in this area at least, the species is common in its free-living mode, and it was not found in association with the *P. australis* present.

SAMPLING AREAS AND METHODS

Details of the plankton sampling programme, including the areas, times, and methods have been described by Booth (1974, 1975, 1977). In brief, three plankton stations were occupied in the Bay of Islands (35° 15'S, 174°10'E) (Apr 1970 – Dec 1971), four in Wellington Harbour (41°16'S, 174°51'E) (May 1970 – Feb 1972) and four at Raumati Beach (40°56'S, 174° 58'E) (Jun 1971 – Jun 1972); the positions of these stations are given in Booth (1977; figs 1 & 2). Details of the hydrology of the Bay of Islands and Wellington Harbour during the sampling period are given in Booth (1974, 1975). Plankton sampling was carried out at approximately monthly intervals with a 120 μm mesh, free-fall net.

Descriptions of larvae use the terminology of Ockelmann (1965) and Chanley & Andrews (1971) for most features, and of Rees (1950) in particular for hinge characters. Terminology relating to the incubatory habit of the species considered is derived from Ockelmann (1965) and Chanley (1969). The dimensions given for pelagic late stage larvae (which, in this study, refer to both late veliger and pediveliger stages) are the range of sizes of larvae most often observed in the plankton samples. Dimensions for incubated larvae are the range of sizes observed at particular stages of development. Hinge line length is the length of the straight edge section of the hinge; other details relating to the descriptions of larvae are noted in Booth (1977).

Adults were collected at various times of the year to obtain incubated larvae. For *Kellia cycladiformis*, a group of adults and juveniles (individuals measured 8 mm, 5 mm, 3 mm, 2 mm, and 1 mm in length) and several pediveligers, all linked by byssal threads, were removed from an empty *Mytilus edulis aoteanus* shell in the low midlittoral zone at Wairoa Bay, near Waitangi, Bay of Islands on 28 October 1970. The largest adult was incubating 12 late stage larvae. In addition, three adults 8 mm long examined at the National Museum, Wellington contained numerous D-shaped larvae. These were collected in March 1976 at Whangarei Heads and D'Urville Island.

Forty adults of *Lasaea rubra hinemoa* (most appearing to be of the *vexata* type — see Ponder 1971) greater than 1.5 mm in length were collected at Wairoa Bay approximately monthly from February 1971 to May 1972. A total of 27 adults of *L. maoria* were collected at Eastbourne, Wellington Harbour on 21 January and 30 March 1972. Forty-five adults of *Borniola reniformis* over 4.0 mm long were collected at Wairoa Bay, Bay of Islands during 1971. Forty adults of *Arthritica crassiformis* more than 2.5 mm long were taken at Te Puna, Bay of Islands, on 12 January and 17 May 1972 from beds of the pholad *Barnea similis*. Thirty to forty adults of *A. bifurca* more than 2.5 mm long were taken approximately monthly at Petone Beach from October 1971 to October 1972 from their association with the tube worm *Pectinaria australis*.

LARVAL DESCRIPTIONS, SEASONAL OCCURRENCE, AND NOTES ON THE BREEDING CYCLE OF SOME ADULTS

The seasonal occurrences of each pelagic late stage larva that was found in significant numbers in the Bay of Islands and Wellington Harbour are presented on a modified log scale (Figs 2 & 8). The occurrence of each species expressed as a percentage of the total number of the 20 most abundant species of late stage bivalve larvae present is given in Fig. 9. The occurrences of larvae at Raumati Beach are given in Table 1.

The occurrence and abundance of the adult bivalve species in the sampling localities are outlined in Table 2.

Kellia cycladiformis (Deshayes) (Figs 1, 2, & 9, Tables 1-3)

DIMENSIONS. Incubated D-shaped larvae 80–130 μm in length; average length to height ratio 1:0.73 and ratio of length of larva to length of hinge line 1:0.73. Larvae from any one adult were about equal in size and appeared to be at the same stage of development. Pelagic late stage larvae measured 330–360 μm in length, average length to height ratio 1:0.82 and ratio of length of larva to length of hinge line 1:0.25.

Late stage larvae removed from the brood chamber of an adult *K. cycladiformis* (8 mm long) at Wairoa Bay on 28 October 1970 measured 350 μm in length and all had a well developed foot.

SHAPE (Fig. 1). D-shaped larva has a skewed form, pointed ends and a rounded ventral margin. In the late stage larva, the umbos are equal in size, broadly rounded and inconspicuous; anterior end is much longer than the posterior end; posterior shoulder slopes more steeply than anterior shoulder, although both are rounded; ventral margin is long and broadly rounded.

HINGE (Fig. 1). In larva 340 μm in length, the hinge has no true provinculum (as defined by Rees 1950), although the straight edge does bear many very small, feebly developed serrations. As far as could be determined, the ligament attachment point lies behind and towards posterior end of straight edge of hinge.

OTHER FEATURES (Fig. 1). In the late stage larva, the prodissoconch 1 shell, with its more punctate texture, is clearly delineated from prodissoconch 2 shell, when observed under Nomarski differential interference contrast (DIC). However, prodissoconch 1 shell lacks the radial striae described for leptonacean (= erycinacean) larvae by Rees (1950), although prodissoconch 2 shell does have both radial striae and fine concentric lamellae. An outer, thickened, dark zone is usually seen in larvae over 330 μm in length. Both the prodissoconch 2 shell shape and the outer zone are clearly seen in the early dissoconch shell (Fig. 1 middle right) removed from the *Mytilus edulis aoteanus* shell.

Oil droplets are frequently observed in the digestive gland region of the late stage larva. The larva tends to become darker grey in appearance with increasing size. There is no visible eyespot.

COMPARISON WITH OTHER SPECIES. The late stage larva resembles in shape the leptonacean *Montacuta ferruginosa* described by Jorgensen (1946), Rees (1950), and Gage (1966), but not *Kellia suborbicularis* described by Lebour (1938) and Gage (1966).

DISTRIBUTION AND SEASONAL ABUNDANCE (Figs 2 & 9, Tables 1–3). The late stage larva, as well as the adults of *K. cycladiformis*, occurred at all sampling localities.

At the Bay of Islands, the larva occurred mainly at the inner stations (Confluence and Brampton Reef) throughout the year except for a short period during autumn.

In Wellington Harbour it occurred much less commonly, but again throughout most of the year, with peaks in late autumn and early winter 1971.

At Raumati Beach, the larva occurred throughout the year, except during spring. These results suggest that spawning and release of larvae in *K. cycladiformis* occur nearly throughout the year, with peaks at different seasons according to locality.

