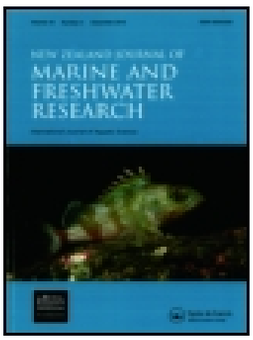

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Larval shell development of the northern tuatua, *Paphies subtriangulata* (Bivalvia, Mesodesmatidae)

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Abstract The larval shell development of *Paphies subtriangulata* is described from larvae reared to settlement in the hatchery. Externally the larval shells of *P. subtriangulata* are very similar to those of *Paphies ventricosa* and, to a lesser extent, *Paphies australis*. Internally the hinge structures of the late-stage larvae of *P. subtriangulata, P. ventricosa*, and *P. australis* are sufficiently different to distinguish the species. The spatulate tooth and the peg tooth of *P. ventricosa* are absent in *P. subtriangulata* and *P. australis*; the ligament of *P. australis* is posterior to the provinculum and central in *P. ventricosa* and *P. subtriangulata*. Straight-hinge stage larvae of *P. subtriangulata* were 88–143 μm long and 67–117 μm high and umbo stage larvae were 125–265 μm long and 97–223 μm high. The larvae settled in about 17 days from a length of 230 μm.

Keywords bivalve larvae; Mesodesmatidae; larval shell development; larval morphology

INTRODUCTION

Tuatua are among the most abundant infaunal bivalves of the littoral and early sublittoral of exposed, open-coast, fine-sand beaches around the New Zealand mainland and the Chatham Islands. The various forms of tuatua that inhabit some beaches in central New Zealand had been confused for many years until Richardson et al. (1982) resolved the situation by proving there were two species. Beu & De Rooij-Schuiling (1982) have determined that the valid names of the species are *Paphies subtriangulata* (Wood, 1828) and *Paphies donacina* (Spengler, 1793).

Beu & De Rooij-Schuiling (1982) summarised the distribution of the two species around the New Zealand mainland: *P. subtriangulata* inhabit beaches all around the North Island and along the north coast of the South Island; *P. donacina* inhabit beaches around the South Island and the north coast of Stewart Island and around the North Island except for the northernmost beaches (Ninety Mile Beach and the east coast north of East Cape). The two species are sympatric in those areas where their distributions overlap. They are replaced by, or, at some places, are sympatric with the toheroa, *Paphies ventricosa* (Gray, 1843), in the littoral of some beaches (Redfearn 1974).

All the New Zealand mesodesmatids (the pipi, *Paphies australis* (Gmelin, 1791), the tuatua, and the toheroa) are epicurean shellfish. The fishery is largely recreational, with some commercial interest in tuatuas and toheroas. Local populations of tuatuas are resurgent and are often very large; Dawson (1954) recorded over 400 million *P. donacina* in the littoral of a 13 km section of beach in Pegasus Bay, South Island. The wide distribution of tuatua around New Zealand with large local populations constitute a considerable economic resource. All the New Zealand mesodesmatids are potential candidates for aquaculture.

This paper describes the larval shell development of *P. subtriangulata*. The larval shell development of the toheroa, *P. ventricosa*, has been described by Redfearn (1982) and the late-stage larval shells of *P. australis* by Booth (1983).

