

LIFE-HISTORY STUDIES ON NEW ZEALAND BRACHYURA
(CRUSTACEA, DECAPODA)

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ABSTRACT

1. Abbreviated or direct development is described in Pilumnus novaezelandiae Filhol, 1886 and P. lumpinus Bennett, 1964 (Xanthidae, Pilumninae) from New Zealand. Embryonic development is separated into Nauplius, Metanauplius, and embryonic Zoea stages. In P. novaezelandiae, larvae hatch at a Megalopa stage and are retained beneath the pleon of the female crab. The Megalopa larva and first five juvenile crab stages are described. In P. lumpinus emergent larvae are advanced, much-modified, and non-natatory Zoeae which are not retained by the parent. The Zoea and Megalopa larvae of this species are described. Abbreviated development has little phylogenetic significance among Brachyura, and has probably evolved as a response to habitat requirements of adult crabs.
2. A brief account is given of the systematics and distribution of the New Zealand xanthid crabs Heterozius rotundifrons A. Milne Edwards, 1867, Ozius truncatus H. Milne Edwards, 1834, and of Heteropanope (Pilumnopeus) serratifrons (Kinahan, 1856). Keys are given to the Zoea larvae of New Zealand xanthid Brachyura and to the Megalopa larvae of Heterozius rotundifrons and Ozius truncatus. Notes are given on the seasonal breeding cycle of Heterozius rotundifrons, and the pre-Zoea larva, two Zoea larval stages, and the Megalopa larva reared in the laboratory are described. Ozius truncatus possesses a pre-Zoea larva, four Zoea larval stages, and a Megalopa larva. These have been reared and are described.

A key is given for the separation of the Zoea larval stages.

The pre-Zoea larva and first stage Zoea larva of Heteropanope (Pilumnopeus) serratifrons are described. There are probably four zoeal stages in the larval development of this species.

3. The characters of Zoea larvae of the family Xanthidae described up to the present time are critically analysed and considered in relation to the status of currently accepted adult genera and species, the generic groupings used by Monod (1956), and the generic composition of the subfamilies proposed by Balss (1957). Xanthid Zoea larvae fall into two natural groups of genera based on larval characters, the most important being the length of the antennal exopod in relation to that of the spinous process. The first group is equivalent to the subfamily Xanthinae as reconstituted by Balss (1957), but there is no larval evidence suggesting that the "Panopean" genera should be separated from the "Xanthian" genera as suggested by Monod (1956). A second natural group is formed by larvae of the subfamily Menippinae as in Balss (1932, 1957), the subfamily Pilumninae of Balss (1957), and the genus Geryon. Larvae of genera in the subfamily Trapeziinae Miers should be removed from the section Hyperolissa and included in this second natural group. Zoea larvae described from the genera Heteropanope and Pilumnopeus form a separate branch of the second group. Zoea larval evidence does not support Monod's (1956) separation of Eriphia from the "Menippian" group of genera.
4. The first stage Zoea larva of Hemiplax hirtipes (Jacquinot, 1853) is described, and present knowledge concerning larvae of crabs of the family Ocypodidae is summarized and discussed. No diagnostic character is common to all ocypodid Zoea larvae,

but affinities are shown with those of the families Hymenosomidae, Pinnotheridae, and Grapsidae.

5. Pre-Zoea and first stage Zoea larvae hatched from the grapsid crabs Leptograpsus variegatus (Fabricius, 1793), Planes marinus Rathbun, 1915, Hemigrapsus crenulatus (H. Milne Edwards, 1837), H. edwardsi (Hilgendorf, 1882), Cyclograpsus lavauxi H. Milne Edwards, 1853, Helice crassa Dana, 1851, and Plagusia chabrus (Linnaeus, 1764) from New Zealand are described. A key is given for the separation of these larvae. Known Zoea larvae of the family Grapsidae show close affinities with those of the brachyrrhynchous families Ocypodidae and Gecarcinidae, and fall into four groups based on larval characters. This system of larval classification agrees with the present arrangement of adult genera into subfamilies except for a division among larvae of the subfamilies Varuninae and Sesarminae. The length of larval life and larval dispersal probably has no bearing on the presence or absence of certain New Zealand species at the Chatham Islands.

FOREWORD

This thesis on the larval life of New Zealand Brachyura (Crustacea, Decapoda) concerns only brachyrhynchous crabs of the families Xanthidae, Ocypodidae, and Grapsidae. The dissertation comprises five separate papers, one published, three in press, and one to be submitted for publication during September, 1968.

AIMS OF THE THESIS

Larvae of New Zealand Brachyura have not been previously studied in detail. In the early stages of this study it was intended to describe the larvae of a large proportion of the New Zealand brachyuran fauna of about 50 species. However, earlier published work showed that in some Australian marine Brachyura, development is abbreviated and free larval life is suppressed. If a similar mode of development was found to occur among New Zealand crabs, detailed study of this remarkable phenomenon was considered justified. Abbreviated development was discovered in two New Zealand species of the family Xanthidae, and the morphological study and resulting discussion presented as a large part of this thesis proved this to be a very rich field of investigation. Subsequent work was confined to the larvae of the three remaining species in the family Xanthidae, and to those of eight species belonging to the brachyrhynchous families Ocypodidae and Grapsidae. Free-living larval stages of species considered are described, larval affinities are fully discussed, and systems of classification based on larval characters are compared with the currently accepted systematic arrangement of adult crabs in each family. The length of planktonic

larval life and larval dispersal are considered in relation to the presence or absence of certain species at the Chatham Islands. During the course of this study larvae were obtained from 34 species in ten families, or about 68% of the New Zealand brachyuran fauna. Larvae not considered here will be the subject of future work.

PRESENTATION OF THE THESIS

The format of the five papers meets all publication requirements of the New Zealand Journal of Marine and Freshwater Research, and the first, second, fourth, and fifth papers will be published in this journal. The third paper is to be published in Crustaceana and is referred thereto in the text of this thesis. The fifth paper has not yet been submitted for publication, but is here referred to as "in press" to avoid unnecessary alteration to gally proofs.

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N.Z. Jl mar. Freshwat. Res. 2 (2), figs 1-88, tpls 1-3

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LIFE-HISTORY STUDIES ON NEW ZEALAND BRACHYURA.

1. Embryonic and Post-Embryonic Development of *Pilumnus novaezelandiae* Filhol, 1886, and of *P. lumpinus* Bennett, 1964 (Xanthidae, Pilumninae)

by
Robert G. Wear

SUMMARY

Abbreviated or direct development is described in *Pilumnus novaezelandiae* Filhol, 1886 and *P. lumpinus* Bennett, 1964 from New Zealand. Embryonic development is separated into Nauplius, Metanauplius and embryonic zoeal stages. The ontogenetic position of the pre-zoeal cuticle suggests that it represents the Metanauplius stage, and the absence of plumose pre-zoeal aesthaetes in *P. novaezelandiae* implies relationship with the more recently evolved brachyuran families. The significance of the pre-zoeal cuticle in brachyuran phylogeny is discussed. In *P. novaezelandiae* four embryonic zoeal phases are recognised as approximately equivalent to the four Zoea larval stages occurring in the majority of xanthid Brachyura. It was not possible to distinguish similar phases in embryonic zoeal development of *P. lumpinus* because of advanced anachronism which is normally associated with abbreviated development. The appearance of relatively advanced structures very early in ontogeny is attributed to the absence of the need for successive developmental stages to be adapted for free life. In the embryonic Zoea, carapace spines considered to assist with flotation and orientation, and natatory setae, are together reduced or absent in abbreviated development where such structures would be of no use within the egg.

In P. novaezelandiae and P. lumpinus increase in egg size during incubation is probably due to absorption of water by the embryo during development, and eclosion is initiated by rupture of the chorion through internal pressure thus created. Larvae of P. novaezelandiae hatch at a Megalopa larval stage and are retained beneath the pleon of the female crab. Those of P. lumpinus hatch as advanced, much-modified, and non-natatory Zoeae which are not retained by the parent. Simultaneous moulting of the pre-zoeal and zoeal skins occurs in both species.

The Megalopa larva and first five juvenile crab stages of P. novaezelandiae are described and compared with equivalent stages of P. vestitus from Australia recorded by Hale (1931). The Megalopa larva of P. lumpinus is described. P. lumpinus is considered as the least evolved of the three species of Pilumnus possessing abbreviated development, while P. vestitus suggests a second stage, and the third and most advanced stage is shown by P. novaezelandiae. Ecology of these three species is correlated with abbreviated development. Retention of potentially free-swimming Megalopa larvae by the parent explains gregariousness among juvenile crabs and adults of both P. novaezelandiae and P. vestitus.

It is probable that abbreviated development has evolved among marine and freshwater Brachyura as a response to habitat requirements of the adult crabs. Partial or complete abbreviation of the planktonic phase and retention of larvae would assist with retaining the stock within a restricted locality or ecological niche. Abbreviated development among Brachyura therefore has little phylogenetic significance.

INTRODUCTION

Five species of the family Xanthidae are known to occur in New Zealand. Of these Heterozius rotundifrons A. Milne Edwards, Ozius truncatus H. Milne Edwards, and Heteropanope (Pilumnopeus) serratifrons (Kinahan) have either two or four Zoea larval stages in their life-histories, and will be discussed in a second publication. The two remaining xanthid crabs which form the subject of this paper are Pilumnus novaezelandiae Filhol and Pilumnus lumpinus Bennett. In these species the Zoea larval phase is passed through within the egg and development is abbreviated. This type of development occurs only rarely among marine Brachyura.

Ovigerous females of Pilumnus novaezelandiae and of P. lumpinus were kept alive in aquaria at the Victoria University of Wellington Marine Biological Station at Island Bay. The embryonic development was traced by removing three or four eggs from the female crabs every five or six days up to the time of hatching. Eggs were preserved in 2-ethoxy-ethanol ("cellosolve"). Larvae were kept alive in covered finger bowls and in small aquaria. In this way the first five juvenile crab stadia of P. novaezelandiae were obtained over a period of 13 months.

The terms used here to describe embryonic development follow those of Brooks and Herrick (1891), Gurney (1926, 1942), and Ōishi (1959). The name embryonic Zoea is applied to the embryo at a stage of development when it possesses characters equivalent to those of a normal free-living Zoea larva. Decapod larval terms pre-Zoea and Zoea follow the nomenclature of Lebour (1928) while the name Megalopa is here employed in the sense suggested by Williamson (1957) and the ambiguous term post-larva has been avoided where possible. Non-larval stages following the Megalopa are termed juvenile crab stages.

Nomenclature of larval limbs and limb-segments follows that of Borradaile (1926), Gurney (1942), Hale (1927), and Lebour (1928) excepting that the suffix "ite" is deleted from limb-segment terms as in Wear and Yaldwyn (1966).

Pilumnus novaezelandiae Filhol, 1886

Two ovigerous female crabs each with a carapace width of 19.0 mm were collected from rock crevices on Takapuna Reef, Auckland, 24/10/1964. One carried 67 eggs and the other 74. The eggs were large (1.50 mm x 1.40 mm), light mauve to purple in colour, and were comparatively freshly laid. At the time of capture the eggs contained embryos at an early post-Nauplius or Metanauplius stage of development. A third ovigerous female (carapace width 22.5 mm) was caught in a small otter trawl in Kau Bay, Wellington Harbour, 12/11/1964. This crab carried 96 eggs containing advanced embryos within one week of hatching. P. novaezelandiae has not been recorded intertidally in the Wellington area.

In the female crab pleopods occur on abdominal segments two to five. The exopods of the pleopods are fringed by plumose hairs which overlap those on the lateral margins of the corresponding abdominal segments to form the sides of the brood pouch as in Naxoides (= Paranaxia) serpulifera (see Rathbun 1914, pp. 653-64), Cryptodromia octodentata, Paradromia lateralis (see Hale 1925, pp. 403-13) and Pilumnus vestitus (see Hale 1927, p. 322). The number of unusually large eggs (Fig. 1) results in the female pleon being held at right angles to the body or, occasionally, at an obtuse angle.

1. EMBRYONIC DEVELOPMENT

NAUPLIUS STAGE

"A well marked Nauplius stage is passed through in the egg by all Decapoda which hatch at a later stage, and embryonic life may be divided into stages, with pauses between, and even moults." (Gurney 1942, pp. 39-40.) However when ovigerous females of Pilumnus novaezelandiae were collected from Takapuna Reef the pre-Nauplius and Nauplius stages had already been passed through within the eggs, and embryos were in a post-naupliar stage of development.

METANAUPLIUS STAGE (Figs 2, 3, 4)

Embryos 36 days from hatching were in a stage of development equivalent to a stage termed Metanauplius by Ōishi (1959, p. 285). Eggs measured 1.50 mm x 1.40 mm and were without eye-pigment. The embryo was visible to the naked eye as a small translucent patch lying on the surface of the yolk mass (Fig. 2).

In the Metanauplius the carapace is not formed. The optic lobes lying either side of the rudimentary brain are large and well developed. Two further pre-oral appendages (first and second antennae) are present as uniramous outgrowths posterior to the optic lobes (Fig. 3). The mandibles are present as tiny buds lateral to the labrum (Fig. 3). Rudiments of the first and second maxillae and of the first and second maxillipeds occur posterior to the labrum, but there is no sign of the third maxillipeds or of the pereopods.

The thoracico-abdominal flexure is folded over the developing post-oral appendages (Fig. 2) but reaches only to the posterior margin of the mandible buds. The abdomen is incompletely divided into five segments, and the sixth segment is not separate from the telson (Fig. 4). The telson is broadly forked and bears five tiny unarmed

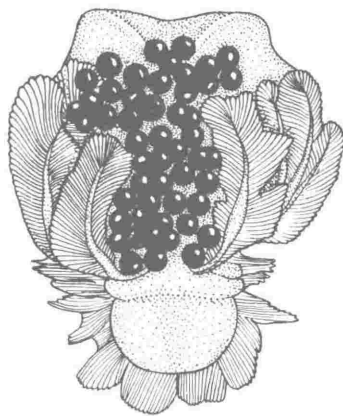
Pilumnus novaezelandiae Filhol

- Fig. 1 Ovigerous female: ventral view of abdomen
(drawn from photograph by M. D. King)
- Fig. 2 Metanauplius stage: embryo in situ; lateral
view (outer egg membrane removed)
- Fig. 3 Metanauplius stage: view of egg showing embryo
in situ (egg membranes removed)
- Fig. 4 Metanauplius stage: abdomen and telson
surrounded by pre-zoeal cuticle; dorsal view

Abbreviations:

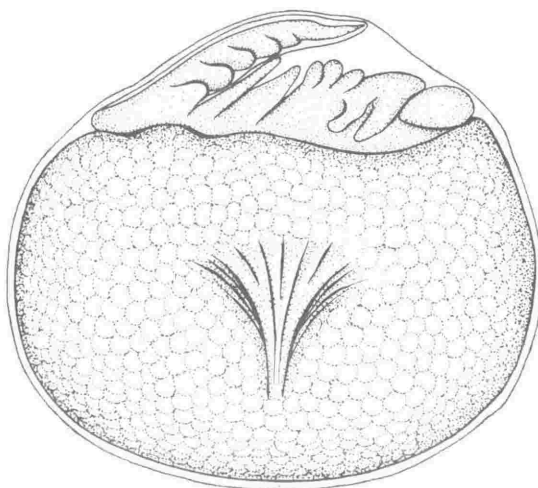
abd.	-	abdomen
ant.	-	antenna
mand.	-	mandible
max.	-	maxilla
mxd.	-	maxilliped
opt. lobe	-	optic lobe

1



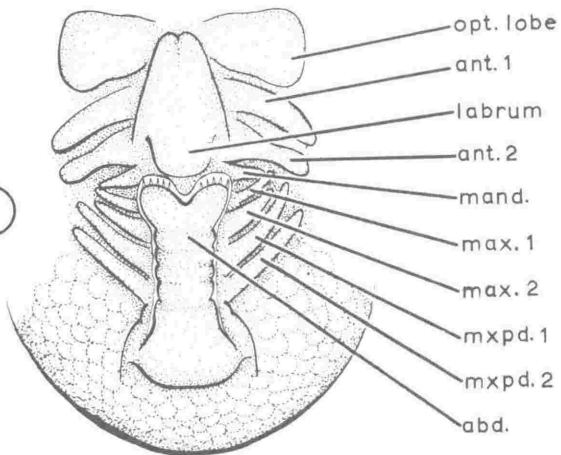
10.00 mm

0.50 mm



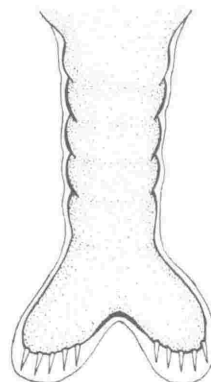
2

3



0.50 mm

4



0.25 mm

setae either side of the shallow cleft in the posterior midline. The abdomen and telson are enclosed within a thin, transparent, unsegmented cuticle which lacks spines or processes (Fig. 4), but this cuticle does not occur elsewhere in the Metanauplius.

EMBRYONIC ZOEAL STAGE (Figs 5-31)

The Metanauplius stage in embryonic development passes without abrupt transition or moult into a stage here termed embryonic Zoea. This stage in ontogeny possesses many characters of the normal free-living brachyuran Zoea larva, but it is here retained within the egg capsule. In P. novaezelandiae it is possible to identify four embryonic zoeal phases. These phases are not separated from each other by ecdyses, but are merely stages in development, characterised by morphological changes which appear to be of sufficient significance to warrant distinction. However the four phases are not completely equivalent to four free-swimming Zoea larval stages in the life-history of Brachyura. For example, in both P. novaezelandiae and P. lumpinus the embryonic zoeal carapace has no spines, and the exopods of the first and second maxillipeds have only rudimentary natatory setae, or these may be completely lacking. Also the normal sequence in the development of larval appendages is upset and some structures commonly found in late stage Zoea larvae appear very early in ontogeny.

As Gurney (1942) points out, successive free-living stages in larval development must be viable, and new structures can only appear in chronological order. When these normally free-living stages are passed through within the egg, there is no necessity for the preservation of such a sequence, or for the persistence of structures required in the planktonic environment. Hence carapace spines which are considered to be organs assisting in flotation and orientation (Lebour 1928; Foxon 1934), and natatory setae which effect thoracic propulsion are reduced in abbreviated development.

Pre-zoeal Cuticle

The pre-zoeal or embryonic cuticle (Lebour 1928; Gurney 1942) is a thin transparent membrane which forms during the embryonic development of all Decapoda which hatch at a Zoea stage, and surrounds the body and appendages of the larva. Generally this cuticle is shed immediately before hatching or during the hatching process (Gurney 1942, p. 53). Gurney considered the pre-zoeal cuticle to represent a pre-"zoeal" stage, once a free larva in ancestral forms, but now relegated to embryonic life. For example, this author regarded the pre-Zoea of the Caridea as equivalent to the Nauplius phase of the Penaeidea.

In the Brachyura the pre-zoeal cuticle is often produced into aesthaetes and long feathered processes on the first and second antennae and on the telson. In many species this cuticle is retained by the larva for several hours after the time of hatching. While the pre-zoeal cuticle is present, the larva is termed a "pre-Zoea" and this implies nothing more than its position in ontogeny (Lebour 1928).

In Pilumnus novaezelandiae the pre-zoeal cuticle is fully developed early in the embryonic zoeal stage and does not change significantly up to the time of hatching. It appears to develop with the appendages, but in the case of the inner ramus of the first antenna and the exopod of the second antenna the cuticle is developed to accommodate underlying structures before they differentiate. As the embryonic Zoea larva develops, the pre-zoeal cuticle extends to cover the first and second antennae, all post-oral appendages, the carapace as it forms, and the abdomen and telson. Processes or aesthaetes normally associated with the pre-zoeal cuticle in Brachyura (Lebour 1928; Gurney 1942) are here either absent or greatly reduced.

First Embryonic Zoeal Phase (Figs 5-8)

The first phase occurs about 28 days from the time of hatching. The carapace is developed to cover the basal sections of the thoracic

Pilumnus novaezelandiae: First embryonic zoeal phase

Fig. 5 Embryonic Zoea in situ; lateral view (inner and outer egg membranes removed)

Fig. 6 First antenna of left side

Fig. 7 Second antenna of left side

Fig. 8 Telson; dorsal view

Pilumnus novaezelandiae: Second embryonic zoeal phase

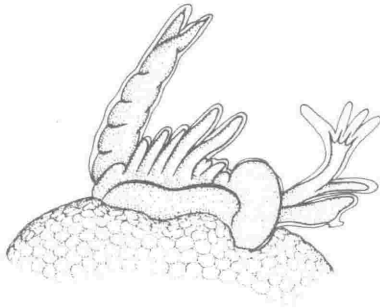
Fig. 9 Embryonic Zoea in situ; lateral view (outer egg membrane removed)

Fig. 10 Embryonic Zoea; lateral view (egg membranes and pre-zoeal cuticle removed);

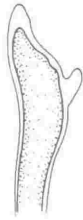
Fig. 11 Telson; dorsal view

Abbreviations:

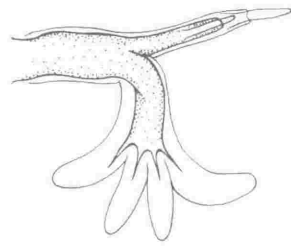
abd.	-	abdomen
cpce	-	carapace
egg mem.	-	egg membrane
p.z. cut.	-	pre-zoeal cuticle



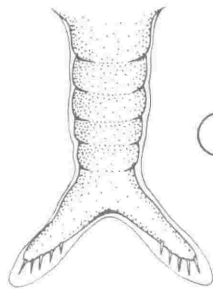
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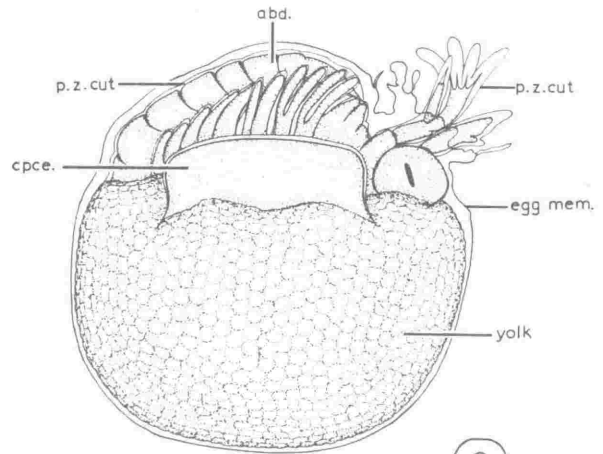


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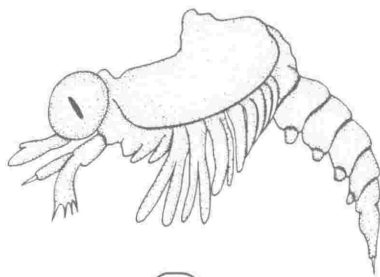


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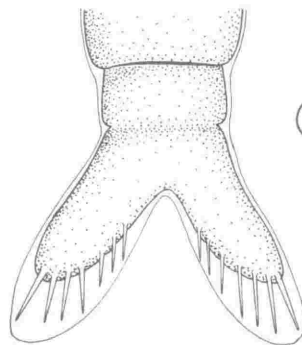
0.40mm



9



10



11

5, 9, 10
0.50mm

6, 7, 11
0.25mm

appendages and the thorax is free from the carapace. The optic lobes are well developed but not differentiated into eye and eye-stalk. Eye pigment is not present.

The first antenna (Fig. 6) is uniramous, but the surrounding pre-zoeal cuticle is produced into a small sac in a position to envelop the inner ramus which later develops. The second antenna (Fig. 7) comprises a short exopod with four terminal unarmed setae and a bud-like spinous process invaginated at its tip. The two rami are not separate from the protopod. The appendage is surrounded by the pre-zoeal cuticle which is only partly evaginated on the spinous process, but on the exopod it is extended distally as four short, unarmed aesthaetes.

Rudiments of eight pairs of post-oral appendages are developed, but the third, fourth, and fifth pereopods have not yet differentiated (Fig. 5). All post-oral appendages are uniramous, without setae, and are covered by the pre-zoeal cuticle.

The telson (Fig. 8) is more widely forked and the rami are narrower than in the Metanauplius stage.

Second Embryonic Zoeal Phase (Figs 9-11)

This occurs about 25 days before hatching and lasts for four or five days. The following characters distinguish the second phase:

The eye is incompletely separated from its stalk, and eye pigment is now present as a small red diagonal strip on the lateral surface of the optic lobes (Fig. 9).

The inner ramus of the first antenna (see Fig. 10) is now present as a tiny bud.

The first, second, and third maxillipeds are biramous, but without terminal setae. The endopod of the third maxilliped arises from near the base of the basipod (Fig. 10).

All five pairs of pereopods are present as uniramous rudiments.

The abdomen is now completely segmented but the sixth abdominal segment is incompletely separated from the telson (Fig. 11). The pre-zoeal cuticle does not follow the segmentation of the abdomen. Pleopods are present as bud-like rudiments on segments two to five. The telson (Fig. 11) now bears seven pairs of short posterior setae which are all similar and without marginal hairs.

Third Embryonic Zoeal Phase (Figs 12-23)

A third phase occurs 21 days before hatching and persists for six to seven days. The egg's size has increased to 1.65 mm x 1.50 mm and the embryo now occupies about half the volume of the egg (Fig. 12).

The carapace extends forward between the eyes as a small triangular rostrum, and the eye is now differentiated from its stalk (Fig. 13). The area of eye pigment has increased and is elliptical in shape.

The second antenna has developed an endopod which is surrounded by the pre-zoeal cuticle. The endopod is almost as long as the spinous process by the time that the embryonic Zoea passes into its fourth phase of development.

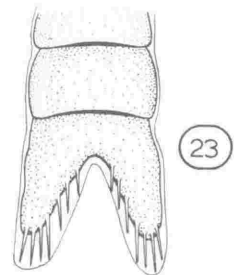
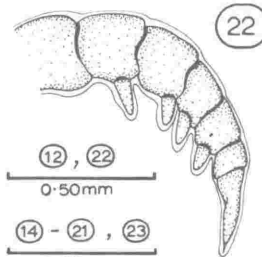
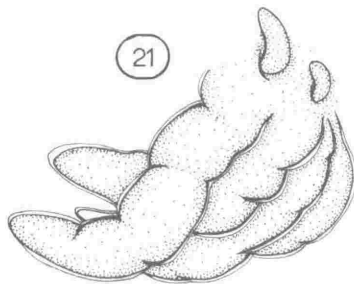
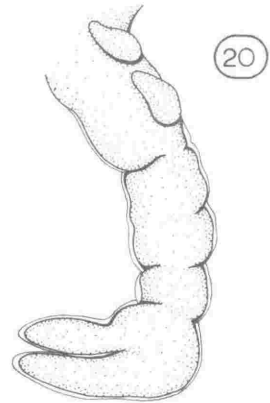
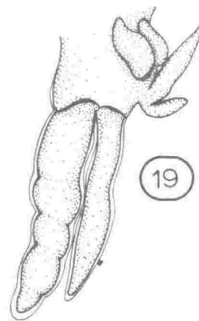
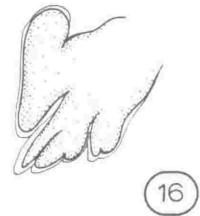
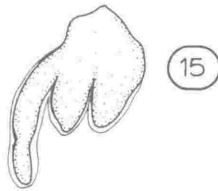
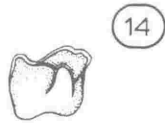
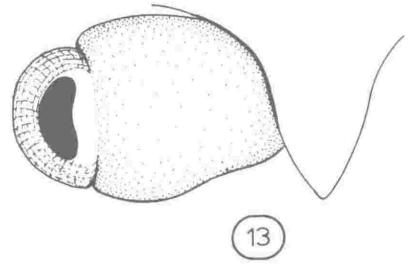
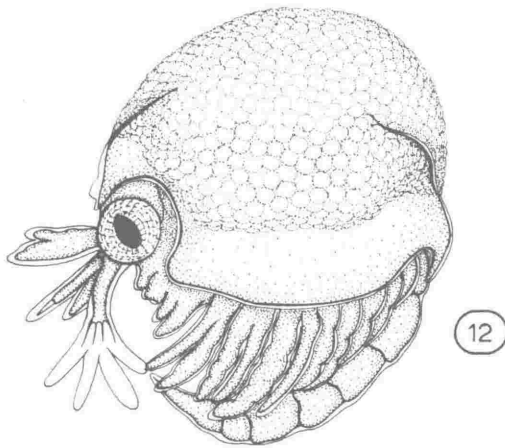
The mandible (Fig. 14) and first and second maxillae (Figs 15, 16) follow the usual brachyuran pattern, except that the scaphognathite of the second maxilla is here without marginal setae and the palps of all three appendages are unsegmented.

Maxillipeds and pereopods (Figs 17-21) have increased in size and show the beginnings of segmentation. The first pereopod (Fig. 20) has a rudimentary chela at its tip. Gill buds are present, but difficult to determine early in this third phase as they are then only tiny rudiments. However, shortly before the embryo passes into a fourth embryonic zoeal phase the gills can be formulated as follows:

Pilumnus novaezelandiae: Third embryonic zoeal phase

- Fig. 12 Embryonic Zoea; lateral view (inner and outer egg membranes removed)
- Fig. 13 Right eye and rostrum; anterior view
- Fig. 14 Mandible of left side
- Fig. 15 First maxilla of left side
- Fig. 16 Second maxilla of left side
- Fig. 17 First maxilliped of left side
- Fig. 18 Second maxilliped of left side
- Fig. 19 Third maxilliped of left side
- Fig. 20 First pereopod of left side
- Fig. 21 Second, third, fourth and fifth pereopods of left side
- Fig. 22 Abdomen; lateral view
- Fig. 23 Sixth abdominal segment and telson; dorsal view

(13)
0.20mm



(12, 22)
0.50mm
(14) - (21), (23)
0.25mm

	MAXILLIPEDS			PEREIOPODS				
	1st	2nd	3rd	1st	2nd	3rd	4th	5th
Pleurobranchiae	-	-	-	-	1	1	-	-
Arthrobranchiae	-	1	2	2	-	-	-	-
Podobranchiae	-	1	1	-	-	-	-	-
Epipodites	1	1	1	-	-	-	-	-
Exopodites	1	1	1	-	-	-	-	-

The arthrobranch of the second maxilliped is very small. It is the last to develop and may not be present until the fourth phase.

The sixth abdominal segment is now separate from the telson (Fig. 23). The pleopod buds are long but still uniramous (Fig. 22).

Fourth Embryonic Zoeal Phase (Figs 24-31)

This final phase is evident 14 days before hatching. The major characters of this phase persist up to the time of the embryonic Zoea-Megalopa transition stage, which occupies the 24 hours before hatching. During this phase the eggs increase in size together with the embryo and its appendages, and the volume of yolk decreases. Fourteen days before hatching the eggs measure 1.65 mm x 1.53 to 1.55 mm, but by the time of hatching this increases to between 1.65 mm x 1.60 mm and 1.75 mm x 1.65 mm.

The embryonic zoeal carapace is now fully formed and covers the remaining yolk (Fig. 24). Eye pigment has now reached almost maximum development.

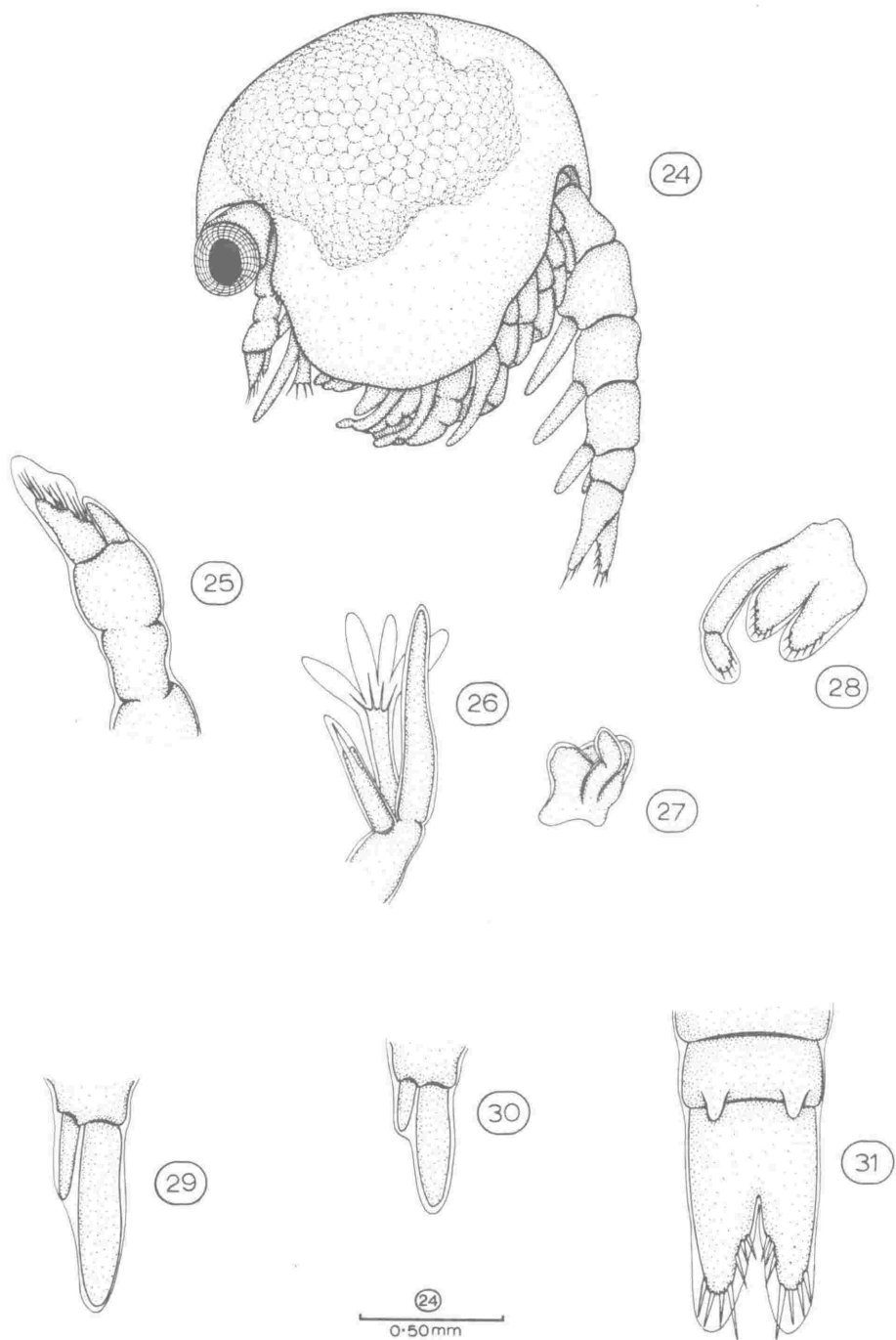
The peduncle of the first antenna is incompletely divided into three unarmed segments of about equal length (Fig. 25).

The endopod of the second antenna (Fig. 26) is now longer than the spinous process whose tip is still invaginated. The exopod has not developed further.

The mandible (Fig. 27) and second maxilla (Fig. 28) each have

Pilumnus novaezelandiae: Fourth embryonic zoeal phase

- Fig. 24 Embryonic Zoea; lateral view (egg membranes and pre-zoeal cuticle removed)
- Fig. 25 First antenna of left side
- Fig. 26 Second antenna of left side
- Fig. 27 Mandible of left side
- Fig. 28 First maxilla of left side
- Fig. 29 Pleopod from left side of second abdominal segment
- Fig. 30 Pleopod from left side of fifth abdominal segment
- Fig. 31 Sixth abdominal segment and telson; ventral view



(24)
0.50mm

(25) - (31)
0.25mm

the palp divided into two segments. Short terminal setae are visible under the pre-zoeal cuticle which surrounds the palp of the second maxilla.

The pereopods are visibly segmented, but the pre-zoeal cuticle surrounding these is not segmented.

Pleopod buds are now biramous. Pleopods of the second abdominal segment (Fig. 29) measure 0.37 mm in length, but pleopods decrease in size posteriorly to those of the fifth segment which are only 0.25 mm long (Fig. 30). Uropod buds (Fig. 31) are present as rudiments arising ventrally from the sixth abdominal segment. The telson (Fig. 31) is deeply cleft with the posterior setae arranged in two groups: a posterolateral group of four setae with the fourth (inner) seta longer than the three lateral setae, and an inner group of three smaller setae lying within the fork of the telson. These setae may protrude through the pre-zoeal cuticle.

The chromatophore pattern is now fully developed, but as no free Zoea exists in this species a detailed study of the distribution is unnecessary. All chromatophores are red and there is complete representation of both the primary and secondary systems (Aikawa 1929, p. 20, fig. 1).

EMBRYONIC ZOEAL TO MEGALOPA TRANSITION STAGE (Figs 32-42)

This stage is equivalent to Czerniawsky's term Pseudozoea for a "Stadium transitans inter zoëas et megalopideas." (Czerniawsky 1884, p. 247 ref. Gurney 1942, p. 37). In the specialised and abbreviated ontogeny of Pilumnus novaezelandiae this stage is not free-living, and a descriptive term is not necessary.

The embryonic Zoea to Megalopa transition stage does not involve a moult or ecdysis, but is rather a series of morphological changes occurring in the embryonic Zoea while it is still within the egg. These

changes occur during the 24 hour period before hatching, and involve a gradual moulding of structures characteristic of the Megalopa stage within a newly formed megalopal skin. The unhatched larvae are at this time surrounded by five membranes - the skin of the Megalopa newly formed, the zoeal cuticle, the pre-zoeal cuticle, and the inner and outer egg membranes. Details of the Megalopa larva visible beneath the transparent zoeal skin are recorded in the description of the Megalopa stage.

Embryonic larvae dissected from the egg show varying degrees of atrophy of the antennal exopod and spinous process, the first maxillipeds and exopods of the second and third maxillipeds, and withdrawal of the abdomen and telson. Other structures such as the carapace, antennal endopod, and pereopods show rapid growth. These trends become more obvious towards hatching and are outlined in the description following:

The Megalopal carapace is wrinkled and folded beneath that of the Zoea.

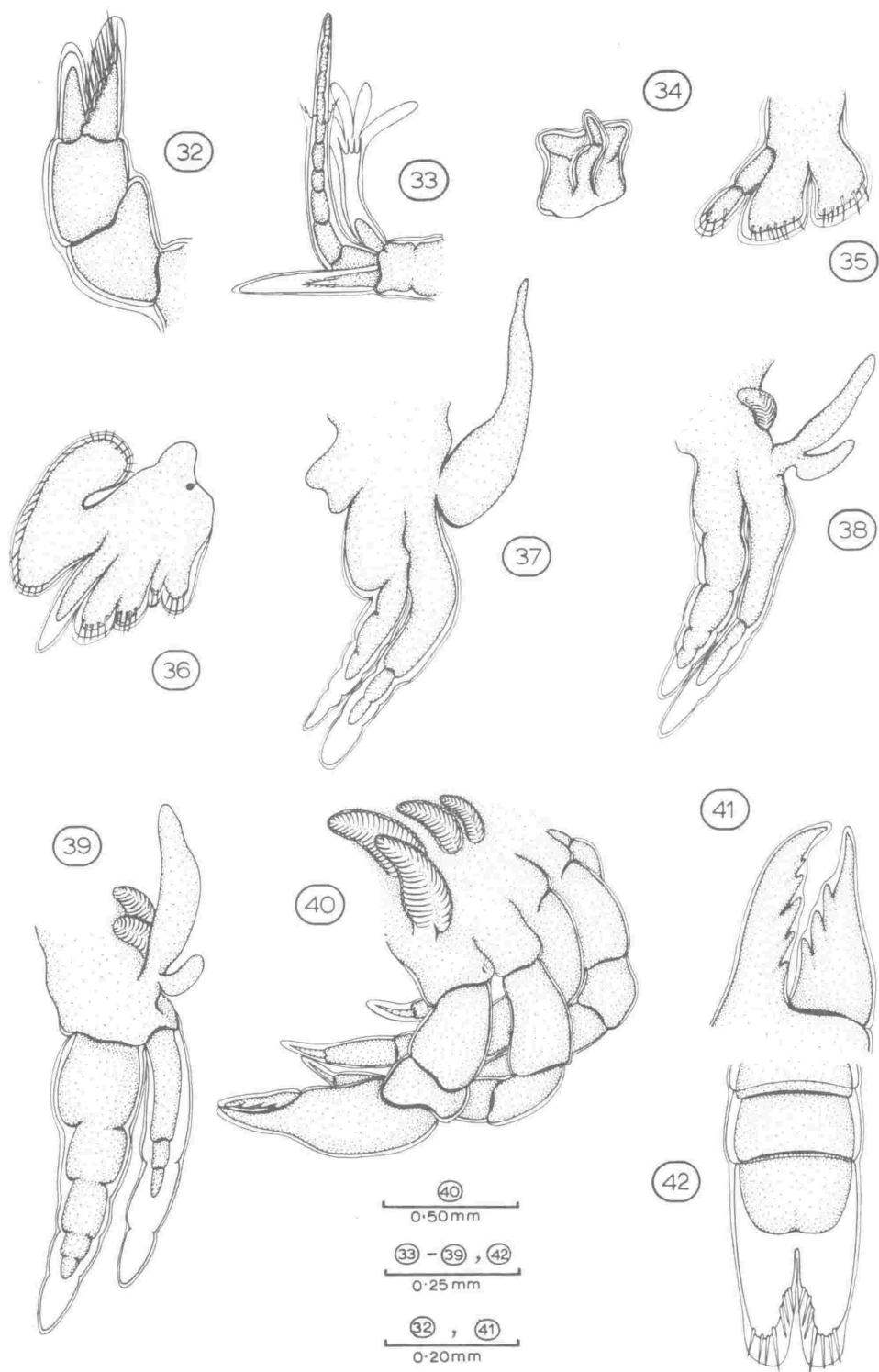
The first antenna (Fig. 32) possesses all structures of the Megalopa larva visible beneath the transparent cuticle.