Lasaea rubra hinemoa Finlay (Figs 3 & 4, Tables 1–3)

DIMENSIONS. Incubated young were observed up to 580 μm in length; average length to height ratio 1:0.76 and ratio of length of larva to length of hinge line 1:0.50 at Wairoa Bay, Bay of Islands during 1971–72. Ponder (1971) reported the prodissoconch to reach 500–600 μm in diameter.

SHAPE (Fig. 3). Late stage larva and postlarva have a skewed D-shaped form with posterior shoulder sloping more steeply than the longer anterior shoulder; anterior end blunt, almost flat; posterior end curves rapidly ventrally; ventral margin gently rounded, almost straight.

OTHER FEATURES (Fig. 3). The shell is colourless and transparent during incubation, and has widely separated concentric lamellae which are clearly visible under Nomarski DIC (Fig. 3, right). The shell thickens, develops a reddish-brown tinge, particularly around the hinge, and the concentric lamellae become more marked just prior to release. There is no visible eyespot.

COMPARISON WITH OTHER SPECIES. The larva and postlarva closely resemble the shape and dimensions of *L. rubra* described by Oldfield (1955, 1964) which, like *L. rubra hinemoa,* are also released as "miniature adults.'

DISTRIBUTION AND SEASONAL OCCURRENCE (Tables 1–3). The postlarva of *L. rubra hinemoa* was taken only very occasionally in the plankton at the Bay of Islands, providing further evidence that larval development is not pelagic.

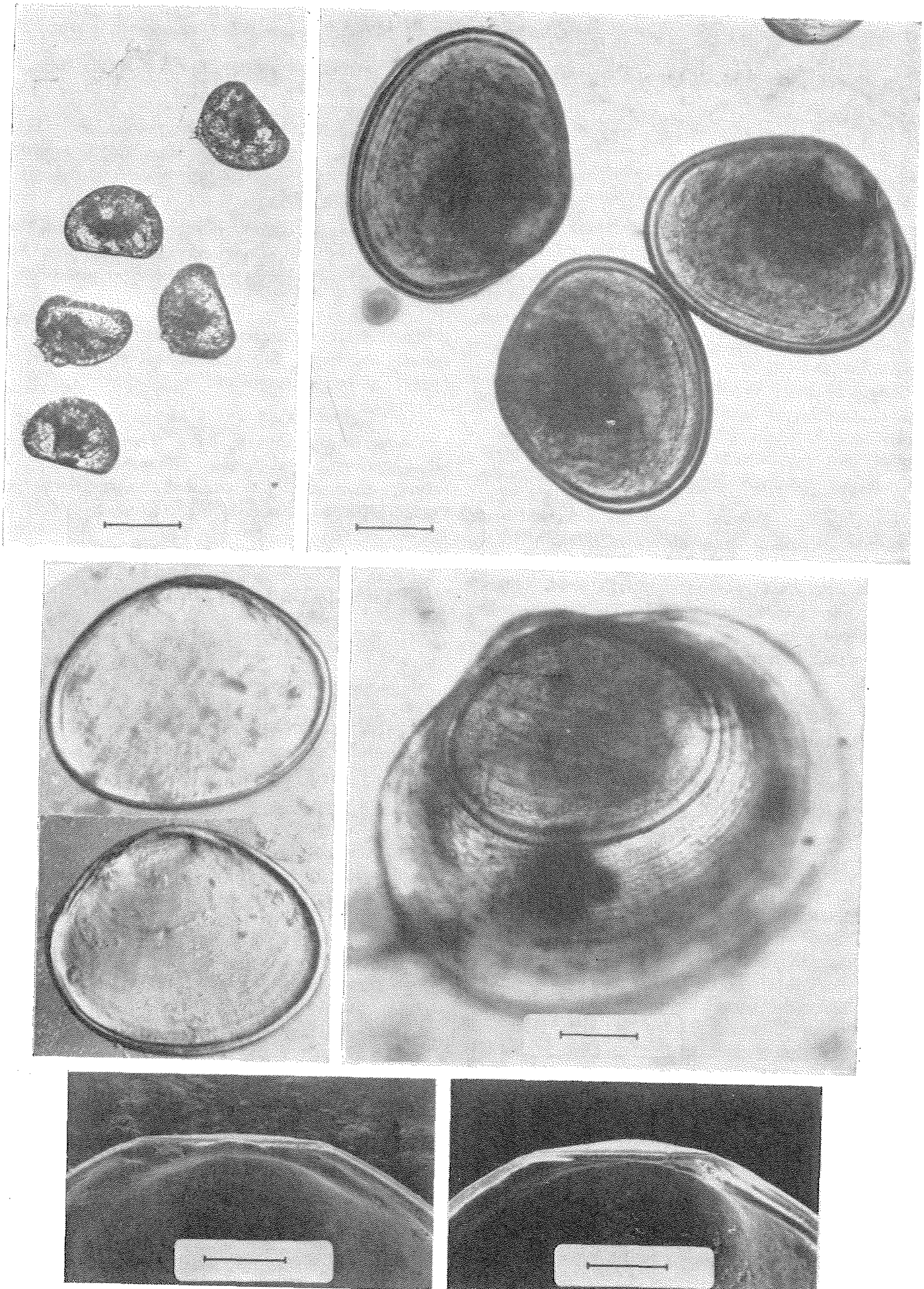


Fig. 1. D-shaped larvae (upper left), late stage larvae (upper right) and single valves of late stage larva (middle left) of *Kellia cycladiformis*; juvenile *K. cycladiformis* taken at Wairoa Bay, Bay of Islands (middle right); scale lines = 100 μm. Hinge of left valve (lower left) and right valve (lower right) of late stage larva (length 340 μm) of *K. cycladiformis* (from different larvae); scale lines = 40 μm.