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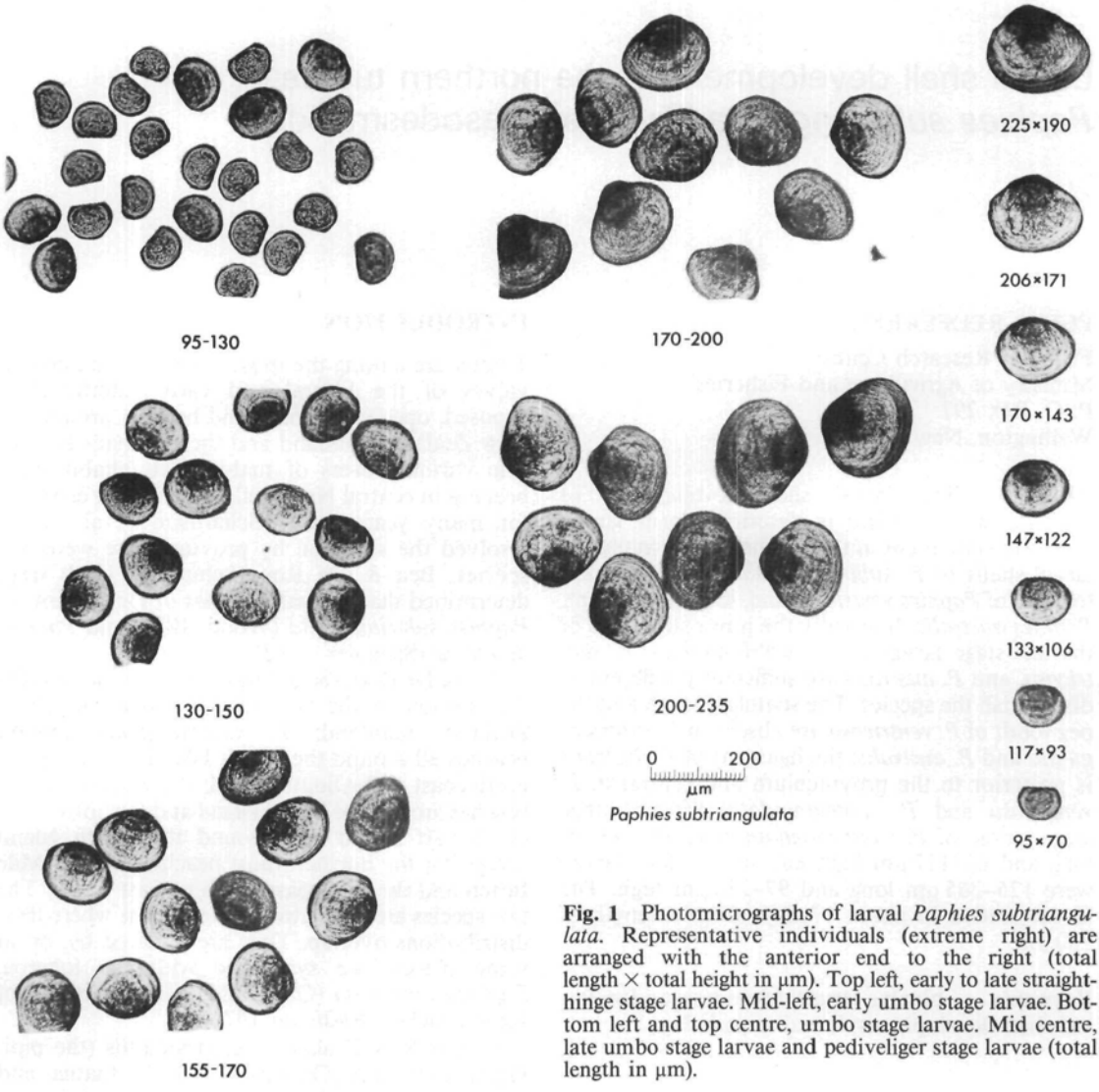


Fig. 1 Photomicrographs of larval *Paphies subtriangulata*. Representative individuals (extreme right) are arranged with the anterior end to the right (total length × total height in µm). Top left, early to late straight-hinge stage larvae. Mid-left, early umbo stage larvae. Bottom left and top centre, umbo stage larvae. Mid centre, late umbo stage larvae and pediveliger stage larvae (total length in µm).

MATERIALS AND METHODS

Adult *P. subtriangulata* were collected from Waikanae Beach, North Island (40° 51′ S, 172°51′ E) when they were sexually ripe and were held for a few days in tanks of running sea water at 15 °C, in the Fisheries Research Division's shellfish hatchery at Mahanga Bay, Wellington. They were spawned and the fertilised eggs and subsequent larvae cultured using the techniques described by Redfearn (1982).