The second antenna (Fig. 33) is characterised by a robust, jointed endopod, but the exopod and spinous process are reabsorbed to a varying degree. The endopod is surrounded by the zoeal skin but the pre-zoeal cuticle is usually ruptured distally. Viable tissue is withdrawn from the zoeal skin defining the exopod and spinous process so that except basally, these two rami are empty sacs. Reabsorption of the exopod and spinous process is often complete by the time of hatching.

The mandible (Fig. 34), first and second maxillae (Figs 35, 36), and first to third maxillipeds (Figs 37-39) all show slight retraction from the periphery of the zoeal cuticle. This withdrawal is more marked in the exopods of these appendages which are smaller in the Megalopa larva than in the fourth embryonic zoeal phase.

Pilumnus novaezelandiae: Embryonic Zoea/
Megalopa transition stage

- | | |
|---------|--|
| Fig. 32 | First antenna of left side |
| Fig. 33 | Second antenna of right side |
| Fig. 34 | Mandible of left side |
| Fig. 35 | First maxilla of left side |
| Fig. 36 | Second maxilla of left side |
| Fig. 37 | First maxilliped of left side |
| Fig. 38 | Second maxilliped of left side |
| Fig. 39 | Third maxilliped of left side |
| Fig. 40 | First to fifth pereopods of left side |
| Fig. 41 | First pereopod of left side; fixed and movable fingers |
| Fig. 42 | Sixth abdominal segment and telson; dorsal view |



The pereopods (Fig. 40) are jointed and well formed. The fixed and movable fingers of the cheliped (Fig. 41) are toothed, and the second to fifth pereopods each have a spine-like claw showing through the zoeal cuticle. The pre-zoeal cuticle is apparently lacking from the pereopods, but rapid growth of underlying tissue may have ruptured this thin membrane.

The abdomen has considerably withdrawn from the zoeal cuticle. Within two or three hours of hatching the posterior margin of the megalopal telson reaches only the proximal third of the embryonic zoeal telson (Fig. 42). The telson of the Megalopa larva is considerably smaller than that of the embryonic Zoea, and its reabsorption and moulding to this smaller size and different shape is almost complete before the megalopal abdomen starts to withdraw from the zoeal skin immediately before hatching.

2. HATCHING

Hatching observed in the laboratory usually took about 30 minutes to complete. The young leave the egg as soft, flaccid, Megalopa larvae. Hatching involves rupture of the outer egg membrane (chorion) followed by considerable movement on the part of the embryo which actively breaks the inner egg membrane. In one process the Megalopa then emerges from the zoeal cuticle, the pre-zoeal cuticle, and the egg. The zoeal and pre-zoeal cuticles apparently rupture along the line of the posterior margin of the carapace as the Megalopa frees itself from the inner egg membrane. The embryonic and extra-embryonic membranes are together shed into the sea water.

3. POST-EMBRYONIC DEVELOPMENT

Eggs of the two ovigerous female crabs from Takapuna Reef hatched 8/12/1964. All eggs hatched within a period of eight hours. Empty egg cases were shed into the sea water while emergent Megalopa larvae remained beneath the pleon of the female. All 28 of the progeny of one female crab were removed on hatching and placed in finger bowls containing sea water which was renewed every two or three days. Those of the second female were not disturbed. Eggs of the Wellington Harbour specimen hatched 22/12/1964 and the progeny were allowed to remain with the parent.

The female crabs did not attempt to feed while in captivity and ignored all organic matter provided. However the undisturbed female collected from Takapuna Reef consumed all its Megalopa larvae as they hatched. Six larvae of the second Auckland specimen survived in finger bowls for 38 days before moulting to the first juvenile crab stage, but all of these died shortly after moulting. Ten larvae hatched from the Wellington Harbour specimen remained beneath the female abdomen for 35 days and then moulted to the first juvenile crab stage. These juveniles showed no interest in returning to the female. Nine of these died while in the second and third juvenile crab stages during the winter of 1965, but one juvenile crab, later found to be female, survived with the parent crab among algae-covered stones in a small aquarium of sea water. This juvenile survived to moult from the fifth to the sixth juvenile crab stage 15/2/1966, but shortly after moulting to the sixth stage it was unfortunately lost.

THE MEGALOPA LARVA

The Megalopa larvae spend the greater part of their life enmeshed in the brood pouch formed by the large exopods of the pleopods and hairs on the sides of the female abdomen (Plate 1A).

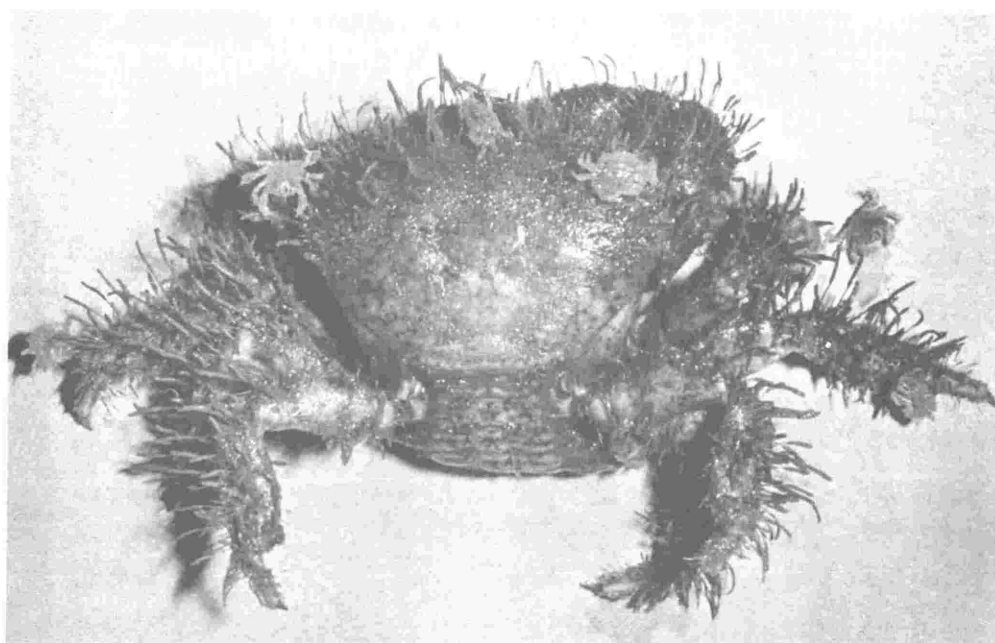
Pilumnus novaezelandiae

- A. Female crab in ventral view showing Megalopa larvae (brood young) beneath pleon

- B. Female crab in dorsal view showing Megalopa larvae positioned over the carapace and in the near vicinity of the parent



A



B

Female crabs carrying a brood of *Megalopa* larvae have also been observed in the field (Prof. J. E. Morton, pers. comm.). During the first few hours of aquarium life the carapace of the *Megalopa* is wrinkled and very soft. During this time the larvae remained exclusively under the protection of the parent abdomen. After about 12 hours they were considerably more robust, and often moved short distances from the female using their natatory pleopods and swimming in the fashion normal for brachyuran *Megalopa* larvae (Foxon 1934). These "exploratory" migrations were of short duration and the young always returned to the parent, either to take up a temporary position on the female carapace or pereopods (Plate 1B) or to crawl immediately back beneath the abdomen.

Description of *Megalopa* Larva (Figs 43-57):

This is based on five larvae hatched from one of the Takapuna Reef specimens, and five hatched from the female crab obtained from Wellington Harbour.

Cephalothorax (Figs 43, 44)

Carapace broadly rounded, 1.66 mm in length and 1.88 mm wide with regions poorly defined. Orbital notch deep; interorbital space 0.70 mm. Rostral region broad, depressed, and fringed on each side with six or seven stout plumose setae directed forwards and upwards. One pair of short forwardly directed spines lateral to these setae in a supraorbital position. Anterolateral margin of carapace with three postorbital spines: inner spine small and situated midway along the posterior border of the orbital notch; central spine larger and more robust; lateral spine situated at the extreme anterolateral margin of the carapace. Margins of carapace otherwise smooth but fringed with fine hairs posteriorly. Dorsal surface of carapace provided with paired groups of two to

four stout plumose setae in each of the protogastric, hepatic, branchial, and cardiac regions (Fig. 43); dorsal surface otherwise with a sparse covering of fine hairs.

Eyes large, extending laterally to the level of the largest post-orbital spine. Anterolateral margin of eye-stalk with two short plumose setae.

Cephalic Appendages (Figs 45-49)

First antenna (Fig. 45) with peduncle of three segments: proximal segment swollen at base to enclose a statocyst and provided with a dense fringe of hairs in this region; second segment smooth; third (distal) segment with one terminal seta on outer margin. Inner ramus unsegmented and bearing two medial and two distal setae. Outer ramus of five segments and twice the length of inner ramus: first segment without setae; second, third and fourth segments each with a tuft of aesthaetes on the inner margin; terminal segment longer with one long seta and one or two shorter setae at its tip.

Second antenna (Fig. 46) with two-segmented protopod: basis about twice the length of the coxa. Endopod of 12 or 13 segments: five proximal segments short; seven or eight distal segments longer and more slender; setae few in number with no consistent arrangement, but generally there are three terminal setae. No sign of an exopod.

Mandible (Fig. 47) with a three-segmented palp; terminal segment with several short distal setae.

First maxilla (Fig. 48) with proximal endite fringed medially with about four long hairs and distally with short plumose setae curved towards the mouth. Distal endite with several short hairs along its inner margin; distal setae similar to those on the proximal endite; two long plumose setae at its outer distal angle. Palp of two segments: proximal segment with several long plumose setae; distal segment with three terminal setae.

Pilumnus novaezelandiae: Megalopa larva

Fig. 43 Megalopa larva; dorsal view

Fig. 44 Megalopa larva; lateral view

Fig. 45 First antenna of right side

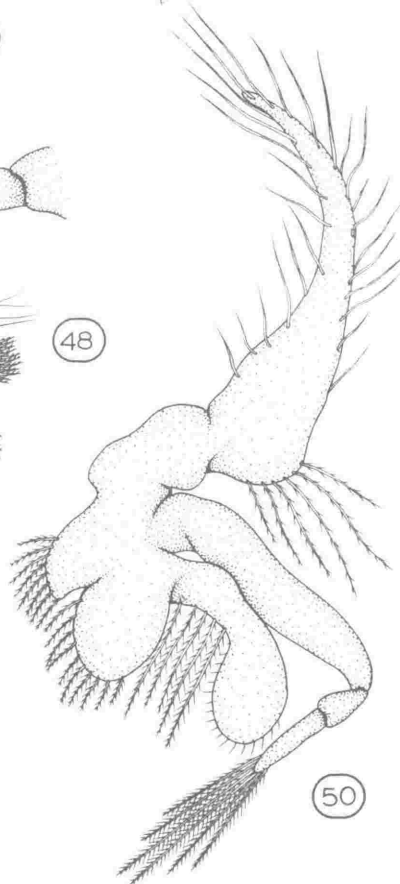
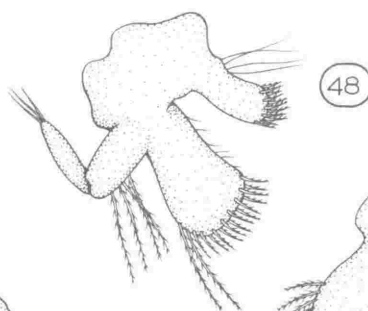
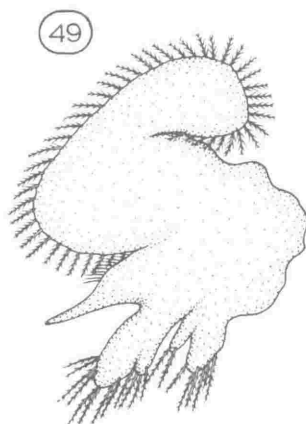
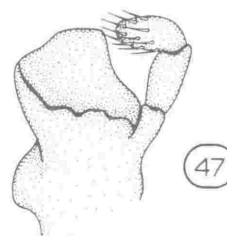
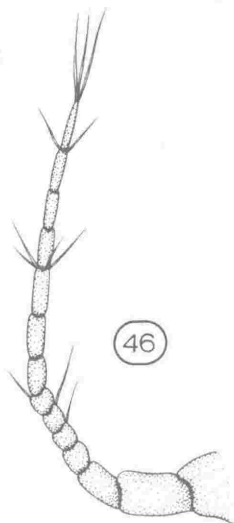
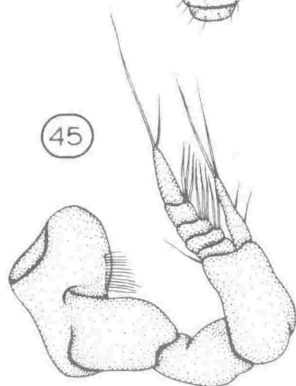
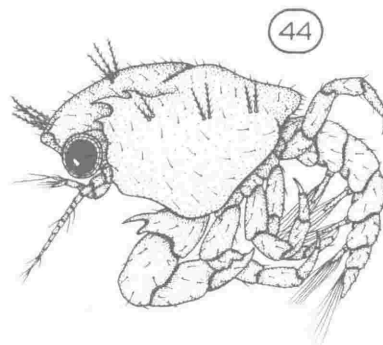
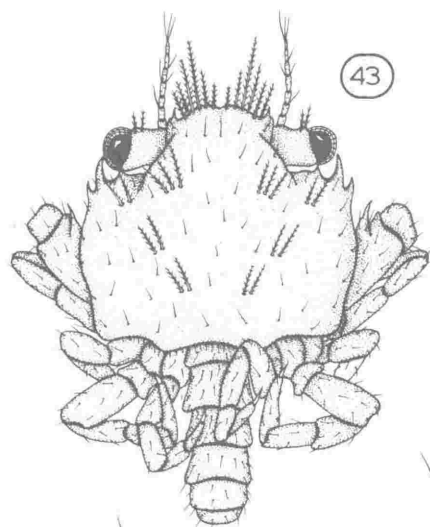
Fig. 46 Second antenna of left side

Fig. 47 Mandible of left side

Fig. 48 First maxilla of left side

Fig. 49 Second maxilla of left side

Fig. 50 First maxilliped of left side



43 , 44
1.00mm

45 - 50
0.25mm

Second maxilla (Fig. 49) follows the usual decapod pattern with two proximal endites separated from two more distal endites by a deep cleft. All four endites are fringed with plumose setae arranged as illustrated in Fig. 49. Palp unsegmented, with short hairs fringing the outer margin of its basal half; distal half smooth and acicular as in the adult. Scaphognathite large, flattened, and fringed with many short plumose setae.

Thoracic Appendages (Figs 50-53)

First maxilliped (Fig. 50) flattened as in the adult. Coxa and basis each fringed with plumose setae. Endopod flattened and spatuliform; proximal half with five or six long plumose setae arising from its inner margin; distal margins fringed with short hairs. Exopod large and three-segmented; basal segment without setae and as long as the endopod; second segment very short, without setae; distal segment about one-third the length of basal segment and bearing six terminal biplumose setae. Epipod strongly developed, flattened and tapering to a point; marginal setae plumose basally but otherwise smooth.

Second maxilliped (Fig. 51) not greatly flattened. Coxa and basis incompletely separated and setose along their inner margins. Endopod of five segments and curved inwards: ischium and merus fringed medially with short plumose setae; carpus and propodus with setae along their distal margins; dactylus with a terminal tuft of stout plumose setae. Exopod strongly developed, three-segmented and similar to that of the first maxilliped described above. Epipod small, slender, and fringed with smooth setae. A rudimentary podobranch arises from the base of the epipod, but is without lamellae and therefore not functional in the Megalopa larva. A rudimentary arthrobranch, differentiated into lamellae at its base only, lies above the epipod.

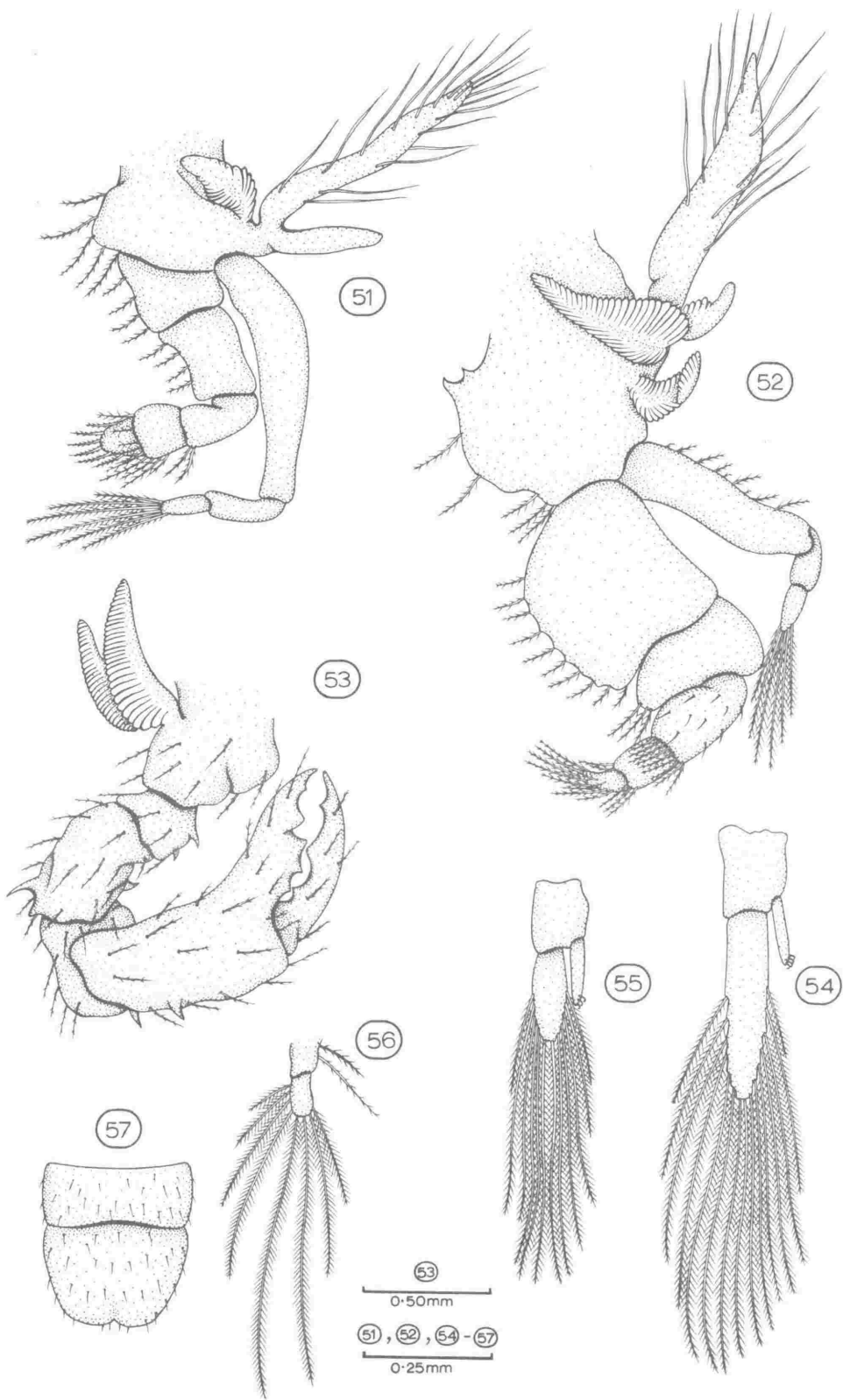
Third maxilliped (Fig. 52) with coxa and basis difficult to separate and sparsely setose. Endopod of five segments is large and laterally expanded: ischium expanded into a broad plate which is serrated medially and fringed with short plumose setae in the same region; merus half the length of ischium, similarly expanded, but without medial serrations; carpus not flattened, provided with a sparse covering of setae but densely fringed along its distal margin; propodus with a few distal setae; dactylus small but with many terminal plumose setae. Exopod smaller than that of first and second maxillipeds and differs in having a fringe of fine plumose hairs along the lateral margin of the basal segment. Gills comprise two well developed arthrobranchs each with lamellae visible, and a small podobranch with lamellae differentiated at its base only. The epipod is considerably smaller than that of the first maxilliped, but is larger than the epipod of the second maxilliped.

First pereopod (Fig. 53) strongly developed, chelate, with all segments sparsely covered with setae. Left and right chelipeds are of equal size. Coxa and basis short and concealed beneath the carapace; ischium short with two small medial spines; merus about twice the length of the ischium, with a small spine midway along its inner face and one large forwardly directed spine arising from its outer distal margin; carpus slightly shorter than merus and without spines; propodus as long as the total length of ischium, merus, and carpus - two spines on its outer face and fixed finger with three large teeth and one or two smaller teeth; dactylus (movable finger) more or less falciform and with three prominent teeth. The first pereopod has no epipod but bears two well formed arthrobranchs.

Second, third, fourth, and fifth pereopods (Figs 43, 44) all similar and differing from each other only in the size and arrangement of the gills. The following description is based on the second pereopod.

Pilumnus novaezelandiae: Megalopa larva

- Fig. 51 Second maxilliped of left side
- Fig. 52 Third maxilliped of left side
- Fig. 53 First pereopod of right side
- Fig. 54 Pleopod from left side of second abdominal
segment
- Fig. 55 Pleopod from left side of fifth abdominal
segment
- Fig. 56 Uropod from left side of sixth abdominal
segment
- Fig. 57 Sixth abdominal segment and telson; dorsal
view



Coxopod, basipod, and five distal segments (endopod) with a sparse covering of short setae. Dactylus terminates in a strong spine, but segments otherwise without spines. Ischium short; merus and dactylus four times the length of ischium; carpus and propodus both about three times the length of the ischium. All walking legs are without epipods. One pleurobranch occurs on each of the second and third pereopods, but the fourth and fifth pereopods are without gills.

Abdomen (Figs 43, 44, 54-57)

The abdomen comprises six segments and a telson (Figs 43, 44, 57). Segments laterally expanded and flattened, sparsely setose dorsally and laterally; first segment two-thirds the length of the second and slightly narrower; second, third, fourth, and fifth segments of about equal length; sixth segment narrower and about half the length of the fifth segment. Pleopods occur on the second to fifth segments (Fig. 44). Pleopods of the second segment (Fig. 54) biramous; protopod of one segment; exopod twice the length of the protopod, more than twice its width, and bears 15 long biplumose setae along the margins of its distal half; endopod a short rod, one-third the length of the exopod and one-third as wide, without setae but with four small hooklets arising from the inner margin just below its tip. Pleopods of the third and fourth segments are similar to those of the second segment, but smaller. Pleopods of the fifth segment (Fig. 55) with a much smaller exopod which bears only 12 marginal biplumose setae; endopod two-thirds the length of exopod and only half as wide, but with three terminal hooklets. Uniramous uropods (Fig. 56) are developed ventrally from the sixth abdominal segment: protopod twice as long as broad, usually with two or three inner proximal setae; exopod about the same size as the protopod, with eight long biplumose setae spaced along its outer, distal, and inner distal margins; no sign of an endopod. Telson (Fig. 57) broadly rounded with a shallow indentation in the posterior midline; posterior margin with a variable

number (usually four or six) tiny posterior setae.

Chromatophore Pattern

Chromatophores of the *Megalopa* larva are variable in position, colour, and number, but it was possible to establish a relatively set pattern. Concentrations of red pigment are found in the eye-stalks, epigastric region of the carapace, and in all segments of the pereopods except in the dactyli of the second to fourth pereopods. These chromatophores are usually rounded when contracted, but are more dendritic in their expanded state and tend towards orange. From six to eight red stellate chromatophores are situated in the branchial region of the carapace, and the hepatopancreas is coloured brown. Additional red stellate chromatophores are scattered over the carapace, especially in the gastric and cardiac regions, but these are variable in position and in number.

FIRST JUVENILE CRAB STAGE (Figs 58, 63, 68, 73, 78, 83)

Sixteen first stage juvenile crabs were obtained by moult from *Megalopa* larvae.

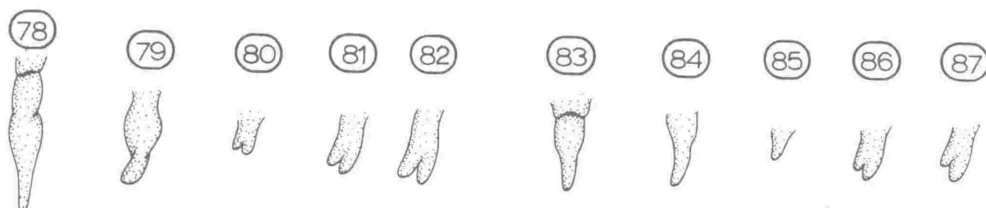
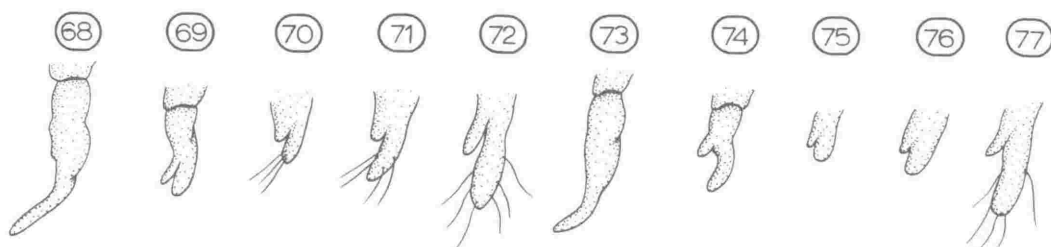
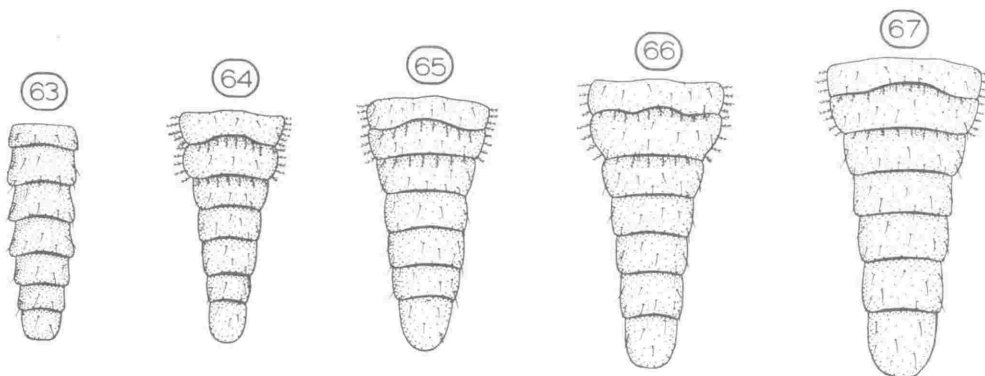
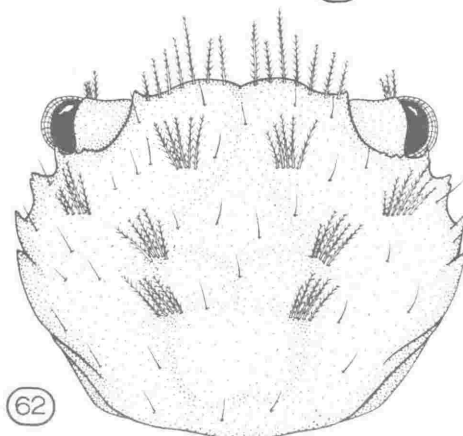
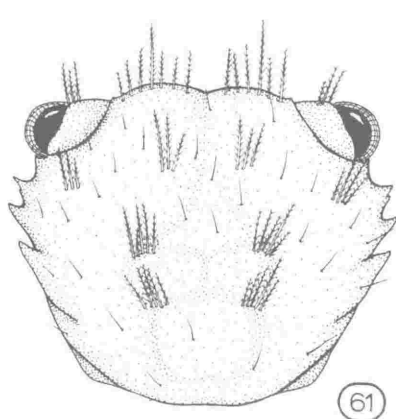
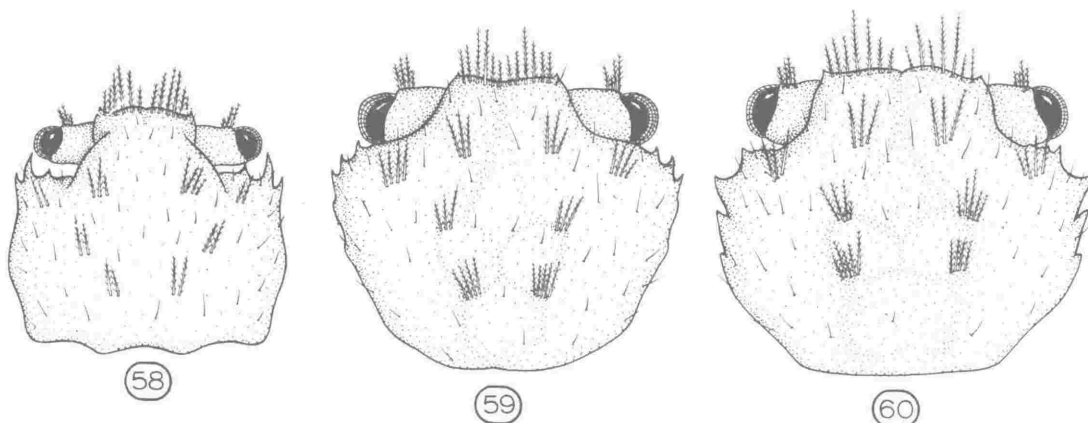
The juveniles are semi-transparent and the chromatophores are less well defined than in the *Megalopa* larva.

The carapace (Fig. 58) is 1.65 mm long and from 1.90 mm to 1.96 mm wide, but otherwise differs little from that of the *Megalopa*.

The pleopods have now atrophied into uniramous rods comprising a short protopod and a long, sometimes shrivelled exopod without natatory setae. As these pleopods are no longer functional as natatory organs the first stage juvenile crabs are not able to swim. Pleopods of the second (Fig. 68), third (Fig. 73), fourth (Fig. 78), and fifth (Fig. 83) abdominal segments respectively measure 0.30 mm, 0.28 mm, 0.26 mm, and 0.17 mm in length. Uropods are absent. The telson (Fig. 63) lacks a median indentation and the posterior margin is now straight and without setae. There is no evidence of sexual dimorphism in either the shape of the abdomen or the nature of the pleopods.

Pilumnus novaezelandiae: Juvenile crab stages

- Figs 58-62 Carapace in dorsal view; first to fifth
juvenile crab stages
- Figs 63-67 Abdomen in dorsal view; first to fifth
juvenile crab stages
- Figs 68-72 Pleopod from left side of second
abdominal segment; first to fifth
juvenile crab stages
- Figs 73-77 Pleopod from left side of third abdominal
segment; first to fifth juvenile crab
stages
- Figs 78-82 Pleopod from left side of fourth abdominal
segment; first to fifth juvenile crab
stages
- Figs 83-87 Pleopod from left side of fifth abdominal
segment; first to fifth juvenile crab stages



58 - 67
1.00mm

68 - 87
0.25mm

The duration of the first juvenile crab stage varied between 41 days and 44 days under laboratory conditions (16°C to 18°C).

SECOND JUVENILE CRAB STAGE (Figs 59, 64, 69, 74, 79, 84)

All ten first stage juvenile crabs reared from the female crab from Wellington Harbour moulted to a second stage between 7/3/1965 and 10/3/1965. Six of these died shortly after moulting.

The crabs are now opaque, coloured brownish white, and nearly all trace of red chromatophores has disappeared.

Carapace (Fig. 59) 1.90 mm long and 2.25 mm wide with regions now moderately well defined. Interorbital space 0.90 mm. Postorbital carapace spines much reduced. Lateral margins of carapace now produced into two indistinct swellings: the first behind the anterolateral carapace spine immediately posterior to the cervical groove; the second posterior to the first in the branchial region.

The cephalic and thoracic appendages are now similar to those of the adult crab. All gills are now functional with lamellae well developed.

The abdomen (Fig. 64) has considerably altered in shape, and measures 1.55 mm in total length. The first and second segments are each 0.70 mm wide, the third 0.50 mm, the fourth 0.43 mm, and the fifth and sixth 0.40 mm and 0.30 mm wide respectively. The telson is now rounded posteriorly. The first and second segments are fringed laterally and posteriorly with fine plumose hairs. The pleopods (Figs 69, 74, 79, 84) have atrophied still further and are all about 0.17 mm in length. Pleopods of the second (Fig. 69) and third segments (Fig. 74) are biramous, the endopods being present as tiny buds.

The four surviving second stage juvenile crabs lived for 72, 82, 82 and 86 days respectively before moulting to a third stage. Water temperatures varied between 12°C and 15°C during this time.

THIRD JUVENILE CRAB STAGE (Figs 60, 65, 70, 75, 80, 85)

Four third stage juvenile crabs were obtained by moult between 20/5/1965 and 5/6/1965. Three of these died within two days of moulting.

The third juvenile crab stage differs from the second stage described above in the following characters:

The carapace (Fig. 60) measures 2.10 mm long and 2.50 mm wide; interorbital space 1.25 mm. Lateral swellings present in the second stage have now developed into prominent lateral spines or tubercles which persist in later juvenile crab stages and in the adult. The lateral postorbital spine apparently remains as the anterior member of three lateral spines or tubercles. The second postorbital spine remains in a lateral postorbital position but the median spine is now absent or represented by one or more granulations or spinelets.

The abdomen (Fig. 65) is similar in shape to that of the second stage, but is now larger - 1.70 mm long and 0.85 mm across its widest (first) segment. Pleopods of the second (Fig. 70), third (Fig. 75), fourth (Fig. 80), and fifth (Fig. 85) abdominal segments measure 0.13 mm, 0.09 mm, 0.06 mm, and 0.03 mm in length respectively. The first three pairs are biramous, the endopod present as a tiny inconspicuous bud; the fourth pleopods are of one ramus only.

The third stage juvenile crab moulted to a fourth stage 2/9/1965. The third stage therefore lasted for 92 days with laboratory water temperatures varying between 10.5° and 13°C.

FOURTH JUVENILE CRAB STAGE (Figs 61, 66, 71, 76, 81, 86)

The fourth stage differs from the third stage in the following characters:

Carapace (Fig. 61) 2.15 mm long and 2.60 mm wide; interorbital space 1.25 mm. Postorbital carapace spines much reduced; anterior lateral carapace spine with a bifid tip, but this is probably an individual variation as this feature is not usually found in adult crabs.

The fixed and movable fingers of the first pereopod are now pigmented dark brown as in adult crabs.

Abdomen (Fig. 66) 1.90 mm in total length with the sixth segment a little longer than any of the first to fifth segments. The widths of the six abdominal segments and telson are respectively 0.87 mm, 0.81 mm, 0.69 mm, 0.56 mm, 0.50 mm, 0.44 mm, and 0.38 mm. All four pairs of pleopods (Figs 71, 76, 81, 86) are biramous, but only slightly longer than those of the third juvenile crab stage.

The duration of the fourth juvenile crab stage was 89 days. Water temperatures varied between 11°C and 17°C.

FIFTH JUVENILE CRAB STAGE (Figs 62, 67, 72, 77, 82, 87)

The fourth stage moulted to the fifth stage 30/11/1965.

The carapace (Fig. 62) is now 2.40 mm long and 3.00 mm wide with the interorbital space 1.50 mm. The postorbital and three lateral carapace spines are more pronounced than in the fourth stage.

The abdomen (Fig. 67) is now 2.13 mm long with segments in the same proportion as those of the fourth stage, but relatively longer. Pleopods of the second and third segments (Figs 73, 77) are each 0.20 mm in length, but their exopods now have a few marginal setae. Pleopods of the fourth and fifth segments (Figs 82, 87) are considerably smaller than those of the anterior segments, without setae, and are 0.12 mm and 0.08 mm long respectively.

The fifth stage lasted for 76 days and moulted to the sixth juvenile crab 15/2/66.

Pilumnus lumpinus Bennett, 1964

Ovigerous females were collected from Takapuna Reef, Auckland, 24/10/1964; from Lyall Bay and Island Bay, Wellington, 2/10/1964; from the Kaikoura Peninsula, 14/12/1964 and 6/2/1966. The collection on which this study is based comprises 32 ovigerous female crabs with eggs in all stages of development.

This species is common intertidally although rarely seen, and invariably inhabits deep and inaccessible crevices among broken rock. P. lumpinus is a solitary species and females are not found living in close proximity to large numbers of juvenile crabs as frequently observed with P. novaezelandiae (Bennett 1964, p. 73).

Eggs are light pinkish brown when freshly laid and measure 1.10 mm x 1.25 mm which is considerably smaller than the eggs of P. novaezelandiae. Female crabs are mature when the carapace width exceeds 12 mm. The smallest ovigerous female collected (carapace width 12.5 mm) carried 53 eggs, and the largest (carapace width 22.5 mm) carried 257 eggs. There is a linear relation between carapace width up to 21.0 mm and the number of eggs carried by female crabs, but between 21.0 mm and 22.5 mm there is no great increase in egg number.

1. EMBRYONIC DEVELOPMENT

NAUPLIUS STAGE (Figs 88, 89)

When first obtained the eggs of two specimens showed no sign of an embryo. The length of time that these eggs had already been incubated was not known, but may not have been more than a few days. A Nauplius embryo (Fig. 88) was differentiated two days from the time of capture.

At this stage the optic lobes and the first antennae are poorly developed, but the second antennae are large biramous buds. Tiny rudiments of the mandibles and first maxillae are also present. The thoracico-abdominal flexure is a rounded and undifferentiated protuberance, and is not folded anteriorly as in later stages.

A later Nauplius stage (Fig. 89) is developed about one week after the embryo first appears. The optic lobes have considerably enlarged but there is no eye pigment in the optic disc. Uniramous buds of the second maxillae and first and second maxillipeds are now present. Hence at this stage there are seven pairs of rudimentary post-oral appendages. The thoracico-abdominal flexure has enlarged considerably, but the abdomen shows no traces of segmentation and the telson is not yet formed. There is no sign of a pre-zoeal cuticle.

METANAUPLIUS STAGE (Figs 90, 91, 92)

A post-naupliar stage of development here termed Metanauplius was distinguished one week following the later Nauplius stage described above. The Metanauplius is characterised by: the presence of a pre-zoeal cuticle; sessile eyes; the presence of all post-oral appendages normal for decapod Crustacea; the differentiation of a forked telson with posterior setae.

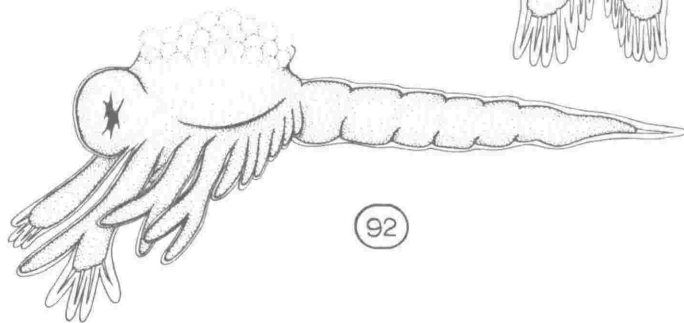
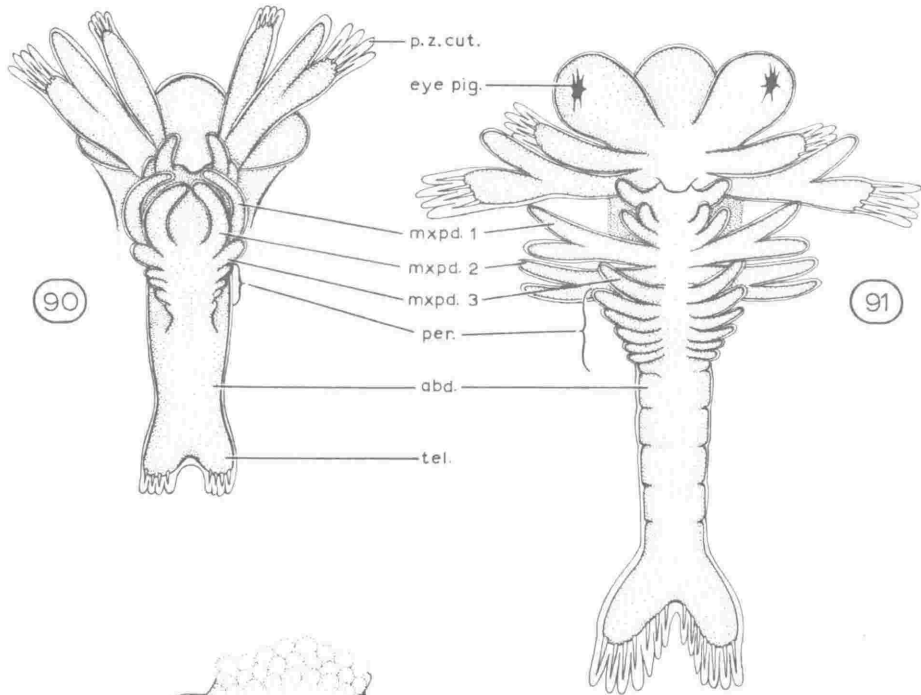
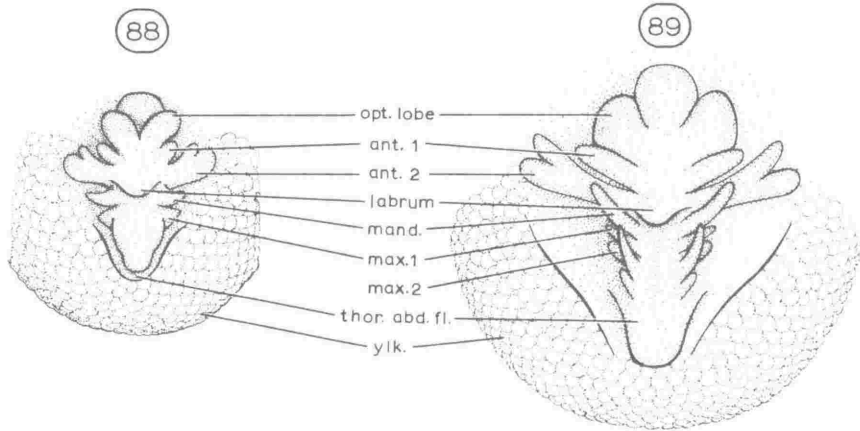
Pilumnus lumpinus Bennett

- Fig. 88 Nauplius stage; view of egg showing embryo
 in situ (egg membranes removed)
- Fig. 89 Late Nauplius stage; view of egg showing
 embryo in situ (egg membranes removed)
- Fig. 90 Metanauplius stage: embryo in first phase
 of development; ventral view with abdomen
 extended
- Fig. 91 Metanauplius stage: embryo in second stage
 of development; ventral view with abdomen
 extended
- Fig. 92 Metanauplius stage: embryo in second phase
 of development; lateral view with abdomen
 extended

Abbreviations:

abd.	-	abdomen
ant.	-	antenna
eye pig.	-	eye pigment
mand.	-	mandible
max.	-	maxilla
mxpd.	-	maxilliped
opt. lobe	-	optic lobe
per.	-	periopods
p.z. cut.	-	pre-zoeal cuticle
tel.	-	telson
thor. abd. fl.	-	thoracico-abdominal flexure
ylk	-	yolk

0.25mm



92

The Metanauplius develops through two phases which are merely stages in the growth of the embryo and are not separated from each other by a moult or ecdysis. These two phases are separated by the following characters:

- (a) Eye pigment absent
 - (b) First two pairs of maxillipeds uniramous
 - (c) Abdomen not segmented
 - (d) Telson with four pairs of posterior setae
- Phase 1 (Fig. 90)

- (a) Eye pigment present
 - (b) First two pairs of maxillipeds biramous
 - (c) Abdomen segmented
 - (d) Telson with seven pairs of posterior setae
- Phase 2 (Figs 91, 92)

Phase 1 (Fig. 90)

The optic lobes are developed as elongate bulbs extending laterally from the cephalic region. First antennae are uniramous with four short terminal setae. The second antennae are slightly longer and biramous. The outer ramus (exopod) bears four terminal setae which are more strongly developed than those of the first antennae, and the inner ramus (spinous process) is unarmed. The inner ramus is not the endopod, as this develops later in ontogeny. Mandibles and first and second maxillae are present as small rudiments lateral and posterior to the labrum. The first and second maxillipeds are now long uniramous rods directed forwards and inwards towards the labrum. The third maxillipeds and pereopods lie posterior to these, but are much shorter and not curved inwards. The abdomen is flexed over the developing post-oral appendages and is unsegmented or possesses only traces of segmentation. The telson is not separated, but is provided with a very shallow posterior median indentation and four pairs of short postero-lateral setae.