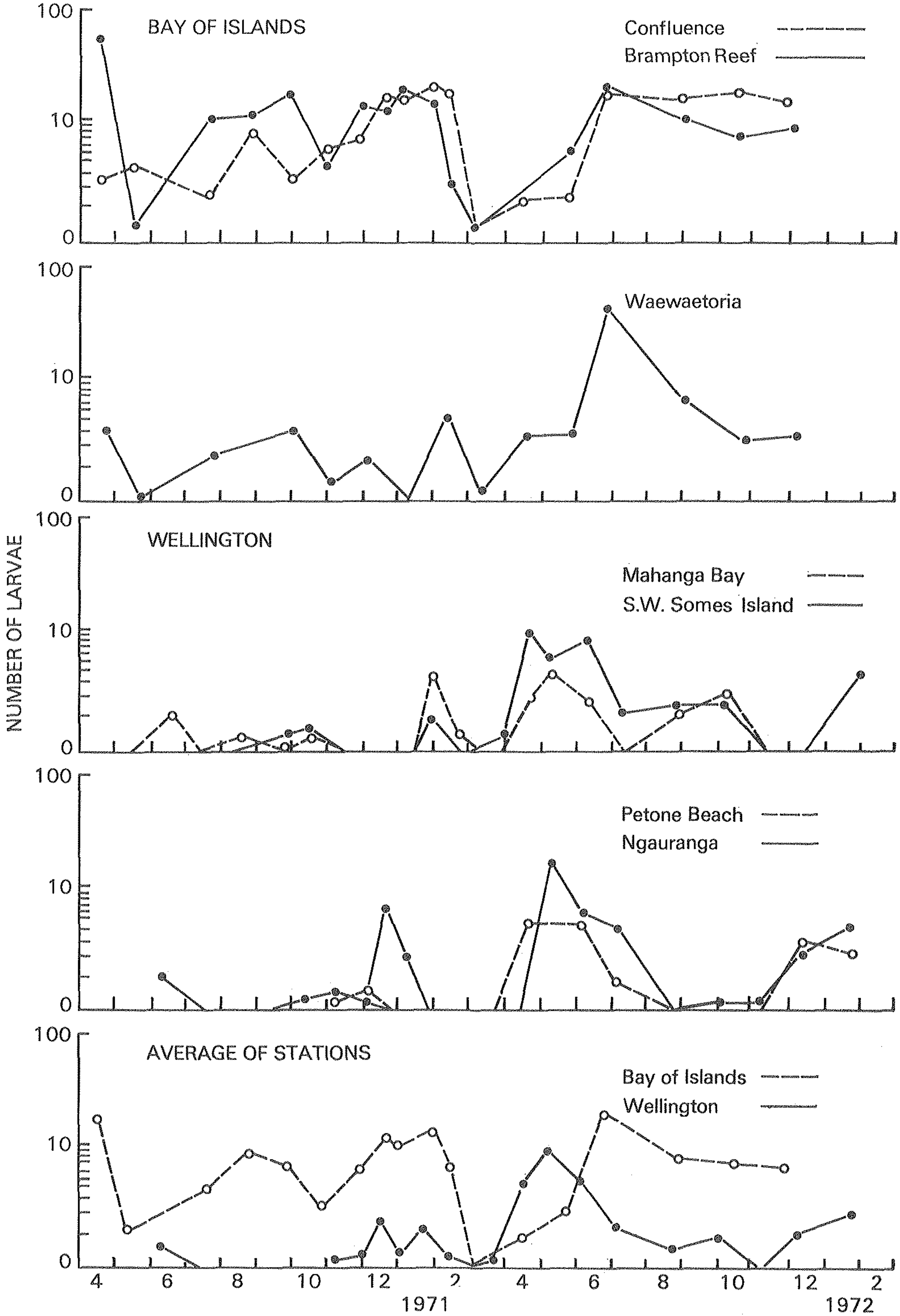


Fig. 2. Monthly variations in abundance (numbers per 1000 litres of seawater) of late stage *Kellia cycladiformis* larvae, Bay of Islands (April 1970 - December 1971) and Wellington Harbour (May 1970 - February 1972).

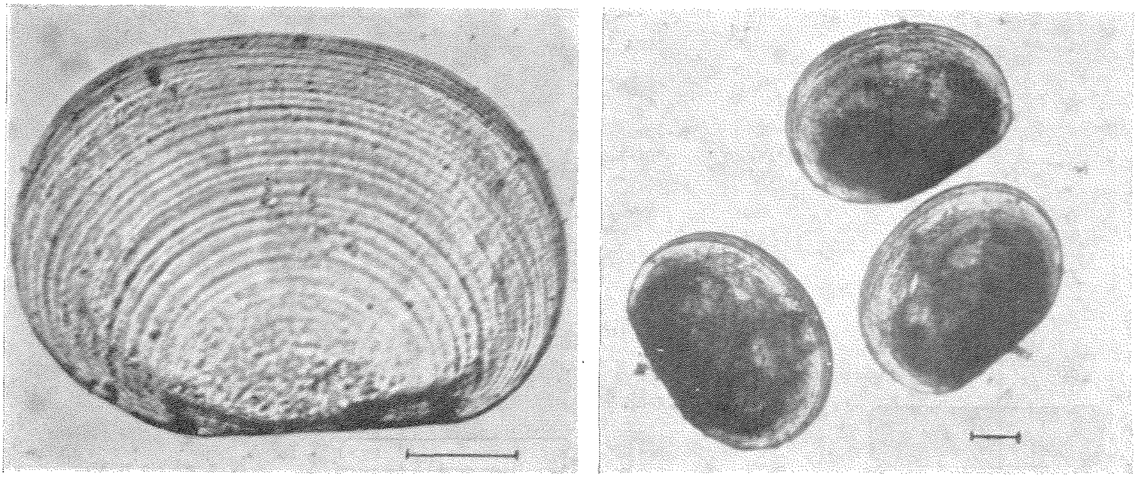


Fig. 3. Single valve of postlarva (left) and postlarvae (right) of *Lasaea rubra hinemoa;* scale lines = 100 μm.

Breeding cycle of the adult (Fig. 4). The young brooded by any one adult were always the same size and appeared to be at the same stage of development. The maximum number of young incubated by any single adult was 33. These were 500 μm long, and occurred in an adult 4.08 mm long. The usual number of incubated young from any one adult was between 5 and 15. The smallest adult carrying young (2 at 400 μm length) was only 1 mm in length. The smallest, easily recognized, shelled larvae were 320 μm in length, while the largest postlarvae encountered were 580 μm long. However, most postlarvae were probably released at about 560 μm long (cf. 600 μm given by Oldfield 1964 for *L. rubra* at Plymouth). Some adults were incubating larvae or juveniles over 320 μm in length in all months. The highest number of incubating adults (25–30%) was in winter 1971 (May–August); the smallest number was in spring 1971, with a major release of young probably having occurred just previously at a sea surface temperature of 16–17°c. A less marked release of larvae appears to have occurred during the summer of both years.

Fig. 4 (lower) shows that at any one sampling date there was a considerable range in the size of young being incubated by different adults. Factors affecting larval size probably include adult size, brood size, and larval growth rates, but the observation is consistent with larval release occurring throughout most of the year.

In summary, the observations, although covering little more than one year, suggest peak spring and summer spawnings and release of larvae, but also trickle releases of larvae throughout the year. This is a more extended breeding season than noted by Oldfield (1964) for *L. rubra* at Plymouth.