The larval cultures were maintained for 20 days at about 20 °C until most of the larvae had settled or were about to settle. Straight-hinge stage larvae were fed with near-axenic cultures of *Pavlova lutheri* (Culture Centre of Algae and Protozoa, Cambridge, Great Britain (CCAP), strain number 931/1) or *Isochrysis galbana* (CCAP 927/1) and umbo stage larvae were fed with mixed cultures of *P. lutheri* and *Skeletonema costatum* (CCAP 1077/1a) or *Tetraselmis suecica* (CCAP 66/4).

Samples of the larvae were removed from the cultures every other day and were preserved as described by Redfearn (1982). The larvae were routinely examined and measured (for details see Chanley & Chanley 1980; Redfearn 1982) with a ×15 filar micrometer eyepiece and a ×10 objective. Details of the hinge structure were examined at

several stages of the shell development using light and scanning electron microscopy techniques (Redfearn 1982) and statistical analyses of shell dimensions were performed using the Minitab statistical system (Ryan et al. 1976).

Total length, total height, anterior end, and anterior and posterior shoulders C were measured on 193 individuals over the entire size range to a total length of 265 μm. Hinge line length was measured on the straight-hinge stage larvae and umbo height on the umbo stage larvae. Total length and depth were measured on an additional 171 individuals over the entire size range to a total length of 234 μm. Provinculum length and total length were measured on the disjointed valves from 116 individuals over the entire size range to a total length of 265 μm. The total length can be measured with greater precision than the other dimensions (Chanley & Dinamani 1980) and has been used as the basis for comparison of the shell dimensions.

DESCRIPTION OF THE LARVAE

"Length" and "height" refer to total length and total height of the larvae, unless otherwise stated, and have been used to avoid repetition. Values given for any other dimension refer to the minimum and maximum values measured at that particular stage of development, unless otherwise stated.

Paphies subtriangulata adults spawned at 15–20 °C. Eggs were more or less spherical with a diameter of 56–61 μm inclusive of a thick (2 μm) vitelline membrane. Sperm were about 48 μm long; the sperm head was 3.5 μm long and 2.1 μm in diameter at the widest section, and the tail was 44 μm long. The sperm head had a short, blunt acrosome and tapered slightly to the posterior end.

Larval development to the straight-hinge stage veliger was completed within 24–48 h after fertilisation and many of the larvae completed their development to the settlement stage within a further 17–18 days. The mean growth, measured by the increase in length, was 8 μm/day.

The earliest straight-hinge stage larvae observed were 88 μm long. The straight-hinge shape was retained by the larvae until they were 125–143 μm long (Fig. 1). Larvae, 88–143 μm long, increased in height from 67 to 117 μm and in depth from 45 to 98 μm. The anterior end increased from 45 to 82 μm and the hinge line length from 47 to 82 μm. The anterior shoulder C increased from 47 to 92 μm and posterior shoulder C from 46 to 75 μm.

Early straight-hinge stage larval shells are almost symmetrical in longitudinal profile with a similar curvature to the anterior and posterior shoulders and ends. The anterior end is longer than the posterior end by about 8 μm in larvae 100 μm long. As the shells develop they become progressively more asymmetrical in longitudinal profile and the anterior shoulders and ends become more elongate and convex than the posterior shoulders and ends. The anterior end is longer than the posterior end by about 17 μm in larvae 140 μm long. The ventral margin is broadly rounded.

Umbo stage larvae are asymmetrical in longitudinal profile (Fig. 1). Umbones are equal in size and first obscure the hinge line as low broad roundings of the dorsal margin in larvae from 125 μm long. The umbones in late-stage larvae are broadly rounded.