Phase 2 (Figs 91, 92)

The second phase occurs in the second week of metanaupliar development which is about 70 days before the time of hatching. It is distinguished from the first growth phase by the characters listed and by a general increase in size. The telson is more distinctly forked but is still not separate from the sixth abdominal segment.

Pre-zoeal Cuticle

A pre-zoeal cuticle forms with the development of the Metanauplius. However at this stage the cuticle is without aesthaetes and processes usually present in the brachyuran pre-Zoea, and is similar to its maximum development in the embryonic Zoea of Pilumnus novaezelandiae.

The cuticle covers the first and second antennae, all post-oral appendages, and the abdomen and telson (see Figs 90, 91, 92). It is produced into unarmed finger-like processes to cover underlying setae of the first and second antennae, and of the posterior margin of the telson (see Figs 90, 91). The pre-zoeal cuticle forms a continuous sheath over the abdomen, and in the second Metanauplius phase it does not follow the segmental indentations.

EMBRYONIC ZOEAL STAGE (Figs 93-117)

As in P. novaezelandiae the Metanauplius passes without abrupt transition into the embryonic zoeal stage. In P. lumpinus structures and larval characters comparable with those of first or second stage planktonic Zoea larvae are here entirely suppressed. The embryo begins to develop into a much modified and advanced Zoea immediately after passing the Metanauplius stage described above. It was not therefore possible to distinguish phases in embryonic zoeal development. Morphological changes are merely associated with growth and are here described chronologically.

Development from the Metanauplius stage is comparatively slow, but structures such as eye pigment, pereopod buds, gill buds, abdominal segmentation, and pleopod buds all appear almost simultaneously. About 50 days before hatching, or 20 days after the second phase in metanaupliar development is distinguished, the embryo reaches a stage comparable with the third embryonic zoeal phase in the ontogeny of P. novaezelandiae. However in P. novaezelandiae the third embryonic zoeal phase occurs only three weeks before hatching. Early development of the embryonic Zoea of P. lumpinus is masked by extreme anachronism, and the ontogenetic sequence on which the previous recognition of phases is based is not followed.

Pre-zoeal Cuticle

Fifty-six days or eight weeks before hatching the pre-zoeal cuticle is fully formed, and does not change significantly thereafter. The thin cuticle covering the peduncle and inner ramus of the first antenna (Fig. 95) is not produced into spines or processes, but on the outer ramus of the first antenna it is extended distally as two or three short plumose processes which are poorly formed and remain only partly evaginated throughout embryonic zoeal development (see Figs 95, 103). The exopod of the second antenna (see Fig. 96) is produced into four large, distal, plumose processes as found in all described pre-Zoea larvae of brachyrrhynchous crabs. These processes are usually incompletely evaginated early in ontogeny (Fig. 96) but extend later (Figs 104, 115). The endopod and spinous process each have a covering cuticle which is without processes (Figs 96, 104).

The pre-zoeal telson is extended posteriorly into seven long paired processes in positions corresponding to seven pairs of posterior setae arising from the embryonic zoeal telson (Figs 102, 114). The first (outer), second, and third processes are long (0.75 mm in length) and plumose. The fourth process is about one half the length of the

three lateral pairs and is non-plumose, while the fifth, sixth, and seventh (inner) processes are each plumose and about 0.65 mm long. The posterior telson processes are invaginated distally when first formed but are fully extended within about 28 days of hatching (Fig. 114).

As the embryonic Zoea increases in size, the pre-zoeal cuticle develops to cover the carapace as it forms, the thoracic appendages, the abdomen and pleopod buds, but is without processes or aesthaetes in these regions (see Figs 93-117).

Embryonic Zoea, Fifty Days Before Hatching (Figs 93-102)

Egg size has increased to 1.40 mm x 1.35 mm and the embryonic Zoea occupies about two-thirds the volume of the egg (Fig. 93). The carapace is incompletely developed but there is a small triangular rostrum (Fig. 94).

Cephalic Appendages (Figs 95-98)

First antenna (Fig. 95) has its peduncle incompletely divided into three segments. The inner ramus is present as a tiny bud.

Second antenna (Fig. 96) now bears an endopod about as long as the spinous process. The exopod is broader and a little longer than either the endopod or the spinous process and bears three unarmed setae at its tip. The fourth (inner) pre-zoeal exopod process is an empty sac and does not enclose a zoeal seta. The Metanauplius has four terminal exopod setae (Figs 90-92) but the inner member does not persist.

The mandible is similar to that of the third phase embryonic Zoea of P. novaezelandiae.

First maxilla (Fig. 97) has its two endites each with small marginal setae which do not protrude through the pre-zoeal cuticle. The palp is unsegmented and without setae.

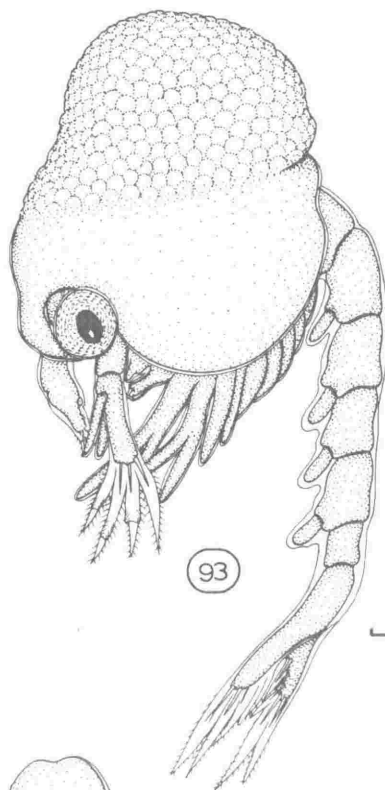
Second maxilla (Fig. 98) has rudimentary setae fringing each

Pilumnus lumpinus: Embryonic Zoea

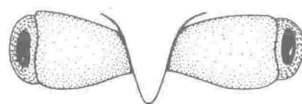
fifty days before hatching

- Fig. 93 Embryonic Zoea; lateral view (egg membranes removed)
- Fig. 94 Eyes and rostrum; anterior view
- Fig. 95 First antenna of left side
- Fig. 96 Second antenna of right side
- Fig. 97 First maxilla of left side
- Fig. 98 Second maxilla of left side
- Fig. 99 First maxilliped of left side
- Fig. 100 Second maxilliped of left side
- Fig. 101 Third maxilliped of left side
- Fig. 102 Telson; ventral view

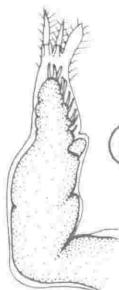
93, 94, 102
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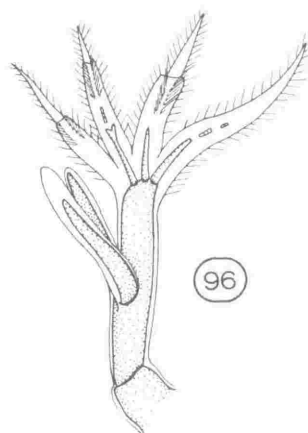
93



94



95



96

95 - 101
0.25mm



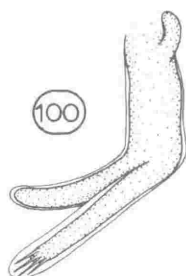
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98



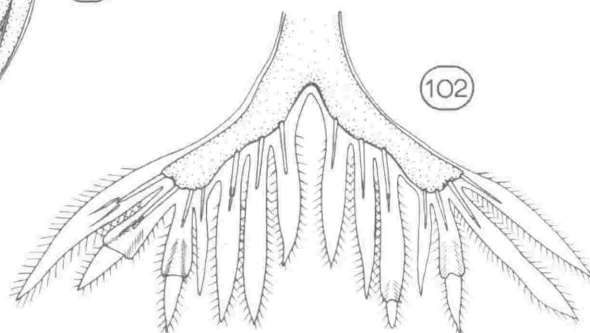
99



100



101



102

of the four endites; scaphognathite has three or four setae arising from its proximal tip.

Thoracic Appendages (Figs 99-101)

First maxilliped (Fig. 99) is biramous; unsegmented endopod a little shorter than the exopod; exopod a slender unjointed rod bearing four short setae at its tip; epipod present as a tiny bud.

Second maxilliped (Fig. 100) is similar to the first maxilliped but bears the rudiment of one arthrobranch. The epipod and podobranch appear later in development.

Third maxilliped (Fig. 101) is biramous; endopod unsegmented and more robust than the exopod; exopod a slender rod without terminal setae; rudiments of the epipod and of two arthrobranches present.

Pereiopods (see Fig. 93) are similarly developed to those occurring in the third phase embryonic Zoea of P. novaezelandiae.

Abdomen (Figs 93, 102)

The abdomen (Fig. 93) comprises six segments and a telson. Segments two to five are each provided with a pair of uniramous pleopod buds. The telson (Fig. 102) comprises two long slender rami separated by a deep central cleft, and is similar to the larval telson of dromiid crabs. Seven setae are spaced along the posterior margin of each ramus and are about equal in size, smooth, and only partly formed. The fourth pair of setae do not form the major part of the telson fork as in the free-living brachyuran Zoea (Gurney 1942, p. 121), and the three inner pairs of setae do not form a distinct group. The three outer pairs of setae are not reduced.

Chromatophore Pattern

Chromatophores are red and located mainly at the bases of the cephalic and thoracic appendages, and ventrally and posteriorly in all six abdominal segments. Remaining yolk is light pink to light brown.

Embryonic Zoea, Twenty-eight Days Before Hatching (Figs 103-114)

The egg size has increased to 1.45 mm x 1.35 mm and the embryonic Zoea occupies the entire egg capsule. Remaining yolk (about one-sixth the volume of the egg) now lies beneath the fully formed carapace as in the fourth embryonic zoeal phase of P. novaezelandiae. Ontogenetic developments distinguishing this four week stage from the seven week stage are described below.

Cephalic Appendages (Figs 103-107)

First antenna (Fig. 103) with a three-segmented peduncle; inner ramus unsegmented with one or two aesthaetes at its tip; outer ramus with two or three terminal aesthaetes and with three groups of aesthaetes subterminally on the inner margin.

Second antenna (Fig. 104) with its unsegmented endopod slightly less than twice the length of the spinous process and longer than the exopod.

Mandibular palp (see Fig. 105) incompletely divided into two segments.

First maxilla (Fig. 106) and second maxilla (Fig. 107) each with marginal endite setae protruding through the pre-zoeal cuticle; scaphognathite of the second maxilla entirely fringed with small setae.

Thoracic Appendages (Figs 108-111)

First maxilliped (Fig. 108) with endopod and exopod about equal in length; epipod bud flexed midway along its length with its distal half curved upwards.

Second maxilliped (Fig. 109) with an epipod similar to that of the first maxilliped; a large arthrobranch bud is now present.

Third maxilliped (Fig. 110) with its endopod incompletely segmented; epipod rudiment similar to that of the first and second

Pilumnus lumpinus: Embryonic Zoea

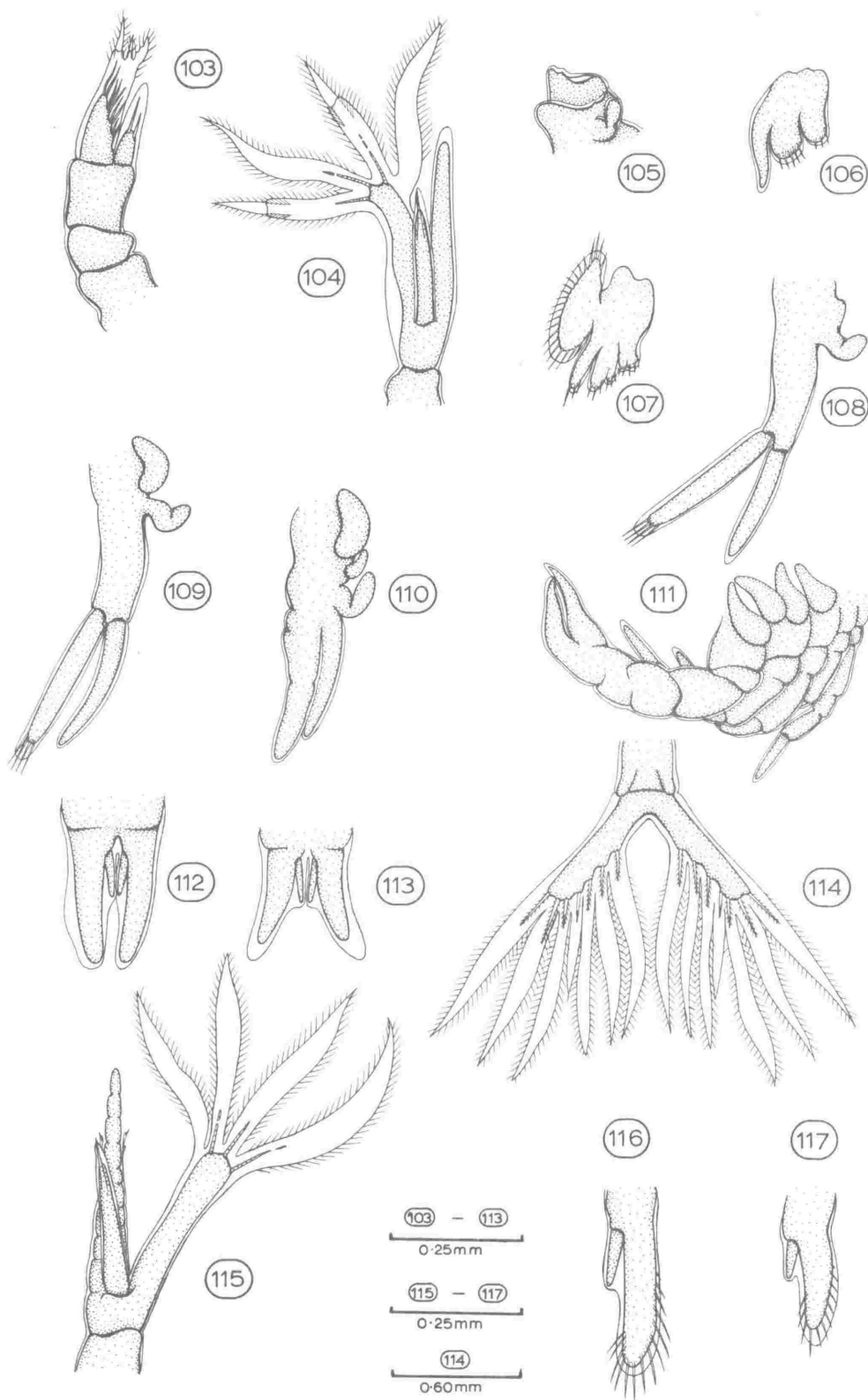
twenty-eight days before hatching

- | | |
|----------|---|
| Fig. 103 | First antenna of left side |
| Fig. 104 | Second antenna of right side |
| Fig. 105 | Mandible of left side |
| Fig. 106 | First maxilla of left side |
| Fig. 107 | Second maxilla of left side |
| Fig. 108 | First maxilliped of left side |
| Fig. 109 | Second maxilliped of left side |
| Fig. 110 | Third maxilliped of left side |
| Fig. 111 | First to fifth pereopods of left side |
| Fig. 112 | Pleopod from left side of second abdominal
segment |
| Fig. 113 | Pleopod from left side of fifth abdominal
segment |
| Fig. 114 | Sixth abdominal segment and telson;
ventral view |

Pilumnus lumpinus: Embryonic Zoea

seven days before hatching

- | | |
|----------|---|
| Fig. 115 | Second antenna of left side |
| Fig. 116 | Pleopod from left side of second abdominal
segment |
| Fig. 117 | Pleopod from left side of fifth abdominal
segment |



maxillipeds; lower arthrobranch bud very small and tucked beneath the much larger arthrobranch situated above and just anteriorly.

Pereiopods (Fig. 111) are visibly segmented; first pereiopod possesses two gill buds; second and third pereiopods each have one; no gill buds on the fourth and fifth pereiopods.

Abdomen (Figs 112-114)

Pleopod buds now biramous. Pleopods of second segment (Fig. 112) are largest: exopod 0.25 mm long; endopod 0.10 mm long, more slender, and arising from the base of the exopod; both rami without setae. Pleopods of fifth segment (Fig. 113) are smallest; exopod 0.19 mm long; endopod 0.10 mm long. Uropods are present as small buds arising ventrally from the sixth abdominal segment (Fig. 114).

Telson (Fig. 114) with all seven paired processes of the pre-zoeal cuticle now completely evaginated; posterior telson setae of the embryonic Zoea now completely formed; all setae except the fourth pair plumose.

Embryonic Zoea, Seven Days Before Hatching (Figs. 115-117)

The egg size has increased to 1.50 mm x 1.40 mm which is the maximum size. Remaining yolk is found beneath the larval carapace and now occupies only about one-fifteenth of the volume of the egg. The entire embryonic Zoea and all appendages have considerably increased in size, but there are few larval characters which differ from those described above.

The endopod of the second antenna (Fig. 115) is now one and one-half times the length of the exopod and is visibly divided into 10 or 11 segments. Rapid growth of the endopod often results in rupture of the pre-zoeal cuticle (see Fig. 115). The spinous process

is still invaginated at its tip. The full complement of gills is not yet present as a rudimentary podobranch later found on each of the second and third maxillipeds is still lacking. The pleopods (Figs 116, 117) have their exopods fringed with short setae which may protrude through the surrounding pre-zoeal cuticle.

2. HATCHING

Individual female crabs required up to five days to hatch all their eggs under laboratory conditions. Eggs which had not hatched after five days disappeared and were presumably eaten by the female. After initial rupture of the chorion, the process of hatching follows that described for P. novaezelandiae with each larva taking about 15 minutes to break free of the inner egg membrane. However the eggs of P. lumpinus hatch as advanced Zoea larvae (see Fig. 118). The pre-zoeal cuticle is not shed during the process of hatching, but remains intact to be discarded together with the zoeal skin when ecdysis to the Megalopa stage occurs.

3. POST-EMBRYONIC DEVELOPMENT

THE ZOEAL LARVA

The emergent larvae of Pilumnus lumpinus here termed Zoea differ from all known brachyuran Zoea larvae in that the exopods of the first and second maxillipeds do not function as natatory organs. Rudimentary natatory setae are present, but these are not used and the larvae do not therefore swim. The larvae also lack dorsal and lateral carapace spines and the long rostral spine usually characterizing the Zoea larvae of brachyrrhynchous crabs. These departures from the normal pattern are probably related to the suppression of Zoea larval stages brought about through abbreviated development, and as such they probably have little phylogenetic significance. Other features of a final stage brachyuran Zoea (Lebour 1928) are all present, so the generally accepted term Zoea is here retained.

The Zoea larval stage is relatively short lived, and lasts from 15 minutes to 30 minutes under laboratory conditions (15°C to 17°C). The larvae are not retained beneath the pleon of the female crab, but they lie on the bottom of the aquarium rapidly flexing and extending the abdomen in attempts to moult from both the zoeal and pre-zoeal skins. Only about 20% of all Zoea larvae obtained from eggs in the laboratory survived through to the subsequent Megalopa larval stage.

Description of Zoea Larva

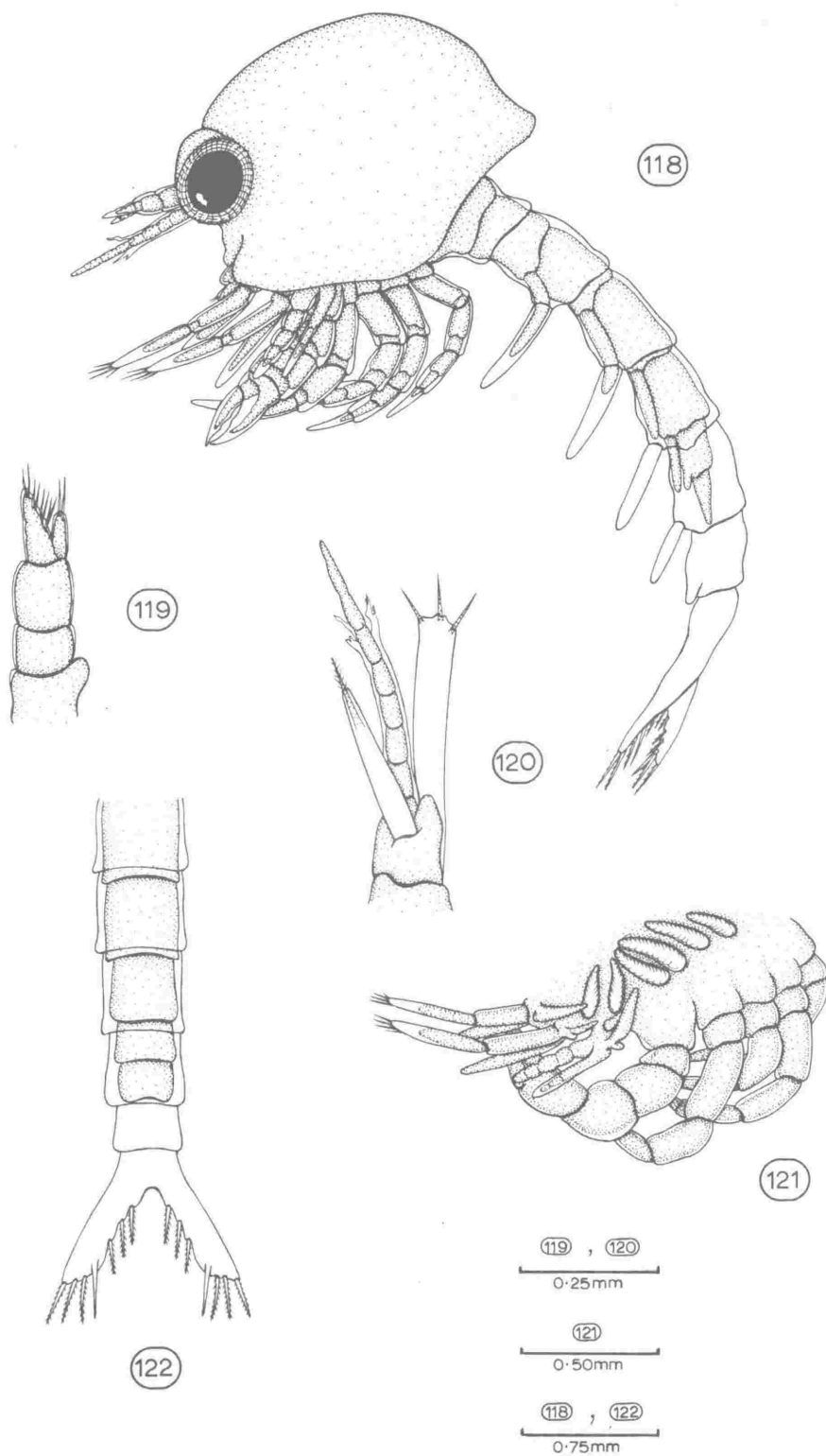
Cephalothorax (Fig. 118)

Total length of larva (measured from anterior margin of eye to tip of lateral telson cornu with abdomen extended) is 7.40 mm to 7.50 mm. The carapace is without dorsal or lateral spines and its margins are smooth. Rostrum small and triangular. Eyes large and stalked.

FIGURES 118 - 122

Pilumnus lumpinus: Zoea larva
(pre-zoeal cuticle removed)

- Fig. 118 Zoea larva; lateral view
- Fig. 119 First antenna of left side
- Fig. 120 Second antenna of left side
- Fig. 121 Maxillipeds and pereopods of left side
- Fig. 122 Abdomen and telson; dorsal view



Cephalic Appendages (Figs 119, 120)

First antenna (Fig. 119) is similar to that described 28 days before hatching, but the megalopal skin has now formed under the zoeal cuticle. The proximal segment of the peduncle is swollen at its base with the formation of a statocyst.

Second antenna (Fig. 120) with viable tissue withdrawn from the spinous process and from the greater length of the exopod; endopod 1.30 mm long, segmented and compressed within the zoeal skin or occasionally protruding (see Fig. 120).

Mandible and first and second maxillae are similar to those of the embryonic Zoea seven days before hatching.

Thoracic Appendages (Fig. 121)

The maxillipeds and pereopods (Fig. 121) are all segmented. The segmental indentations are all well defined within the megalopal skin which has now formed beneath the zoeal cuticle.

The full complement of gills is now present (Fig. 121) and tabulated as follows. (This gill formula is the same as for the adult crabs).

	MAXILLIPEDS			PEREIOPODS				
	1st	2nd	3rd	1st	2nd	3rd	4th	5th
Pleurobranchiae	-	-	-	-	1	1	-	-
Arthrobranchiae	-	1	1+r	2	-	-	-	-
Podobranchiae	-	r	r	-	-	-	-	-
Epipodites	1	r	1	-	-	-	-	-
Exopodites	1	1	1	-	-	-	-	-

Note: r = rudimentary gill or rudimentary epipodite

Abdomen (Fig. 122)

The abdomen measures 5.40 mm to 5.50 mm in length and is structurally similar to that of the earlier described stage. One or two days before hatching the abdomen and telson start to withdraw from the boundaries of the zoeal skin. On hatching, the two rami of the telson have withdrawn almost to the level of the median cleft in the posterior midline.

Immediately before moulting to the Megalopa larva a considerable amount of the zoeal abdomen is reabsorbed, and the tip of the telson has usually withdrawn to about the level of the posterior margin of the fifth abdominal segment (see Figs 118, 122) leaving the sixth abdominal segment and telson of the Zoea larva empty. At this stage zoeal pleopods of the fourth and fifth abdominal segments are empty sacs with the megalopal pleopods lying flush with the ventral surface of the abdomen, (Fig. 118).

THE MEGALOPA LARVA

Megalopa larvae were obtained by moult from Zoea larvae hatched from the eggs of two specimens from Takapuna Reef, 27, 29/12/1964; three from Lyall Bay, Wellington, 21, 22/12/1964; two from the Kaikoura Peninsula 9/2/1966. Larvae left in an aquarium lived apart from the parent and did not shelter beneath its pleon at any time.

Larvae spent the greater part of their megalopal life sheltering in crevices among stones, coralline outgrowths, and weed provided in the aquarium. Crawling was the usual means of locomotion but the Megalopa larvae used their natatory pleopods to swim more frequently and for longer periods than did those of P. novaezelandiae. From aquarium observations the Megalopa larvae of P. lumpinus swim mainly to find a crevice in which to hide. When completely concealed the larvae rarely moved again except during the night when

swimming was more frequent and the larvae more active. The majority of larvae appeared to favour an individual crevice, and at night returned to this almost directly after swimming. The Megalopa larvae were not observed to feed on Artemia nauplii, mussel, and other forms of organic matter provided.

Description of Megalopa Larva (Figs 123-133)

This description of the Megalopa larval stage is shortened to a comparison with that of P. novaezelandiae and is based on twelve larvae, two obtained from each of two female crabs from Auckland, Wellington, and Kaikoura.

Cephalothorax (Figs 123, 124)

Carapace similar in shape to that of P. novaezelandiae: 1.36 mm long; 1.38 mm wide; interorbital space 0.50 mm. Rostrum short, triangular and depressed. Frontal region with five or six stout plumose setae on each side directed forwards and upwards. One pair of supraorbital spines situated at lateral angles of the frontal region. Anterolateral margin of carapace with one strong spine arising from the posterolateral corner of the orbit. Carapace margins otherwise smooth. Dorsal surface of carapace with a sparse covering of fine hairs, but without the groups of stout setae present in P. novaezelandiae. Eyes large, not extending laterally to the level of the postorbital carapace spine; eyestalks without setae.

Cephalic Appendages (Figs 125, 126)

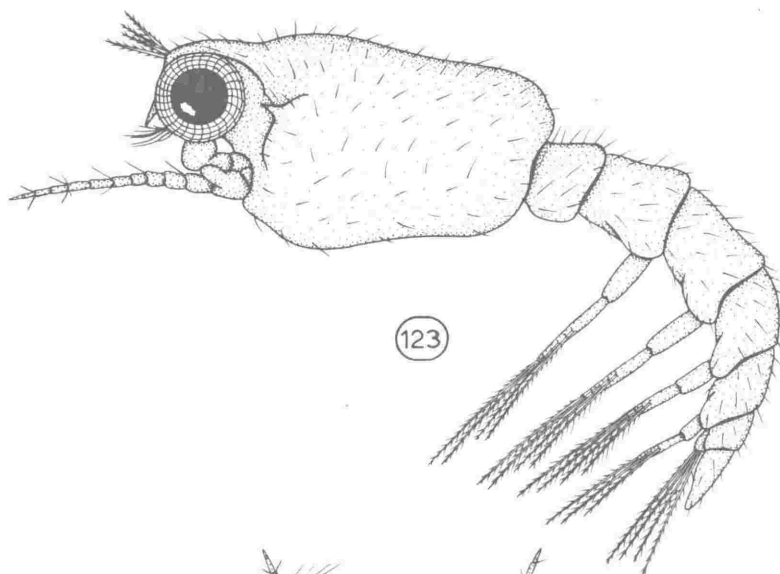
First antenna (Fig. 125) is shorter than that of P. novaezelandiae; inner ramus of two segments but the appendage is otherwise similar to that described for the previous species.

Second antenna (Fig. 126) with a two-segmented protopod; basis about twice the length of coxa. Endopod of 10 or 11 segments: two proximal segments larger than distal segments; setae few in number

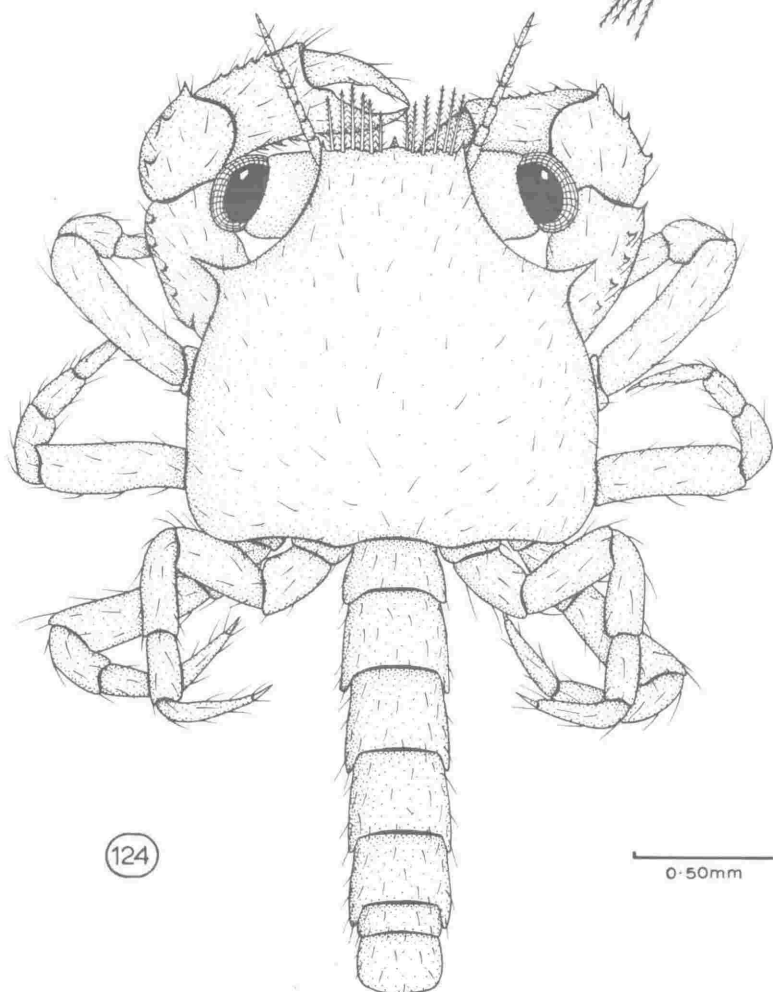
Pilumnus lumpinus: Megalopa larva

Fig. 123 Megalopa larva; lateral view
(thoracic appendages removed)

Fig. 124 Megalopa larva; dorsal view



123



124

0.50mm

and irregularly arranged, but there are usually three terminal setae. Exopod present in the Megalopa as a small flap without spines or setae, but absent in the adult crab.

The mandibles and first and second maxillae are similar to those of P. novaezelandiae described and illustrated earlier; minor differences occur only in details of setation.

Thoracic Appendages (Figs 127-130)

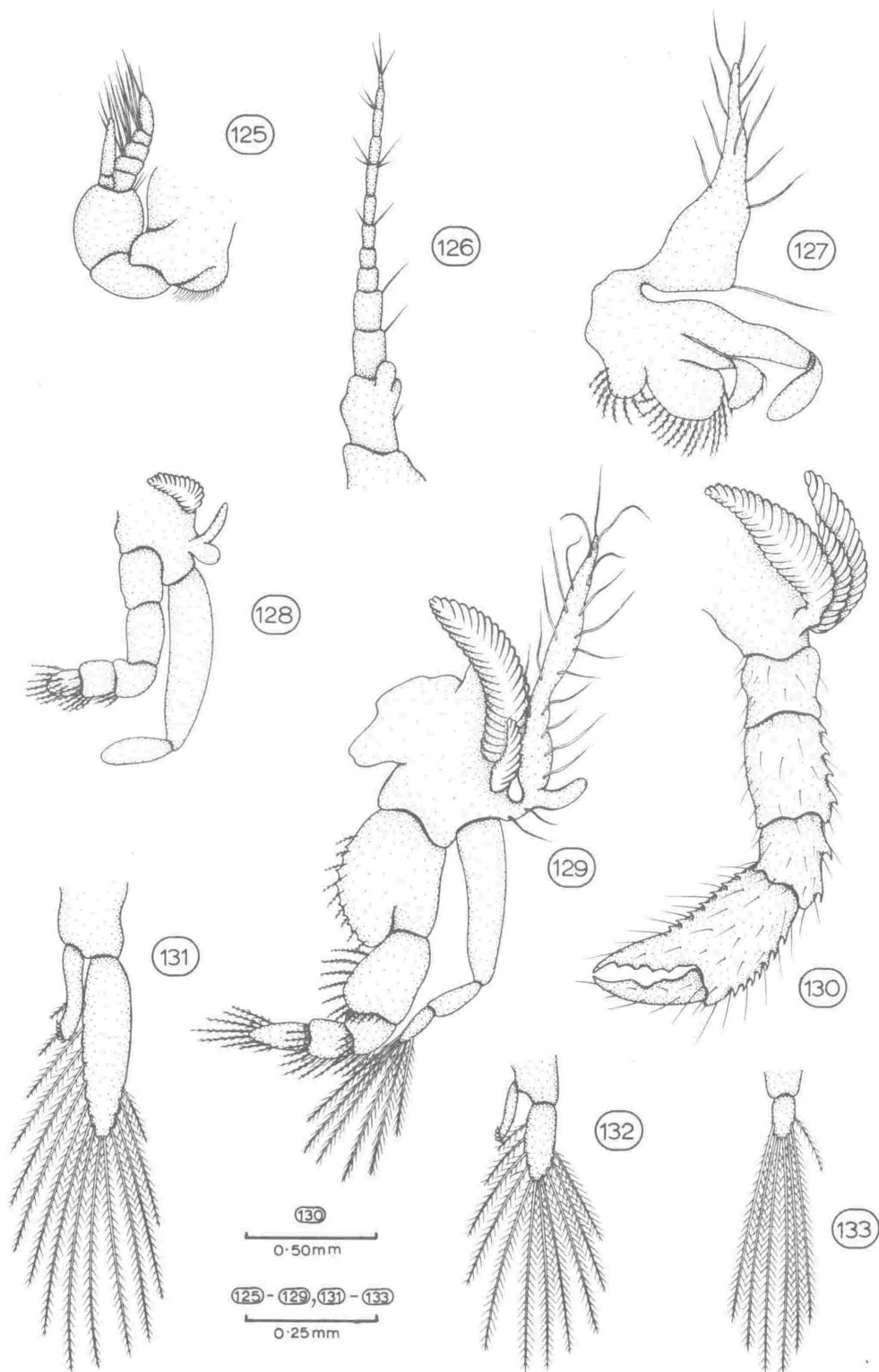
First maxilliped (Fig. 127) flattened, similar to that of P. novaezelandiae, but differs in having the endopod fringed only with a few short hairs along its outer distal margin. Exopod is more reduced, of two segments only, and without terminal setae. Epipod strongly developed as in P. novaezelandiae.

Second maxilliped (Fig. 128) with endopod smaller than the exopod: endopod with setae on its three distal segments only; exopod strongly developed, two-segmented and without setae. The gills of the second maxilliped are of the same number and are similarly arranged to those of P. novaezelandiae but are greatly reduced in comparison: epipod a small and slender rod without setae; podo-branch a small bud without lamellae arising ventrally from near the base of the epipod; arthrobranch also small but differentiated into lamellae.

Third maxilliped (Fig. 129) with endopod more slender than that of P. novaezelandiae; ischium and merus not expanded laterally to the same degree, but the ramus otherwise similar to that of P. novaezelandiae. Exopod of three segments: no lateral hairs along the margins of the basal segment; tip of distal segment with six long biplumose setae. The gills are similarly arranged to those on the first maxilliped of P. novaezelandiae but differ in the degree of development: anterior arthrobranch much larger than the lower and more posterior arthrobranch; epipod smaller than in P. novaezelandiae and here about the same size as the anterior

Pilumnus lumpinus: Megalopa larva

- Fig. 125 First antenna of right side
- Fig. 126 Second antenna of left side
- Fig. 127 First maxilliped of left side
- Fig. 128 Second maxilliped of left side
- Fig. 129 Third maxilliped of left side
- Fig. 130 First pereopod of left side
- Fig. 131 Pleopod from left side of second abdominal
segment
- Fig. 132 Pleopod from left side of fifth abdominal
segment
- Fig. 133 Uropod from left side of sixth abdominal
segment.



arthrobranch; podobranch small, rudimentary and without lamellae.

First pereopod (Fig. 130) chelate with all segments sparsely covered with setae. Left and right chelae of equal size. Coxa and basis short and concealed beneath the carapace; ischium short and without spines; merus about twice the length of ischium with a row of four small spines laterally; carpus about half the length of merus with two spines on its lateral face and one blunt spine on its inner distal margin; propodus subequal in length to ischium, merus, and carpus combined, bearing six or seven small spines along both the medial and lateral faces, teeth on fixed finger poorly defined; dactylus without spines, slender, and with only rudimentary protuberances along its inner face. The two arthrobranchs are well formed, and each of these gills comprises about 18 or 20 pairs of lamellae.

Second, third, fourth, and fifth pereopods (Fig. 124) similar to those of P. novaezelandiae: One small pleurobranch is present on each of the second and third pereopods.

Abdomen (Figs 123, 124)

The abdomen measures 1.5 mm in length and comprises six segments and a telson. The abdominal segments are in the same relative proportions as those of the *Megalopa* larva of P. novaezelandiae.

Pleopods occur on the second to fifth abdominal segments (Fig. 123) and differ from those of P. novaezelandiae only in details of setation and in the number of hooklets present on the endopods. Pleopods of second segment (Fig. 131) with endopod bearing six distal hooklets; exopod bearing 15 marginal setae. Pleopods of third, fourth, and fifth segments having endopods with six, six, and four distal hooklets respectively, and their exopods fringed with 14, 13 and 11 marginal biplumose setae. A pleopod of the fifth segment is illustrated (Fig. 132). Pleopods otherwise similar to those on

corresponding segments of the Megalopa of P. novaezelandiae. Uropods (Fig. 133) uniramous with six, sometimes seven long marginal biplumose setae.

Chromatophore Pattern

The Megalopa larva of P. lumpinus is considerably more opaque than that of P. novaezelandiae. Small red chromatophores, difficult to see, are scattered over the carapace and in all segments of the pereopods and of the abdomen. It was not possible to establish a pattern in the distribution of chromatophores in the Megalopa larva of P. lumpinus.