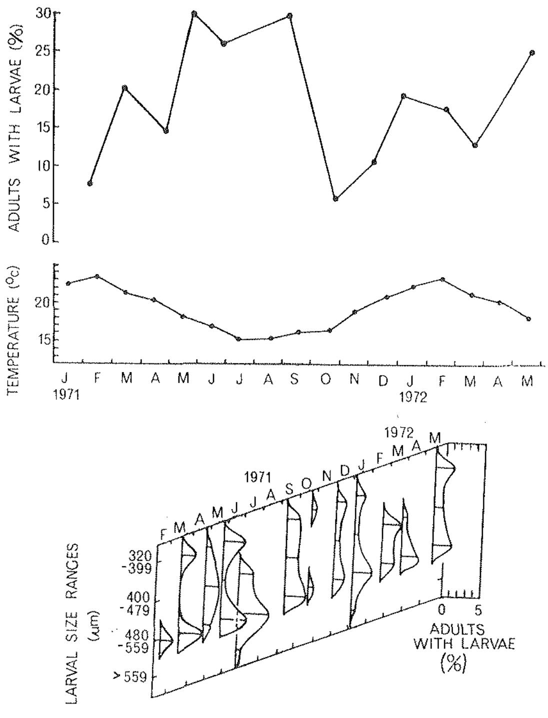


Fig. 4. Monthly variations in the percentage of 40 adult *Lasaea rubra hinemoa* greater than 1.5 mm length incubating larvae and postlarvae over 320 μm in length (upper), and the size of the incubated young (μm) on each sampling date (lower), Wairoa Bay, Bay of Islands, February 1971 - May 1972. Bay of Islands sea surface temperatures (middle) from Booth (1974).

Table 1. Monthly abundance of late stage leptonacean larvae at Raumati Beach, 1970–72. Tow-net data, listing from most abundant species present in order of decreasing abundance, from two 3-minutes tows (Stns 1 & 2, right part of fig. 2, Booth 1977); free-fall net data, in numbers of larvae per 1000 litres of seawater, from the average of two net drops (Stns 3 & 4, right part of fig. 2, Booth 1977). (—, no sample; *, 1 tow only; zero, no *K. cycladiformis* or Leptonacean 1 larvae taken)

Date	Sea surface temp (°c)		Free fall net *K. cycladiformis*	Free fall net Leptonacean 1	Total late stage bivalve larvae
26 Nov 1970	19.0	*K. cycladiformis*	—	—	—
12 Dec 1970	21.0	*K. cycladiformis*, Leptonacean 1*	0.34	0.30	2.50
17 Jun 1971	12.3	zero	0	0	9.80
25 Jul 1971	12.5	*K. cycladiformis*	0.99	0.56	11.10
30 Sep 1971	13.8	zero	0	0	6.80
4 Nov 1971	15.9	zero	0	0	0.90
15 Dec 1971	19.2	*K. cycladiformis*, Leptonacean 1	0.28	0.14	5.50
17 Jan 1972	19.6	*K. cycladiformis*	5.53	0.09	11.60
15 Feb 1972	17.5	*K. cycladiformis*, Leptonacean 1	0.34	0.17	11.70
18 Mar 1972	18.3	*K. cycladiformis**	35.70	9.52	176.00
15 Apr 1972	16.2	*K. cycladiformis*, Leptonacean 1*	0.33	0.12	5.40
4 Jun 1972	12.8	*K. cycladiformis*, Leptonacean 1*	0.80	0.15	16.80

Table 2. Relative abundance of the adult leptonacean species at Bay of Islands and Wellington Harbour, 1970–72. The most abundant species present in each locality are listed in order of decreasing abundance (a, abundant; c, common; f, frequent). Other leptonacean species were either much less common or absent in each locality. Sources of data: shore and benthic surveys (Booth 1972) and Beu & Climo (1971)

Species	Abundance	Distribution
Bay of Islands		
Lasaea rubra hinemoa	a	estuaries & basins
Arthritica bifurca	c	estuaries
Borniola reniformis	f	basin
Wellington Hbr		
Arthritica bifurca	c	mainly upper hbr
Lasaea rubra hinemoa	f	throughout hbr

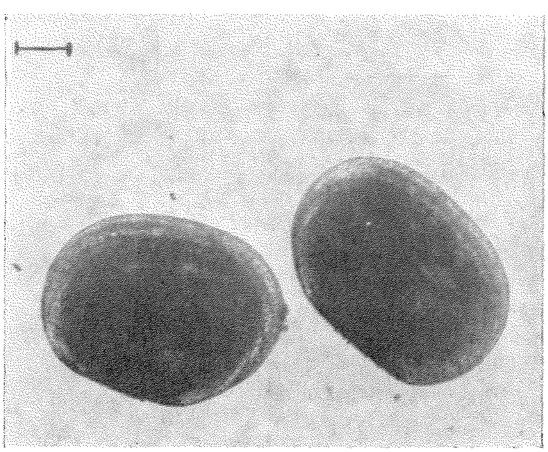


Fig. 5. Postlarvae of *Lasaea maoria;* scale line = 100 μm.

Lasaea maoria (Powell) (Fig. 5)

Adults were collected at Eastbourne, Wellington Harbour on 21 January 1972 (12) and 30 March 1972 (15). On each date 2 adults contained 12–15 young in the brood chamber.

DIMENSIONS. Incubated young 400–560 μm in length; length to height ratio 1:0.73, ratio of length of larva to length of hinge line 1:0.50.

SHAPE (Fig. 5). Late stage larva and postlarva very similar in shape to *L. rubra hinemoa,* except that the posterior end is slightly higher.

OTHER FEATURES. Late stage larva and postlarva appear whiter than *L. rubra hinemoa,* although there is usually a reddish-brown tinge around the umbos. Marked concentric lamellae seen under Nomarski DIC. No visible eyespot.

Borniola reniformis (Suter) (Fig. 6)

Forty-five adults were collected at Wairoa Bay, Bay of Islands during 1971, and one (collected on 12 February) contained numerous D-shaped larvae.

DIMENSIONS. Incubated D-shaped larvae 120 μm in length; length to height ratio 1:0.89, ratio of length of larva to length of hinge line 1:0.60.

SHAPE (Fig. 6). D-shaped larva is high, and the ventral margin rounded. Except for the area of the hinge, the larva appears almost round.

Arthritica crassiformis Powell (Fig. 6)

Eighty adults were collected from their commensal habit with the pholad *Barnea similis* at the Te Puna Inlet, Bay of Islands on 12 January 1972 (40) and 17 May 1972 (40); on each occasion 10% contained numerous D-shaped larvae.

DIMENSIONS. Incubated D-shaped larvae 110–150 μm in length; length to height ratio 1:0.72, ratio of length of larva to length of hinge line 1:0.57.

SHAPE (Fig. 6). D-shaped larva has a skewed form with posterior shoulder sloping more steeply than the longer anterior shoulder; ventral margin gently rounded.

SEASONAL OCCURRENCE. The occurrence of incubated larvae in January and May (summer and autumn) is consistent with Ponder's (1965) record from Takapuna (near Auckland) of incubating adults in February and early March, with the larvae 109 μm long.