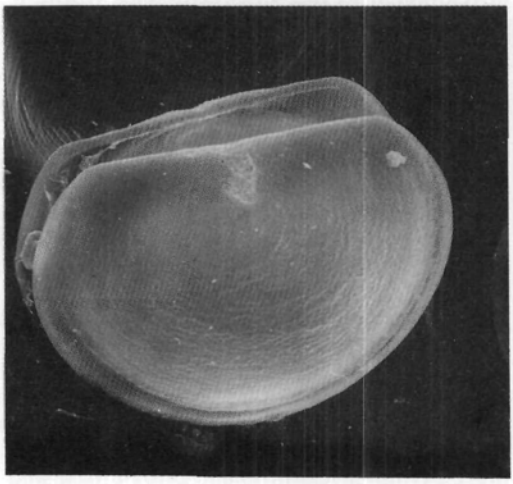
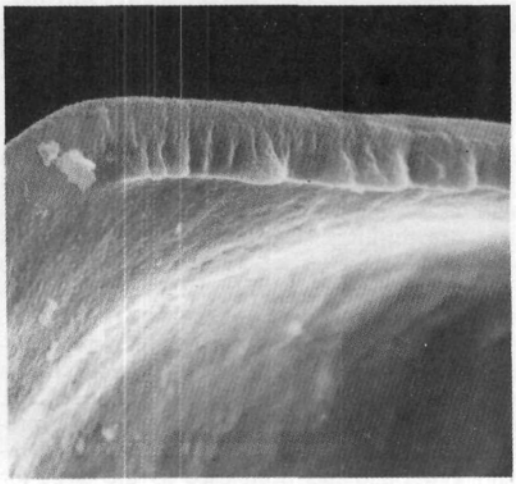
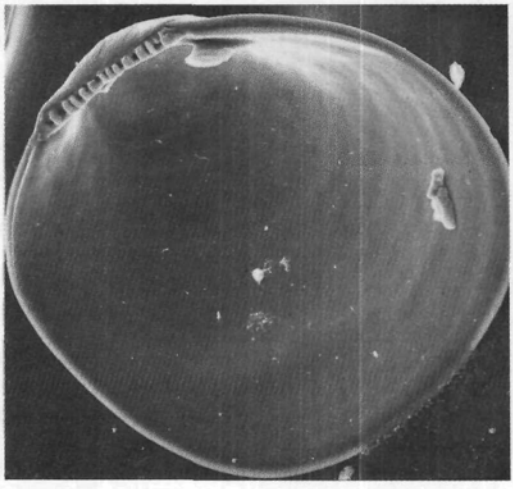
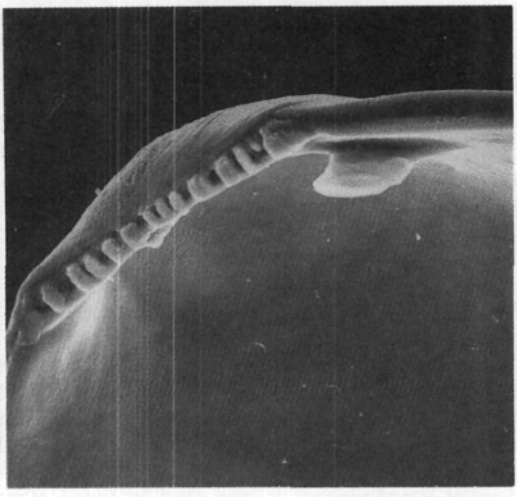
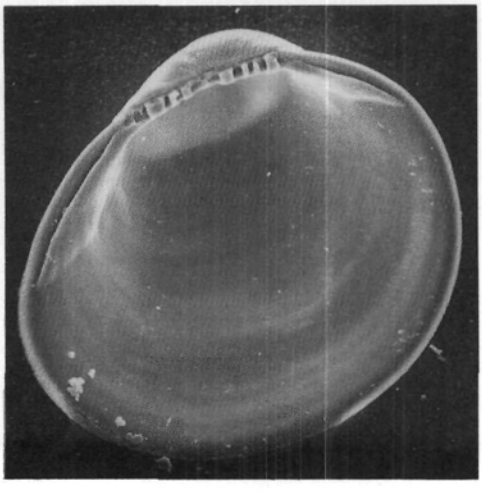
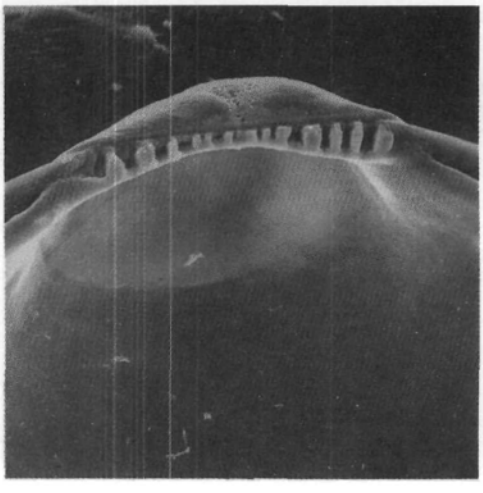
Height, in larvae 125–265 μm long, increased from 97 to 223 μm and depth from 86 to 141 μm. The anterior end increased from 67 to 167 μm and the maximum height of the umbo extension above the shoulders was 26 μm. The anterior shoulder C increased from 71 to 206 μm and the posterior shoulder C from 63 to 152 μm.