DISCUSSION

RECORDS OF ABBREVIATED DEVELOPMENT IN MARINE BRACHYURA

Abbreviated, or direct development occurs only rarely among marine Brachyura. Species showing this type of development have been recorded from Australia and New Zealand only, and these occur in each of the three families Dromiidae (Dromiacea), Majidae, and Xanthidae (Brachygnatha).

In the Dromiidae, Hale (1925, 1927) and Montgomery (1922) described abbreviated development in Petalomera lateralis (Gray). It is also recorded in Cryptodromia octodentata Haswell (Hale 1925, 1927) and probably occurs in Epipedodromia (= Platydromia) thompsoni (Fulton and Grant) as suggested by Hale (1925, p. 405) and in Dromidia australis (Rathbun) which has very large yolky eggs 2 mm in diameter (Hale 1927, pp. 106-7). Petalomera wilsoni (Fulton and Grant) occurs in Australia (Hale 1927), New Zealand, and South Africa (Barnard 1950) but eggs of this species measure only 0.75 mm in diameter and probably hatch as planktonic Zoea larvae. Developmental stages of this species are probably similar to those of Dromia vulgaris from Europe (Lebour 1934) which has eggs of about the same size as those of Petalomera wilsoni.

In the Australian Majidae, Rathbun (1914) recorded abbreviated development in Naxoides (= Paranaxia) serpulifera (Guerin) but it is not known among other members of this family.

In the family Xanthidae, abbreviated development occurs in Pilumnus vestitus Haswell, from Australia (Hale 1931), and in P. novaezelandiae Filhol and P. lumpinus Bennett, from New Zealand, described in this paper. All other New Zealand xanthid crabs (Heterozius rotundifrons A. Milne Edwards, Ozius truncatus H. Milne Edwards, and Heteropanope (Pilumnopeus) serratifrons (Kinahan)) have a series of planktonic Zoea larval stages (Wear, in press, a). The affinities of Heteriozium rotundifrons with the family

Xanthidae are uncertain (Balss 1930) but there is evidence suggesting that development is incompletely abbreviated in this species. The eggs of H. rotundifrons are larger than usual (0.95 mm x 0.80 mm) and the four zoeal stages usually occurring in xanthid development are here reduced to two (Wear, in press, a). No literature is available concerning the life-histories of Australian xanthid species other than Pilumnus vestitus. I have examined eggs of Pilumnus rufopunctatus Stimpson¹, P. tomentosus Latreille², and P. vespertilio Fabricius², but these Australian species have small eggs about 0.50 mm to 0.60 mm in diameter with little yolk, and the morphology of embryos dissected from the eggs does not suggest that development is abbreviated.

There is clearly no phylogenetic pattern for the phenomenon of abbreviated development. Isolated species with large eggs and abbreviated larval life occur in most groups of Decapoda (Gurney 1942, pp. 54-61). In all these, including the Brachyura discussed above, systematic relationship does not necessarily imply similarity in development.

MORPHOLOGICAL SIGNIFICANCE OF ABBREVIATED DEVELOPMENT IN THE GENUS PILUMNUS

Nauplius Stages

In the early embryonic development of Pilumnus novaezelandiae and P. lumpinus the term Nauplius can only be applied in a very general way. The structure of the early embryo merely supports the widely accepted theory that a free Nauplius was at one time universal among decapod Crustacea (Gurney, 1942, p. 40). As a result of anachronistic development, characters such as rudimentary compound eyes

¹ Ovigerous females kindly provided by Dr D.J.G. Griffin, Australian Museum, Sydney, Australia

² Eggs received through the courtesy of Dr J. C. Yaldwyn, Australian Museum

and post-oral appendages appear early in the egg-Nauplius. These characters are not found in any free-living decapod Nauplius known. Similarly the Metanauplius stage of both P. novaezelandiae and P. lumpinus shows quite advanced development of the above characters, and at this stage there is also abdominal segmentation. This appearance of relatively advanced structures very early in ontogeny can be attributed to the absence of the need for successive developmental stages to be adapted for free life, as they are here passed through within the egg.

The egg-Nauplius of P. lumpinus (Fig. 88) is at about the same stage of development as the one-week old Nauplius of Alpheus saulcyi figured by Brooks and Herrick (1891), but is apparently younger than that of Willemoesia challengerii illustrated by Gurney (1942, p. 40, fig. 8). In known decapod Nauplii the three anterior pairs of appendages develop simultaneously (Brooks and Herrick 1891; Ōishi 1959; Dobkin 1961; Korschelt 1944). However in the Nauplius stage of P. lumpinus there is an appreciable lag in the development of the first antennae. The egg-Nauplius of a brachyuran species has not been described previously, and it is therefore not known if development of the first antennae is similarly retarded in other brachyuran species.

The second antennae are biramous in the first embryonic zoeal phase of P. novaezelandiae and in the egg-Nauplius of P. lumpinus, but in both species the inner ramus can be traced as being the spinous process. The endopod appears between the inner ramus and the exopod later in embryonic development. First stage Zoea larvae of Brachyura with non-abbreviated development hatch with the antennae differentiated into exopod and spinous process only, and in these species it is probable that early separation of these two rami occurs in the egg-Nauplius.

Pre-Zoeal Cuticle

The significance of the pre-zoeal or embryonic cuticle was first discussed by Conn (1884). All early authors thought that the pre-zoeal cuticle represented the Protozoeal stage relegated to embryonic life. This view is no longer considered valid. Gurney (1926) suggested that the pre-zoeal cuticle is equivalent to the Metanauplius stage, but this author later considered it to represent the Nauplius stage (1942, pp. 48-9) relegated to embryonic life.

In abbreviated development the normal sequence in which larval stages appear is upset through anachronism and the merging of one larval stage into another in a process of gradual growth within the egg rather than by specific ecdyses. It is therefore misleading to draw conclusions regarding the order of appearance of larval appendages in embryology when development is abbreviated. However, anachronism is unlikely to change the position of the pre-zoeal cuticle in ontogeny.

In the embryonic development of P. lumpinus the pre-zoeal cuticle is not represented in the egg-Nauplius. The cuticle first forms with the Metanauplius of P. lumpinus, and probably represents this stage, even though the development of plumose pre-zoeal processes continues past the Metanauplius stage into embryonic zoeal development. In P. novaezelandiae it is not known when the pre-zoeal cuticle first appears, but it is certainly present in the Metanauplius stage of this species.

These observations therefore support Gurney's earlier suggestion (1926) that the pre-zoeal cuticle represents the Metanauplius, once a free larva, but now relegated to embryonic life. In P. lumpinus further support for this theory can be found in the basic structure of the cuticle, seen, for instance, in the unsegmented abdomen and the presence of plumose processes on the first and second antennae and on the telson - all probably functional natatory processes in free life. These characters are present in the last planktonic Nauplius stage of

the Penaeidea (Gurney 1942). In the Penaeidea the last Nauplius stage (Metanauplius) is followed by three protozoal stages. These are thought to persist as much-modified but free-living Zoea larvae in the Caridea (Gurney 1926, 1942). As the embryonic Zoea of both P. novaezelandiae and P. lumpinus has a well-formed cuticle of its own, and as this stage is probably equivalent to a Protozo^o_λ, the pre-zoeal cuticle present at this time cannot represent the same stage in development. This further supports the view that the pre-zoeal cuticle represents the preceding Metanauplius stage. However it will be necessary to determine the time at which the pre-zoeal cuticle first appears in the embryology of many more decapod species before its ontogenetic position becomes clear.

Sollaud (1923) found that in Leander serratus (Palaemonidae), where larvae hatch in the adult form, the zoeal stage in the egg is marked by the formation of the pre-zoeal cuticle which moulds the maxillipeds but not the pereopods. This is also the case in Decapoda with non-abbreviated development, as in these species the pereopods are not formed at the pre-zoeal stage. In Pilumnus novaezelandiae and P. lumpinus the pre-zoeal cuticle surrounds both the maxillipeds and the pereopods, but this may again be attributed to anachronism which results in the pereopod buds first appearing in the Metanauplius stage when the pre-zoeal cuticle is being formed. The cuticle appears to grow with the pereopods, and must therefore be either continuously formed or show a considerable degree of elasticity.

Significance of the Pre-zoeal Cuticle in Brachyuran Phylogeny

The pre-zoeal cuticle surrounding the embryonic Zoea of Pilumnus novaezelandiae lacks plumose aesthaetes and processes considered to be characteristic of brachyuran pre-Zoea larvae

(Lebour 1928; Gurney 1942). This may be in some way related to abbreviated development, but it is not necessarily so, as pre-zoeal processes are well developed in P. lumpinus.

Larvae hatched from the eggs of New Zealand crabs show that the pre-zoeal cuticle may quite commonly lack these plumose processes. This is the case in ten species in the family Hymenosomidae (Oxyrhyncha) and in the following brachyrrhynchous crabs: Heterozius rotundifrons Milne Edwards³ (?Xanthidae); Pinnotheres novaezelandiae Filhol (Pinnotheridae); Hemigrapsus crenulatus (Milne Edwards), H. edwardsi (Hilgendorf), Helice crassa Dana, Cyclograpsus lavauxi Milne Edwards, Leptograpsus variegatus (Fabricius), Planes marinus Rathbun (Grapsidae); Hemiplax hirtipes (Jacquinot) (Ocypodidae). This list does not include foreign genera and species within these two superfamilies, but, these apart, I have found no reference to a pre-Zoea larva possessing a fully developed pre-zoeal cuticle with plumose aesthaetes in any species belonging to the families Hymenosomidae, Goneplacidae, Pinnotheridae, Ocypodidae, Grapsidae, and the terrestrial family Gecarcinidae.

Hence in the Brachyura, suppression of the pre-zoeal cuticle appears to have taken place in those families which have evolved more recently (see Glaessner 1960, p. 47) especially in the Goneplacidae, Ocypodidae, Grapsidae, and the highly specialised family Pinnotheridae. In a recent phylogenetic arrangement of the Brachyura (Balss 1957) the family Xanthidae is placed immediately before Goneplacidae. If this implies close relationship, it is not surprising to find the pre-zoeal cuticle reduced in Heterozius rotundifrons and in Pilumnus novaezelandiae, and this reduction may also occur in other specialised xanthid crabs.

³ Reinstated in the Atelecyclidae by Balss (1957) but retained in the Xanthidae by Bennett (1964). See also Wear (in press, a).

Larval evidence does not support the inclusion of the family Hymenosomidae in the Oxyrhyncha, as hymenosomid larvae lack carapace spines and possess other characters which show little relationship with those of the families Majidae and Parthenopidae (Aikawa 1929; Gurney 1942, p. 282). Zoea larval characters suggest a close relationship between the Hymenosomidae and the Pinnotheridae (Gurney 1942) and between the Pinnotheridae and the Leucosiidae (Lebour 1928; Gurney 1942). However the family Leucosiidae (Ebalia) has a Megalopa larva (Lebour 1928) but this stage is absent in the Hymenosomidae and Pinnotheridae. This, together with the presence of strongly developed pre-zoeal cuticular processes suggests that Ebalia may be more primitive than is implied by the similarity of Zoea larval characters. Reduction of zoeal carapace spines among the Leucosiidae may, therefore, have developed independently as an ecological factor and may not be evidence of phylogenetic relationship with either the Hymenosomidae or the Pinnotheridae.

Embryonic Zoea Stage

In the embryonic development of Pilumnus novaezealandiae anachronism does not completely mask the sequence of events normally found in decapod ontogeny. It is therefore possible to recognise four phases approximately equivalent to the usual four Zoea larval stages in the life-history of xanthid Brachyura (see page 8). However, it was not possible to distinguish comparable embryonic zoeal phases in the development of P. lumpinus because of advanced anachronism. For example, characters such as segmentation of the peduncle of the first antennae, the appearance of gill buds and of pleopod buds, the separation of the sixth abdominal segment and the telson, and the appearance of chromatophores occur almost simultaneously. The relatively different degree of anachronism characterising the embryonic development of these two species is of uncertain significance.

In the ontogeny of P. lumpinus the embryonic Zoea possesses setae on the exopods of the first and second maxillipeds and a widely forked telson bearing long plumose setae. Also a single zoeal stage occurs after hatching, but this is short-lived and it does not swim. The absence of such features in the ontogeny of P. novaezelandiae and the much shorter incubation period observed in this species suggests that in P. lumpinus abbreviated development is probably more recently evolved.

Dorsal, lateral, and rostral carapace spines are characteristic of all known xanthid Zoea larvae other than those of the genus Heteropanope (see Wear, in press a, in press b) and small lateral papillae occur on the second abdominal segment of all known brachyuran Zoeae (Lebour 1928). These characters are absent in the embryonic Zoea of P. novaezelandiae and of P. lumpinus. Carapace spines which are considered to be of assistance in flotation and orientation (Lebour 1928; Foxon 1934) and natatory setae which effect thoracic propulsion are together reduced in abbreviated development where such structures are of no use. Lateral protuberances on the abdomen appear to have no function and their absence is therefore more difficult to explain.

Hatching

During embryonic development the eggs of P. novaezelandiae increase in size from 1.50 mm x 1.45 mm when freshly laid to 1.75 mm x 1.65 mm shortly before hatching, while those of P. lumpinus increase from 1.10 mm x 1.25 mm to 1.50 mm x 1.40 mm. This size increase is apparently caused by a slow uptake of water from the environment. This process was demonstrated by Davis (1965) using the eggs of Callinectes sapidus Rathbun (Portunidae). Davis considered that in this species a period of swelling of the eggs during embryonic development is followed by osmotic swelling of the inner egg membrane at the start of hatching. The swelling inner egg membrane then ruptures the chorion by pressure from within and the larva plays no part.

The inner membrane is subsequently ruptured by mechanical action of the larval abdomen and telson. This sequence is followed by both Pilumnus novaezelandiae and P. lumpinus, but in these two species the mechanism of eclosion appears to differ from that described for Callinectes. The embryo and the inner egg membrane of Pilumnus novaezelandiae and P. lumpinus are closely applied to each other at the time of hatching, and the amount of fluid apparent beneath the inner egg membrane at this time is insufficient to suggest that internal pressure is built up by osmotic swelling of the inner membrane and not of the embryo. As the volume of the embryonic Zoea immediately before hatching is greater than that of the original yolk mass in freshly laid eggs of Pilumnus novaezelandiae and P. lumpinus, it is more probable that absorption of water by the larva during embryonic development is responsible for the increase in internal egg pressure. The process by which the chorion is broken and sloughed off appears to be similar to that observed in Homarus americanus Milne Edwards (Astacura) by Davis (1964).

In Pilumnus novaezelandiae larvae hatch from the eggs at a Megalopa stage. It was observed that the pre-zoeal cuticle still surrounded the empty zoeal skin, and after hatching these were found together either inside the inner egg membrane or nearby. Hence both the pre-zoeal and zoeal cuticles are shed together, either in the process of hatching from the inner egg membrane or immediately afterwards, and there is apparently no post-hatching ecdysis from the pre-zoeal cuticle as occurs normally in the Brachyura.

The eggs of P. lumpinus hatch as an advanced and much-modified Zoea larva, and simultaneous shedding of both the pre-zoeal and zoeal cuticles occurs also in this species. However the moult does not take place until about 30 minutes after hatching. The process of moulting involved tearing of both membranes below the posterior margin of the carapace by violent movement of the larval abdomen, followed by withdrawal of the cephalothorax and abdomen of the Megalopa in the manner normal for Brachyura.

The degree of assistance to hatching provided by periodic flapping of the maternal abdomen is uncertain. During the period of hatching several eggs removed from females of both P. novaezelandiae and P. lumpinus hatched quite successfully without such aid. Therefore flapping of the abdomen may take place only to remove empty egg cases and stalks attaching these to the pleopod hairs of the female.

Megalopa Larval Stage

In Pilumnus lumpinus, Megalopa larvae obtained by moult from the short-lived Zoea stage are free-swimming. After hatching, the Megalopa larvae of P. novaezelandiae are retained beneath the pleon of the female crab as in P. vestitus (see Hale 1931). Megalopa larvae of P. vestitus possess pleopods, but natatory setae are absent and they are therefore unable to swim. Natatory setae similar to those on the megalopal pleopods of P. novaezelandiae and P. lumpinus are developed in the first juvenile crab stage which is also retained beneath the parental abdomen. As this juvenile crab stage of P. vestitus possesses functional natatory pleopods, it may be more correctly termed a second Megalopa stage⁴ to follow the terminology of Lebour (1928). Hale (1931) suggested that these natatory pleopods could be used for swimming away from parental protection shortly before ecdysis to the first juvenile crab stage (Hale's second juvenile crab stadium) which lacks natatory pleopods. However during the second Megalopa stage, the young may occasionally swim away from the parent as observed in P. novaezelandiae, otherwise their natatory pleopods are not used as suggested for the brood young of P. vestitus (Hale 1931), Petalomera lateralis, and Cryptodromia octodentata

⁴Two Megalopa stages occur only rarely and are known in Charybdis bimaculata Miers, Plagusia dentipes (de Haan) (Aikawa 1937), and in Pachygrapsus marmoratus (Fabricius) (Hyman 1924). From my own observations there are also two Megalopa stages in Plagusia chabrus (Linnaeus) from New Zealand.

(Hale) 1925) without the support of aquarium observations.

Pleopods of the Megalopa larva of both P. novaezealandiae and P. lumpinus bear distal hooklets on the endopods (see Figs 54, 55, 131, 132). These have also been observed in the first juvenile crab stage (second Megalopa) of P. vestitus (see Hale 1931, p. 324, fig. 2A) and in the brood young of both Petalomera lateralis and Cryptodromia octodentata (see Hale 1925). Hale considered that these hooklets are used to link each segmental pair of pleopods to ensure a synchronous beat. However the endopods from which the hooklets arise are greatly reduced, and it is difficult to see how this small and unstable linkage between the left and right pleopods is effective. The pleopods of many other brachyuran Megalopa larvae beat together without the aid of such hooklets and it is therefore difficult to suggest a realistic function for these structures.

The degree of development of the gills in Pilumnus novaezealandiae and P. lumpinus provides an additional specific distinction. The Megalopa larvae of both species possess the same gill formula, but in P. lumpinus the podobranch and epipod of the second maxilliped, and the podobranch and posterior arthrobranch of the third maxilliped are greatly reduced in size. This reduction is evident in adult crabs of this species. In P. novaezealandiae, however, no such reduction is apparent in either the Megalopa larvae or the adults.

Juvenile Crab Stages

The first five juvenile crab stages of Pilumnus novaezealandiae reared in the laboratory are described here, but P. lumpinus was not reared beyond the Megalopa stage. Hale (1931) separated and described the first seven juvenile crab stages of P. vestitus obtained from shore collections and commented on subsequent stages. These juvenile crab stadia were separated on the basis of biometric grouping, and were not verified by laboratory rearing.

In *P. novaezelandiae* atrophy of larval pleopods starts in the first juvenile crab stage as in Macropodia longirostris (Fabricius) (Lebour 1927, p. 808), Carcinus maenas Pennant (Williamson 1903, p. 160), and in Pachygrapsus marmoratus (Fabricius) (Hyman 1924, p. 5). The larval pleopods of Pilumnus novaezelandiae continue to atrophy through to the third juvenile crab stage as recorded in Uca pugilator by Hyman (1922, p. 456). These pleopods are smallest at this time, but do not disappear completely. After the third juvenile crab stage the pleopods begin to grow as primordial adult (female) pleopods, and continue to develop into the adult form. Complete loss of larval pleopods during post-larval development has been recorded only in Uca (= Gelasimus) pugnax by Hyman (1920) and in the second juvenile crab stage of Pilumnus vestitus described by Hale (1931).

Further growth changes involving loss and development of carapace spines occur in successive juvenile crab stages of Pilumnus novaezelandiae. The inner postorbital carapace spine present in the Megalopa and first two juvenile crab stages (Figs 43, 58, 59) apparently degenerates to one or two small granulations or spinelets by the third stage. The larger central spine arising from the posterior border of the orbit in the first and second juvenile crab stages persists as an extra-orbital or lateral postorbital spine in later stages. The outer postorbital spine of the Megalopa larva and first two juvenile crab stages is retained as the anterior lateral carapace spine of subsequent juvenile stages and of the adult. Two further adult lateral carapace spines first appear as swellings in the second juvenile crab stage, and develop later. In the fifth juvenile stage the interorbital space is still about one-half of the carapace width, while in the adult it is about two-fifths the carapace width.

The fate of the large extra-orbital or postorbital carapace spine in the Megalopa of P. lumpinus (see Fig. 124) is unknown, although it possibly persists as one of the lateral carapace spines of the adult crab.

The first to fifth juvenile crab stages of P. vestitus may also show loss and subsequent development of carapace spines similar to that described for P. novaezelandiae. The possibility of such a sequence can be seen in Hale's (1931) carapace diagrams, but the author has not suggested that this may occur.

There is a rather more gradual increase in carapace width in successive juvenile crab stages of P. novaezelandiae than occurs in P. vestitus (see Table 1).

TABLE 1 - Mean carapace width in juvenile crab stages of
P. novaezelandiae and P. vestitus

<u>P. novaezelandiae</u>		<u>P. vestitus</u>	
Crab stage	Mean carapace width	Crab stage	Mean carapace width
Megalopa	1.88 mm	2nd Megalopa (1)	1.55 mm
1	1.93 mm	1 (2)	1.80 mm
2	2.25 mm	2 (3)	2.35 mm
3	2.50 mm	3 (4)	2.85 mm
4	2.60 mm	4 (5)	3.45 mm
5	3.00 mm	5 (6)	4.80 mm

(1) to (6) = Juvenile crab stages as identified by Hale (1931).

There is, however, a possibility that one or more stages of P. vestitus may have been overlooked, as Hale's (1931) measurements and stages are based on biometric groupings from field collections. For example, there may be an additional stage between Hale's first and second juvenile crab stages, as pleopods are present as quite large structures in the first stage, but are entirely absent in the

second stage. It is unlikely that such complete atrophy should occur in only one moult.

It is also possible that post-larval development in P. novaezelandiae may have been retarded by laboratory conditions, and growth may in fact be more rapid in the field. P. novaezelandiae required about 13 months to pass through five juvenile crab stages, but Hale found nine stages of P. vestitus about five months from the time of hatching under natural conditions. On the other hand, some of Hale's later juvenile crab stages may have been the product of the previous breeding season. This would account for the apparently more rapid growth in P. vestitus.

Evolution of Abbreviated Development in the Genus Pilumnus

Pilumnus lumpinus appears to be the least evolved of the three species of Pilumnus in the Australasian region showing abbreviated development. Eggs (1.50 mm x 1.40 mm when ready to hatch) are incubated over a period of at least four months and hatch as advanced, non-natatory Zoeae. They show full development of the usual brachyuran pre-zoeal cuticular processes (Lebour 1928) and possess four rudimentary setae on the exopods of each of the first and second maxillipeds. The telson is widely forked and bears posterior plumose setae. This stage is very short and the Zoea larva quickly moults to a free-swimming Megalopa which leaves the parent crab.

P. vestitus suggests a second stage in this series. The eggs measure 1.50 mm in diameter near the time of hatching, but the incubation period is not known. The pre-zoeal cuticle is greatly reduced in embryonic development, and lacks long feathered aesthaetes on the first and second antennae and on the telson⁵. The

⁵Eggs from Hale's (1931) collection kindly provided by Dr J.C. Yaldwyn.

embryonic Zoea lacks setae on the maxillipeds, while the telson is not widely forked and bears only rudimentary posterior setae. The eggs hatch as Megalopa larvae without natatory pleopods (Hale 1931). This first stage Megalopa is retained beneath the female pleon where it moults to a second stage Megalopa with natatory pleopods (Hale's first juvenile crab stage). This second stage Megalopa is also associated with the parent crab.

The third and most advanced stage in this evolutionary sequence is shown by P. novaezelandiae. The eggs are the largest (1.75 mm x 1.65 mm) and are incubated over a probable period of only two months. The pre-zoeal cuticle is reduced to a degree similar to that of P. vestitus. Eggs hatch as Megalopa larvae with natatory pleopods. There is only one Megalopa larval stage, and this is retained beneath the pleon of the female crab.

ECOLOGICAL SIGNIFICANCE OF ABBREVIATED DEVELOPMENT IN MARINE BRACHYURA

The ecology of P. novaezelandiae, P. lumpinus, and P. vestitus can be correlated with their respective larval life-histories. Adult females of P. novaezelandiae carrying juvenile progeny beneath the pleon have been observed on Takapuna Reef by Professor J. E. Morton (pers. comm.). In this species the Megalopa larva is the only potentially free-swimming stage in the life-history, but is retained by the female crab. Subsequent juvenile crab stages lack natatory pleopods and cannot swim. This would keep the juvenile crabs in the vicinity of the parent, and explain gregariousness noted in this species by Bennett (1964, p. 71).

In P. lumpinus the Megalopa larvae swim actively and are not retained by the female. Dispersal is not therefore restricted as in P. novaezelandiae, and the adults are solitary (Bennett 1964, p. 73).

Large numbers of juvenile crabs were obtained from bryozoan detritus from five or six fathoms in Kau Bay, Wellington Harbour (12/11/1964), but no adults were present. Active dispersal of *Megalopa* larvae may explain the presence of these juvenile crab stages in deeper water.

Juvenile crab stages of *P. vestitus* were collected in large numbers close to adult crabs (Hale 1931), and it would appear that this Australian species also is gregarious. The only potentially natatory stage is the second *Megalopa*, and this is retained by the female. Hence dispersal is restricted as in *P. novaezelandiae*.

The above three species of the genus *Pilumnus* and all other *Brachyura* known to have abbreviated development, have the following features in common:

1. All occur in the Southern Hemisphere, either in Australia or New Zealand. (*Homolaspis plana* (A. Milne Edwards) from Southern Chile is known to have non-abbreviated development (Guiata 1960), otherwise little is known of the life-histories of South African or South American *Brachyura*⁶).
2. They are all shallow water species and usually found on reefs, or wave-washed rock platforms.
3. They are all recluse.

⁶*Pilumnoides perlatus* (Poeppig) has small eggs 0.33 mm in diameter (2 ovigerous females kindly provided by Dr A. Carvacho, Antofagasta) and this is probably a second Chilean xanthid crab with non-abbreviated development. Similarly, the small size of eggs recorded from *Gaudichaudia gaudichaudi* (Milne Edwards), *Paraxanthus barbiger* (poeppig), and *Platyxanthus orbignyi* (Milne Edwards and Lucas) from Central Chile by Antezana, Fagetti, and Lopez (1965) does not suggest that development is abbreviated in these species.

Bate (1868) recorded abbreviated development in *Uca cunninghami* from Rio de Janeiro, but Dr R. O. Cunningham's account suggests that this species is a strictly freshwater form (Bate 1868, p.445).

Among the Brachyura, the three features listed above are shared by many species having non-abbreviated development, but the second and third characters may have some significance. Wave-washed reefs and shallow water rock platforms with deep crevices occur only in isolated areas of our coastline. Under these conditions abbreviated development, and retention of larvae by the female would be an additional safeguard against dispersal by tidal currents, and might assist in retaining the stock within a restricted locality or ecological niche. Finally it results in the gregariousness seen in Pilumnus novaezelandiae and P. vestitus. Larval polychaetes, echinoderms, and presumably also prosobranchs, may prolong their pelagic life for days or weeks until they find a suitable substratum (Thorson 1950, p. 36) but it is doubtful if larval Brachyura are able to do this.

Thorson (1950) pointed out that most animal populations on the sea floor maintain their composition over long periods of time, but the individual species concerned may have either abbreviated development or varying periods as planktonic larvae. Consequently high planktonic larval mortality is compensated for by relatively larger numbers of eggs, but species with abbreviated development must have a much lower mortality to maintain their optimum numbers in a community.

In marine bottom invertebrates pelagic development occurs in about 70% of all species and reaches maximum development among the shelf fauna of warmer waters, but is nearly or totally suspended in the deep sea and in arctic and antarctic regions (Thorson 1950, p. 36). The decapod Crustacea follow a similar pattern, but abbreviated larval life is more commonly found among species from land or freshwater, and to a considerably less degree among those of the arctic and antarctic regions and of the deep sea (Gurney 1942, pp. 54-64). However, all Brachyura with abbreviated development (including the freshwater

Potamonidae) may have in common a need to minimise dispersal, and this could be achieved by partial or complete abbreviation of the planktonic phase. It would appear, therefore, that abbreviated development in Brachyura may be an adaptation to a habitat requirement⁷, and as such it would have little phylogenetic significance. These remarks may also apply to the majority of Decapoda with abbreviated development, but the examples cited by Gurney (1942) include a number of phylogenetically unrelated species from varying habitats, in which the length of larval life is reduced without apparent reason.

⁷Korschelt (1944, p. 841) stated that "Besondere Lebensumstände sind es auch bei anderen Brachyuren, welche eine mehr oder weniger weitgehende bis beinahe direkte Entwicklung veranlassen," but offered no substantiating evidence or discussion.

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LIFE-HISTORY STUDIES ON NEW ZEALAND BRACHYURA.

2. Family Xanthidae. Larvae of *Heterozius rotundifrons* A. Milne Edwards, 1867, *Ozius truncatus* H. Milne Edwards, 1834 and *Heteropanope* (*Pilumnopus*) *serratifrons* (Kinahan, 1856)

by

Robert G. Wear

SUMMARY

A brief account is given of the systematics and distribution of *Heterozius rotundifrons* A. Milne Edwards, *Ozius truncatus* H. Milne Edwards, and of *Heteropanope* (*Pilumnopus*) *serratifrons* (Kinahan). Keys are given for the separation of Zoea larva of New Zealand xanthid Brachyura and to the Megalopa larvae of *Heterozius rotundifrons* and *Ozius truncatus*.

Notes are given on the seasonal breeding cycle of *Heterozius rotundifrons*, and the pre-Zoea larva, two Zoea larval stages, and Megalopa larva reared in the laboratory are here described. Larval characters of *H. rotundifrons* are specialised and do not support its recently suggested classification in the family Atelecyclidae. The larvae show no relationships with those of the Cancridae or of the Corystidae, and affinities with described larvae of the Xanthidae or even the Brachyryncha are obscure. Larval development is incompletely abbreviated possibly to reduce dispersal in response to restricted inter-tidal habitat requirements of the adult crabs.

The pre-Zoea larva, four Zoea larval stages, and the Megalopa larva of *Ozius truncatus* reared in the laboratory are described. A key

to the Zoea larval stages is given. Larvae of this species are distinct both at the generic and specific levels, but are generally similar to those known of xanthid crabs. It is difficult to relate the genus Ozius to other xanthid genera on the basis of larval characters alone.

The pre-Zoea larva and stage one Zoea larva of Heteropanope (Pilumnopeus) serratifrons are described. There are probably four Zoea larval stages in the development of this species. Zoea larval characters suggest that in the family Xanthidae, Heteropanope and Pilumnopeus should be separated from other genera in the subfamily Pilumninae with which they are currently classified.

INTRODUCTION

In a previous paper (Wear 1967) abbreviated development in Pilumnus novaezelandiae Filhol and P. lumpinus Bennett was described. The present publication concerns the larval stages of the three remaining New Zealand species in the family Xanthidae.

SYSTEMATICS AND DISTRIBUTION OF ADULTS

Heterozius rotundifrons A. Milne Edwards

The systematic position of this species is uncertain. The adult was recognised by Balss (1930) as a primitive xanthid related to the South American Homolaspis, but nevertheless distinct from this genus. Heterozius was considered by Balss (1930, p.203-4) to lessen the gap between the Xanthidae on one hand and Acanthocyclus (Corystidae) on the other, but it bears no relationship to Ozius and the similarity in the generic name is unfortunate (Balss 1930; Bennett 1964).

Heterozius rotundifrons was placed in the Cancridae by Richardson (1949a), but was included among the Atelecyclidae by Balss (1957). Bennett (1964) following Balss (1930, 1932) described the adult as a xanthid crab, and until claims to the contrary can be fully substantiated, it is probably desirable and less confusing to retain Heterozius rotundifrons in the family Xanthidae. The species is however difficult to place in any existing subfamily, and is here considered as a primitive form following the suggestion of Balss (1930).

Heterozius rotundifrons is the monotype of a genus endemic to New Zealand and the Chatham Islands (Bennett 1964). The species is common intertidally on rocky shores throughout New Zealand, especially in the Cook Strait area, and is sympatric with Petrolisthes elongatus (Milne Edwards) in all localities. Ovigerous female crabs were collected from Mangonui Estuary and Whangaroa Harbour (North Auckland) 23-10-1964, the University of Auckland Marine Station at Leigh, 15-10-1964, the Wellington area, 1964-65, and from Patterson Inlet (Stewart Island) 24-10-1965. Larvae were hatched from at least two specimens from each of the above localities, and comparison of larvae revealed no significant morphological variation over the geographical range.

Ozius truncatus H. Milne Edwards

The genus Ozius, previously of the subfamily Oziinae is at present included in the Menippinae (sensu emendato Balss 1932) which is now reconstituted to embrace the subfamilies Oziinae and Eriphiinae distinguished in earlier systems of classification (see Balss 1957; Bennett 1964).

Ozius truncatus is found mainly in northern New Zealand, and its distribution follows that outlined by Bennett (1964, p. 69). The species is also particularly common in Australian waters (Hale 1927). Adult crabs are considered to occur rather sparsely under stones, close inshore but apparently always in the water (Bennett 1964), but I collected several specimens from under large rocks about the mid-tide level in only damp conditions. Ovigerous females were collected from many North Island localities including the following: Wainui Bay, Whangaroa, 25-10-1964; McLeod's Bay, Whangarei Harbour, 22-10-1964; Pukerua Bay, Wellington, 1-1-1965. Larvae were hatched from three females from Pukerua Bay.

Heteropanope (Pilumnopeus) serratifrons (Kinahan)

The genus Heteropanope has been removed from the Menippinae by Balss (1932) and placed in the subfamily Pilumninae. Systematics of the closely related genera Heteropanope, Pilumnopeus, and Eurycarcinus is confused. Balss (1933) separated the genera Heteropanope and Pilumnopeus which most authors considered to be synonymous (Buitendijk and Holthuis 1949), but the opinion followed here is that of Monod (1956, p. 264) who considers some distinction between these two genera necessary, at least to the level of subgenus.

Heteropanope (Pilumnopeus) serratifrons, previously known from Australia (Hale 1927, p. 161; Bennett 1964, p. 69) was recorded on the New Zealand faunal list (as Pilumnopeus serratifrons) by Richardson (1949b) but is not included by Bennett (1964). However its presence in northern New Zealand has been known for some time (Prof. J. E. Morton, pers. comm.). Specimens for study were collected from McLeod's Bay, Whangarei Harbour, where adult crabs appeared to be plentiful around the mid-tide level, but the species was not found south of this area. Four ovigerous females and several males were found living in burrows similar to those of Helice crassa Dana (Grapsidae) and Hemiplax hirtipes (Jacquinot) of the family Ocypodidae, but in Australia Heteropanope (Pilumnopeus) serratifrons is not typically a burrowing species (Hale 1927). Larvae were hatched from two of the above female crabs.

METHODS

Ovigerous female crabs obtained from various New Zealand localities were kept singularly in small aquaria until their eggs hatched. Larvae were reared in covered finger bowls using newly hatched Artemia Nauplii as food. Larval stages of Heterozius rotundifrons and of Ozius truncatus obtained in the laboratory were

compared with larvae from the plankton of the Wellington area, and in both cases the reared developmental stages were found to be normal. The very tiny first stage Zoea larvae of Heteropanope (Pilumnopeus) serratifrons did not feed, and died within three or four days of hatching while still in the first zoeal stage.

Chromatophores of living material were observed using the synthetic anaesthetic ethyl m-aminobenzoate (SANDOZ MS-222) about 1/3,000 parts in seawater. Larvae thus immobilised for sketching purposes later recovered when returned to fresh seawater. In this paper major chromatophore colours are represented in drawings of the first stage Zoea larva only. Black is indicated by solid black and red is represented by stippling. Additional colours and details of distribution are confined to the text in either tabular or descriptive form.

TERMINOLOGY AND MEASUREMENTS

Decapod larval terminology used throughout this publication follows that of the previous paper (Wear 1967). The majority of Zoea and Megalopa larval characters used here in keys for the separation of species are those suggested by Lebour (1928).

Measurements referred to in the text are defined below.

- | | |
|----------------------------|--|
| Length of Rostral Spine: | Taken from ventral margin of eye to tip of spine. |
| Length of Dorsal Spine: | Taken from junction with carapace to tip of spine. |
| Length of Antennal Exopod: | Excluding distal setae and measured as a fraction of the spinous process from point of junction. |

Length of Spinous Process cf. Rostral Spine:	Measured from the ventral margin of eye to its tip, and recorded as a fraction of the length of rostral spine.
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Length of Spinous Process cf. Dorsal Spine:	Measured from the ventral margin of eye to its tip, and recorded as a fraction of the length of dorsal spine.
--	---

Total Length of Larva:	Measured from anterior margin of eye to tip of lateral telson cornua with abdomen extended.
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A KEY TO THE ZOEAL LARVAE OF
NEW ZEALAND XANTHID BRACHYURA

The following key does not include Pilumnus novaezelandiae and P. lumpinus as these two species do not possess free-swimming Zoea larval stages (Wear 1967).

- 1 (2) - 2 larval stages; lateral carapace spines directed downwards; rostrum greater than half the length of dorsal spine; antennal exopod short, about $1/7$ the length of spinous process; spinous process robust and extremely long, about $1\frac{1}{2}$ times the length of dorsal spine; lateral protuberances on 2nd abdominal segment only; segment 5 without ventrolateral spines but with a pair of long dorsolateral spines; pleopod buds in stage 1 larva; telson with one small dorsal spine on telson cornu.
.....Heterozius retundifrons
- 2 (1) - 4 larval stages; lateral carapace spines directed outwards almost at right angles to dorsal spine in posterior view; rostrum half or much less than half the length of dorsal spine; antennal exopod about $2/3$ the length of spinous process; spinous process slender, considerably shorter than dorsal spine; lateral protuberances on 2nd and 3rd abdominal segments; segment 5 with a pair of ventrolateral spines but without dorsolateral spines; no pleopod buds in stage 1; telson with two or three spines on telson cornu.
- a (b) - Rostrum long, straight, about half the length of dorsal spine; lateral carapace spines long; carapace with a median frontal tubercle and a similar tubercle behind dorsal carapace spine; antennal exopod with terminal setae; spinous process considerably shorter than rostral spine and less than half the length of dorsal spine; first abdominal segment with a

median dorsal spine; telson with one large and one small dorsal spine on lateral cornu, inner margin of telson cornu without setae.

.....Ozius truncatus

b (a) - Rostrum a tiny process, about $1/20$ the length of dorsal spine; carapace smooth and without bumps or tubercles; antennal exopod without terminal setae; spinous process much longer than rostral spine and greater than half the length of dorsal spine; first abdominal segment without a median dorsal spine; telson with one small dorsal spine and two small lateral spines on lateral cornu, inner margin of telson cornu setose.

.....Heteropanope (Pilumnopous) serratifrons

A KEY TO THE MEGALOPA LARVAE OF
Heterozius rotundifrons AND Ozius truncatus

- 1 (2) - Carapace 1.12 mm long, without ridges or tubercles; frontal region wide, poorly defined; eyes not reaching lateral carapace margins; antennal flagellum very short, 3-segmented; 1st and 2nd maxillipeds reduced; 3rd maxilliped with arthrobranch and podobranch; ischium of 1st pereopod without spines; 5th pereopods without long terminal setae; 6th abdominal segment without pleopods (uropods).

.....Heterozius rotundifrons

- 2 (1) - Carapace 2.00 mm long, strongly ridged, two posterior tubercles; frontal region narrow, elongate and well defined; eyes reaching lateral carapace margins; antennal flagellum long, 8 or 9-segmented; 1st and 2nd maxillipeds not reduced; 3rd maxilliped with two arthrobranches and rudimentary podobranch; ischium of 1st pereopod with a strong ventral spine; 5th pereopods with three long terminal setae; 6th abdominal segment with natatory pleopods (uropods).

.....Ozius truncatus

Heterozius rotundifrons A. Milne Edwards, 1867

Female crabs apparently reach maturity when the carapace length exceeds about 13mm. The smallest ovigerous female collected (carapace width 13.4 mm) carried 395 eggs, and the largest female (carapace width 23.0 mm) carried 1,574 eggs. There is a linear relationship between increasing carapace width and the number of eggs carried by individual female crabs. Eggs freshly laid are orange-yellow and measure 0.70 mm in diameter. Colour intensifies during incubation, and by the time eye pigment is visible the remaining yolk is bright orange-red. As the embryo continues to develop egg colour loses intensity and fades to light yellow towards the time of hatching. Eggs about to hatch measure 0.95 mm x 0.80 mm.

During 1964 and 1965 a very extended but variable breeding period was noted at Island Bay, Wellington. Mating took place mainly during January and February, but occasional mating pairs were found from October through to March. Ovigerous females were more common between the months of May and November than at other times, but also occurred over the summer and autumn seasons (December to April). At no time were more than 50% of mature female crabs in berry. Incubation of eggs is long and occupies at least five months, and it is therefore probable that breeding occurs only once a year, with the majority of females mating in January and February and bearing eggs from May through to November. Many mature female crabs apparently breed outside this seasonal pattern.

THE PRE-ZOEAL LARVA

The majority of larvae shed the pre-zoeal cuticle as they hatch from the inner egg membrane, and are able to swim strongly immediately after hatching. In each brood there are a few larvae which do not moult from the pre-zoeal cuticle for five or six minutes after hatching. During this time the larvae lie on the bottom, flexing and extending the abdomen in efforts to rupture the thin pre-zoeal cuticle.

Larvae dissected from eggs showed that the pre-zoeal cuticle completely covers the cephalothorax, cephalic and thoracic appendages, and abdomen of the first stage Zoea. As is usual in brachyuran pre-Zoea larvae (see Gurney 1942, p. 52) this cuticle does not follow segmental indentations of the zoeal abdomen. It does not possess long aesthaetes arising from the first antennae, the exopod of the second antennae or the posterior margin of the telson.