Table 3. Summary of main occurrences of late stage leptonacean larvae, Bay of Islands, Wellington Harbour, and Raumati Beach, 1970–72. (a, abundant, i.e., ⩾ 100 larvae per 1000 litres of seawater; c, common, i.e., ⩾ 10 but < 100; f, frequent, i.e. ⩾ 1 but < 10; o, occasional, i.e., < 1; n.o., never observed)

Species	Bay of Islands	Wellington Hbr	Raumati Beach
K. cycladiformis	May–Feb (f,c)	Apr–Jul (f) Dec–Jan (o,f)	Dec–Jul (o,f,c)
L. rubra hinemoa	Insignif. nos	n.o.	n.o.
L. maoria	n.o.	n.o.	n.o.
Leptonacean 1	Mar–Nov (f,c,a) Dec–Feb (c,a)	Feb–Nov (f,c,a) Dec–Jan (c,a)	Dec–Jul (o,f,c)

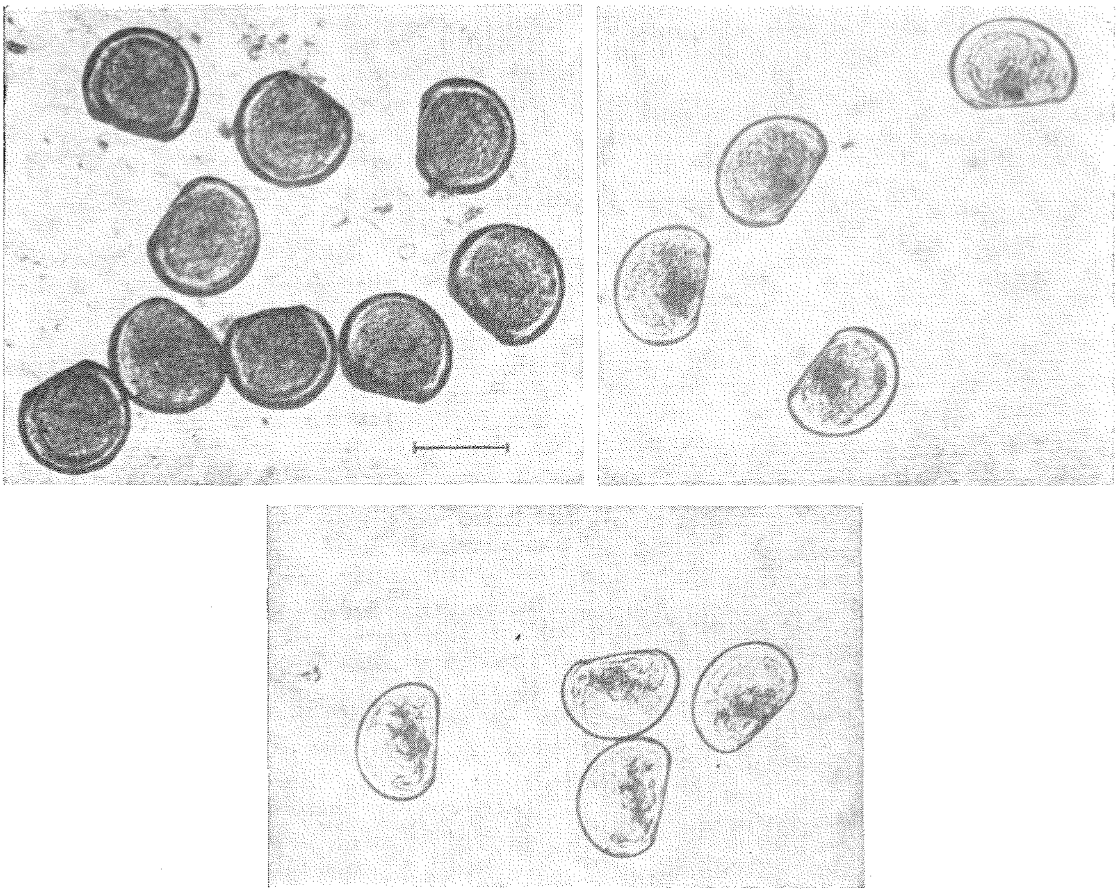


Fig. 6. D-shaped larvae of *Borniola reniformis* (upper left), *Arthritica crassiformis* (upper right) and *Arthritica bifurca* (lower); scale line = 100 μm.