The inclinations of the anterior and posterior shoulders from the umbo are similar. The anterior shoulder is much longer and slopes from the umbo in a gentle curve to the anterior end which is very

Table 1 Comparative dimensional relationships of *Paphies subtriangulata* and *Paphies ventricosa* larvae. Regression equations and R^2(%) correlating the length (TL) with the other dimensions.

	Paphies subtriangulata			*Paphies ventricosa*†		
	Regression equation	R^2(%)	*n*	Regression equation	R^2(%)	*n*
Height	= −4.07 + 0.87 TL	98.1	193	= −4.04 + 0.89 TL	98.4	379
Depth	= 1.68 + 0.60 TL	92.5	171	= 14.06 + 0.46 TL	91.2	213
Anterior end	= −18.01 + 0.70 TL	97.1	193	= −14.06 + 0.66 TL	96.6	379
Anterior shoulder C	= −34.19 + 0.91 TL	97.2	193	= −33.10 + 0.86 TL	96.1	379
Posterior shoulder C	= −2.72 + 0.56 TL	94.0	193	= 11.79 + 0.45 TL	94.1	379
Hinge line length	= 59.82 + 0.04 TL	−1.4	52	= 41.21 + 0.16 TL	26.4	87
Umbo height	= −0.13 + 0.09 TL	40.7	141	= −0.07 + 0.09 TL	62.0	286
Provinculum length	= 54.11 + 0.07 TL	43.7	116	—	—	—

† Data from Redfearn (1982).

convex. The posterior shoulder is truncated and the posterior end is broadly rounded or slightly angular. The ventral margin is broadly rounded. The anterior end is longer than the posterior end by about 54 μm in larvae 250 μm long. The linear relationships between the length and the other dimensions for all measured values, straight-hinge to umbo stage, are given in Table 1.

Hinge structure and development

Straight-hinge stage larvae have a thickened, almost straight and uniformly wide provinculum bearing about 35 small irregular teeth (Fig. 2). Provinculum length increases as the larvae develop, but there is considerable variation in the provinculum length for any particular shell length. The provinculum, in larvae 88–143 μm long, increased in length from 41 to 70 μm and in width from 2 to 4 μm.

Umbo stage larvae have a thicker, more arched provinculum (Fig. 2) which is about 4 μm wider at the ends than at the centre. The provinculum, in larvae 125–265 μm long, was variable with the length ranging from 56 to 89 μm. The small irregular teeth of the straight-hinge stage provinculum are fused to form 11–14 rectangular teeth and corresponding sockets. Tooth development starts at each end of the provinculum in some larvae 110–120 μm long before the umbo development is evident externally. In late-stage larvae the 3–4 teeth at the anterior and posterior ends of the provinculum are more peg-like and regular than those in the centre and in some larvae some teeth are double or bifid (Fig. 2).