The chromatophore pattern is fully developed in the pre-Zoea, but is recorded in description of the first Zoea larva.

THE ZOEAL LARVAL STAGES

The seasonal abundance of larvae of Heterozius rotundifrons in the Wellington Harbour plankton has been discussed previously and the first stage Zoea illustrated (Wear 1965, p. 17, Fig. 6H). First and second stage Zoea larvae of H. rotundifrons are strong and constant swimmers and are attracted by light.

STAGE ONE

Figs 1 - 7

The duration of this first stage under laboratory conditions was about seven or eight days.

Description

Cephalothorax (Figs 1, 2)

Total length of larva 2.38 mm to 2.40 mm. Rostrum 0.56 mm long, straight or curved slightly forwards at its tip; dorsal carapace spine 0.80 mm long and curved posteriorly; lateral spines very short, about 0.19 mm long and directed downwards. Carapace with a median tubercle behind the base of dorsal spine and one small setae below this tubercle on each side; carapace and carapace spines otherwise without hairs or setae. Eyes large and sessile.

Cephalic Appendages (Figs 3-6)

First antenna (Fig. 3) uniramous with two long aesthaetes and two shorter aesthaetes at its tip.

Second antenna (see Figs 1, 2) with exopod lacking terminal setae and only 0.19 mm long; spinous process 1.25 mm long and very robust, hairy along its entire anterior margin and at posterior tip, greater than twice the length of rostrum and about $1\frac{1}{2}$ times that of the dorsal spine; endopod not yet developed.

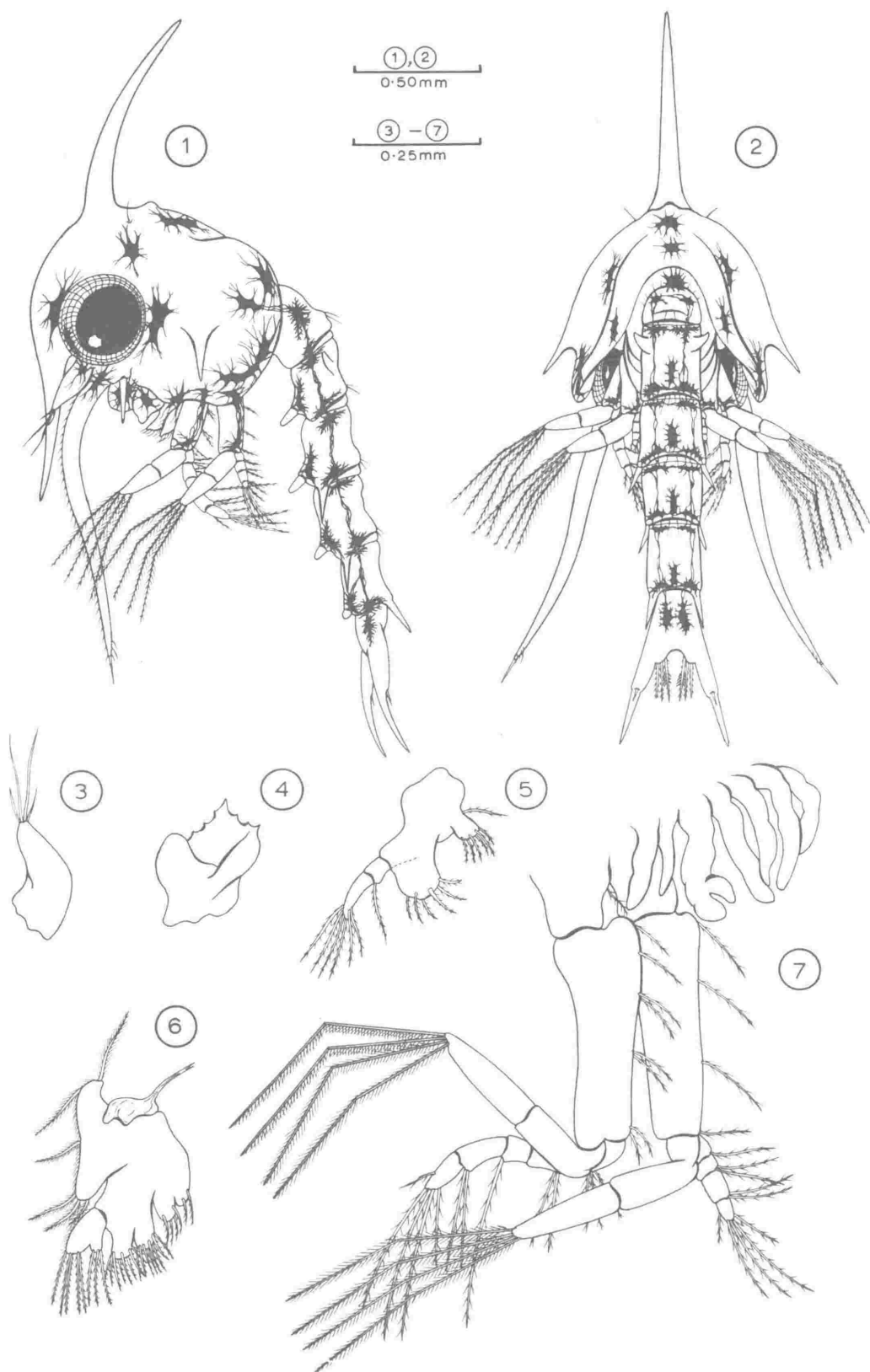
Mandible (Fig. 4) strongly toothed but without a palp.

First maxilla (Fig. 5) with proximal and distal endites each having an inner row and an outer row of three short plumose setae; proximal endite with one medial seta near its base. Palp of two segments; proximal segment with one terminal plumose seta; distal segment having six sparsely plumose setae at its tip.

Second maxilla (Fig. 6) with first (proximal), second, third, and fourth (distal) endites having two, four, eight, and eight marginal plumose setae respectively. Palp with a shallow terminal cleft dividing it into two rami; slender inner ramus with three terminal plumose setae; broader outer ramus provided with five such setae; lateral margin fringed with fine hairs. Scaphognathite with one long biplumose

Heterozius rotundifrons: Stage 1 Zoea Larva

- Fig. 1 Stage 1 Zoea; lateral view
- Fig. 2 Stage 1 Zoea; posterior view
- Fig. 3 First antenna of left side
- Fig. 4 Mandible of left side
- Fig. 5 First maxilla of left side
- Fig. 6 Second maxilla of left side
- Fig. 7 Maxillipeds and pereopods of left side



seta arising from its proximal tip, two such setae on the outer margin which is otherwise fringed with fine hairs, and three long biplumose setae distally.

Thoracic Appendages (Fig. 7)

First maxilliped with one seta arising from the posterior margin of coxa. Basis with eight or nine plumose setae along its inner margin. Endopod of five segments; ischium short with three inner distal setae; merus twice the length of the ischium with two setae mid-way along its inner margin; carpus about equal in length to ischium and bearing one long inner distal seta; propod slightly longer than carpus and with two distal setae; dactylus equal in length to propod and with three long terminal setae, one shorter subterminal seta and one very small seta mid-way along the outer margin. All setae of endopod are sparsely plumose. Exopod of two segments and as long as the endopod; tip of distal segment with four very long biplumose natatory setae.

Second maxilliped similar to the first, but differs mainly in having a much shorter endopod of four segments each of about equal length. Coxa without setae. Basis with four setae spaced along its inner margin. Endopod about half the length of that of the first maxilliped: first, second and third segments with one, two and two short plumose setae respectively arising from their inner distal margins; setation of the terminal segment is similar to that of the equivalent first maxilliped segment, but the setae are here shorter. Exopod as in the first maxilliped.

Third maxilliped biramous: rami of equal length, short, unsegmented and without setae.

Pereiopods all present as short, uniramous, unsegmented buds; first pereiopod with a rudimentary chela at its tip.

Gill buds are not present in the first stage Zoea larva.

Abdomen

Abdomen (see Figs 1, 2) of five segments and a telson: sixth segment and the telson are fused. Five abdominal segments each of about equal length (0.25 mm): first segment without spines but with three or four median dorsal hairs; second segment with a paired lateral papilla or protuberance as in all known brachyuran larvae; unarmed pair of ventrolateral spines on each of the third and fourth segments; fifth segment with a pair of long dorsolateral spines; two or three posterior dorsal hairs on all segments except the fifth. Short uniramous pleopod buds occur on the second to fifth abdominal segments.

Telson (see Fig. 2) widely forked: one small dorsal spine occurs mid-way along each of the lateral cornu; 3+3 plumose setae arise from the posterior margin of the telson inside the fork; inner seta with four or five strong marginal hairs centrally.

Chromatophore Pattern (Figs 1, 2)

Chromatophores in the Zoea larva of H. rotundifrons are both numerous and intense, and it is difficult to determine the centres of coloration to establish a distribution pattern. The larvae have an overall colour of olive green when observed with the naked eye.

The chromatophore pattern characterising the first stage Zoea larva of H. rotundifrons is tabulated (Table 1). The chromatophore classification is that of Aikawa (1929), modified to cover the larvae of New Zealand Brachyura. All Aikawa's chromatophore groups are used and additional groups are indicated where necessary.

TABLE 1

Heterozius rotundifrons A. Milne Edwards
Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

1.	(1)	Supracerebral	-----
2.	x	Antennular	black
3.	(2)	Antennal	black
4.	(3)	Labral	polychromatic, black to green to yellow
5.	(4)	Mandibular	" " "
6.	(5)	Maxillar	" " "
7.	(6)	Maxillipedal	black, coalesced with 18 below
8.	(7)	Lateral Intestinal	dichromatic, black to yellow
9.	x	Subintestinal	" " "

B. Visceral Group

10.	(8)	Median Gastric	polychromatic, black to green to yellow
11.	(9)	Precardiac	" " "
12.	(10)	Subcardiac	" " "
* 13.	(11)	Postcardiac	" " "

SECONDARY SYSTEM

14.	x	Posterior Carapacial	2 pairs, dichromatic, black to yellow
15.	(12)	Posteroventral Carapacial	polychromatic, black to green to yellow
16.	(12)	Lateral Carapacial	-----
17.	x	Dorsal Carapace Spine	-----

- | | | |
|----------|----------------------|-------------------------------|
| 18. (13) | Maxillipedal | black, coalesced with 7 above |
| 19. (14) | Optic | black |
| 20. (15) | Median Ocular Centre | black |
-

NOTE:

(1) to (15) numerical status of chromatophores after
Aikawa (1929)

- x not included in Aikawa's system
- * not homologous with Aikawa's equivalent
- chromatophore absent

STAGE TWO

Figs 8-13

The second zoeal instar was obtained by moult from the first stage Zoea in the laboratory. The duration of the second stage varied between 11 and 12 days. Significant morphological changes only are described below.

Description

Cephalothorax (Fig. 8)

Total length of larva 3.06 mm. Rostrum 0.69 mm; dorsal carapace spine 1.00 mm; lateral spines 0.22 mm. Eyes now borne on short stalks.

Cephalic Appendages (Figs 9-12)

First antenna (Fig. 9) with an inner ramus now present as a tiny subterminal bud.

Second antenna (see Fig. 8) with spinous process 1.31 mm long, now slightly less than twice the length of the rostral spine but still longer than the dorsal spine; endopod present as a bud-like rudiment.

Mandible (Fig. 10) with a short rudimentary palp.

First maxilla (Fig. 11) with endites each having seven marginal setae.

Second maxilla (Fig. 12) with the scaphognathite fringed with about 30 biplumose setae spaced along its entire margin.

Thoracic Appendages (see Fig. 8)

First and second maxillipeds each with eight long natatory setae and one shorter lateral seta arising from the tips of the exopods. The setation is otherwise unchanged from that of the first stage Zoea. The third maxillipeds and pereopods have increased in size. The

Heterozius rotundifrons: Stage 2 Zoea Larva

Fig. 8 Stage 2 Zoea; lateral view

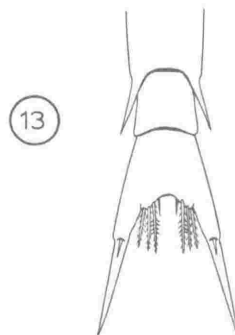
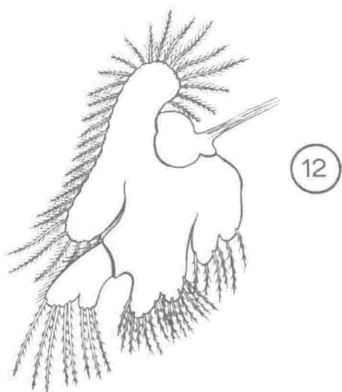
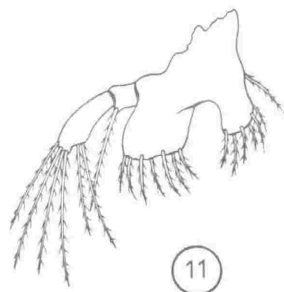
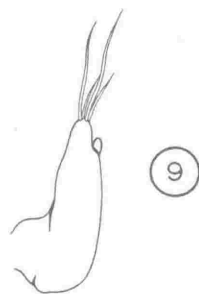
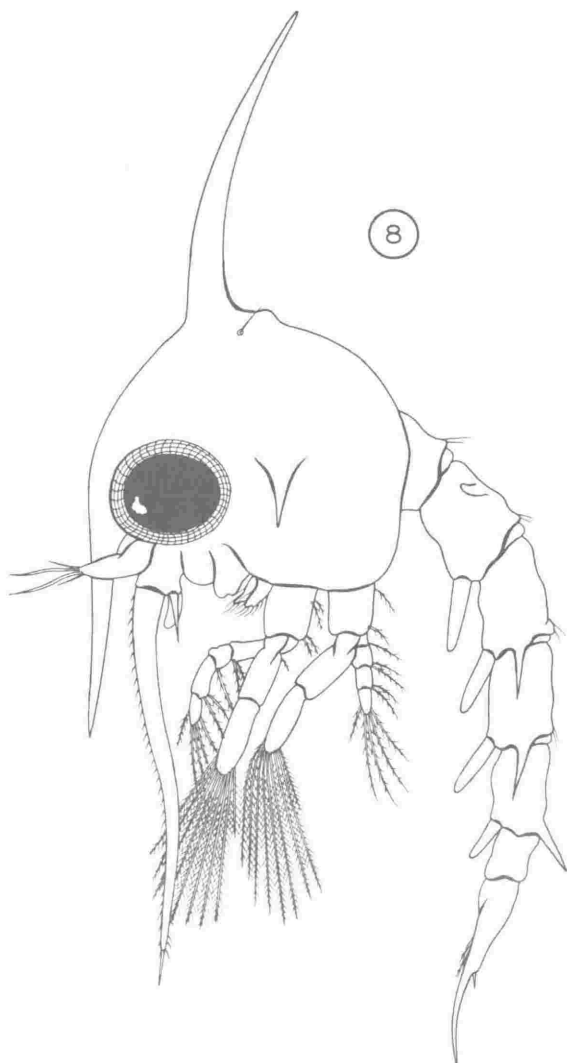
Fig. 9 First antenna of right side

Fig. 10 Mandible of left side

Fig. 11 First maxilla of left side

Fig. 12 Second maxilla of left side

Fig. 13 Fifth, sixth abdominal segments and telson; dorsal
view



(8), (13)
0.50mm

(9) - (12)
0.25mm

endopod of the third maxilliped and the pereopods are obscurely segmented beneath the zoeal cuticle. Gills are present in the second stage Zoea as short and non-functional bud-like rudiments, but the gill formula is difficult to determine and is recorded in description of the Megalopa larva.

Abdomen

Abdomen (see Fig. 8) now comprises six segments and a telson; sixth segment about half the length of the anterior segments and is without spines or setae; ventrolateral spines and dorsolateral spines longer than in the first stage Zoea.

Telson (Fig. 13) with four pairs of posterior setae inside the fork; additional pair of setae are very small, unarmed, and occur in a position medial to the 3+3 larger plumose setae.

Chromatophore Pattern

The newly separated sixth abdominal segment is provided with the same chromatophore pattern as the anterior five segments. The distribution and number of chromatophores is otherwise unchanged from that of the first stage Zoea larva described earlier.

THE MEGALOPA LARVA

The Megalopa larva was obtained by moult from the second zoeal stage in the laboratory. The duration of the Megalopa stage under laboratory conditions (15°C to 17°C) varied between 15 days and 17 days before moulting to the first juvenile crab stage. Megalopa larvae of H. rotundifrons were not found in the Wellington plankton.

Description

Cephalothorax (Figs 14, 15)

Carapace 1.12 mm long and of the same width; broadly rounded and

without ridges, spines or setae, but sparingly covered with very short fine pubescence; frontal region wide with rostrum poorly defined or virtually absent; interorbital space 0.56 mm. Eyes large and not reaching the lateral margin of the carapace; eye-stalks short and without spines or setae.

Cephalic Appendages (Figs 16-19)

First antenna (Fig. 16) with a peduncle of three short segments; inner ramus of one segment, short and with two terminal aesthaetes; outer ramus more robust and bearing many aesthaetes at its tip and along the inner margin.

Second antenna (Fig. 17) much reduced: peduncle of two short unarmed segments; flagellum (endopod) 0.12 mm long and comprising three short segments only, distal segment provided with one long terminal seta; exopod absent.

Mandible with a palp of three short segments each of equal length; terminal segment with a tuft of short setae.

First maxilla (Fig. 18) with its palp now reduced to a flattened and unsegmented process without setae.

Second maxilla (Fig. 19) also having a reduced palp which is similar to that of the adult crab; scaphognathite now fringed with 40 or more plumose setae.

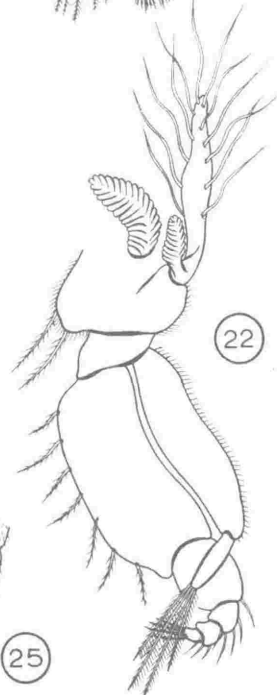
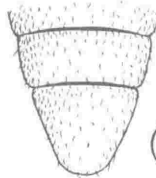
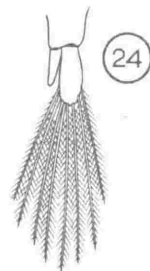
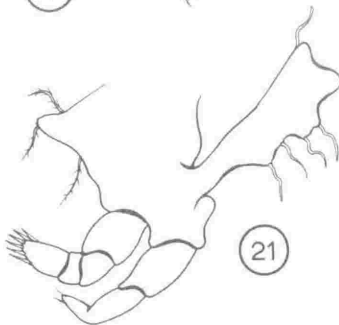
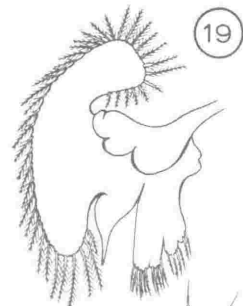
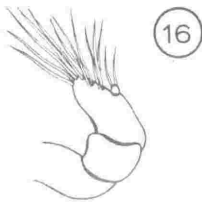
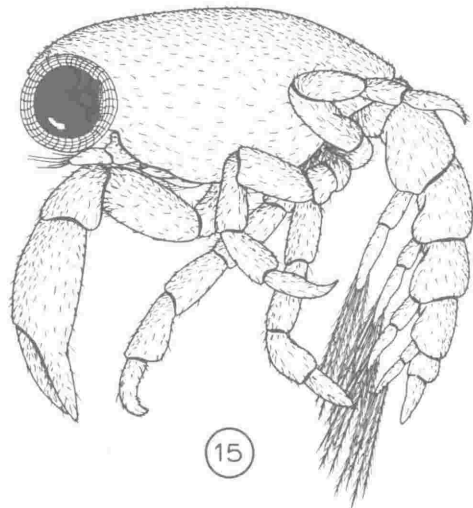
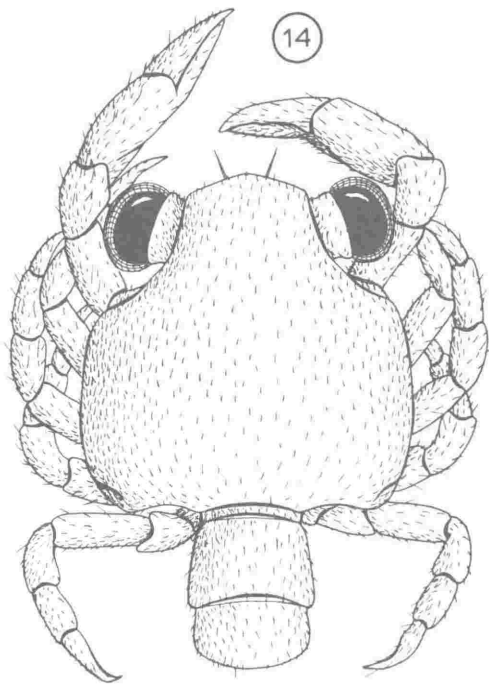
Thoracic Appendages (Figs 20-22)

First maxilliped (Fig. 20) similar to that of the adult; coxa and basis fringed with setae; endopod of one segment, much reduced and provided with only a few short setae irregularly arranged; exopod slightly longer than endopod, three-segmented and without setae. Epipod large, flattened, with one large plumose seta arising laterally and two or three similar setae at its tip.

FIGURES 14 - 25

Heterozius rotundifrons: Megalopa Larva

- Fig. 14 Megalopa larva; dorsal view
- Fig. 15 Megalopa larva; lateral view
- Fig. 16 First antenna of left side
- Fig. 17 Second antenna of left side
- Fig. 18 First maxilla of left side
- Fig. 19 Second maxilla of left side
- Fig. 20 First maxilliped of left side
- Fig. 21 Second maxilliped of left side
- Fig. 22 Third maxilliped of left side
- Fig. 23 Pleopod from left side of second abdominal segment
- Fig. 24 Pleopod from left side of fifth abdominal segment
- Fig. 25 Sixth abdominal segment and telson; dorsal view



14, 15
 0.50 mm
 16 - 25
 0.25 mm

Second maxilliped (Fig. 21) also small: coxa and basis not easily separated and fringed with only two or three setae; endopod of four segments, distal segment bearing six or seven stout setae, otherwise unarmed; exopod as long as endopod, two-segmented, but bears only two or three short distal setae. Epipod broad, flattened, and provided with only a few marginal setae. Other gill structures are not present on the second maxilliped.

Third maxilliped (Fig. 22) considerably larger than second maxilliped: coxa fringed with two or three plumose setae and with fine hairs; basis short and lacks hairs or setae. Endopod of five segments: ischium large and flattened with its inner margin setose; merus not greatly flattened, about one third the length of the ischium, and lacks setae; carpus, propod and dactylus very tiny, with each segment bearing a few lateral setae and the dactylus provided with terminal setae. Exopod shorter than endopod and comprises two segments: first segment as long as the ischium but narrower, and bears many fine hairs along its lateral margin; distal segment about one third the length of the proximal segment and provided with four short biplumose setae. Epipod smaller than that of the second maxilliped and is more setose. The gills of the third maxilliped comprise one small podobranch and a large arthrobranch, each with lamellae visible.

The pereopods (see Figs 14, 15) are similarly proportioned to those of the adult crab. In the *Megalopa* all segments are without accessory spines or setae, but are covered with a fine pubescence similar to that found on the carapace. There are no long setae present on the dactylus of the fifth pereopods. The first pereopod possesses two arthrobranchs and the second and third pereopods each have one pleurobranch.

The complete gill formula of the Megalopa larve of Heterozius rotundifrons is tabulated below. This formula may also be referred to the adult crabs.

	<u>MAXILLIPEDS</u>			<u>PEREIOPODS</u>				
	1	2	3	1	2	3	4	5
Pleurobranchiae:	-	-	-	-	1	1	-	-
Arthrobranchiae:	-	-	1	2	-	-	-	-
Podobranchiae:	-	-	1	-	-	-	-	-
Epipodites:	1	1	1	-	-	-	-	-
Exopodites:	1	1	1	-	-	-	-	-

Abdomen

Abdomen (see Figs 14, 15) of six segments and a telson; 1.25 mm long and sparingly pubescent. First segment very short, 0.38 mm wide; second segment 0.30 mm long, 0.40 mm wide; third, fourth, and fifth segments each respectively smaller; sixth segment (see Fig. 25) smallest, 0.09 mm long and 0.38 mm wide. Lateral pleura of second to fifth segments extended ventrally.

Biramous pleopods (Figs 23, 24) occur on segments two to five: inner ramus (endopod) rudimentary and lacks setae, distal hooklets or serrations; outer ramus (exopod) well developed and in each case fringed with eight long biplumose setae. Pleopods of the second segment (Fig. 23) are largest, and those of the fifth segment (Fig. 24) are smallest. The sixth abdominal segment lacks pleopods (uropods).

Telson (Fig. 25) triangular, pubescent but without marginal setae.

Chromatophore Pattern

The Megalopa larva of H. rotundifrons is similarly coloured to the Zoea larvae of this species. However, the primary chromatophore system is now considerably masked by great development of the secondary system (see Table 1 p.99). The pereopods are also pigmented with dichromatic black to yellow chromatophores.

Ozius truncatus H. Milne Edwards, 1834

Eggs freshly laid measure 0.50 mm x 0.45 mm and are dark maroon in colour. This colour loses intensity as the embryo develops. Eggs about to hatch measure 0.70 mm x 0.65 mm.

Breeding takes place only once every year and occurs at about the same time throughout New Zealand. Ovigerous females were found only during October and January, and carried eggs for about three months.

THE PRE-ZOEA LARVA

Pre-Zoea larvae (Fig. 26) were obtained from the eggs of three females from Pukerua Bay, 6, 9, 10-1-1965. The pre-zoeal cuticle is not moulted in the process of hatching, but is retained by the larvae for periods varying between 60 minutes and 90 minutes under laboratory conditions (17°C to 19°C).

The pre-Zoea larvae do not swim, but move spasmodically by violent flexing of the abdomen which becomes more frequent during the process of moulting from the pre-zoeal cuticle. In the majority of larvae observed the first and second maxillipeds were free from the pre-zoeal cuticle and functional as natatory organs some time before the abdomen and telson had moulted completely and before the carapace spines were fully evaginated, but at this time swimming lacked orientation.

Pre-Zoea larvae were not found in plankton samples from the Wellington area.

Description

Cephalothorax (Fig. 26)

The cuticle covering the cephalothorax (see Fig. 26) is smooth and without processes, but the carapace spines of the first stage Zoea larva are folded beneath: dorsal carapace spine is folded forwards to lie between the eyes and is considerably invaginated; the rostrum is telescoped and compressed but not greatly invaginated, and extends posteriorly beneath the thorax; lateral spines are difficult to see, only partly invaginated, and lie flush against the sides of the carapace.

Cephalic Appendages (Figs 27, 28)

First antenna (Fig. 27) with the pre-zoeal cuticle extended distally as one long plumose process and one smaller unarmed process.

Second antenna (Fig. 28) with cuticle produced into a simple unarmed sac to surround the partly invaginated zoeal spinous process; exopod extended as four very long and flattened plumose processes which are often invaginated distally early in the pre-zoeal stage.

Mandible, first and second maxillae of the first stage Zoea are all sheathed by the pre-zoeal cuticle which is without spines or processes on these appendages. However, setae belonging to the first stage Zoea may protrude.

Thoracic Appendages

First and second maxillipeds are the only thoracic appendages present in the pre-zoeal stage (see Fig. 26). These are covered by the pre-zoeal cuticle which lacks spines or setae other than those of the stage one Zoea which may protrude.

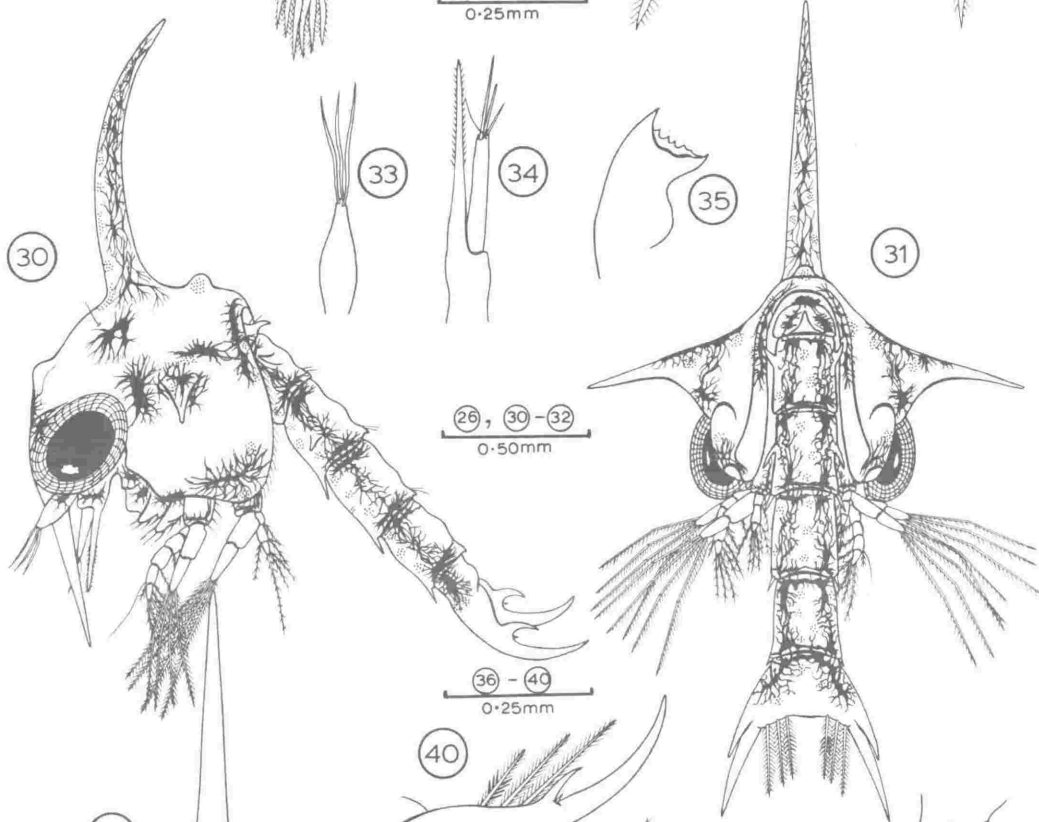
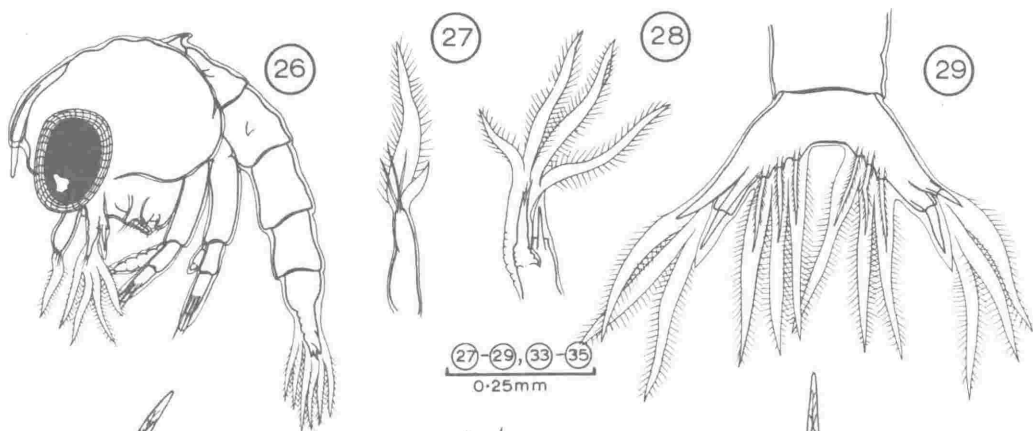
FIGURES 26 - 40

Ozius truncatus: Pre-Zoea Larva

- Fig. 26 Pre-Zoea larva; lateral view
- Fig. 27 First antenna of left side
- Fig. 28 Second antenna of left side
- Fig. 29 Fifth abdominal segment and telson; dorsal view

Ozius truncatus: Stage 1 Zoea Larva

- Fig. 30 Stage 1 Zoea; lateral view
- Fig. 31 Stage 1 Zoea; posterior view
- Fig. 32 Cephalothorax; anterior view
- Fig. 33 First antenna of left side
- Fig. 34 Second antenna of right side
- Fig. 35 Mandible of left side
- Fig. 36 First maxilla of left side
- Fig. 37 Second maxilla of left side
- Fig. 38 First maxilliped of left side
- Fig. 39 Second maxilliped: endopod of left side
- Fig. 40 Left lateral telson cornu; dorsolateral view



Abdomen

The abdominal segments of the Zoea are covered by the pre-zoeal cuticle which itself shows no sign of segmentation (see Fig. 26).

The telson (Fig. 29) is more widely forked than in the first Zoea (see Figs 31, 32) and the lateral cornua and posterior telson setae of the Zoea larva remain invaginated during the pre-zoeal stage. Lateral to the telson cornua the pre-zoeal cuticle is extended into three long plumose processes each of about equal length (see Fig. 29). The tips of the cornua are enclosed within a much smaller unarmed process less than one third the length of the three lateral processes. Three further pairs of long plumose processes enclose the 3+3 zoeal setae lying within the fork of the telson. Hence there are 7+7 pre-zoeal telson processes.

Chromatophore Pattern

The chromatophore pattern is described with the first stage Zoea larva to which it more properly applies.

THE ZOEAL LARVAL STAGES

The swimming habits of Zoea larvae of O. truncatus in the laboratory are similar to those of Heterozius rotundifrons described above. Only the first three Zoea larval stages occurred in plankton samples from the Wellington area, and these were taken only very rarely. The fourth zoeal stage was not found in the plankton, but was reared from stage three in the laboratory.

A KEY TO THE ZOEAL STAGES OF Ozium truncatus H. Milne Edwards

- 1 (4) - Total length less than 3.50 mm; 1st antenna uniramous; mandible without palp; gill buds absent; 6th abdominal segment not separate from telson; pleopod buds absent; telson with 3+3 posterior setae inside fork.
- 2 (3) - Total length 2.38 mm to 2.40 mm; eyes sessile; 2nd antenna without endopod bud; exopods of 1st and 2nd maxillipeds with 4 natatory setae; 3rd maxilliped and pereopod buds absent.
..... STAGE ONE (Figs 30-40)
- 3 (2) - Total length 3.00 mm; eyes stalked; 2nd antenna with short endopod bud; exopods of 1st and 2nd maxillipeds with 6 natatory setae; 3rd maxilliped and pereopod buds present.
..... STAGE TWO (Figs 41-46)
- 4 (1) - Total length greater than 3.50 mm; 1st antenna biramous, inner ramus a short bud; mandible with a rudimentary palp; gill buds present; 6th abdominal segment separate from telson; pleopod buds (5 pairs) present; telson with 5+5 posterior setae inside fork.
- 5 (6) - Total length 4.00 mm; 2nd antenna with endopod about half the length of exopod; exopods of 1st and 2nd maxillipeds with 8 natatory setae; pereopod buds unjointed; pleopods short, bud-like; 4th and 5th pairs of posterior telson setae inside the fork very tiny and much less than half the length of 3rd setae.
..... STAGE THREE (Figs 47-53)

- 6 (5) - Total length 4.75 mm; 2nd antenna with endopod only slightly shorter than exopod; exopods of 1st and 2nd maxillipeds with 10 natatory setae; pereopod buds visibly but incompletely jointed; pleopods long uniramous rods; 4th and 5th pairs of posterior telson setae inside the fork one quarter to one half the length of 3rd setae.
..... STAGE FOUR (Figs 54-61)

STAGE ONE

Figs 30-40

The duration of the first zoeal stage was six days under laboratory conditions.

Description

Cephalothorax (Figs 30, 31, 32)

Total length of larva 2.35 mm to 2.40 mm. Rostrum straight and 0.50 mm long; dorsal carapace spine 0.94 mm long and curved posteriorly; lateral spines about 0.40 mm in length, straight and directed outwards at right angles to the carapace. Carapace with a median dorsal tubercle as in Heterozius rotundifrons but without dorsal setae; additional median tubercle in frontal region; one small seta behind frontal tubercle arising from each side of the base of the dorsal carapace spine; posterior border of the carapace fringed with fine hairs. Eyes sessile.

Cephalic Appendages (Figs 33-37)

First antenna (Fig. 33) uniramous with three long terminal aesthaetes.

Second antenna (Fig. 34) with exopod 0.31 mm in length, possessing three terminal setae of unequal length and one fine hair; spinous process as long as the exopod and its terminal setae, about three fifths the length of the rostrum and one third that of the dorsal spine; spinous process setose distally; endopod not yet developed.

Mandible (Fig. 35) without a palp.

First maxilla (Fig. 36) with endites each bearing five or six marginal setae; palp as described for Heterozius rotundifrons.

Second maxilla (Fig. 37) with the four endites each having four terminal setae; palp as described for the first Zoea of Heterozius rotundifrons; scaphognathite with four marginal biplumose setae but margins otherwise fringed with fine hairs, proximal tip extended and falcate.

Thoracic Appendages (Figs 38, 39)

First maxilliped (Fig. 38) having one plumose seta on inner margin of coxa. Basis with from 10 to 12 inner marginal setae. Endopod comprises five segments each of approximately equal length: first to fourth segments each bearing one distal seta on the inner margin; fourth segment (propod) sometimes with two inner setae, and also possesses one long hair and a small seta on its outer distal margin; dactylus provided with four long and sparsely plumose setae arising from its tip. Exopod of two segments is about twice the length of the endopod and bears four natatory setae at its tip.

Second maxilliped similar to the first; coxa without setae; basis with two medial and two distal setae. Endopod (Fig. 39) of three segments only and is about one third as long as the exopod: first segment short with one distal seta; second segment twice the

length of the first and bears two distal setae; third segment very small and with three terminal setae and one outer subterminal seta. Exopod as in the first maxilliped (see Fig. 38).

Third maxillipeds, pereopod buds and gill buds are all absent in the first stage Zoea larva.

Abdomen

The abdomen (see Figs 30, 31) comprises five segments and a telson: sixth abdominal segment not separate from the telson. Five abdominal segments each about 0.25 mm long: first segment with a posterior dorsal spine; second segment with a pair of procurved dorsolateral protuberances; third segment with a lateral protuberance which is curved posteriorly (see Fig. 31); third, fourth, and fifth segments each with a pair of short, unarmed ventrolateral spines, but the fifth segment has no dorsolateral spines as present in Heterozius rotundifrons Zoea larvae; dorsal hairs present on the first four abdominal segments. No sign of pleopod buds.

Telson (see Figs 30, 31, 40) more widely forked and with shorter rami than in the first Zoea of H. rotundifrons: lateral cornua armed with a large and conspicuous spine arising dorsally and curved posteriorly, spine fused with cornu on each side and not articulating; one small axillary seta is situated between the dorsal spine and the cornu (see Figs 30, 40). Three pairs of posterior setae occur inside the fork of the telson: setae plumose but medial pair with from three to six pairs of spines or coarse hairs as in H. rotundifrons.

Chromatophore Pattern (Figs 30, 31)

Chromatophores are considerably less diffuse than in the Zoea of Heterozius rotundifrons, and the centres of coloration are more readily seen. The general colour of larvae to the naked eye is greenish yellow. The chromatophore distribution pattern characterising the first stage Zoea larva of Ozius truncatus is tabulated in Table 2.

TABLE 2

Ozius truncatus H. Milne Edwards

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

1. Supracerebral	-----
2. Antennular	dichromatic, black to yellow
3. Antennal	" " "
4. Labral	" " "
5. Mandibular	" " "
6. Maxillar	" " "
7. Maxillipedal	" " "
	coalesced with 18 below
8. Lateral Intestinal	dichromatic, black to yellow
9. Subintestinal	red, small and numerous

B. Visceral Group

10. Median Gastric	dichromatic, black to yellow
11. Precardiac	" " "
* 12. Subcardiac	red
* 13. Postcardiac	dichromatic, black to yellow

SECONDARY SYSTEM

14. Posterior Carapacial	dichromatic, black to yellow +1 or 2 red
15. Posteroventral Carapacial	dichromatic, black to yellow +1 or 2 red
16. Lateral Carapacial	dichromatic, black to yellow +2 red

17. Dorsal Carapace Spine	numerous dichromatic black to yellow + 6 or 7 red
18. Maxillipedal	dichromatic, black to yellow coalesced with 7 above
19. Optic	dichromatic, black to yellow
20. Median Ocular Centre	" " " "

NOTE: * not homologous with Aikawa's (1929) equivalent
 - chromatophore absent

STAGE TWO

Figs 41 - 46

The second stage Zoea larva was obtained from the first stage by moult in the laboratory. The duration of the second zoeal stage was six days. The main characters by which the second stage Zoea may be distinguished from the stage one Zoea are detailed below.

Description

Cephalothorax (Fig. 41)

Total length of larva 3.00 mm. Rostral spine 0.87 mm; dorsal carapace spine 1.45 mm; lateral carapace spines 0.45 mm. The eyes are now stalked.

Cephalic Appendages (Figs 42-45)

First antenna (Fig. 42) with two additional aesthaetes arising from the base of the outer ramus which is now separate from the peduncle.

Second antenna (Fig. 43) with endopod bud now present; spinous process about half as long as the rostrum and slightly more than one quarter the length of the dorsal spine.

First maxilla (Fig. 44) with distal endite possessing seven or eight setae; palp of three segments with a lateral seta arising from the base of the proximal segment.