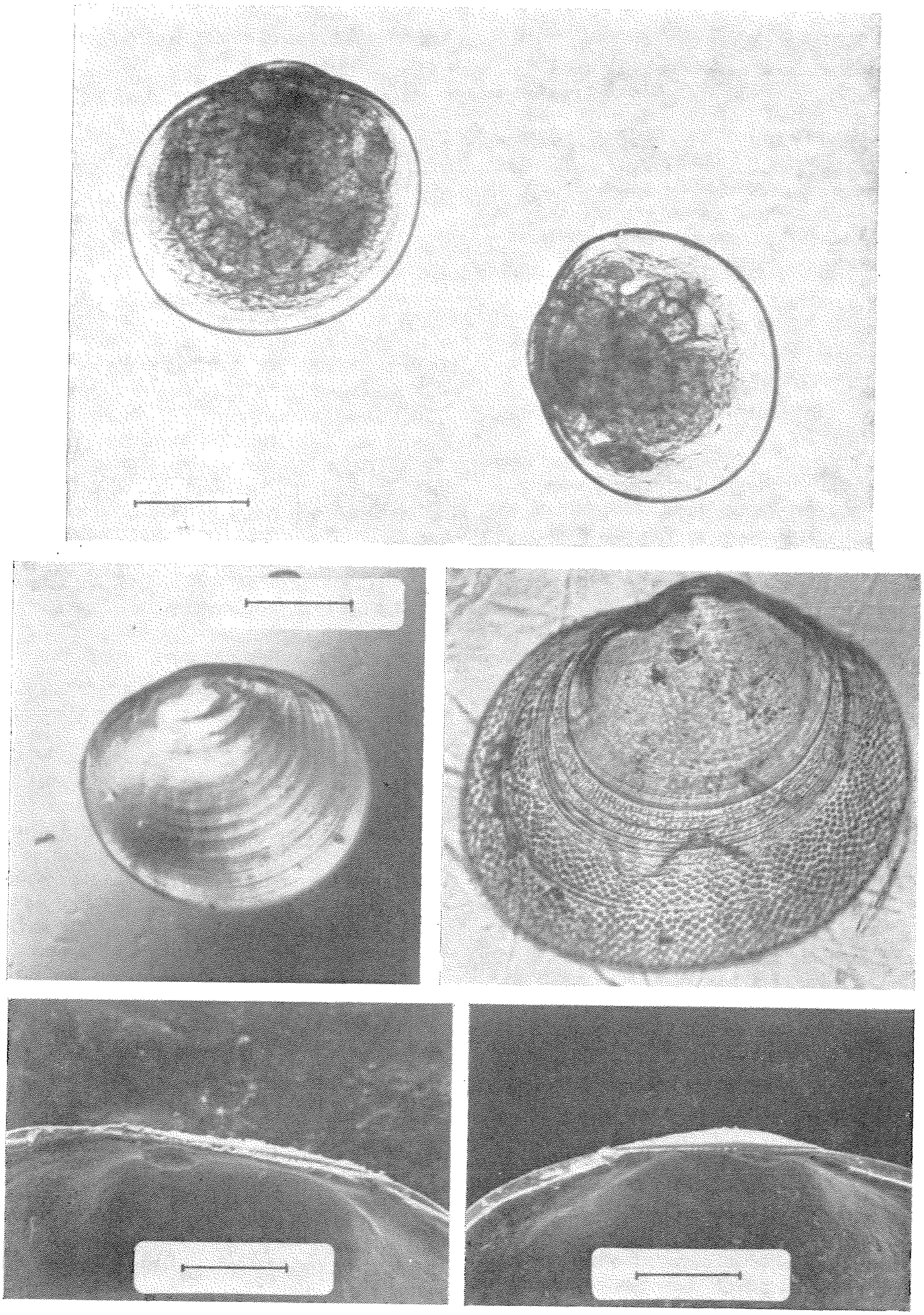


Fig. 7. Late stage larvae (upper) and single valve (middle left) of Leptonacean 1: postlarva (middle right), probably *Arthritica bifurca,* from Bay of Islands; scale lines = 100 μm. Hinge of left valve (lower left) and right valve (lower right) of late stage larvae (lengths 270 μm and 230 μm respectively) of Leptonacean 1; scale lines = 40 μm.

Arthritica bifurca (Webster) (Fig. 6)

Thirty to forty adults were collected monthly (Oct 1971–Oct 1972) at Petone Beach, Wellington Harbour from their association with the tubeworm *Pectinaria australis.* Fifteen to thirty-five percent were incubating larvae at all times of the year, except during spring when the percentage dropped to 5–10%. The larvae in any one adult were always the same size and appeared to be at the same stage of development.

DIMENSIONS. Incubated D-shaped larvae 110–130 µm in length; length to height ratio 1:0.72, ratio of length of larva to length of hinge line 1:0.57.

SHAPE (Fig. 6). D-shaped larva very similar in shape to that of *A. crassiformis.*

SEASONAL OCCURRENCE. The presence of incubating adults at all times of the year and the narrow size range of incubated larvae suggest larval release throughout the year, with the main release period sometime in early spring. Wear (1966) found incubating adults with early prodissoconch larvae in March and April at Petone Beach, but does not state whether he also sampled for them at other times of the year.

LEPTONACEAN 1 (? *Arthritica bifurca* (Webster)) (Figs 7, 8, & 9, Tables 1–3)

DIMENSIONS. Pelagic larvae 210–280 µm in length; average length to height ratio 1:0.88, ratio of length of larva to length of hinge line 1:0.32.

SHAPE (Fig. 7). In the late stage larva the umbos are equal in size and knobby to broadly rounded; both shoulders slope gently, but posterior shoulder is slightly higher than anterior shoulder; both ends are of similar length; ventral margin is rounded.

HINGE (Fig. 7). In larva 250 µm long, hinge has no true provinculum (as defined by Rees 1950), although the straight edge does bear many very small, feebly developed serrations. Ligament attachment point lies behind and towards posterior end of straight edge of hinge.

OTHER FEATURES (Fig. 7). Quite marked concentric lamellae over larval shell, particularly prodissoconch 2, clearly seen under Nomarski DIC (Fig. 7, middle left); prodissoconch 1 shell often more punctate in texture when viewed under Nomarski DIC. No visible eyespot. The early dissoconch shell (Fig. 7, middle right) recovered from amongst adult *A. bifurca* in the Kerikeri Estuary, Bay of Islands displays a prodissoconch 2 shell consistent with the shape of Leptonacean 1.

COMPARISON WITH OTHER SPECIES. The late stage larva resembles the shapes of the leptonaceans *Montacuta bidentata* described by Jorgensen (1946) and Rees (1950), and *Mysella bidentata* described by Gage (1966).

DISTRIBUTION AND SEASONAL ABUNDANCE (Figs 8 & 9, Tables 1–3). This larva, as well as the adults of *A. bifurca,* occurred at all sampling localities.

In Bay of Islands it occurred at all stations throughout the year, in greatest numbers at the inner stations. Peak abundance occurred during the late autumn of 1970 and 1971, and during summer 1970–71. Except for a short period during the spring, it was one of the most common bivalve species in the plankton.

In Wellington Harbour the larva also occurred at all stations, with peaks during mid summer 1970–71 and late autumn 1971 (possibly also mid summer 1971–72 and late autumn 1970). Again the larva was one of the most common species in the plankton. These results indicate spawning throughout most of the year, and are consistent with the occurrence of adults incubating larvae at Petone Beach throughout the year.

At Raumati Beach, the larva occurred throughout the year except spring, with a peak during the early autumn of 1972. In summary, the species appears to spawn throughout most of the year with peaks during summer and late autumn.

DISCUSSION

The late stage pelagic larva, Leptonacean 1 has been allocated to superfamily Leptonacea because several aspects of its hinge structure are consistent with that described for this group by Rees (1950). However, the position of the ligament at the posterior end of the hinge line, rather than the anterior end, is at odds with Rees's (1950) description. Oldfield (1964) reports a posterior ligament for the late stage larva of the leptonacean *Lasaea rubra,* indicating that not all leptonacean larvae have an anterior ligament. Furthermore, Ponder (1965) reported an internal, posterior ligament in the adults of *Arthritica* spp.

The hinge structure of the other pelagic late stage leptonacean larva described in this study (*Kellia cycladiformis*) is also consistent with Rees's (1950) description, except for the posterior position of the ligament. Again the adult internal ligament is posterior (Ponder 1971).

Leptonacean 1 has been provisionally identified to species level (*Arthritica bifurca*) using the following criteria.

(1) The distribution and abundance of the larva is consistent with that of the adults of *A. bifurca.*

(2) An early dissoconch shell, possibly that of *A. bifurca,* displays the Leptonacean 1 prodissoconch 2 shell shape.

(3) The seasonal occurrence of the larva in the

plankton in Wellington Harbour is broadly consistent with the observations at Petone Beach on the adults of *A. bifurca,* which indicated release of larvae throughout the year.