The lateral hinge system was fully developed in larval shells 150 μm long and consisted of flanges anterior and posterior to the provinculum on the left valve with corresponding grooves on the right valve (Fig. 2). A special tooth was fully developed in larval shells 200 μm long, on the left valve, anterior to the provinculum and ventral to the lateral hinge flange. The special tooth is lamelliform and extends downwards as a broad plate some 12–25 μm long at the base and 10–14 μm wide. It articulates against a thickening of the lateral hinge groove just anterior to the provinculum of the right valve (Fig. 2). The special tooth development was apparent in some shells 180 μm long.

The larval ligament was developed in some shells from 180 μm long and was conspicuous in late-stage larvae. The chondrophore lies just ventral to and to the centre of the provinculum and is about 13 μm across at its widest section in larvae over 200 μm long (Fig. 2).

Larval settlement

The foot was evident in some larvae 180 μm long and pediveliger larvae were noted from a length of 200 μm. Some larvae settled at 230 μm, but others retained the pediveliger condition until they were at least 260 μm long. About 50% of the larvae over 200 μm long settled by day 17 and about 90% of these larvae had settled by day 20 when the experiment was terminated. The larvae did not have an obvious apical flagellum or a discernable eyespot at any stage during their development.

DISCUSSION

The external shape of larvae of *P. ventricosa* described by Redfearn (1982) and of *P. subtriangulata* are very similar at all stages of their development. The shell dimensions are similar and although the depth and the anterior and posterior shoulders of *P. subtriangulata* tend to be longer than those of *P. ventricosa* for a particular length, the differences are insufficient to be useful for larval differentiation. The shoulders and ends of *P. subtriangulata* are generally more angular and pointed than those of *P. ventricosa* which are more broadly rounded. Late-stage larvae of *P. australis* described by Booth (1983) are also similar in longitudinal profile although larvae of *P. australis* tend to be more rounded than of the other species.

Internally the provincular shape and dentition of *P. australis, P. ventricosa,* and *P. subtriangulata* are also similar. Late-stage larvae of *P. australis* have about 12, *P. ventricosa* 12–13, and *P. subtriangulata* 11–14 provincular teeth. However, there are differences in the special teeth and the position of the ligament. The spatulate tooth and the peg tooth of *P. ventricosa* are absent in *P. australis* and *P. subtriangulata.* The ligament is central to the provinculum in *P. subtriangulata* and *P. ventricosa* and towards the posterior end of the provinculum in *P. australis.*

Umbo stage larvae of the New Zealand mesodesmatids are rounded, with anterior ends longer than posterior ends, anterior margins less broadly rounded than posterior margins and broadly

Fig. 2 (opposite page) Scanning electron micrographs of the hinge structure of larval *Paphies subtriangulata.* Top, provinculum and external right valve of straight-hinge stage larva; total length about 110 μm (× 800) and detail (right) of provinculum with small irregular teeth (× 2000). Middle, left valve of late umbo stage larva; total length about 220 μm (× 500) and detail hinge structure (right) (× 1000), showing provinculum, lateral hinge flanges, lamelliform tooth and the larval ligament. Bottom, right valve of late umbo stage larva; total length about 220 μm (× 450) and detail hinge structure (right) (× 950) showing provinculum, lateral hinge grooves, thickened articulation facet anterior provinculum and the chondrophore.

rounded ventral margins. Umbones are broadly rounded and posterior to the centre. The provinculum is taxodont with well developed terminal teeth. Lateral hinge flanges develop on the left valves and ridges on the right valves anterior and posterior to the provinculum and a lamelliform special tooth on the left valve articulates with a thickened ridge tooth on the right valve. The ligament is either central or towards the posterior end of the provinculum.

The North American species *Mesodesma arctatum* has a hooked lamelliform tooth on the left valve which articulates with a heavy ridge tooth on the right valve, and it has a posterior chondrophore (J. G. Goodsell pers. comm.) which is similar to the arrangement in *P. australis*. A lamelliform tooth (left valve) and a ridge tooth (right valve) may be characteristic of the late-stage larvae of bivalves in the family Mesodesmatidae.

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