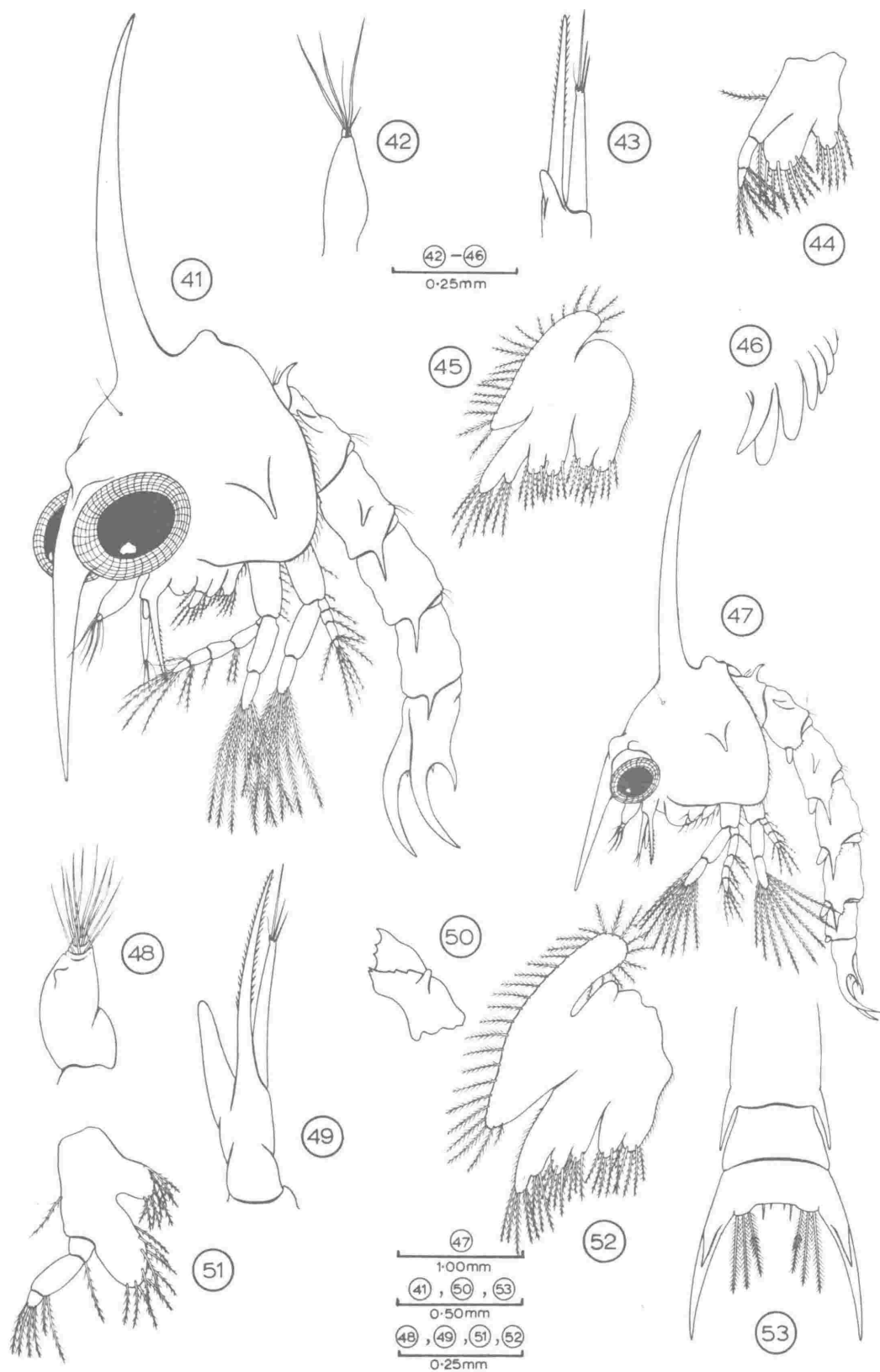
Second maxilla (Fig. 45) with the two distal endites each bearing five setae; fine hairs fringe the inner margin of the proximal endite and also the outer margin of the palp; scaphognathite rounded at its proximal tip and fringed with 19 or 20 plumose setae.

Ozius truncatus: Stage 2 Zoea Larva

- Fig. 41 Stage 2 Zoea; lateral view
- Fig. 42 First antenna of left side
- Fig. 43 Second antenna of right side
- Fig. 44 First maxilla of left side
- Fig. 45 Second maxilla of left side
- Fig. 46 Third maxilliped and pereopods of left side

Ozius truncatus: Stage 3 Zoea Larva

- Fig. 47 Stage 3 Zoea; lateral view
- Fig. 48 First antenna of right side
- Fig. 49 Second antenna of right side
- Fig. 50 Mandible of right side
- Fig. 51 First maxilla of left side
- Fig. 52 Second maxilla of left side
- Fig. 53 Fifth, sixth abdominal segments and telson;
dorsal view



Thoracic Appendages

Exopods of the first and second maxillipeds now have six natatory setae (see Fig. 41); endopod of the second maxilliped is four-segmented. Third maxillipeds and pereopods are present as rudimentary buds (Fig. 46); third maxillipeds biramous.

Abdomen

The abdomen (see Fig. 41) has increased in size and the ventro-lateral spines of the third to fifth segments are longer and more robust. The abdomen is otherwise little different from that of the first stage Zoea larva.

STAGE THREE

Figs 47-53

The duration of the third zoeal stage is between five and six days under laboratory conditions. The stage three Zoea larva differs from the second stage in the characters recorded below.

Description

Cephalothorax (Fig. 47)

Total length of larva 4.00 mm. Rostral spine 1.10 mm; dorsal carapace spine 2.00 mm; lateral carapace spines 0.48 mm.

Cephalic Appendages (Figs 48, 52)

First antenna (Fig. 48) with an inner ramus now present as a tiny subterminal bud; outer ramus provided with from eight to ten aesthaetes.

Second antenna (Fig. 49) with a robust endopod now about half the length of the exopod; spinous process 0.50 mm long and slightly less than half the length of the rostrum and about one quarter as long as the dorsal spine.

Mandible (Fig. 50) with a rudimentary palp.

Endites of the first maxilla (Fig. 51) each fringed with 10 or 11 short plumose setae.

Second maxilla (Fig. 52) with its palp bearing eight setae; scaphognathite with about 30 marginal setae.

Thoracic Appendages

First and second maxillipeds (see Fig. 47) now with eight natatory setae. Third maxillipeds and pereopods have increased in size; first pereopods terminate in a rudimentary chela. Gill buds are present as tiny rudiments.

Abdomen (Figs 47, 53)

The abdomen (see Figs 47, 53) comprises six segments and a telson: second segment with its ventrolateral border strongly toothed; lateral spines on third to fifth segments longer than before, and with strong basal teeth on their upper borders; sixth segment (see Fig. 53) without spines or setae and about half the length of the anterior segments. Short pleopod buds are present on the second to sixth abdominal segments; those of the sixth segment (uropods) are very small.

Telson (Fig. 53) now with five pairs of setae arising from its posterior margin medial to the lateral cornua. The inner pair of setae is simple and tiny.

Chromatophore Pattern

The sixth abdominal segment is provided with chromatophores of the same colour and distribution pattern characterising the more anterior abdominal segments described earlier.

STAGE FOUR

Figs 54-61

Laboratory-reared Zoea larvae remained in the fourth stage for periods of between six days and ten days before moulting to the Megalopa larval stage.

Description

Cephalothorax (Fig. 54)

Total length of larva 4.75 mm. Rostral spine 1.25 mm; dorsal carapace spine 2.40 mm long and only very slightly curved; lateral carapace spines 0.50 mm.

Cephalic Appendages (Figs 55-59)

First antenna (Fig. 55) with peduncle incompletely divided into two segments; inner ramus conspicuous but small; outer ramus armed with about 20 aesthaetes arranged in three groups along its inner margin.

Second antenna (Fig. 56) with endopod now only slightly shorter than exopod; spinous process has not increased in size and is now only two fifths the length of the rostrum and less than one quarter that of the dorsal spine.

Mandible (Fig. 57) strongly ridged and toothed; palp long but not segmented.

First maxilla (Fig. 58) with the two distal palp segments now apparently fused, but armature is similar to that of the stage three Zoea; endites each with about 12 marginal setae.

Second maxilla (Fig. 59) now broad and well developed as in the adult; scaphognathite now fringed with 50 or more marginal setae.

Ozius truncatus: Stage 4 Zoea Larva

Fig. 54 Stage 4 Zoea; lateral view

Fig. 55 First antenna of right side

Fig. 56 Second antenna of right side

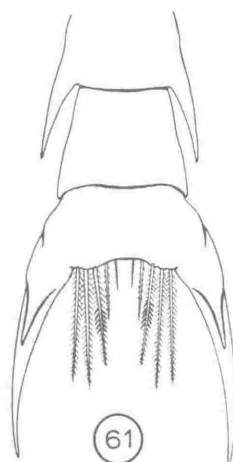
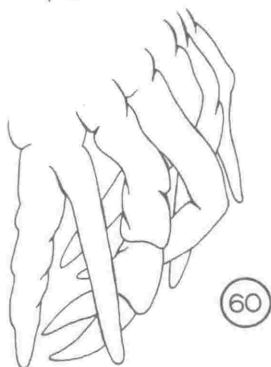
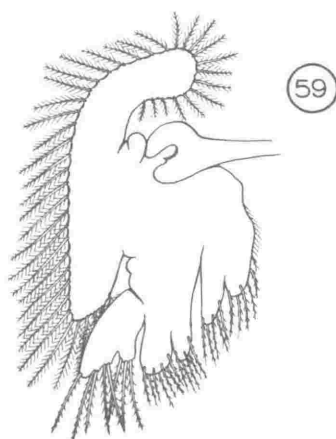
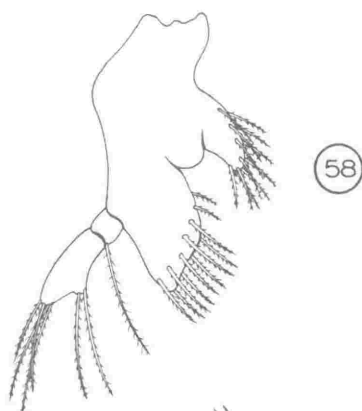
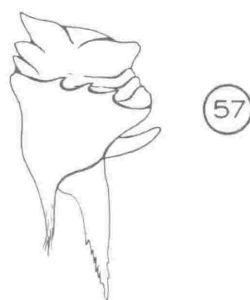
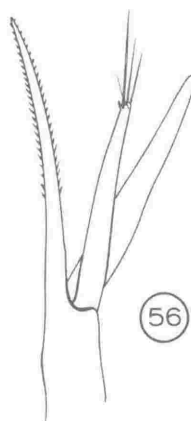
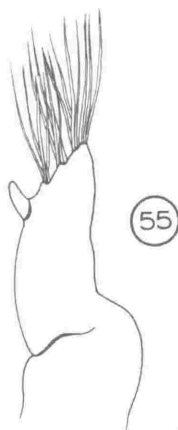
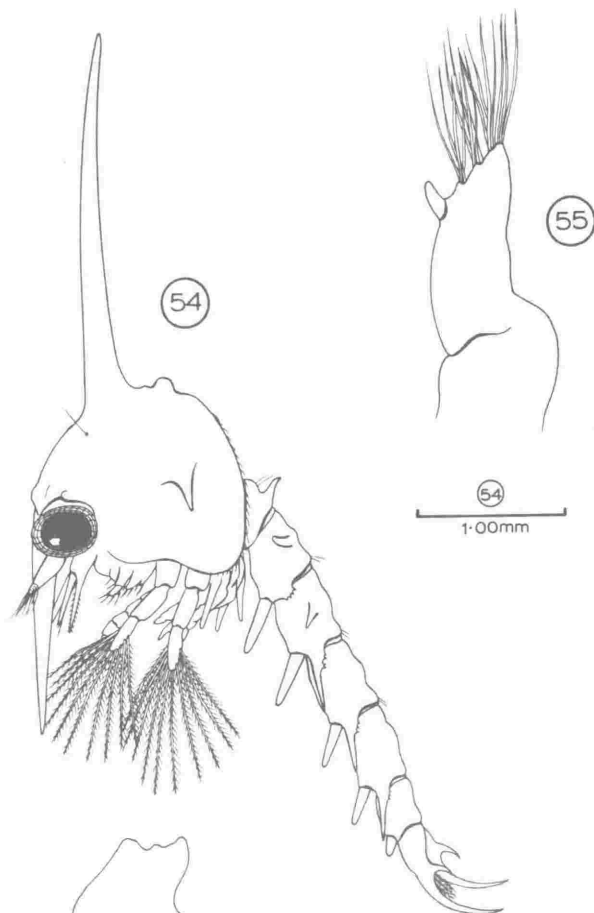
Fig. 57 Mandible of left side

Fig. 58 First maxilla of left side

Fig. 59 Second maxilla of left side

Fig. 60 Third maxilliped and pereopods of left side

Fig. 61 Fifth, sixth abdominal segments and telson;
dorsal view



61
0.50mm

55 - 60
0.25mm

Thoracic Appendages (Fig. 60)

First and second maxillipeds (see Fig. 54) now bear ten natatory setae. Third maxilliped and pereopods (Fig. 60) are robust and well developed, but show only partial segmentation beneath the zoeal skin.

All gill buds are visible as rudiments, but are without lamellae and are non-functional at this stage.

Abdomen (Figs 54, 61)

The abdomen (see Fig. 54) is considerably larger than that of the stage three Zoea; lateral spines very long and strongly developed. Pleopods of second segment 0.38 mm in length but still uniramous; remaining pleopods decrease in size posteriorly to those of the sixth segment which are only 0.13 mm long.

Telson (Fig. 61) with the fourth posterior seta about half the length of the third seta; fifth (medial) seta a little smaller. Axillary dorsal seta of telson cornua very tiny and may be absent in many specimens.

THE MEGALOPA LARVA

Megalopa larvae were obtained by moult from the fourth stage Zoea in the laboratory, and two specimens were obtained from the plankton. There is only one Megalopa stage in Ozium truncatus which moulted to the first juvenile crab stage after 12 to 14 days.

Description

Cephalothorax (Figs 62, 63)

Carapace 2.00 mm long, 1.95 mm wide, sparingly pubescent and strongly ridged; lateral and posterior margins fringed with fine

hairs; frontal region longer than broad and the rostrum is rounded but not depressed; interorbital space 0.63 mm; posterior margin of carapace with a pair of prominent tubercles. Eyes large and reaching the level of the lateral carapace margins; eye-stalks long, sparsely pubescent and without spines or setae.

Cephalic Appendages (Figs 64-66)

First antenna (Fig. 64) with sparingly setose peduncle of two short proximal segments and a larger distal segment; inner ramus of two segments and with four or five terminal aesthaetes; outer ramus of six segments, more robust but only slightly longer than inner ramus, inner margin with many aesthaetes but with only two at its tip.

Second antenna (Fig. 65) not reduced: peduncle of two segments; flagellum 0.72 mm long and comprising eight or nine segments most of which possess four distal setae, but two or three segments often lack setae; exopod absent.

Mandible with a palp of three segments but otherwise similar to that of the fourth stage Zoea larva.

First maxilla (Fig. 66) with palp now flattened, two-segmented and with few setae; endites with many more setae than in the fourth stage Zoea larva.

Second maxilla is similar to that of the Megalopa larva of Heterozius rotundifrons (see Fig. 19) but in Ozius truncatus the palp possesses five or six basal setae.

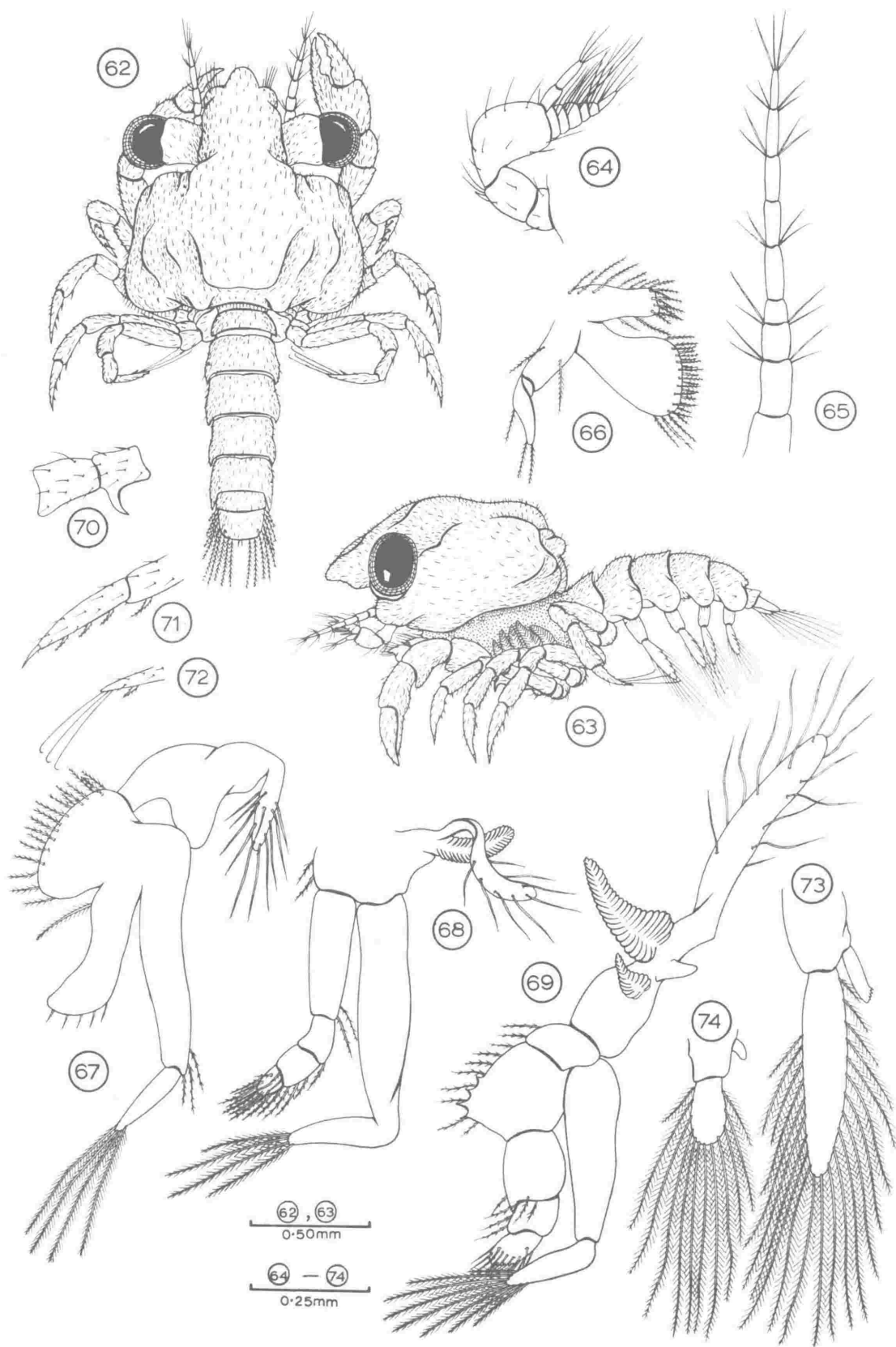
Thoracic Appendages (Figs 67-72)

First maxilliped (Fig. 67) is not reduced to the degree found in the Megalopa of Heterozius rotundifrons: coxa and basis setose; endopod flattened, short and with one proximal inner seta and five or six distal setae which are not plumose; exopod twice the length of

FIGURES 62 - 74

Ozius truncatus: Megalopa Larva

- Fig. 62 Megalopa larva; dorsal view (abdomen extended)
- Fig. 63 Megalopa larva; lateral view
- Fig. 64 First antenna of right side
- Fig. 65 Second antenna of left side
- Fig. 66 First maxilla of left side
- Fig. 67 First maxilliped of left side
- Fig. 68 Second maxilliped of left side
- Fig. 69 Third maxilliped of left side
- Fig. 70 First pereopod: ischium and merus
- Fig. 71 Second pereopod: dactylus
- Fig. 72 Fifth pereopod: dactylus
- Fig. 73 Pleopod from left side of second abdominal
segment
- Fig. 74 Pleopod (uropod) from left side of sixth
abdominal segment



the endopod and of two segments, proximal segment with a few outer distal setae, distal segment with four long biplumose setae at its tip. Epipod large and without setae for the greater part of its length, but the distal third is more slender and provided with many setae.

Second maxilliped (Fig. 68) much larger than that of Heterozius rotundifrons, and differs mainly in the comparative lack of reduction of both the endopod and exopod. Other differences include the presence of four well developed setae at the tip of the exopod, a much smaller epipod, and the occurrence of a podobranch which is not found in Heterozius rotundifrons.

Third maxilliped (Fig. 69) with coxa and basis having few setae. Endopod of five segments: ischium short; merus broad with its inner margin having four strong serrations and numerous setae; carpus, propodus and dactylus respectively smaller and with similar armature to the corresponding segments of H. rotundifrons. Exopod longer than endopod and comprises two segments: first segment almost as long as the entire endopod and is without setae; distal segment about half the length of the proximal segment and provided with eight biplumose setae. Epipod larger than that of the second maxilliped. Gills comprise one rudimentary podobranch without lamellae, two arthrobranchs - the lower gill of these two being the smaller.

Pereiopods differ greatly from those of the *Megalopa* larva of H. rotundifrons. First pereiopod (see Figs 62, 63) chelate and sparingly pubescent; ischium (Fig. 70) with a strong ventral spine. Second to fourth pereiopods (see Figs 62, 63) pubescent and similar to each other; propodus with a single ventral setose spine; dactylus with three such spines and terminating as a single smooth spine (Fig. 71). Fifth pereiopod similar to the anterior pereiopods, but the dactylus (Fig. 72) bears one ventral setose spine and three long terminal setae ("feelers" - Lebour, 1928).

The gill formula applicable to the *Megalopa* larva and adults of *Ozius truncatus* is tabulated below

	<u>MAXILLIPEDS</u>			<u>PEREIOPODS</u>				
	1	2	3	1	2	3	4	5
Pleurobranchiae:	-	-	-	-	1	1	-	-
Arthrobranchiae:	-	-	2	2	-	-	-	-
Podobranchiae:	-	1	r	-	-	-	-	-
Epipodites:	1	1	1	-	-	-	-	-
Exopodites:	1	1	1	-	-	-	-	-

NOTE: r = rudimentary gill

Abdomen

Abdomen (see Figs 62, 63) of six segments and a telson, 1.90 mm long and sparingly pubescent. Abdominal segments are similarly proportioned to those of the *Megalopa* of *H. rotundifrons*: second and third segments are widest (0.56 mm); lateral pleura of the second to fifth segments are extended ventrally.

Biramous pleopods occur on segments two to six (see Fig. 63). Pleopods of the second segment (Fig. 73) are largest: protopod 0.18 mm in length and without setae; endopod 0.13 mm long, slender and serrated along its inner distal margin; exopod 0.44 mm in length, broader than endopod and fringed with 22 long biplumose setae. Pleopods of the third and fourth segments similar to those of the second segment, but smaller. Pleopods of the fifth segment with exopod 0.25 mm long and fringed with 20 marginal setae. Pleopods of the sixth segment (Fig. 74) very small; protopod and exopod each 0.13 mm long; exopod provided with 12 marginal setae; endopod tiny and without setae.

Telson (see Fig. 62) with its posterior margin broadly rounded, almost straight; two or four minute posterior setae.

Chromatophore Pattern

The Megalopa larva of Ozium truncatus possesses similar chromatophores to the Zoea larvae, but has additional chromatophores in the legs and carapace. As in Heterozium rotundifrons the secondary system of chromatophore distribution is greatly developed and effectively masks the primary system.

Heteropanope (Pilumnopus) serratifrons (Kinahan, 1856)

Each female carried 2,000 or more very small eggs. The eggs of two specimens were comparatively freshly laid, dark brownish-green in colour, and measured 0.40 mm x 0.38 mm or 0.39 mm x 0.39 mm. Those of the two remaining crabs were almost ready to hatch at the time of collection, light olive green and measured 0.45 mm x 0.40 mm.

THE PRE-ZOEAL LARVA

Pre-Zoea larvae hatched from two specimens carrying the more mature eggs 7, 10-12-1964. The duration of the pre-zoeal stage in the laboratory was about one hour. During this time larvae lay on the bottom of the aquarium and did not swim until ecdysis to the first stage Zoea larva was complete. Processes of the pre-zoeal cuticle differ from those described for Ozius truncatus only in the details described below.

Description

First antenna (Fig. 75) produced into two long plumose processes of about equal length.

Second antenna (Fig. 76) with the cuticle surrounding its exopod extended into only two long plumose processes.

Telson (Fig. 77) narrow with a deep cleft in the posterior mid-line. The seven pairs of posterior telson processes are similar to those of O. truncatus, but the fourth (unarmed) process differs in being about half the length of the other six.

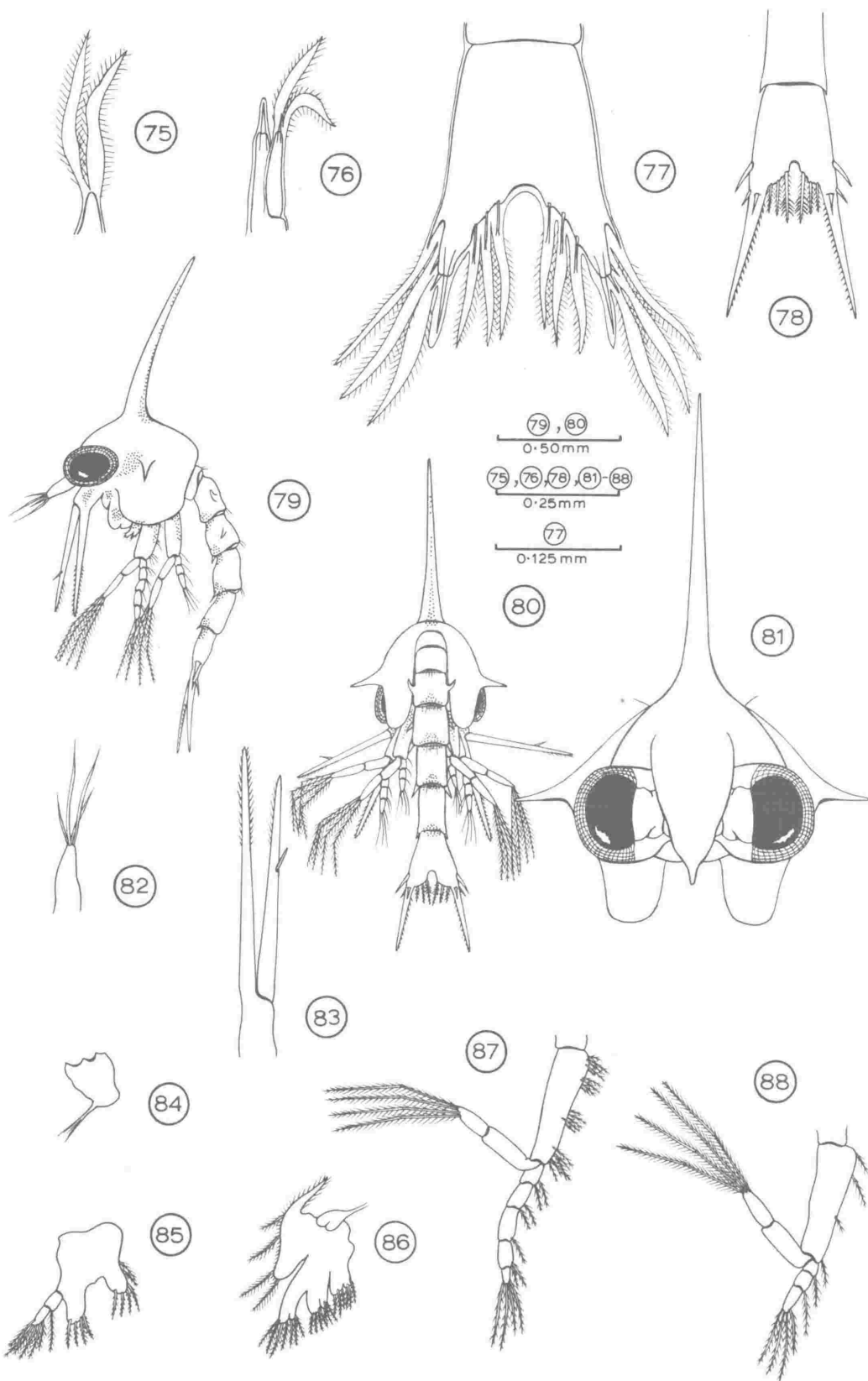
FIGURES 75 - 88

Heteropanope (Pilumnopous) serratifrons: Pre-Zoea Larva

- Fig. 75 First antenna of left side
Fig. 76 Second antenna of right side
Fig. 77 Telson; dorsal view

Heteropanope (Pilumnopous) serratifrons: Stage 1 Zoea Larva

- Fig. 78 Telson; dorsal view
Fig. 79 Stage 1 Zoea; lateral view
Fig. 80 Stage 1 Zoea; posterior view
Fig. 81 Cephalothorax; anterior view
Fig. 82 First antenna of left side
Fig. 83 Second antenna of right side
Fig. 84 Mandible of left side
Fig. 85 First maxilla of left side
Fig. 86 Second maxilla of left side
Fig. 87 First maxilliped of left side
Fig. 88 Second maxilliped of left side



THE FIRST STAGE ZOEAL LARVA

Description

Cephalothorax (Figs 79, 80, 81)

Total length of larva 1.75 mm. Rostrum virtually absent and reduced to a tiny process; dorsal carapace spine 0.63 mm long and only slightly curved; lateral carapace spines short and straight. Carapace smooth and without tubercles, but with frontal hairs as in the Zoea larvae of Ozius truncatus. Eyes sessile.

Cephalic Appendages (Figs 82-86)

First antenna (Fig. 82) uniramous with two long and two shorter terminal aesthaetes.

Second antenna (Fig. 83) with exopod 0.44 mm in length and possessing inner distal hairs and one strong lateral spine arising from its distal third; spinous process with distal setae, only slightly longer than the exopod and four fifths the length of the dorsal carapace spine; endopod absent.

Mandible (Fig. 84) first maxilla (Fig. 85) and second maxilla (Fig. 86) similar to those described of the stage one Zoea of O. truncatus but are here smaller. The proximal tip of the scaphognathite (2nd maxilla) is plumose and tapers to a point.

Thoracic Appendages (Figs 87, 88)

First maxilliped (Fig. 87) with the coxa lacking setae; basis with four groups of five or six setae along its inner margin; endopod with ischium, merus and propodus each bearing two inner distal setae, carpus with one seta and dactylus with four terminal setae;

exopod shorter than the endopod, two-segmented and with four terminal natatory setae.

Second maxilliped (Fig. 88) differs from the first maxilliped mainly in that the endopod is of only three segments. Details of setation are illustrated (see Fig. 88).

Third maxilliped is present as a tiny rudiment but there is no sign of periopods.

Abdomen (Figs 78, 79, 80)

Abdomen of five segments and a telson; fourth and fifth segments longer and more narrow than the anterior segments; the first segment lacks a posterior dorsal spine but the armature of all segments is otherwise the same as in the stage one Zoea of O. truncatus. There is no sign of pleopod buds.

Telson (Fig. 78) narrower than in the two species previously described: lateral margins of the telson and the cornua are a continuous straight line; inner margins of the cornua armed with numerous stout spines. There are three pairs of lateral telson setae: anterior pair largest and arising from the lateral telson margins at the level of the median cleft; second pair also lateral, much smaller, and situated at the base of the lateral cornua; third pair dorsal, of intermediate size, and also situated at the base of the telson cornua. There are three pairs of setae situated inside the fork of the telson. These are similar to those described in both Heterozius rotundifrons and Ozius truncatus, but they are here relatively smaller.

Chromatophore Pattern (Figs 79, 80)

The larvae of Heteropanope (Pilumnopeus) serratifrons are almost transparent as the chromatophores present are very small and lightly coloured. The distribution is tabulated in Table 3.

TABLE 3

Heteropanope (Pilumnopeus) serratifrons (Kinahan)

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

- | | | |
|----|--------------------|-------|
| 1. | Supracerebral | ----- |
| 2. | Antennular | ----- |
| 3. | Antennal | red |
| 4. | Labral | red |
| 5. | Mandibular | red |
| 6. | Maxillar | red |
| 7. | Maxillipedal | red |
| 8. | Lateral Intestinal | ----- |
| 9. | Subintestinal | red |

B. Visceral Group

- | | | |
|-----|----------------|----------------------------------|
| 10. | Median Gastric | red |
| 11. | Precardiac | ----- |
| 12. | Subcardiac | red, extending into dorsal spine |
| 13. | Postcardiac | ----- |

SECONDARY SYSTEM (Not represented in this species)

DISCUSSION

Heterozius rotundifrons

The breeding of this species is not as well defined as in the majority of British Brachyura (Lebour 1928, pp.501-2) or in other New Zealand species observed during the course of this study. Bennett (1964, p. 66) recorded ovigerous females both in mid-summer (February) and mid-winter (July) and Dell (1963) suggested that H. rotundifrons breeds bi-annually. These observations can almost certainly be explained by the extended breeding and incubation periods. It is possibly the low percentage of ovigerous females present at any one time that led Chilton and Bennett (1928) to suggest that female crabs incubating eggs may remain secluded. During incubation the eggs of H. rotundifrons increase in volume by about 50%. This size increase is probably due to slow uptake of water from the environment during incubation as shown by Davis (1964) for Callinectes sapidus.

The pre-Zoea larva of Heterozius rotundifrons lacks the usual feathered processes or aesthaetes on the antennules, antennae, and on the telson (see Lebour 1928, pp. 474-6), and may therefore show phylogenetic relationship with the more specialised and recently evolved families of brachyrrhynchous crabs in which these pre-zoeal processes are also absent (see Wear 1967).

Four Zoea larval stages are characteristic of xanthid crabs described up to the present time (see Wear, in press) but in H. rotundifrons the eggs are larger than any recorded from xanthid crabs with planktonic development and there are only two zoeal stages. In an earlier paper (Wear 1967) I suggested that abbreviated development has evolved sporadically among phylogenetically unrelated species in

which the adult crabs possess specialised and restricted habitat requirements. In these species the length of free larval life is shortened, dispersal is therefore restricted, and the population is maintained within a given ecological niche. As adults of H. rotundifrons are recluse and live in a restricted intertidal habitat, the number of Zoea larval stages may here be reduced in response to this habitat requirement.

The Zoea larvae of Heterozius rotundifrons possess a prominent median tubercle situated posterior to the dorsal carapace spine. This structure is found also in Homolaspis plana (see Guiata 1960), Ozius truncatus, and in O. rugulosus (see Chhapgar 1956), but its significance if any is uncertain. Similarly, the antennal spinous process is developed to a degree not previously seen in xanthid Zoea larvae, and the structure of this appendage in Heterozius rotundifrons cannot be related to that of any other brachyrynchous crab. A further Zoea larval character of uncertain significance is the presence of a long pair of dorsolateral spines arising posteriorly from the fifth abdominal segment. Other than in the first stage Zoea of Menippe rumphii (see Prasad and Tampi 1957) a spine is not known to occur in this position in any brachyuran Zoea larva. The absence of lateral papillae on the third abdominal segment, and of lateral telson spines in the Zoeae of H. rotundifrons is probably only a specific character, but these characters are usually present in xanthid Zoea larvae (see Wear, in press).

Characters such as the form of the rostrum, the presence or absence of a median dorsal spine or other spines on the carapace, presence or absence of long setae on the dactylus of the fifth pereopods, number of setae on the last pair of pleopods (uropods), and the number of accessory hooks or spines present on the pereopods have together been used to distinguish the Megalopa larvae

of British crabs (see Lebour 1928, p. 489). The status given to these characters by Lebour has not been seriously undermined by subsequent work on species from outside the British Isles. Considering the Megalopa larva of Heterozius rotundifrons in the light of these characters the following observations were made: absence of a definite rostrum is not known to occur in any Megalopa other than those of the Leucosiidae and of Pinnotheres veterum (Lebour 1928); absence of a median dorsal carapace spine shows no relationship with the Cancridae (suggested by Richardson 1949a) which typically possess such a spine; absence of setae on the dactylus of the fifth pereopod differs from the presence of such setae found in all British Brachyryhyncha except the Pinnotheridae (Lebour 1928) and in the great majority of brachyryhynchous Megalopa larvae subsequently described¹; the absence of hooks or spines on the pereopod segments of H. rotundifrons is of uncertain significance; so far as is known H. rotundifrons is the only species described in which uropods are entirely absent throughout larval life².

From the larval characters therefore, it is difficult to establish close relationship with other known brachyuran larvae. Reduction of the pre-Zoea larval cuticle can possibly be related with the similar trend seen in the more highly evolved families of Brachyryhyncha, but on the other hand this may be a specialisation commonly associated with abbreviated development and would therefore have little phylogenetic significance. Two Zoea larval stages is a character of the Oxyryhyncha (Lebour 1928, p. 478; Gurney 1942, p. 279), but in

¹ Lack of these setae in H. rotundifrons may be related in some way to abbreviated development, as they are also absent in the Megalopa of Pilumnus novaezelandiae and P. lumpinus (see Wear 1967).

² Rudimentary in the stage four Zoea of Chlorodiella nigra (Forskål) but absent in the Megalopa (see Gohar and Al-Kholy 1957).

Heterozius rotundifrons this cannot be taken as evidence of relationship. Relationship with Homolaspis suggested by Balss (1930) is not obvious when comparing the first stage Zoea larva of Heterozius rotundifrons with that of Homolaspis plana described by Guiata (1960). Affinity is suggested by the presence of a median dorsal carapace tubercle in both species, but in other respects the Zoea of H. plana is typical of the subfamily Xanthinae (see Wear, in press) and is quite unlike that of Heterozius rotundifrons. The Megalopa larva of H. rotundifrons is highly specialised and has no known affinities among brachyuran Megalopas described. However there are so many genera in which the Megalopa is unknown, that the value of this stage is limited (Gurney 1942, p. 272).

Larval relationships of the Brachyura are normally of considerable value when considered in the light of adult systematics (Lebour 1928; Gurney 1942). However, in the case of Heterozius rotundifrons, I consider that there is little larval evidence to support its present position in the Atelecyclidae, or to suggest any relationship with larvae of the Cancridae (see Lebour 1928) or with those of the Corystidae (see Gurney 1902; Lebour 1928). Similarly, there is no support for the suggestion of Balss (1930, pp. 203-4) that Heterozius is intermediate between the Corystidae and the Xanthidae. On larval characters alone, it is difficult to retain H. rotundifrons in the Xanthidae or even in the Brachyrhyncha.

The only conclusions which may be reasonably drawn from the larval evidence are that H. rotundifrons is a highly specialised crab related perhaps more closely to the Xanthidae than to any other family. Development is incompletely abbreviated possibly to reduce dispersal in response to restricted intertidal habitat requirements of the adult crabs. For the present it would seem desirable to retain the species

in the family Xanthidae following Bennett (1964), but larval characters suggest that H. rotundifrons could be more properly classified as the monotype of a separate and specialised brachyrrhynchous family with uncertain relationships.

Ozium truncatus

Pre-Zoea larvae of European xanthid crabs have been characterised by Lebour (1928, p.503) but many xanthid larvae described from other localities do not conform to these characters. In the British Brachyrrhyncha the pre-zoeal posterior telson processes are long and plumose except the first (outer) and the fourth processes which are comparatively shorter and smooth. In the pre-Zoea of O. truncatus the first process is plumose and only the fourth is smooth. Among xanthid crabs this also occurs in Menippe mercenaria Say and Panopeus herbstii Milne Edwards (see Hyman 1925), in Cycloxanthops novemdentatus (Lockington) described by Knudsen (1960), Pilumnus lumpinus Bennett (Wear 1967) and Heteropanope (Pilumnopeus) serratifrons here described. Hence this character, previously thought to be characteristic of the genus Ebalia and of the Oxyrrhyncha (Lebour 1928, p. 475) is no longer a distinction between the Oxystomata and Oxyrrhyncha on one hand and the Brachyrrhyncha on the other.

Characters of O. tuncatus Zoea larvae which conform with those of the family Xanthidae described up to the present time are: the presence of four zoeal stages; the development of the antennal exopod as a distinct segment; the presence of a pair of lateral papillae on each of the second and third abdominal segments; the occurrence of ventrolateral spines on the third to fifth abdominal segments (see Wear, in press). The presence in O. truncatus of

a median dorsal carapace tubercle similar to that seen in Heterozius and Homolaspis, and the occurrence of a median frontal tubercle is of uncertain phylogenetic significance. Other distinctive zoeal characters of Ozius truncatus are the development of accessory basal teeth on the ventrolateral abdominal spines which is not known to occur in other xanthid species, and the presence of a dorsal spine on the first abdominal segment which has not been previously recorded in any brachyuran larvae. The extreme development of the dorsal spine on the lateral telson cornua is paralleled only in O. rugulosus Stimpson (see Chhapgar 1956) and this may be a good generic character.

The Megalopa larva of O. truncatus possesses all the general characters used in the diagnosis of British species (Lebour 1928, pp. 503, 529) and also conforms well with xanthid Megalopa larvae subsequently described from elsewhere.

Hence the pre-Zoea, Zoea, and Megalopa larval stages of Ozius truncatus are generally similar to those known for xanthid crabs, but they are quite distinct both at the generic and specific levels. However many larval characters of O. truncatus are considerably specialised, and it is therefore difficult to relate the genus Ozius to other xanthid genera on the basis of larval characters alone.

Heteropanope (Pilumnopeus) serratifrons

The pre-Zoea larva of this species is similar to that of Ozius truncatus and significant differences are seen only in the nature of the first and second antennae. However, the possession of only two plumose processes on the exopod of the second antenna is otherwise found only in the genus Ebalia (see Lebour 1928, p. 539) but there are

no other apparent relationships between Ebalia and Heteropanope. There is little evidence to suggest that this character is anything more than an individual specific (possibly generic) variation, but in view of unusual Zoea larval characters discussed below, it supports separation of the genus Heteropanope from other genera included in the family Xanthidae based on known larval characters (see Wear, in press).