The identification of Leptonacean 1 must remain tentative until the species has been reared in the laboratory. As always with indirect identification of bivalve larvae, there is the possibility of confusion in the identifications of the late stage larvae because of the similarity in shape between species. For example, the late stage larvae of *A. crassiformis* and *A. hulmei* may be very similar in appearance to those of *A. bifurca,* although neither of these species would be expected to occur as commonly as *A. bifurca* in the plankton because the adults were much less common in the sampling localities. Furthermore, there may be larvae of other genera that are also similar in appearance.

In *Kellia cycladiformis,* however, the identification is positive since the late stage larvae were obtained from the brood chamber of the adult. The period for which the *K. cycladiformis* larva is pelagic is unclear, and the evidence appears contradictory. The presence of 12 late stage larvae 350 μm long in the brood chamber of an adult taken at Wairoa Bay on 28 October 1970 suggests either non-pelagic development (larvae probably being lecithotrophic and incubated nearly throughout their entire development) or hyperlarviparous (probably lecithotrophic development, with a short planktotrophic stage) with the larvae being released sometime after a length of 350 μm is reached. That there was a group of adults, juveniles, and pediveligers together in the *Mytilus edulis aoteanus* shell suggests a non-pelagic development.

Other evidence, however, points to hyperlarviparous or larviparous development: the numerous (many hundreds) D-shaped larvae, 80–130 μm long, in the brood chamber of the three adult *K. cycladiformis* about 8 mm in length collected near Whangarei Heads and D'Urville Island is consistent with overseas observations (Lebour 1938, Howard 1953, Oldfield 1964) on *K. suborbicularis* and *K. laperousi* in which the larvae are incubated to a size of 60–120 μm. The plankton observations also point to a definite, and possibly prolonged, pelagic period since the larvae were common at certain times of the year. Furthermore, the late stage larval features, with a discernible inner and more punctate prodissoconch 1 shell and typical prodissoconch 2 zone, are those of a planktotrophic larval shell and not of an embryonic shell when considered in the light of Ockelmann's (1965) definitions.

These observations suggest that the life history of *K. cycladiformis* is more complicated than that described for other *Kellia* spp., with the possibilities including:

(a) Most larvae are released at a small size (approximately 130 μm long) but a small proportion are incubated to a late stage of development and have a short pelagic period.

(b) Considerable variation may occur intraspecifically regarding both the number of larvae and the duration of their incubation period. The possibility that this may depend upon population density and distribution of breeding adults is a strong one.

(c) Some late stage larvae return to the brood chamber of the adult after a pelagic period.

(d) The occurrence of dwarf parasitic or complemental males in certain allied species, e.g. *Montacuta percompressa* (Chanley and Chanley 1970), point to a need for further investigation of the anomalous broods.

Both *Arthritica crassiformis* and *A. bifurca* are presumably hypolarviparous, or certainly no more than larviparous, with most of the larval development taking place outside the parent. The evidence is the observation that the larvae in the brood chamber of both species were always small (110–150 μm in length for *A. crassiformis* and 110–130 μm for *A. bifurca*) and numerous (many hundreds), and yet the adults were small (generally less than 4 mm long for *A. crassiformis* and *A. bifurca*). *A. crassiformis* larvae are probably released at 140–150 μm long, which is consistent with Ponder's (1965) conclusions that, since no larvae beyond the 'prodissoconch' stage were found, there must be a fairly long free swimming period. *A. bifurca* larvae are probably released at 120–130 μm in length, which is at variance with Wear's (1966) suggestion that the pelagic period is short.

The adults of several of the species considered in this study are among the smallest of the Bivalvia, and exhibit the tendency outlined by Chia (1974) for smaller animals in any given taxa to produce large eggs; they therefore have lecithotrophic, brooding, or ovoviviparous development. Represented in this group of leptonaceans are examples of various developmental strategies which occur in the Bivalvia concerning the degree of protection afforded to the young. At one end of the scale is *Arthritica bifurca,* which incubates its numerous larvae for only a short period of their development (up to 130 μm long), thereby allowing wide dispersal of the larvae by water currents upon release. At the other end of the scale is *Lasaea rubra hinemoa* with non-pelagic development. This species is the culmination of the trend towards protection of the larvae by the adults, thereby ensuring a less hazardous larval development period, but considerably reducing the dispersal potential of the species. Within this range is *Kellia cycladiformis,* although the exact duration of the pelagic development in this species remains unclear.

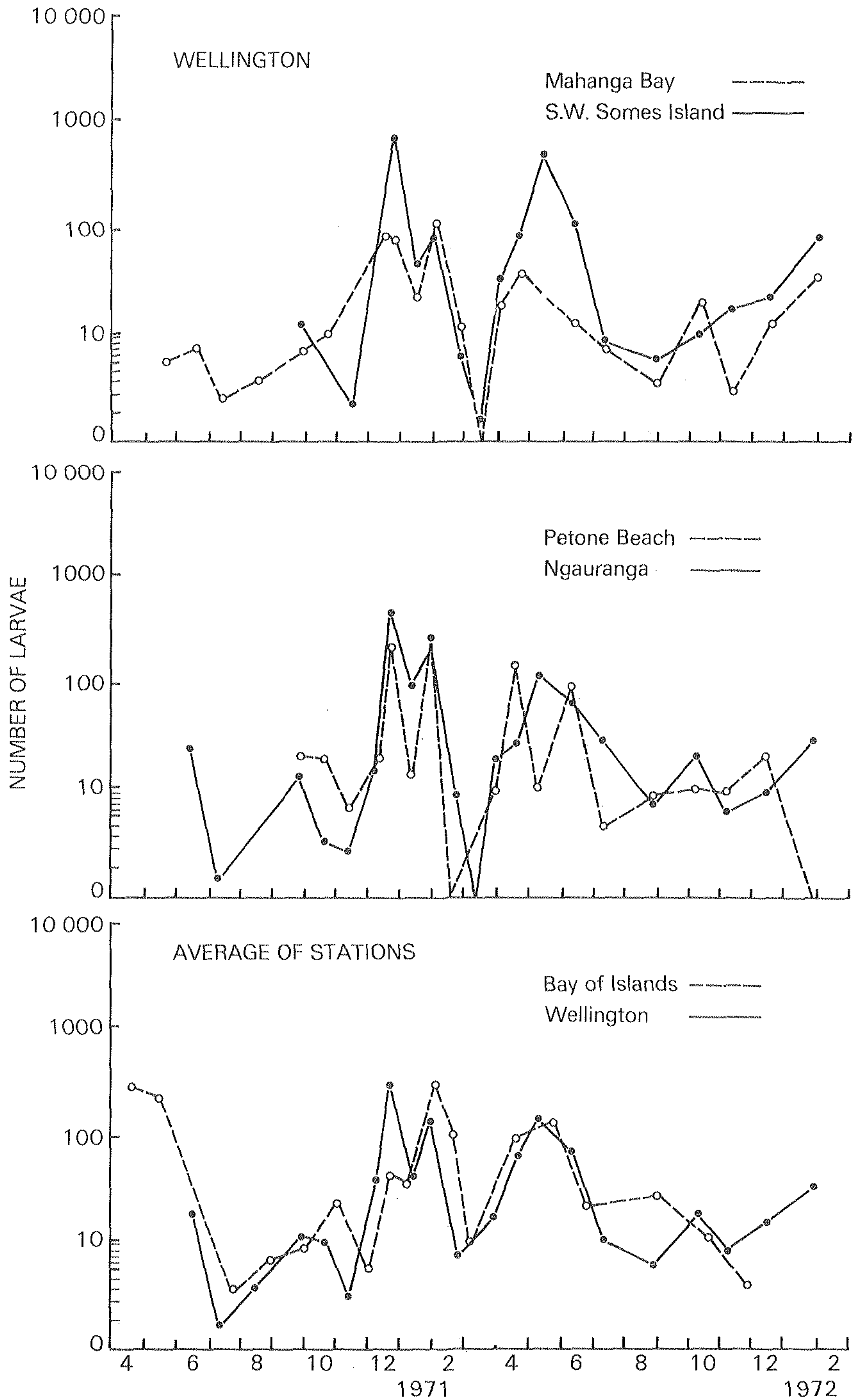
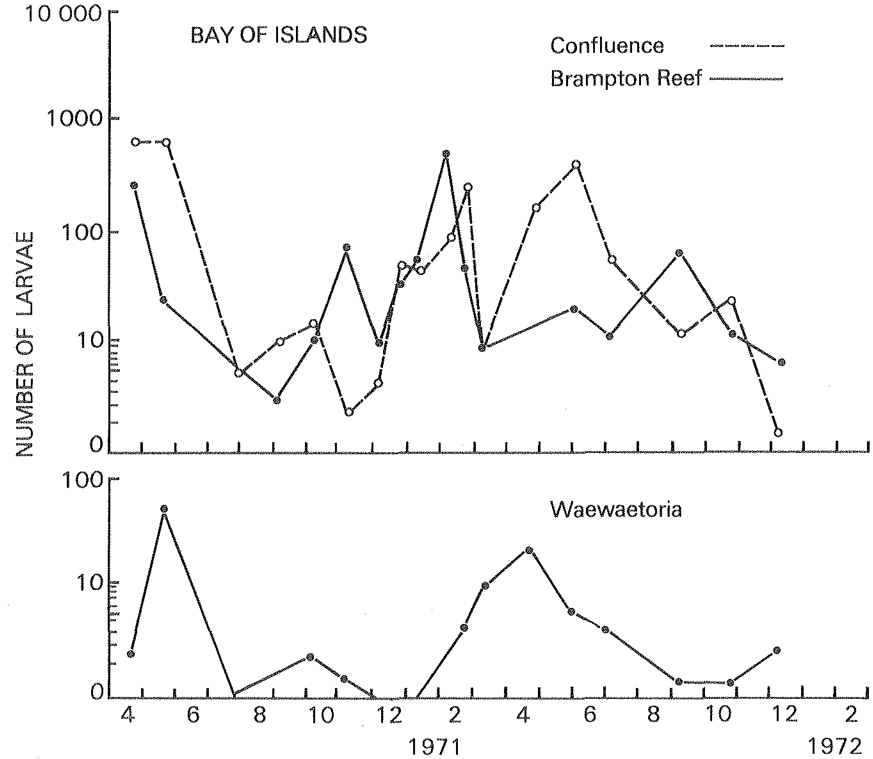


Fig. 8. Monthly variations in abundance (numbers per 1000 litres of seawater) of late stage larvae of Leptonacean 1; (above) Wellington Harbour (May 1970–February 1972) and (opposite) Bay of Islands (April 1970–December 1971).



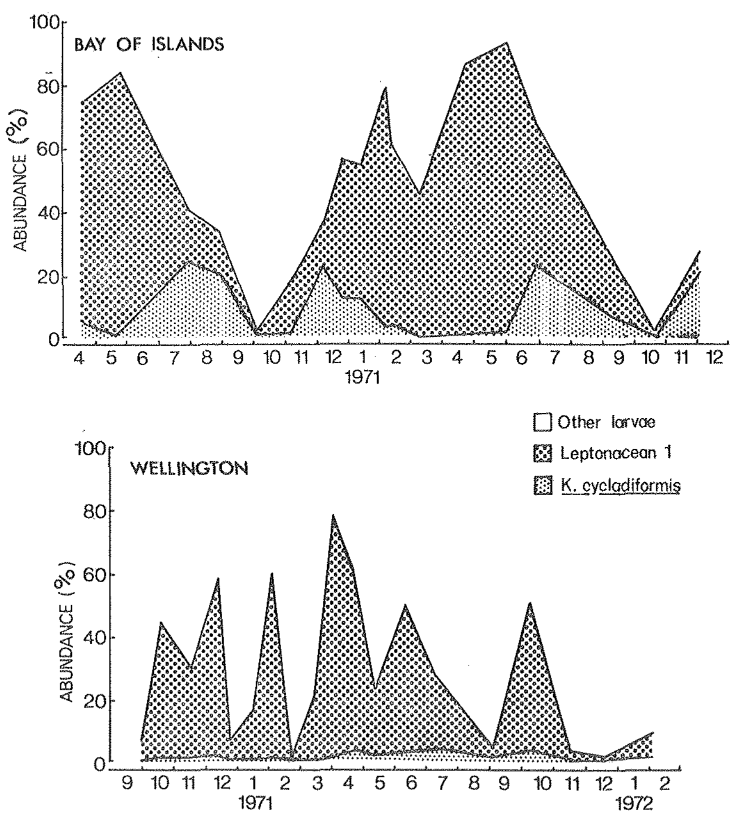


Fig. 9. Variations in relative abundance of the late stage larvae of *Kellia cycladiformis* and Leptonacean 1 and the late stage larvae of the other 18 most abundant species in Bay of Islands (upper) and Wellington Harbour (lower), 1970–72.

The observations on the occurrence of the late stage larva provisionally identified as *Arthritica bifurca*, and the late stage larva of *Kellia cycladiformis* suggest that superfamily Leptonacea contributes extensively to the bivalve larval complement of the plankton in both the Bay of Islands and Wellington Harbour (Fig. 9) particularly during summer, autumn and winter. Morton & Miller's (1968) observation that superfamily Leptonacea are numerically the commonest bivalves on the shore also applies to their larvae in the plankton at most times of the year, although the larva identified as *Arthritica bifurca* may have a longer than average pelagic phase which makes it appear more prominent in the plankton.

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