Although only the first stage Zoea larva has been obtained, there are probably four zoeal stages as in other xanthid crabs except Heterozius rotundifrons³. The possession of only a vestigial third maxilliped and the absence of pereopod buds and of the antennal endopod bud virtually eliminates the possibility of only two stages. It is also unlikely that three zoeal stages occur in Heteropanope (Pilumnopeus) serratifrons, as three zoeal stages are rare, and are known to occur only in Sesarma reticulatum Say (see Costlow and Bookhout 1962) and in some New Zealand species of the families Pinnotheridae and Hymenosomidae⁴.

The first stage Zoea larva of Heteropanope (Pilumnopeus) serratifrons possesses only a minute and vestigial rostral process, but is in all other characters a typical xanthid Zoea. Such drastic reduction of the rostrum is also seen in the Zoea larva of Heteropanope (Heteropanope) glabra Stimpson described by Aikawa (1929) but among the Brachyrrhyncha this is otherwise known to occur

³ Menippe mercenaria Say possesses five possibly six laboratory-reared zoeal stages (Porter 1960) but these were not verified from the plankton.

⁴ Further details are given in the text of an unpublished review paper entitled "The Significance of Abbreviated and Non-abbreviated Development among Australian and New Zealand Marine Brachyura" prepared by this author for the Australia/New Zealand Conference on Decapod Crustacea, Sydney, Australia, October, 1967.

only in the genus Pinnotheres to which Heteropanope and Pilumnopeus are not closely related⁵. Hence among xanthid crabs the vestigial rostrum appears to be a generic character of both Heteropanope and Pilumnopeus. The relationships of these two genera are not clear (Monod 1956) but this very significant Zoea larval character suggests that in the family Xanthidae, Heteropanope and Pilumnopeus may together form a natural group which should be removed from other genera in the subfamily Pilumninae with which they are currently classified (see Wear, in press).

⁵ Larvae of Heteropanope tridentata (Maitland) described by Tesch (1922) can now be attributed to Rhithropanopeus harrisi (Gould) s. sp. tridentatus (Maitland) (see Buitendijk and Holthuis 1949) and are not therefore relevant to this discussion.

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THE BEARING OF THE LARVAL PHASE ON CLASSIFICATION
OF CRABS OF THE FAMILY XANTHIDAE ALCOCK, 1898

by
Robert G. Wear

SUMMARY

The status and generic composition of subfamilies within the family Xanthidae (Crustacea, Decapoda, Brachyura) as originally constituted by Alcock (1898) have been considerably revised in recent years. The two most recent opinions are those of Monod (1956) and of Balss (1957).

Zoea larvae of the family Xanthidae show affinities with those of other brachyrhynchous families, but it is not possible to suggest phylogenetic relationships of a more precise nature. Pre-Zoea, Zoea, and Megalopa larval characters of xanthid crabs given by Lebour (1928) cannot now be considered valid for all species.

All previous attempts to correlate larval characters with the systems of classification proposed for adult crabs by Alcock (1898) and by Balss (1927, 1932) have proved unsuccessful.

In this account, Zoea larval characters of species described up to the present time are critically analysed and considered in relation to the status of currently accepted adult genera and species, the generic groupings used by Monod (1956), and the generic composition of the subfamilies proposed by Balss (1957).

Xanthid Zoea larvae fall into two natural groups of genera based on larval characters, the most important character being the length of the antennal exopod in relation to that of the spinous process. The first group is equivalent to the subfamily Xanthinae as reconstituted by Balss (1957), but there is no larval evidence suggesting that "Panopean" genera should be separated from "Xanthian" genera as suggested by Monod (1956). A second natural group is formed by larvae of the subfamily Menippinae as in Balss (1932, 1957), the subfamily Piluminae of Balss (1957), and the genus Geryon. Larvae of genera in the subfamily Trapeziinae Miers should be removed from the section Hyperolissa and included in this second natural group. Zoea larvae described from the genera Heteropanope and Pilumnopoeus lack rostral or lateral carapace spines and form a separate branch of the second group. Zoea larval evidence does not support Monod's (1956) separation of Eriphia from the "Menippian" group of genera.

INTRODUCTION

Recent Advances in Adult Classification

In the family Xanthidae the majority of species occur on littoral or sub-littoral shores in temperate to tropical regions. The family includes a great number of genera, but the status of several genera is uncertain, and in many cases phylogenetic relationships are obscure. In recent years there have been many attempts to revise the major divisions within the Xanthidae, and attention has been focussed particularly on the status of the various subfamilies and their respective generic composition.

Alcock (1898) listed seven subfamilies and grouped these into the sections Hyperolissa and Hyperomerista. This arrangement was accepted by Ortmann and by Borradaile (see Bennett 1964, p.66). Balss (1927) distinguished eight subfamilies in the above sections, but later (1932) this author reconstituted the subfamily Menippinae to include the Oziinae and Eriphiinae, and separated Pilumnus Leach and related genera as the subfamily Pilumninae. Among later authors Stephenson (1945) and Bennett (1964) have followed Balss in this arrangement.

Monod (1956) discussed 18 African genera and arranged these as follows: The section Hyperolissa Alcock was divided into three groups of genera: (a) a "Xanthian" group which included the genus Chlorodiella Rathbun, (b) a "Panopean" group to include Panopeus H. Milne Edwards and presumably related genera formerly classified with the Hyperomerista (see Balss 1932) and (c) a third unspecified group for the genus Geryon Kröyer (see Table 1). Monod also ordered genera of the section Hyperomerista Alcock into three groups: (a) a "Menippian" group, (b) a "Pilumnian" group and (c) an "Eriphian" group. In this system of classification the genus

Globopilumnus Balss was included in the Menippian group (as in Balss (1933) who included this genus in the subfamily Menippinae), and the genus Pseudozius Dana was placed in the Pilumnian group rather than in the subfamily Menippinae where it is placed by Bennett (1964) following Balss (1932) (see Table 1). Hence five of the seven xanthid subfamilieis suggested by Balss (1932) were replaced by six "groups" without the status of subfamily, but Alcock's sections Hyperolissa and Hyperomerista were retained with a redistribution of genera within these sections (see Monod 1956, pp. 27-28, 217-338).

The most recent classification is that of Balss (1957) who discussed 122 xanthid genera on a world basis. This work was published shortly after that of Monod (1956), and apparently without knowledge of its existence. There is a marked similarity in both arrangements, but Balss's major groups of genera within the Xanthidae were given the status of subfamily. Balss (1957, p. 1646) considered the Carpilinae and Etisinae to be unnatural subfamilies as unrelated genera such as Chlorodopsis and Etisodes were taken together, and closely related genera such as Etisus and Leptodius were separated from one another. Based on this evidence the generic composition of the subfamily Xanthinae was extended to include the Carpilinae and Etisinae, together with Panopeus and related genera which were formerly classified with the subfamily Piluminae (see Balss 1932, 1933). Hence in this arrangement of Balss (1957, pp. 1647-50) the generic composition of the subfamily Xanthinae is equivalent to Monod's Xanthian and Panopean groups combined (Table 1). However, Balss included the genus Geryon in the family Geryonidae Beurlen. The genera placed in the subfamily Menippinae included Pseudozius as in Balss (1932) but otherwise comprises genera found in both the Menippian and Eriphian groups of Monod (1956). The third subfamily Pilumninae is now without Panopeus and related genera but retains

Heteropanope Stimpson, and Pilumnopous A. Milne Edwards which is probably only a subgenus of Heteropanope (Monod 1956). This arrangement differs from Monod's Pilumnian group only in the exclusion of Pseudozius. The Trapeziinae as originally constituted by Miers was recognised by Balss (1957) as a fourth subfamily, but none of the five recent genera concerned were discussed by Monod.

Hence there is almost complete agreement between Monod and Balss concerning relationships between the various xanthid genera and the distinction of Xanthian, Menippian, and Pilumnian groups of genera. The uncertain question is apparently whether or not a Panopean group should be distinguished from the Xanthinae, and similarly if an Eriphian group should be separated within the subfamily Menippinae (see Table 1).

Some workers (eg. Rathbun 1930; Barnard 1950) considered that any subdivision of the family Xanthidae does not include all existing genera satisfactorily, and these authors consequently discarded the subfamilies but offered no alternative system of classification.

The arrangement of adult subfamilies adopted here is that of Balss (1957), and this system is compared with those of Balss (1927, 1932) and with the generic groupings proposed by Monod (1956) in the light of evidence from larval characters.

Larvae of Crabs of the Family Xanthidae

Decapod systematists have rarely attempted to draw supporting evidence from the larval phase (Gurney 1942, p. 12). It is desirable that such evidence should be taken into account in order to produce a natural and soundly based system of adult classification. It is generally recognised that phylogenetic conclusions drawn from larval stages alone without reference to adult systematics can be very misleading, but the two approaches considered together can be of value. This is especially so in the Decapoda, both in the separation of allied species and in the

assessment of relationships at all levels. However there are several exceptions to this generalisation, more especially in the Caridea where some closely related genera possess widely differing larvae (Gurney 1942, p. 15). Among the Brachyura larval characters are usually more reliable, and a species will usually possess characters shared by all other species within a given genus. Similarly, generic larval characters usually vary only within limits which determine the brachyuran family to which a genus belongs (see Lebour 1928). The larvae of a sufficient number of brachyuran genera and species are now known for considerable confidence to be given to the view that if a larva departs significantly from a family or generic type it is unwise to dismiss this fact as irrelevant. This is clearly demonstrated here in larvae of the genus Heteropanope.

In brachyuran development the pre-Zoea and Zoea larval stages are considered to be of phylogenetic significance (Lebour 1928; Gurney 1942). More importance has been attached to the Zoea than to the pre-Zoea larval stage, as the Zoea larvae are more widely known and more readily observed in the laboratory. The Megalopa larva is more properly considered as a post-larval stage (Gurney 1942) and its significance as an aid to classification is limited by the small number of genera in which Megalopa larvae are known.

Hyman (1925, p. 2) was the first author to recognise a division within the Xanthidae based on Zoea larval characters. Hyman divided larvae described up to that time into two groups: (a) those with the antennal exopod minute (Xantho, Panopeus, Eurypanopeus, Neopanope) and (b) those with the antennal exopod present as a distinct segment (Menippe, Eriphia, Pilumnus, Trapezia).

Lebour (1928) described the larval stages of three British xanthid crabs and noted that Hyman's observations were also true of the British species. Lebour characterised all known larvae of the family Xanthidae

and pointed out their affinities with other described larvae of the Brachyryncha, but no further significant conclusions were drawn at this time.

Aikawa (1929, 1933, 1937) used Zoea larval characters to formulate a system of classification divorced from that of the adults. In the group "Xanthozoea" Planes, Pachygrapsus (Grapsidae), and genera of the family Ocypodidae are included together with Xantho and the Panopean genera, while Menippe, Eriphia, and Sphaerozoeus are placed in the group "Grapsizoea" (see Aikawa 1937, pp. 157-158). In the opinion of Gurney (1942, pp. 270-271) these heterogeneous larval groupings serve little purpose and throw little or no light upon adult systematics.

Gurney (1938) and Lebour (1944) both pointed out that groupings of primary larval characters usually sufficient to separate families and genera within the Brachyura did not apply in the Xanthidae. These conclusions were based on Zoea larvae described from 14 genera representing six of the eight subfamilies classified according to Balss (1927).

Since 1944 the Zoea larvae of many more species have been described from 12 additional xanthid genera and Geryon. In only a few of these have the pre-Zoea and Megalopa larvae been discussed. However sufficient data are now available to assess the value of larval characters as an aid to adult taxonomy and the bearing of the larval phase on the different systems of classification proposed for xanthid crabs during the past 40 years.

DIAGNOSTIC CHARACTERS OF KNOWN
XANTHID LARVAE

Pre-Zoea Larvae

Lebour (1928) considered that all pre-Zoea larvae of the family Xanthidae shared the following characters;

- a. - 4 processes on antennal exopod
- b. - Telson with 7+7 posterior processes; outer process smooth (a character then common to all Brachyrrhyncha)

Review of the above characters in the light of recent work shows that there are four plumose processes arising from the antennal exopod in all pre-Zoea larvae described other than in Heteropanope (Pilumnopus) serratifrons (Kinahan) which has two plumose processes only (Wear, in press).

The pre-zoeal telson bears seven pairs of posterior processes, but since 1928, only Chlorodopsis spinipes (Heller) and Trapezia cymodoce (Herbst) have been described as having the first (outer) process smooth (Gurney 1938) to conform with the British Brachyrrhyncha. Among xanthid crabs there are now six species representing the genera Cycloxanthops, Panopeus, Menippe, Ozius, Heteropanope, and Pilumnus which are known to have this outer process plumose as in Ebalia and the Oxyrrhyncha (see Wear, in press). Hence the presence of a smooth outer process is not a reliable character of pre-Zoea larvae of the family Xanthidae or of the Brachyrrhyncha.

Zoea Larvae

Zoea larval characters of the family Xanthidae given by Lebour (1928) are listed below and evaluated in the light of all xanthid larvae described up to the present time.

- a. - 4 zoeal stages
- b. - Carapace with dorsal, rostral, and one pair of smaller lateral spines
- c. - Antenna with vestigial exopod or with exopod nearly as long as the spinous process
- d. - Abdomen with lateral papillae (knobs) on somites 2 and 3; somites 3 to 5 (sometimes 6) with lateral spines
- e. - Telson cornu with 3 lateral spines or with one of these tending to disappear in later stages.

The number of zoeal stages in the Xanthidae is quite firmly established as four (see Table 2). However Porter (1960) described six stages for Menippe mercenaria Say, but considered that probably only five true stages exist. These observations were based on larvae reared in the laboratory, and the zoeal stages obtained were not compared with natural planktonic stages. Heterozius rotundifrons A. Milne Edwards has only two zoeal stages (Wear, in press), but this species is placed only provisionally in the family Xanthidae.

The majority of known xanthid Zoea larvae have four carapace spines (Table 2). Exceptions occur in only two genera. Gurney (1938) noted the presence of a pair of accessory lateral spines in the first Zoea of Tetralia glaberrima (Herbst). In the genus Heteropanope, H. (H.) glabra Stimpson possesses a dorsal carapace spine but no lateral spines or rostral spine (Aikawa 1929), while H. (Pilumnopeus) serratifrons has dorsal and lateral carapace spines but only a vestigial rostral spine (Wear, in press).

The division of xanthid Zoea larvae into two groups as based on the character of the second antenna by Hyman (1925) was followed by Lebour (1928). Lebour suggested that Eriphia and Menippe which possess an antennal exopod developed to about three quarters the length of the spinous process should form a third group situated

between Pilumnus on one hand and Xantho on the other. In this paper the development of the antennal exopod in relation to that of the spinous process is used to separate major groups of larvae within the family Xanthidae (see Table 2), and this appears to be very helpful when considered in relation to different groupings of adult genera into subfamilies. However, as the antenna of Zoea larvae belonging to the genera Eriphia, Menippe, Ozius, and Trapezia also resembles that of the Portunidae and Grapsidae, this character is of no value in separating xanthid Zoea larvae from those of other families.

Lateral papillae ("knobs", Lebour 1928) are known to occur on the second abdominal segment of all brachyuran Zoea larvae. In the Xanthidae, papillae are usually present also on the third abdominal segment (Lebour 1928). However, more recent work shows that the posterior pair of papillae may be absent. Lateral spines on the third to fifth abdominal segments is also a variable character, but these occur in the great majority of xanthid larvae (Table 2).

The possession of one dorsal spine and two lateral spines on the telson cornu is the last of Lebour's xanthid Zoea larval characters listed above. However it is now known that one or two of these spines may be absent (see Table 2), or much modified as in the genus Ozius (Wear, in press), while in the first Zoea of Menippe rumphii (Fabricius) all three pairs of spines are absent (Prasad and Tampi 1957). The presence or absence of these spines is therefore a character only useful in distinguishing species, or occasionally genera.

Thus the characters given by Lebour (1928) are variable and are of no value in separating Zoea larvae of the Xanthidae from those of other brachyrhynchous families except perhaps the Pinnotheridae. As a group, xanthid Zoea larvae conform with Lebour's characters in a very general way, but the larvae are nevertheless similar to those of other brachyrhynchous crabs. From the larval evidence it is not possible to

suggest more precise phylogenetic relationships. However, within the family Xanthidae, Zoea larval characters are of considerable significance, and they separate the species effectively, and distinguish major groups of genera. The most important single character is the length of the antennal exopod in relation to that of the spinous process.

Megalopa Larvae

Lebour (1928) considered Megalopa larvae of the family Xanthidae to possess the following characters:

- a. - Rostrum pointed and bent or rudimentary
- b. - 1st pereopod with a hook on the ischium
- c. - Dactylus of 5th pereopod with long setae (feelers)
which are common to all Brachyrrhyncha except the
Pinnotheridae

Review of the literature indicates that Lebour's characters of xanthid Megalopa larvae are not valid for all species. There is no character which can be used safely beyond the level of genus, but exceptions occur more rarely than among the Zoea larvae. The Megalopa larva of Heterozius rotundifrons departs more significantly from these characters than that of any other species described, and this evidence suggests that the species does not belong to the family Xanthidae (see Wear, in press).

THE BEARING OF ZOEAL LARVAL CHARACTERS ON CLASSIFICATION

FAMILY XANTHIDAE

Subfamily Xanthinae Ortmann (emend. Balss 1957)

With few exceptions described Zoeal larvae of the Xanthinae are characterised by having:

- a. - Dorsal, lateral, and rostral carapace spines.
- b. - Antennal exopod vestigial or not more than one third the length of the spinous process.
- c. - Ventrolateral spines on the third to fifth abdominal segments.
- c. - Lateral papillae on the second and third abdominal segments.
- e. - Telson cornu with one dorsal spine and usually with two lateral spines.

Reduction in the length of the antennal exopod is the only character which does not also occur in species of remaining subfamilies (see Table 2). Variation in characters (c) to (e) appears to be only of generic or specific status.

Monod (1956) suggested that Panopeus and related genera should be classified with the Hyperolissa rather than in the subfamily Pilumninae (Hyperomerista), and that Chlorodiella (= Chlorodius) is more naturally placed among the "Xanthian" genera. The close similarity of the larvae of these genera supports Monod's suggestion (see Table 2). Similarly Balss's (1957) reconstitution of the sub-

family Xanthinae is fully supported by the Zoea larval evidence. Larvae of Chlorodiella (Carpilinae) and of Chlorodopsis (Etisinae) are clearly related to those of Xantho and other genera comprising the Xanthinae as recognised by Balss (1932). In the Panopean genera Eurypanopeus, Hexapanopeus, Lophopanopeus, Neopanope, Panopeus, and Rhithropanopeus, the nature of the second antenna also compares well with that of Xantho, but the Zoea larvae of these genera do not form a natural group apart from those of the Xanthian genera. Hence Monod's separation of Panopeus from the Xanthian group of genera is not supported by Zoea larval characters.

The two species which depart significantly from this pattern are Panopeus bermudensis Benedict and Rathbun, and P. parvulus H. Milne Edwards described by Lebour (1944). These species each have the antennal exopod and spinous process equal in length, as in the Pilumninae (Table 2). This character therefore suggests that P. bermudensis and P. parvulus may be incorrectly placed in this genus. The first Zoea of P. parvulus was described by Lebour (1944) as belonging to the genus Leptodius which is now considered to be a synonym of Xantho (ref. Gordon 1934; Balss 1957) or at the most a subgenus of Xantho (Monod 1956). This larva however does not belong with Xantho, as all known Zoea larvae belonging to this genus (or to Leptodius) possess a reduced antennal exopod (see Table 2). However the Zoea larvae of Panopeus bermudensis and P. parvulus appear to be closely related to those of the Pilumninae. The Zoea larvae of P. bermudensis and of Lobopilumnus agassizii var bermudensis Rathbun can be distinguished from each other only by one minor character (Lebour 1950), and this seems insufficient to warrant the present generic separation of the two species.

Homolaspis plana A. Milne Edwards was considered by Balss (1930) as a primitive xanthid closely related to Heterozius and intermediate

between Acanthocyclus (Corystidae) and the remainder of the Xanthidae. However, the first stage Zoea larva of Homolaspis plana described by Guiata (1960) shows no close relationship with that of Heterozius rotundifrons (see Wear, in press), and the recognition of Homolaspis as a true xanthid crab and the inclusion of this genus in the subfamily Xanthinae by Balss (1957, p. 1648) is supported by Zoea larval characters (see Table 2).

Many genera and species in the subfamily Xanthinae have been recently revised. Consequently larvae have often been attributed to a genus or species which is now only a synonym. In some cases authors have been unaware of name changes, and the same larva has been described more than once, but each time under a different name.

Gurney (1938) described the first stage Zoea of Chlorodiella niger (Forskål). However, the gender of Chlorodiella is feminine, and linguistically this species would be more correctly named C. nigra. Chlorodiella was treated as being feminine by Gohar and Al-Kholy (1957) who described four zoeal stages of C. nigra from the Red Sea. Gurney's work was referred to, but no comparison was made. The first stage Zoea of Chlorodius niger (Forskål) was described by Prasad and Tampi (1957). As the genus Chlorodius is listed as a synonym of Chlorodiella by Balss (1957), there can be little doubt that this work represents a third description of the first stage Zoea of Chlorodiella nigra (Forskål). All three descriptions (Gurney 1938; Gohar and Kholy 1957; Prasad and Tampi 1957) agree in essential detail. However, Prasad and Tampi apparently overlooked the presence of a second small lateral spine on the telson cornu recorded by Gurney (1938) and by Gohar and Al-Kholy (1957) (see Table 2).

Tesch (1922) described four Zoea larval stages and the Megalopa larva of Heteropanope tridentata (Maitland) from the Zuiderzee which

Buitendijk and Holthuis (1949) have now shown to be conspecific with the American Rhithropanopeus harrisii (Gould). Tesch's larvae are widely different from others of the genus Heteropanope, and clearly belong with those of Xantho and the Panopean genera in the subfamily Xanthinae (Table 2). Hood (1962) described the four zoeal stages and the Megalopa of Rhithropanopeus harrisii, but this author was apparently unaware of the synonymy published by Buitendijk and Holthuis and that larvae of this species had been previously described by Tesch (1922). However, in the Zoea larvae Tesch noted a small lateral spine on the fourth abdominal segment, but this spine was not recorded by Hood (1962). This minor difference appears to support the view of Buitendijk and Holthuis (1949) that the European form should be named R. harrisii (Gould) s. sp. tridentatus (Maitland) as a subspecies of R. harrisii (Gould) from America.

Chhapgar (1956) described the first Zoea of Leptodius exaratus (A. Milne Edwards), but this species is now known as Xantho exaratus (A. Milne Edwards) (see Stephenson, 1945, p. 149) and the larvae have been previously described as belonging to Xantho by Aikawa (1929). Chhapgar (1956) either overlooked the two lateral spines on the telson cornua recorded by Aikawa (see Table 2) or described the first Zoea of a different species.

Four zoeal stages of the Atlantic species Xantho incisus Leach were described by Lebour (1928) and the first Zoea agrees in detail with that of X. floridus (Montagu) which is considered by Drach and Forest (1953) to be the same species as X. incisus. Bourdillon-Casanova (1960) described the Zoea larval stages of the Mediterranean subspecies X. incisus var granulicarpus Forest. These larvae differ from those described by Lebour (1928) only in the presence of an extra seta on the second maxilliped in the third and fourth zoeal stages not found in X. incisus (see Bourdillon-Casanova 1960, p. 171). Although this may support the status of X. incisus granulicarpus as a subspecies, it does not suggest the recognition of this form as a full species which

has been suggested by Holthuis (1954, p. 104).

Described Zoea larvae of Xantho poressa (Olivi) (Bourdillon-Casanova 1960), X. rivulosus Risso (Gourret 1884) and of X. hydrophilus Herbst (Lebour 1928) all agree in detail (see Table 2). These three species are now considered to be the same, with the name Xantho poressa remaining valid (Holthuis 1954). Zoea larval evidence is therefore in support of this combination.

Subfamily Trapeziinae Miers, 1886

Zoea larvae of this subfamily have the antennal exopod developed as a distinct segment, but in all species described the antennal exopod is shorter than the spinous process (Table 2). These antennal characters suggest that Zoea larvae of the Trapeziinae are distinct from those of the Xanthinae (Hyperolissa), and are perhaps closer to the Menippinae (Hyperomerista) than to any other subfamily. In all other characters, Zoea larvae of the Trapeziinae are not distinguishable as a group from those of other xanthid crabs. Gurney (1938) did not consider the presence of an accessory pair of lateral carapace spine in the Zoea of Tetralia glaberrima (Herbst) to be of great phylogenetic importance. However, this is probably a generic character of Tetralia, as a xanthid Zoea larva from the Great Barrier Reef is similarly adorned (Gurney 1938).

Subfamily Menippinae Ortmann (emend. Balss 1932)

Zoea larvae of six species representing four genera are known, but there appears to be no larval character which separates these larvae from those of the subfamily Pilumninae with any reliability. Zoea larval characters support the view that the subfamily Menippinae should embrace the genera as proposed by Balss (1957), but Monod's (1956) suggestion that Eriphia should be removed from the remainder

of the Menippinae is not supported by Zoea larval characters. However, larvae of the genus Ozius are distinct, and possess specialised larval characters which make it difficult to relate this genus to other xanthid genera (see Wear, in press).

Larvae of Menippe mercenaria Say were described by Hyman (1925) and by Porter (1960), but these descriptions do not agree in the number and position of lateral spines on the abdomen (see Table 2). It is just possible that these authors have each described a different species.

A more probable case of mistaken identification is seen in Eriphia spinifrons (Herbst). In the Zoea larval stages of this species Bourdillon-Casanova (1960) noted the presence of lateral papillae on the fourth and fifth abdominal segments and the occurrence of a small dorsal spine on the lateral telson cornua, but these characters were not recorded in Hyman's (1925) description of larvae of the same species.

Subfamily Pilumninae Alcock (emend. Balss 1932, 1957)

Zoea larvae of the subfamily Pilumninae are generally similar to those of the Menippinae, and possess an antennal exopod of about the same length as the spinous process (Table 2). Panopeus and related genera formerly classified in the Pilumninae (Balss 1932) possess a vestigial antennal exopod, and as other genera in the Pilumninae have a well developed antennal exopod, the Panopean genera form a natural division within this subfamily. Hence both the removal of Panopeus and related genera from the Pilumninae to follow Monod (1956) and the inclusion of these genera in the subfamily Xanthinae by Balss (1957) is supported by this evidence from the Zoea larvae.

Larvae of the genus Heteropanope are difficult to place in the subfamily Pilumninae. The first stage Zoea of Heteropanope (H.) glabra

Stimpson has a dorsal carapace spine but no lateral spines or rostral spine (see Aikawa 1929), while the first stage Zoea of H. (Pilumnopeus) serratifrons (Kinnahan) has a vestigial rostral spine but is in all other respects a typical xanthid Zoea larva (see Wear, in press). The presence of lateral carapace spines in the Zoea larva of the subgenus Pilumnopeus, and the absence of these spines in that of the subgenus Heteropanope, supports the opinion of Balss (1933) who recognised Pilumnopeus and Heteropanope as full genera. Similarly, as the Zoea larvae of both Pilumnopeus and Heteropanope lack a normally developed rostral process, it is evident that these larvae together form a group apart from other xanthid larvae and certainly separate from those of the genera Actumnus, Lobopilumnus and Pilumnus in the subfamily Pilumninae. The structure of the pre-zoeal antenna of Heteropanope (Pilumnopeus) serratifrons is also unique among those of other xanthid crabs (see Wear, in press).

The genera Actumnus, Lobopilumnus and Pilumnus are clearly related by the degree of development of the zoeal antennal exopod (see Table 2), but the abdominal armature shows considerable variation between the species representing these genera. Three species of the genus Pilumnus have abbreviated development, and these are fully discussed in an earlier publication (Wear 1967).

FAMILY GERYONIDAE

Zoea larvae of Geryon tridens Kröyer described by Brattegard and Sankarankutty (1967) show that on larval characters this family is closely related to the Xanthidae, and more especially to larvae of the subfamilies Trapeziinae and Mennipinae (Table 2). Larval characters cannot therefore be used to support the separation of Geryon from the family Xanthidae as in Balss (1957). Brattegard and Sankarankutty considered the stage one Zoea larva of G. tridens to fall within the group embracing European genera of the

family Portunidae described by Lebour (1928), but this observation is apparently based on characters shared by Zoea larvae of the majority of brachyrhynchous crabs, and cannot therefore imply closer relationship between Geryon and the Portunidae.

CONCLUSIONS

Zoea larvae described of crabs of the family Xanthidae do not support the arrangement of adult subfamilies given by Balss (1927, 1932). The groupings of genera used by Monod (1956) are followed in part, as Zoea larval characters suggest that Chlorodiella is closely related to Monod's "Xanthian" genera, and that Panopeus and related genera belong with the "Xanthian" group rather than with the remainder of the subfamily Pilumninae. All these larvae have a vestigial antennal exopod and form a natural group (see Table 1) but there is no evidence suggesting that the "Panopean" genera should be separated from the "Xanthian" genera. The "Menippian" and "Pilumnian" genera of Monod (1956) together form a second natural group, as Zoea larvae of species included in both of these groups of genera possess a well developed antennal exopod. However the larval evidence does not suggest that Eriphia should be separated from the "Menippian" group as proposed by Monod.

The system of classification given by Balss (1957) is almost fully supported by Zoea larval characters (see Table 1). Larval evidence suggests that Chlorodiella (Carpilinae), Chlorodopsis (Etisinae), and Homolaspis should be included in the subfamily Xanthinae together with Panopeus and related genera to constitute a natural group of larvae within the family Xanthidae. This first natural group is equivalent to the subfamily Xanthinae of Balss (1957). However, it appears that the subfamily Trapeziinae could be more appropriately removed from the section Hyperolissa containing the Xanthinae and placed together with the Menippinae and Pilumninae in a second natural group more or less equivalent to the section Hyperomerista (see Table 1). Zoea larvae of genera and species

in this section are characterised by the possession of a well developed antennal exopod (see Table 2). There are no larval characters which clearly separate the Pilumninae (apart from the genera Heteropanope and Pilumnopeus) from the Menippinae, but the genus Ozius perhaps deserves some distinction. Heteropanope and Pilumnopeus fall into the second major natural group based on the zoeal second antenna, but the larvae of these two genera are together sufficiently distinct to warrant major status as a third larval type within the family Xanthidae.

TABLE 1

MAJOR GROUPS OF GENERA IN THE FAMILY XANTHIDAE PROPOSED
BY MONOD (1956) AND BY BALSS (1957) RELATED TO NATURAL GROUPS
FORMED BY ZOEAL LARVAE

MONOD 1956 (Based on 18 African genera)		BALSS 1957 (Based on 123 genera)		NATURAL GROUPS BASED ON ZOEAL LARVAL CHARACTERS - WEAR (Based on 27 genera)	
Section Hyperolissa					
XANTHIAN GROUP (including <i>Chlorodiella</i>)	SUBFAMILY XANTHINAE (including subfamilies Carpilinae and Etisinae listed in Balss (1932) and the genus <i>Homolaspis</i>)	SUBFAMILY XANTHINAE as in Balss (1957)		NATURAL GROUP 1	
ANOPEAN GROUP (included in subfamily Pilumninae by Balss, 1932)	FAMILY GERYONIDAE	SUBFAMILIES TRAPEZIINAE, MENIPPINAE, and PILUMNINAE as in Balss (1957) + the genus Geryon		NATURAL GROUP 2	
Genus Geryon					
-					
Section Hyperomerista					
MENIPPAN GROUP (including <i>Globopilumnus</i>)	SUBFAMILY MENIPPINAE (including subfamilies Eriphiinae and Oziinae listed in Balss (1927) and the genus <i>Pseudozoeus</i> as in Balss, 1932)	SUBFAMILIES TRAPEZIINAE, MENIPPINAE, and PILUMNINAE as in Balss (1957) + the genus Geryon		(a) genus <i>Heteropanope</i> Stimpson, and genus <i>Pilumnopeus</i> A. Milne Edwards	
ERIPHIAN GROUP				(b) genus <i>Ozius</i> H. Milne Edwards	
PILUMNAN GROUP (including <i>Pseudozoeus</i>)				(c) all other genera	

TABLE 2

ZOEAL LARVAL CHARACTERS OF XANTHID CRABS

SPECIES	REFERENCE TO SYNONYM ⁺	No. OF ZOEAL STAGES	CHARACTERS OF STAGE ONE ZOEAL LARVAE					AUTHOR
			Carapace Spines	Antennal Exopod ^x	Lateral Spines on Abdominal Segments	Lateral Abdominal Papillae	Spines on Telson Cornu	
Section Hyperolissa								
<i>Heterozius rotundifrons</i> Milne Edwards		2	D. 2L. R.	1/7	3, 4, 5 ⁽¹⁾	2	1D. -	Wear (in press)
Subfamily XANTHINAE								
<i>Chlorodiella nigra</i> (Forskål)		4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Gohar & Al-Kholy 1957
= <i>Chlorodiella niger</i> (Forskål)			D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Gurney 1938
= <i>Chlorodius niger</i> (Forskål)	Balss 1957		D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 1L.	Prasad and Tampi 1957
<i>Chlorodopsis spinipes</i> (Heller)			D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Gurney 1938
<i>Cycloxanthops novemdentatus</i> (Lockington)								
= <i>Cycloxanthops novemdentatus</i> (Stimpson)	Monod 1956: 302	4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Knudsen 1960
<i>Cymo andreossyi</i> var. <i>melanodactyla</i> de Haan			D. 2L. R.	1/5	3, 4, 5	2, 3	1D. 2L.	Gurney 1938
<i>Eurypanopeus depressus</i> (Smith)		4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Hyman 1925
<i>Heteractaea ceratopsis</i> (Stimpson)			D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Gurney 1936
<i>Hexapanopeus augustifrons</i> (Benedict & Rathbun)			D. 2L. R.	?	?	?	?	Hyman 1925
<i>Homolaspis plana</i> Milne Edwards			D. 2L. R.	1/3	3, 4, 5	2, 3	1D. 2L.	Guiata 1960
<i>Lophopanopeus bellus bellus</i> (Stimpson)		4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. -	Hart 1935

TABLE 2 (Continued)

SPECIES	REFERENCE TO SYNONYM ⁺	No. OF ZOEAL STAGES	CHARACTERS OF STAGE ONE ZOEAE LARVAE						AUTHOR
			Carapace Spines	Antennal Exopod*	Lateral Spines on Abdominal Segments	Abdominal Papillae	Lateral Spines on Telson Cornu		
<i>Lophopanopeus bellus diegensis</i> (Rathbun)		4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Knudsen 1959a	
<i>Lophopanopeus leucomanus</i> <i>leucomanus</i> (Lockington)		4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. —	Knudsen 1958	
<i>Neopanope texana sayi</i> (Smith)		4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Hyman 1925	
<i>Panopeus bermudensis</i> Benedict & Rathbun			D. 2L. R.	1	4, 5	2, 3 4, 5	— 1L.	Lebour 1944	
<i>Panopeus herbstii</i> Milne Edwards			D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Hyman 1925	
<i>Panopeus herbstii</i> Milne Edwards		4	D. 2L. R	vestigial	3, 4, 5	2, 3	1D. 2L.	Costlow and Bookhout 1961	
<i>Panopeus parvulus</i> (Milne Edwards)									
= <i>Leptodius parvulus</i> (Fabricius)	Monod 1956: 330		D. 2L. R.	1	3, 4, 5	2, 3	1D. 2L.	Lebour 1944	
<i>Paraxanthias taylori</i> (Stimpson)		4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Knudsen 1959b	
<i>Rhithropanopeus harrisi</i> (Gould)									
= <i>Rithropanopeus harrisi</i> (Gould)	Buitendijk and Holthuis 1949	4	D. 2L. R.	vestigial	5	2	1D. —	Hood 1962	
<i>Rhithropanopeus harrisi</i> <i>tridentatus</i> (Maitland)									
= <i>Heteropanope tridentata</i> (Maitland)	Buitendijk and Holthuis 1949	4	D. 2L. R.	vestigial	4, 5	2	1D. —	Tesch 1922	
<i>Xantho</i> sp.									
<i>Xantho</i> 3 spp.		4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Williamson 1915	
<i>Xantho</i> sp.									
<i>Xantho denticulatus</i> White									
= <i>Xanthodius denticulatus</i> (White)	Monod 1956: 280		D. 2L. R.	1/4	3, 4, 5	2, 3	1D. 2L.	Lebour 1944	

TABLE 2 (Continued)

SPECIES	REFERENCE TO SYNONYM ⁺	No. OF ZOEAL STAGES	CHARACTERS OF STAGE ONE ZOEAL LARVAE					AUTHOR
			Carapace Spines	Antennal Exopod ^x	Lateral Spines on Abdominal Segments	Lateral Abdominal Papillae	Spines on Telson Cornu	
<i>Xantho exaratus</i> (Milne Edwards)								
= <i>Leptodius exaratus</i> (Milne Edwards)	Gordon 1934: 29		D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Aikawa 1929
<i>Xantho inciscus</i> Leach			D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. -	Chhappag 1956
= <i>Xantho floridus</i> (Montagu)	Drach and Forest 1953	4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Lebour 1928
= <i>Xantho florida</i> (Montagu)			D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Williamson 1915
<i>Xantho inciscus</i> var <i>granulicarpus</i> Forest		4	D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Bourdillon- Casanova 1960
<i>Xantho poressa</i> (Olivier)			D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Bourdillon- Casanova 1960
= <i>Xantho hydrophilus</i> Herbst	Holthuis 1954:	4	D. 2L. R.	vestigial	3, 4, 5	2, 3	?	Lebour 1928
= <i>Xantho rivulosus</i> Risso	Holthuis 1954: 105-6		D. 2L. R.	vestigial	3, 4, 5	2, 3	1D. 2L.	Gourret 1884
Subfamily TRAPEZIINAE								
<i>Trapezia</i> sp.			D. 2L. R.	4/5	3, 4, 5	2, 3	?	Hyman 1925
<i>Trapezia cymodoce</i> (Herbst)			D. 2L. R.	1/3	3, 4, 5	2, 3	1D. 2L.	Gurney 1938
<i>Trapezia guttata</i> Rüppell			D. 2L. R.	2/5	3, 4, 5	2, 3	1D. 2L.	Gurney 1938
<i>Trapezia maculata</i> (Macleay)			D. 2L. R.	1/2	3, 4, 5	2, 3	1D. 2L.	Al-Kholy 1963
<i>Tetralia glaberrima</i> (Herbst)			D. 4L. R.	1/2	3, 4, 5	2	1D. 2L.	Gurney 1938
Section Hyperomerista								
Subfamily MENIPPINAE								
<i>Eriphia spinifrons</i> (Herbst)		4	D. 2L. R.	2/3	3, 4, 5	2, 3	- 2L.	Hyman 1925
<i>Eriphia spinifrons</i> (Herbst)		4	D. 2L. R.	1/2	3, 4, 5	2, 3 4, 5	1D. 2L.	Bourdillon- Casanova 1960

TABLE 2 (Continued)

SPECIES	REFERENCE TO SYNONYM ⁺	No. OF ZOEAL STAGES	CHARACTERS OF STAGE ONE ZOEAL LARVAE						AUTHOR
			Carapace Spines	Antennal Exopod ^x	Lateral Spines on Abdominal Segments	Lateral Abdominal Papillae	Spines on Telson Cornu		
<i>Menippe mercenaria</i> Say			D. 2L. R.	3/4	4, 5	2, 3	1D. 1L.	Hyman 1925	
<i>Menippe mercenaria</i> Say		5	D. 2L. R.	3/4	3, 4, 5 ⁽²⁾	2, 3	1D. 1L.	Porter 1960	
<i>Menippe rumphii</i> (Fabricius)			D. 2L. R.	1	5 ⁽¹⁾	2, 3	—	Prasad and Tampi 1957	
<i>Ozium truncatus</i> Milne Edwards		4	D. 2L. R.	2/3	3, 4, 5	2, 3	2D. —	Wear (in press)	
<i>Ozium rugulosus</i> Stimpson			D. 2L. R.	1	3, 4, 5	2, 3	1D. —	Chhapgar 1956	
<i>Sphaerozium nitidus</i> Stimpson = <i>Sphaerotius nitidus</i> Stimpson			D. 2L. R.	2/3	?	2, 3	1D. —	Aikawa 1933	
Subfamily PILUMNINAE									
<i>Actumnus setifer</i> (de Haan)			D. 2L. R.	1	4, 5	2, 3	1D. 2L.	Aikawa 1937	
<i>Heteropanope</i> (<i>Pilumnopeus</i>) <i>serratifrons</i> (Kinahan)			D. 2L. —	1	3, 4, 5	2, 3	1D. 2L.	Wear (in press)	
<i>Heteropanope</i> (<i>Heteropanope</i>) <i>glabra</i> Stimpson									
= <i>Heteropanope glabra</i> de Haan	Monod 1956: 264		D. — —	1	3, 4, 5	2	— 1L.	Aikawa 1929	
<i>Lobopilumnus agassizii</i> var <i>bermudensis</i> Rathbun			D. 2L. R.	1	4, 5	2, 3 4, 5	— 1L.	Lebour 1950	
<i>Pilumnus</i> sp.			D. 2L. R.	1	3, 4, 5	2, 3	1D. 2L.	Williamson 1915	
<i>Pilumnus</i> 3 spp.			D. 2L. R.	1	3, 4, 5	2, 3	1D. 2L.	Hyman 1925	
<i>Pilumnus hirtellus</i> (L.)			D. 2L. R.	1	3, 4, 5	2, 3	1D. 2L.	Williamson 1915	
<i>Pilumnus hirtellus</i> (L.)		4	D. 2L. R.	1	2, 3, 4, 5	2, 3	1D. 2L.	Lebour 1928	
<i>Pilumnus longicornis</i> Hilgendorf			D. 2L. R.	1	3, 4, 5	2, 3	1D. 1L.	Prasad and Tampi 1957	
<i>Pilumnus lumpinus</i> Bennett								Wear 1967	
ABBREVIATED			DEVELOPMENT						

ABBREVIATED DEVELOPMENT

TABLE 2 (Continued)

SPECIES	REFERENCE TO SYNONYM ⁺	No. OF ZOEAL STAGES	CHARACTERS OF STAGE ONE ZOEAL LARVAE						AUTHOR
			Carapace Spines	Antennal Exopod ^x	Lateral Spines on Abdominal Segments	Abdominal Papillae	Lateral Abdominal Papillae	Spines on Telson Cornu	
<i>Pilumnus minutus</i> de Haan			D. 2L. R.	1	2, 3, 4, 5	2, 3, 4	-	2L.	Aikawa 1929
<i>Pilumnus novaezelandiae</i> Filhol			ABBREVIATED	DEVELOPMENT					Wear 1967
<i>Pilumnus vespertilio</i> Fabricius			D. 2L. R.	2/3	?	2	-	2L.	Aikawa 1929
<i>Pilumnus vestitus</i> Haswell			ABBREVIATED	DEVELOPMENT					Hale 1931
Family Geryonidae									
<i>Geryon tridens</i> Kröyer			D. 2L. R.	1/2	3, 4, 5	2, 3, 4	1D. 2L.		Brattegard and Sankarankutty 1967

Note:

⁺ Synonym given only when larvae are described under a name differing from currently accepted adult nomenclature

^x Length of antennal exopod (excluding distal setae) expressed as a fraction of the spinous process

D. Dorsal spine

L. Lateral spine

R. Rostral spine

(1) Spine dorsolateral and not ventrolateral

(2) Paired dorsolateral spine in addition to normal ventrolateral pair of spines

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LIFE-HISTORY STUDIES ON NEW ZEALAND BRACHYURA.

3. Family Ocypodidae. First Stage Zoea Larva of *Hemiplax hirtipes* (Jacquinot, 1853)

by

Robert G. Wear

SUMMARY

The stage one Zoea larva of Hemiplax hirtipes (Jacquinot, 1853) from New Zealand is described, and present knowledge concerning larvae of crabs of the family Ocypodidae is summarised and discussed. No diagnostic character is common to all ocypodid Zoea larvae and larval relationships within the family are obscure. Megalopa larvae of this family are structurally modified in response to specialised ecological requirements, and this may also be true of the adult crabs. The original relationships of ocypodid genera may be preserved in the planktonic Zoea larvae which show close affinities with those of the Hymenosomidae, Pinnotheridae, and Grapsidae.

INTRODUCTION

Hemiplax hirtipes (Jacquinot) is the only representative of the family Ocypodidae known to occur in New Zealand. The species is endemic to the mainland and does not occur in the Chatham Islands or in the islands to the south of New Zealand. Collections were made from the Mangonui Estuary (Doubtless Bay) in the north, to Bluff Harbour in the south of New Zealand.

The species occurs on mudflats and in tidal estuaries. Adults are gregarious and generally inhabit burrows (Bennett 1964, p.85). Adult crabs comprise 8% by volume of the total diet of the snapper Chrysophrys auratus (Forster) trawled from between 5 fms and 25 fms in the Hauraki Gulf (Mr B. L. Godfriaux, pers. comm.). It is therefore probable that H. hirtipes also occurs in abundance subtidally.

During 1964-67 ovigerous crabs were collected from June through to November, and it is probable that each female incubates more than one batch of eggs over this long breeding period. Eggs measure 0.25 mm X 0.24 mm when freshly laid and are dark brown in colour. Eggs ready to hatch measure 0.28 mm X 0.26 mm and remaining yolk is coloured light brown.

Laboratory methods, larval terminology, measurements, and diagrammatic representation of chromatophores follow those of previous publications (Wear 1967, in press, a, c).

LARVAL DEVELOPMENT

THE PRE-ZOEAL LARVA

Larvae hatch at a pre-Zoea stage which is short-lived. A thin pre-zoeal cuticle surrounds the larva and all appendages, but plumose pre-zoeal processes are lacking, as in larvae of the family Grapsidae (see Wear, in press, c). First stage Zoea larvae moult from the pre-zoeal cuticle within five or ten minutes from the time of hatching.

FIRST STAGE ZOEAL LARVA

Larvae were hatched from ovigerous crabs collected from the Mangonui Estuary, Whangarei Heads, the Wellington area, the Avon River Estuary (Christchurch) and from Port Chalmers (Dunedin). No significant morphological variation was found among adults or larvae obtained over this geographical range. The Zoea larvae are continuous swimmers and are strongly phototactic. Hatched larvae were kept alive for up to eight days, but these did not feed, and died while still in the first zoeal stage.

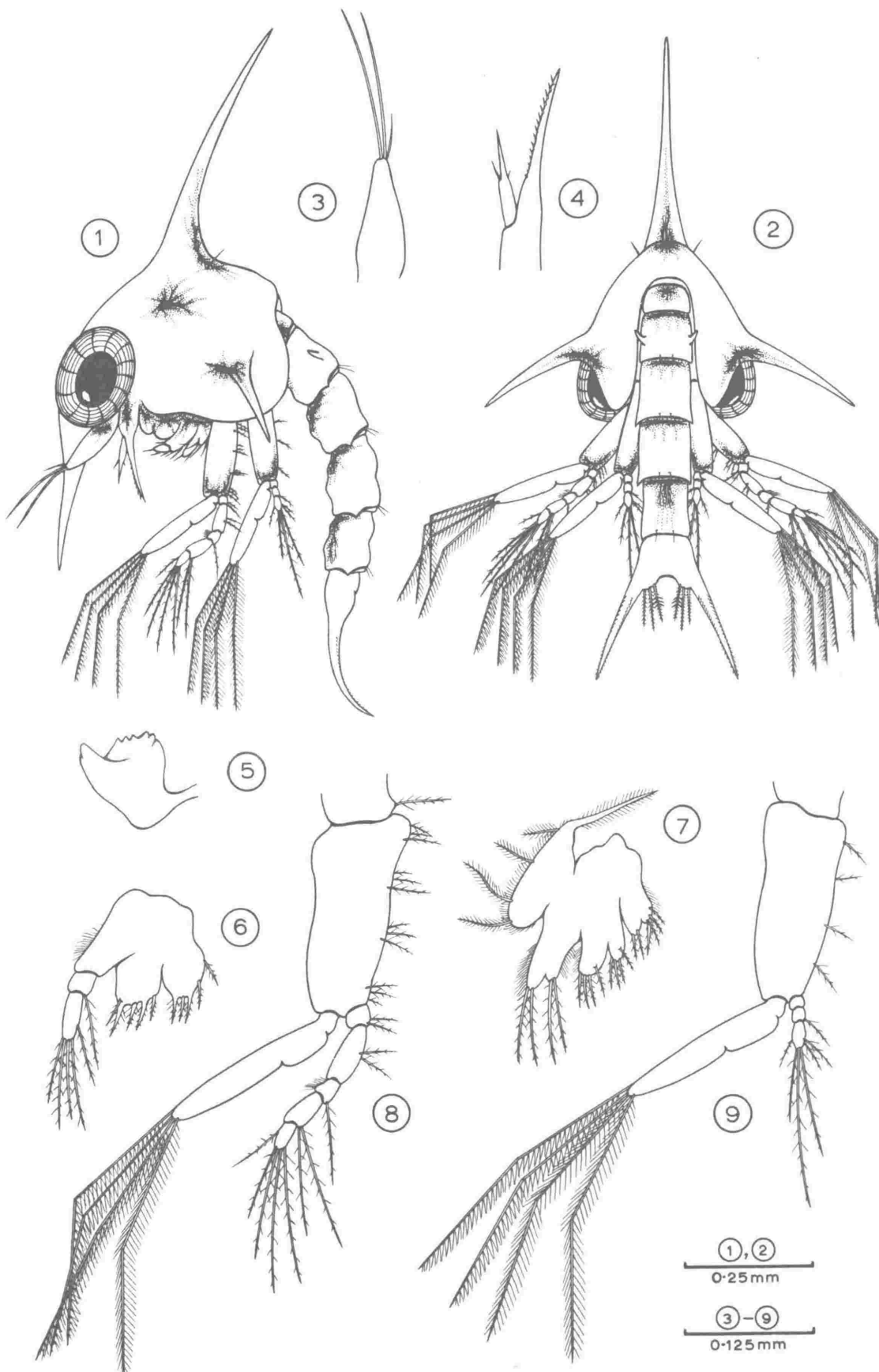
Description

Cephalothorax (Figs 1, 2)

Total length of larva 1.25 mm. Rostral spine 0.29 mm long and straight; dorsal carapace spine 0.46 mm long and slightly curved posteriorly; lateral carapace spines 0.25 mm long, slightly depressed and directed posteriorly as in larvae of the grapsid genera Hemigrapsus, Helice, and Cyclograpsus (see Wear, in press, c). Carapace with a pair of dorsolateral setae situated just behind the dorsal carapace spine; posterior margins fringed with fine, very

Hemiplax hirtipes: Stage 1 Zoea Larva

- Fig. 1 Stage 1 Zoea; lateral view
- Fig. 2 Stage 1 Zoea; posterior view
- Fig. 3 First antenna of left side
- Fig. 4 Second antenna of left side
- Fig. 5 Mandible of left side
- Fig. 6 First maxilla of left side
- Fig. 7 Second maxilla of left side
- Fig. 8 First maxilliped of left side
- Fig. 9 Second maxilliped of left side



short hairs; carapace and carapace spines otherwise smooth and without hairs or setae. Eyes sessile.

Cephalic Appendages (Figs 3-7)

First antenna (Fig. 3) uniramous with two long aesthaetes and one shorter aesthaete at its tip.

Second antenna (Fig. 4) with exopod one half the length of the spinous process. Exopod terminating as a slender spine and bearing one strong subterminal seta laterally and a fine hair-like seta adjacent to this on the inner margin; spinous process including fused protopod 0.19 mm long and armed with a single anterolateral row of small spines along its distal half.

Mandible (Fig. 5) strongly toothed with a well developed incisor process and a ridged molar process; palp lacking.

First maxilla (Fig. 6) comprises two flattened endites and a well developed palp. Proximal and distal endites each with five stout plumose setae arranged as illustrated in Fig. 6. Palp of three segments: proximal segment fused with protopod and bearing fine hairs laterally; short medial segment with one long plumose seta arising from the inner distal margin; distal segment twice the length of the medial segment and bearing four long terminal plumose setae and one subterminal seta.

Second maxilla (Fig. 7) with first (proximal), second, third, and fourth (distal) endites having four, two, four, and four marginal plumose setae respectively; setae arranged as illustrated in Fig. 7; fine hairs occur along the inner margin of proximal endite and outer margin of distal endite. Palp with a shallow terminal cleft; distal margin with two long plumose setae each side of cleft; palp otherwise fringed with fine hairs. Scaphognathite with its proximal tip acicular

and plumose; four finely plumose setae are spaced along the outer and distal margins which are otherwise fringed with fine hairs.

Thoracic Appendages (Figs 8, 9)

First maxilliped (Fig. 8) with one plumose seta arising from the inner margin of coxa. Basis about three times longer than wide and bearing four groups of three short, sparsely plumose setae along its inner margin. Endopod of five segments: ischium short with two inner distal setae; merus three times the length of ischium with two setae mid-way along its inner margin; carpus about as long as the ischium and bearing one long inner distal seta; propod twice the length of ischium and carpus and provided with two long distal setae; dactylus shorter than propod and with three long terminal setae, one long subterminal seta and one very small seta mid-way along its outer margin. All setae of endopod are sparsely plumose. Exopod as long as the basis, slightly longer than endopod, and incompletely divided into two segments of unequal length; tip of exopod with four, very long, biplumose natatory setae.

Second maxilliped (Fig. 9) similar to the first, but with a much shorter endopod of three segments. Coxa without setae. Basis with four short, sparsely plumose setae spaced along its inner margin. Endopod only one third the length of endopod of first maxilliped: first segment without setae; second segment with one short inner distal seta; third segment about twice as long as the two more proximal segments, incompletely divided into two segments about the point indicated by two short inner setae and one outer seta, and with three setae each of different length arising from its tip. All setae of endopod sparsely plumose. Exopod as in the first maxilliped described above.

There is no sign of the third maxillipeds, pereopods or of gill buds.

Abdomen (Figs 1, 2)

The abdomen comprises five segments each of about equal length (0.12 mm) and a telson: first segment without spines or setae; second with a paired lateral papilla or protuberance as in all known brachyuran larvae; second to fifth segments with a pair of rudimentary ventro-lateral spines and two dorsal setae; pleopod buds absent.

Telson (see Fig. 2) forked, 0.28 mm in length and with the same distance separating the tips of the lateral cornua; each ramus (cornu) slender with almost straight sides in dorsal or ventral view, but curved strongly dorsally; cornua without dorsal or lateral spines but with two dorsolateral rows of tiny hairs; median cleft in posterior margin of telson wide and crescent-shaped; three plumose setae arising from the posterior margin of the telson either side of the median cleft; inner seta with three or four centrally placed strong marginal hairs.

Chromatophore Pattern (Figs 1, 2)

Chromatophores of the stage one Zoea of Hemiplax hirtipes are often indistinct. Black centres of colouration are small and fade rapidly in preservative. The larvae are transparent or faint red when observed under low magnification. The chromatophore pattern characterising the stage one Zoea larva of this species is tabulated (Table 1). The chromatophore classification is based on that of Aikawa (1929) but is modified to cover larvae of New Zealand Brachyura as in previous papers (Wear, in press, a, c).

TABLE 1

Hemiplax hirtipes (Jacquinot)

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

1	(1)	Supracerebral	-----
2	x	Antennular	dichromatic, black to red
3	(2)	Antennal	dichromatic, black to red
4	(3)	Labral	dichromatic, black to red
5	(4)	Mandibular	dichromatic, black to red
6	(5)	Maxillar	dichromatic, black to red
7	(6)	Maxillipedal	-----
8	(7)	Lateral Intestinal	dichromatic, black to red; in 1st abdominal segment only.
9	x	Subintestinal	dichromatic, black to red

B. Visceral Group

10	(8)	Median Gastric	-----
11	(9)	Precardiac	dichromatic, black to red or orange
12	(10)	Subcardiac	dichromatic, black to red; extending into dorsal carapace spine
13	(11)	Postcardiac	-----

SECONDARY SYSTEM

14	x	Posterior Carapacial	-----
15	(12)	Posteroventral Carapacial	-----
16	(12)	Lateral Carapacial	dichromatic, black to red
17	x	Dorsal Carapace Spine	-----
18	(13)	Maxillipedal	dichromatic, black to red
19	(14)	Optic	-----
20	(15)	Median Ocular Centre	dichromatic, black to red

NOTE: (1) to (15) numerical status of chromatophores after Aikawa(1929)

x not included in Aikawa's system

- chromatophore absent

DISCUSSION

Brachyuran pre-Zoea larvae usually possess long plumose processes arising from the exopod of the first and second antennae and from the telson (Lebour 1928; Wear 1967). These pre-zoeal cuticular processes are absent in Hemiplax hirtipes as in all other known larvae of the family Hymenosomidae and the more highly evolved brachyrhynchous crabs of the families Goneplacidae, Pinnotheridae, Ocypodidae, Grapsidae and Gecarcinidae (Wear 1967, pp. 63-5).

Zoea larvae of 14 species belonging to the family Ocypodidae have been described. These species cover the three subfamilies Ocypodinae, Scopimerinae, and Macrophthalminae, and seven of the 18 extant genera recognised by Balss (1957) are represented. Balss (1957, pp. 1663-5) grouped these seven genera as follows:

SUBFAMILY OCYPODINAE

<u>Ocypode</u>	Weber
<u>Uca</u>	Leach

SUBFAMILY SCOPIMERINAE

<u>Dotilla</u>	Stimpson
<u>Ilyoplax</u>	Stimpson
<u>Scopimera</u>	de Haan

SUBFAMILY MACROPHTHALMINAE

<u>Hemiplax</u>	Heller
<u>Macrophthalmus</u>	Desmarest

Described Zoea larvae fall into two major groups, each subdivided. To separate these larvae I have given major significance to the presence

or absence of lateral carapace spines, and secondary importance to the expansion of the fourth and fifth abdominal segments and to the degree of development of the exopod of the second antenna.

The relative importance of the two secondary characters is uncertain.

The following key has been compiled from the descriptive work of authors indicated.

A KEY TO DESCRIBED ZOEAL LARVAE
OF THE FAMILY OCYPODIDAE

1. Lateral carapace spines absent AUTHOR
- (1) 4th abdominal segment expanded laterally
- (a) Antennal exopod reduced:
- Uca annulipes (Latreille)
- = Gelasimus annulipes Latreille Chhapgar 1956
- (b) Antennal exopod not reduced
-
- (2) 4th abdominal segment not expanded laterally
- (a) Antennal exopod reduced:
- Uca minax (Le Conte) Hyman 1920
- Uca pugilator (Bosc) Hyman 1922
- Uca pugnax (Smith) Hyman 1920
- (b) Antennal exopod not reduced:
- Dotilla blandfordi Alcock Raja Bai 1959
- Macrophthalmus depressus Rüppell Aikawa 1929
- Macrophthalmus diatatus de Haan Aikawa 1929
- Macrophthalmus japonicus de Haan Aikawa 1929
2. Lateral carapace spines present
- (1) 5th abdominal segment expanded laterally
and posteriorly:
- Dotilla sulcata (Forskål) Ramadan 1940;
Gohar &
Al-Kholy 1957
- (2) 5th abdominal segment not expanded
- (a) Antennal exopod reduced:
- Ilyoplax pusillus (de Haan)
- = Tympanomeres pusillus de Haan Aikawa 1929

<u>Ocypode gaudichaudii</u> M.E. & Lucas	Crane 1940
<u>Ocypode platytarsis</u> Milne Edwards	Raja Bai 1951
<u>Scopimera globosa</u> de Haan	Aikawa 1929

(b) Antennal exopod not reduced:

<u>Hemiplax hirtipes</u> (Jacquinot)	Wear
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From this key, no larval character can be considered as being common to all ocypodid Zoea larvae, and no grouping of larval characters brings the Zoea larvae into closer conformity with the arrangement of adult genera into subfamilies listed by Balss (1957). Thus in the first major division of larvae occur the genera Dotilla, Macrophthalmus, and Uca, and in the second major division occur the genera Dotilla, Hemiplax, Ilyoplax, Ocypode, and Scopimera. Only Dotilla occurs in both divisions. Larval relationships between genera of the subfamilies Ocypodinae, Scopimerinae, and Macrophthalminae suggested by Aikawa (1937, pp. 154-5) correspond to the classification of adults. However Aikawa's conclusions were based on larvae of only four genera, and this view is not supported by genera and species since described. Zoea larval characters mainly support the present arrangement of adult genera in the Xanthidae (Wear, in press, b) and Grapsidae (Wear, in press, c), but this apparently does not apply in the family Ocypodidae.

Although larval relationships within the family Ocypodidae are obscure, their Zoea larvae appear to be closely related to species outside this family. For example among the Hymenosomidae, Pinnotheridae, and Grapsidae, there are larvae showing greater affinities with larvae of the Ocypodidae than can be found within ocypodid larvae themselves.

Gurney (1938; 1942, pp. 278-9) considered that Zoea larval characters indicate close relationship between the Hymenosomidae (Oxyrhyncha) and the Pinnotheridae (Brachyrhyncha) (see also Wear 1967, p. 65), and this distinctive larval group can now be extended to include Dotilla sulcata (Forskål) described by Ramadan (1940). Ramadan noted that in D. sulcata the broadly expanded fifth abdominal segment and small, narrow telson occurred only in Pinnixia (Pinnotheridae) and in Elamena (Hymenosomidae). This character also occurs in

the Zoea larvae of E. producta Kirk and Hymenicus pubescens Dana from New Zealand. The Zoea larvae of H. pubescens possess four short carapace spines and are strikingly similar to those of D. sulcata, thus providing further evidence in support of larval affinities between the Hymenosomidae and those of the brachyrynchous crabs.

A second group of ocypodid Zoea larvae has affinities with larvae of genera classified in the Sesarminae and Varuninae (Grapsidae). The Zoea larva of Hemiplax hirtipes is very similar to those of the genera Cyclograpsus, Helice, and Hemigrapsus (Wear, in press, c) and strongly supports Aikawa's view (1937) that the Macrophthalminae may have arisen from the Grapsidae. The stage one Zoea larva of Dotilla blanfordi Alcock described by Raja Bai (1959) possesses no lateral carapace spines, a well developed antennal exopod, and larval affinities closer to the Sesarminae and Varuninae (Wear, in press, c) than to D. sulcata. The marked differences between larvae of the two species of Dotilla suggests that adult systematics of this genus may benefit from re-examination.

The third distinctive larval group in the family Ocypodidae shows close affinity with those of the Grapsinae (see Wear, in press, c), and is formed by three species of the genus Macrophthalmus Desmarest (Aikawa 1929) and Uca annulipes Latreille (Chhapgar 1956). However the larvae of U. minax (Le Conte), U. pugilator (Bosc), and U. pugnax (Smith) described by Hyman (1920, 1922) all lack lateral carapace spines which are also absent in the Grapsinae, but possess antennal, abdominal and telson characters intermediate between those of the Grapsinae on one hand and the Sesarminae and Varuninae on the other. Zoeal characters therefore suggest that U. annulipes is not closely related to the other three species of Uca from which larvae have been described.

The remaining known ocypodid Zoea larvae can also be placed between the Grapsinae, and the Sesarminae and Varuninae. Larvae of Ocypode gaudichaudii Milne Edwards and Lucas described by Crane (1940) and O. platytarsis Milne Edwards (RajaBai 1951) possess four carapace spines as in the Sesarminae and Varuninae, but the form of the second antenna, armature of the abdomen, and shape of the telson is intermediate between these and the Grapsinae. Zoea larvae of Nyoplax pusillus (de Haan) and Scopimera globosa de Haan are very similar (Aikawa 1929). These larvae possess long and very distinctive toothed rostral and dorsal carapace spines, short lateral carapace spines and an unmodified abdomen as in the Sesarminae and Varuninae, but the second antenna comprises a reduced hair-like exopod and a robust spinous process as in Planes, Pachygrapsus, and Leptograpsus (Grapsinae) (Wear, in press, c).

Crane (1940) described the Megalopa larvae of Ocypode albicans Bosc, O. gaudichaudii, Milne Edwards and Lucas, and O. occidentalis Stimpson, and summarised the characters and ecology of known ocypodid Megalopa larvae. RajaBai (1954, 1959) and Gohar and Al-Kholy (1957) described Megalopa larvae of four additional species and discussed Crane's conclusions. In summary, the Megalopa larvae of beach-dwelling ocypodid crabs are all similar, and are provided with a thick cuticle and specialised grooves to allow close application of all appendages to the body. Hence the Megalopa larvae are structurally modified for protection against dessication, wave action, and sand abbrasion in the upper tidal zone of sandy beaches where they lie just below the surface of the sand awaiting moult to the first juvenile crab stage. The juvenile crabs migrate up the beach to live in the semi-terrestrial habitat of the adults (Crane 1940; RajaBai 1954).

It is therefore well established that ocypodid Megalopa larvae

are structurally modified in response to ecological requirements. Balss (1957) listed all adults of this family as amphibious, littoral and estuarine, mainly burrowing, and gregarious. Hence the characters distinguishing adults of the family Ocypodidae from other brachyrrhynchous crabs may also be ecological adaptations, and true relationships of the genera may be masked by specialisation. Genera now classified in the Ocypodidae may have diverse origins, with ancestral forms having affinities with the Pinnotheridae, Hymenosomidae, or with either the Grapsinae or Sesarminae/Varuninae in the family Grapsidae. As the specialised habitat requirements of adult and juvenile ocypodid crabs do not extend to the planktonic Zoea larvae, it may be only in these that original affinities of the genera have been preserved.

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LIFE-HISTORY STUDIES ON NEW ZEALAND BRACHYURA.

4. Zoea Larvae hatched from New Zealand Crabs of the family Grapsidae.

by

Robert G. Wear

SUMMARY

Pre-Zoea and first stage Zoea larvae hatched from Leptograpsus variegatus (Fabricius) Planes marinus Rathbun, Hemigrapsus crenulatus (H. Milne Edwards), H. edwardsi (Hilgendorf), Cyclograpsus lavauxi H. Milne Edwards, Helice crassa Dana, and Plagusia chabrus (Linnaeus) from New Zealand are described. A key is given for the separation of these larvae.

All grapsid Zoea larvae so far described fall into four groups based on larval characters. The first group includes the genera Grapsus, Leptograpsus, Metopograpsus, Pachygrapsus, and Planes (subfamily Grapsinae). The second group is made up of genera included in the subfamily Varuninae (Brachynotus, Hemigrapsus, Heterograpsus, Eriocheir) and the subfamily Sesarminae (Chasmagnathus, Cyclograpsus, Helice). These two larval groups are distinct. The third group of Zoea larvae also includes genera from the subfamilies Varuninae (Gaetice) and Sesarminae (Metasesarma, Sesarma). These larvae share characters of those in the first and second groups above, and suggest that larvae of the subfamilies Varuninae and Sesarminae can be divided into two related groups of genera. The fourth group shows few affinities with other grapsid Zoea larvae, and comprise the genera Percnon and Plagusia (subfamily Plagusiinae). Larvae of New Zealand species fall into the first, second, and fourth of these groups. Characters used here to

define the four larval groups are given in a key. This larval classification agrees with the present arrangement of adult genera into subfamilies except for the division among larvae of the subfamilies Varuninae and Searminae. This system is compared with the classification of grapsid Zoea larvae proposed by Bourdillon-Casanova (1960). Zoea larvae of the family Grapsidae show close affinities with those of genera in the brachyrynchous families Ocypodidae and Gecarcinidae.

Among New Zealand species, only Hemigrapsus edwardsi breeds during late autumn and winter. The remainder breed in late spring and summer. In each species there are four, possibly five Zoea larval stages and a Megalopa larva. The length of larval life and larval dispersal probably has no bearing on the presence or absence of certain species at the Chatham Islands east of New Zealand.

INTRODUCTION

Nine species belonging to the family Grapsidae have been reliably recorded from the New Zealand mainland. These comprise six genera representing all four subfamilies currently recognised (Balss 1957). Stage one Zoea larvae hatched from seven species are described in this paper. The only species listed in the New Zealand fauna not obtained for study are the oceanic crab Planes cyaneus Dana, and Cyclograpsus insularum Campbell and Griffin recently rediscovered in New Zealand by Dell and Marshall (1967).

Attempts to rear later larval stages of New Zealand grapsid crabs met with only limited success. The stage one Zoea larvae are very small, did not feed in the laboratory, and usually died before moulting. Stage two Zoea larvae were reared only from Hemigrapsus edwardsi (Hilgendorf) and Helice crassa Dana.

A small and readily accessible colony of Hemigrapsus edwardsi provided the basis of detailed study to determine seasonal fluctuations in sex ratio and in the reproductive state of mature females for this species. For the remaining species the limits of the breeding season were assessed only on the presence or absence of "berried" females collected from various localities over a period of four years (1964-67).

Laboratory methods, larval terminology, measurements, and diagrammatic representation of chromatophores drawn from living larvae follow those employed in earlier papers in this series (Wear, in press, a, b).

A KEY TO KNOWN ZOEAL LARVAE OF
NEW ZEALAND CRABS OF THE
FAMILY GRAPSIDAE

The following key is based on the first stage Zoeal larvae only. Characters used for the separation of species are those most readily observed without dissection of the larvae.

- 1 (4) Lateral carapace spines absent: antennal exopod reduced to a short fine seta; abdomen with posterolateral margins of 3rd to 5th segments expanded laterally into a broad ridge; telson narrowly forked, more or less rectangular with lateral cornua short and stout.
- 2 (3) 2nd antenna with spinous process about as long as rostral spine; spinous process bearing a longitudinal series of 10 or 11 strong spines; telson cornua with one lateral seta; 1st and 2nd maxillipeds without chromatophores.
.....Leptograpsus variegatus (Fabricius) (Figs 1-9)
- 3 (2) 2nd antenna with spinous process shorter than rostral spine; spinous process bearing a longitudinal series of only 7 small spines; telson cornua with two lateral setae; 1st and 2nd maxillipeds with strong black chromatophores.
.....Planes marinus Rathbun (Figs 10-18)
- 4 (1) Lateral carapace spines present; antennal exopod not greatly reduced; abdomen with posterolateral margins of 3rd to 5th segments not expanded laterally; telson widely forked with lateral cornua long and slender.
- 5 (12) Rostral spine much less than 0.5 mm long, shorter than dorsal carapace spine, and without tubercles; lateral carapace spines smooth and without hairs or tubercles; 2nd antenna with exopod about half the length of spinous process; 4th and 5th abdominal segments without lateral papillae; telson cornua without lateral

setae; 2nd maxillipeds without chromatophores.

- 6 (9) Total length of larva greater than 1.20 mm; tip of rostral spine to tip of dorsal carapace spine greater than 1.0 mm.
.....genus Hemigrapsus Dana

- 7 (8) Rostral spine much more than half the length of dorsal carapace spine; dorsal carapace spine not recurved anteriorly; 1st maxilliped with propodus of endopod lacking tuft of fine hairs; 3rd to 5th abdominal segments without fine denticles along posterior dorsal margins; lateral telson cornua with two dorsolateral rows of short hairs; dorsal carapace spine with a large red chromatophore at its base.
.....Hemigrapsus crenulatus (H. Milne Edwards)
(Figs 19-26)

- 8 (7) Rostral spine about one half the length of dorsal carapace spine; dorsal carapace spine recurved anteriorly in its distal half; 1st maxilliped with propodus of endopod bearing a tuft of fine hairs; 3rd to 5th abdominal segments with fine denticles along posterior dorsal margins; lateral telson cornua without dorsolateral rows or hairs; dorsal carapace spine without basal chromatophore.
.....Hemigrapsus edwardsi (Hilgendorf)
(Figs 28-33)

- 9 (6) Total length of larva less than 1.20 mm; tip of rostral spine to tip of dorsal carapace spine less than 1.0 mm.

- 10 (11) Dorsal carapace spine recurved anteriorly in its distal half; 1st maxilliped with carpus of endopod lacking tuft of fine hairs; 3rd abdominal segment with a small pair of dorso-lateral papillae.
.....Cyclograpsus lavauxi (H. Milne Edwards)
(Figs 34-41)

- 11(10) Dorsal carapace spine not recurved anteriorly; 1st maxilliped with carpus of endopod bearing a tuft of fine hairs; 3rd abdominal segment without dorsolateral papillae.
.....Helice crassa Dana (Figs 42-50)
- 12 (5) Rostral spine about 0.5 mm long, about as long or occasionally longer than dorsal carapace spine, and bearing a number of small tubercles; lateral carapace spines with small tubercles and short hairs basally; 2nd antenna with exopod much less than half the length of spinous process; 4th and 5th abdominal segments with a pair of small lateral papillae; telson cornua with one lateral seta; 2nd maxillipeds with strong black to yellow chromatophores.
.....Plagusia chabrus (Linnaeus) (Figs 51-64)

SUBFAMILY GRAPSINAE

Leptograpsus variegatus (Fabricius, 1793)

Leptograpsus variegatus commonly known as the "purple rock crab" is fast-running, generally elusive, and shelters under large boulders and in deep crevices from mid tide level to about spring high water level. L. variegatus also occurs in Australia (Hale 1927), and in Chile (Garth 1957) where the species occupies a similar habitat (Antezana, Fagetti, and Lopez 1965).

Ovigerous female crabs were collected from the Wellington area during December and January, 1964 and 1967. Ovigerous females were recorded only between the months of November and January, with all mature females observed bearing eggs during December. The incubation period is about six weeks, and after liberation of larvae ovaries showed no sign of regeneration for a second spawning.

Eggs measure 0.37 mm x 0.35 mm (0.36 mm x 0.36 mm) when freshly laid and are dark brown or almost black in colour. Eggs ready to hatch measure 0.44 mm x 0.42 mm with remaining yolk coloured light brown. Larvae within mature eggs possess very large eyes, and black to greenish yellow chromatophores are strongly developed. In daylight this colouration imparts a green iridescence to mature eggs.

THE PRE-ZOEA LARVA

Larvae hatch from the eggs as pre-Zoeae. These possess a thin pre-zoeal cuticle (Lebour 1928; Wear 1967) which surrounds the body and all appendages, but plumose pre-zoeal processes on the first and second antennae and on the telson are lacking. The stage one Zoea larva moults free of the pre-zoeal cuticle within 15 minutes of hatching.

THE FIRST STAGE ZOEAL LARVA

Description

The following description is based on larvae hatched from five female crabs collected in the Wellington area.

Cephalothorax (Figs 1, 2)

Total length of larva 1.31 mm. Rostral spine 0.26 mm long, straight but slightly expanded midway along its length; dorsal carapace spine 0.30 mm long and slightly curved posteriorly; tip of rostral spine to tip of dorsal spine 0.96 mm; lateral carapace spines absent. Carapace with posterolateral regions distinctly swollen; posterior margin of carapace fringed with short, fine hairs; one pair of dorsolateral setae situated just behind the dorsal carapace spine. Eyes sessile and very large relative to the overall size of the larva.

Cephalic Appendages (Figs 3-7)

First antenna (Fig. 3) uniramous with two long aesthaetes and two shorter and finer aesthaetes arising from its tip.

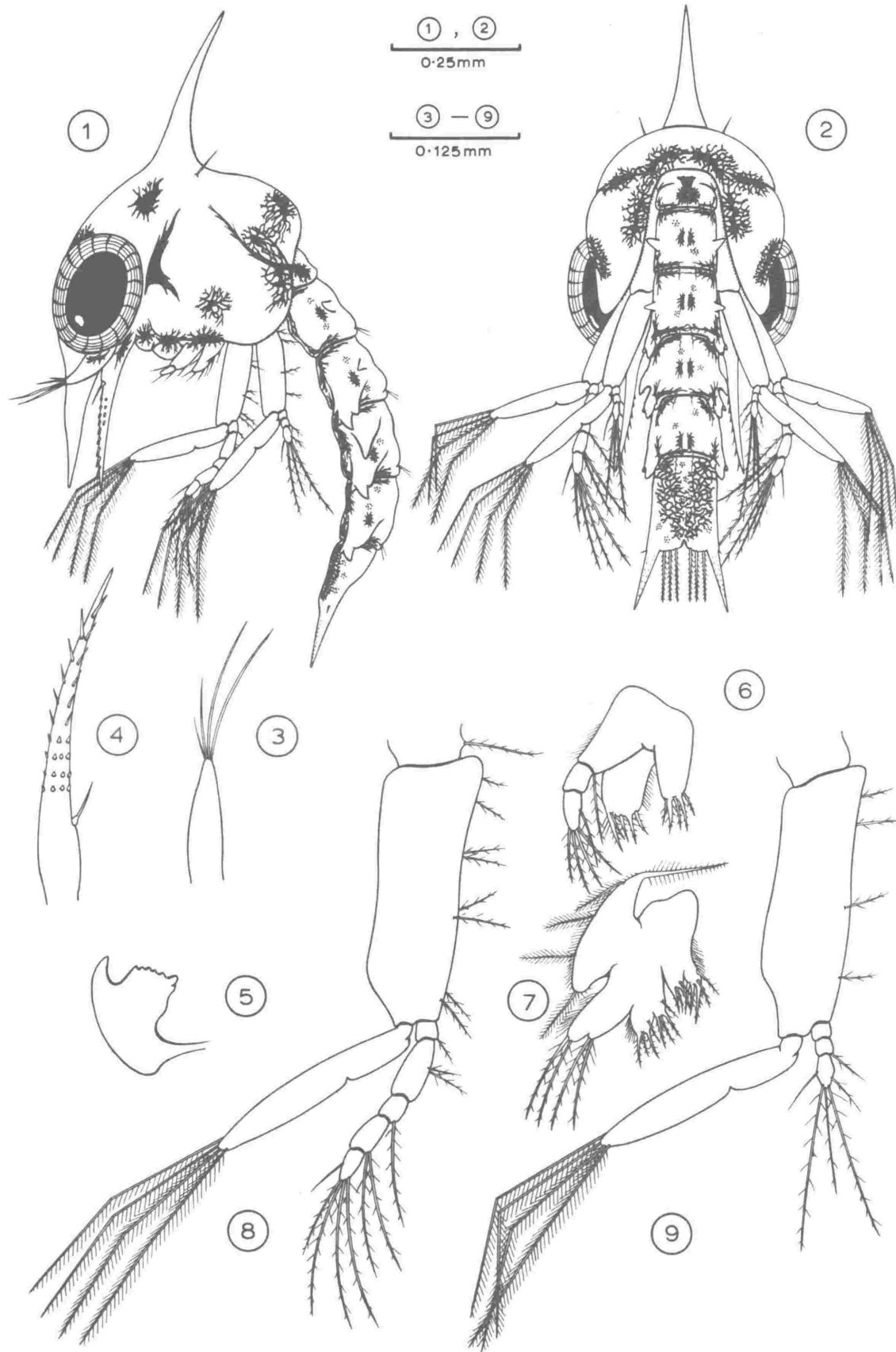
Second antenna (Fig. 4) comprises a well developed spinous process and a vestigial exopod seta: spinous process 0.31 mm long, slightly curved posteriorly, and bearing four anterior rows of small basal spines decreasing to a double row of longer spines towards its tip; spines number 10 or 11 in longitudinal series.

Mandible (Fig. 5) strongly toothed with a well developed incisor process and a ridged molar process; palp lacking.

First maxilla (Fig. 6) comprises two flattened endites and a well developed palp. Proximal and distal endites each bearing two large plumose setae and three smaller plumose setae arranged as illustrated in Fig. 6; distal endite fringed with fine hairs along its

Leptograpsus variegatus: Stage 1 Zoea Larva

- Fig. 1 Stage 1 Zoea; lateral view
- Fig. 2 Stage 1 Zoea; posterior view
- Fig. 3 First antenna of left side
- Fig. 4 Second antenna of right side
- Fig. 5 Mandible of left side
- Fig. 6 First maxilla of left side
- Fig. 7 Second maxilla of left side
- Fig. 8 First maxilliped of left side
- Fig. 9 Second maxilliped of left side



inner margin. Palp of three segments: proximal segment fused with protopod, bearing fine hairs laterally and with one long plumose seta arising from the inner distal margin; short medial segment without hairs or setae; distal segment with four terminal plumose setae and one subterminal seta mid-way along its inner margin.

Second maxilla (Fig. 7) with first (proximal), second, third and fourth (distal) endites possessing five, four, four and four marginal plumose setae respectively; setae arranged as illustrated in Fig. 7; fine hairs fringing the inner margin of proximal endite and outer margin of the distal endite. Palp with a shallow terminal cleft forming two distal lobes of unequal size; lateral lobe and smaller medial lobe both with two long plumose setae arising distally; palp fringed with fine hairs along its outer margin. Scaphognathite with its proximal tip acicular and plumose; four finely plumose setae are spaced along the outer and distal margins which are otherwise fringed with fine hairs.

Thoracic Appendages (Figs 8, 9)

First maxilliped (Fig. 8) with one plumose seta arising from the inner margin of coxa. Basis about three times longer than wide and bearing four groups of two short, sparsely plumose setae along its inner margin. Endopod of five segments: ischium short and bearing one inner distal seta; merus three times the length of ischium with two setae mid-way along its inner margin; carpus about as long as the ischium and bearing one long inner distal seta; propodus about twice the length of ischium and carpus and with two inner distal setae; dactylus shorter than propodus and with four long terminal setae and one very small seta arising mid-way along its outer margin. All setae on endopod are sparsely plumose excepting the small unarmed

seta on the outer margin of the dactylus. Exopod a little shorter than basis, slightly longer than the endopod, and is incompletely divided into two segments of unequal length; tip of exopod with four, very long, biplumose natatory setae.

Second maxilliped (Fig. 9) similar to the first, but with a much shorter endopod of three segments. Coxa without setae. Basis with four short sparsely plumose setae spaced along the inner margin. Endopod about one third the length of that of the first maxilliped: first segment without setae; second segment with one short inner distal seta; third segment about twice the length of the two more proximal segments, incompletely divided into two segments about the point indicated by one short plumose seta on the inner margin and one short smooth seta laterally, and with two long plumose setae and one shorter plumose seta arising from its tip. Exopod as in the first maxilliped described above.

There is no sign of buds of the third maxillipeds, pereopods or gills.

Abdomen (Figs 1, 2)

The abdomen comprises five segments of about equal length (0.125 mm) and a telson: first segment without spines or setae; second segment with a paired dorsolateral papilla or protuberance as in all known brachyuran larvae; third segment with a paired dorsolateral papilla directed slightly posteriorly and with its posterolateral margins expanded laterally as a trilobed ridge bearing a single ventral spine; fourth segment without papillae but with a broad lateral ridge and a second posterolateral trilobed ridge lacking a ventral spine, dorsal lobe not as well defined as that of the third segment (see Fig. 1); fifth segment with a posterolateral ridge only, trilobed but with dorsal lobe poorly defined; second to fifth segments each with two dorsal setae; pleopod buds absent.

Telson (see Fig. 2) 0.30 mm in length with 0.18 mm separating the tips of the lateral cornua; telson plate rectangular, 0.19 mm long, 0.13 mm wide; lateral cornua short, straight, not curved posteriorly, and bearing two dorsolateral rows of short hairs; telson with one pair of tiny lateral spines at base of the lateral cornua. Median cleft in posterior margin of telson a small and shallow indentation; three plumose setae arise from the posterior margin of the telson either side of the median cleft; inner setae without stronger marginal hairs centrally.

Chromatophore Pattern (Figs 1, 2, Table 1)

Stage one Zoea larvae of Leptograpsus variegatus are intensely coloured and appear black or very dark green under low magnification. The colour and distribution of chromatophores is listed in Table 1. The classification of chromatophores is based on that of Aikawa (1929) but is modified to cover larvae of New Zealand Brachyura as in previous papers (Wear, in press, a, b).

TABLE 1

Leptograpsus variegatus (Fabricus)

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A	<u>Neural Group</u>	
1 (1)	Supracerebral	dichromatic, black to greenish-yellow
2 x	Antennular	dichromatic, black to greenish-yellow
3 (2)	Antennal	dichromatic, black to greenish-yellow
4 (3)	Labral	dichromatic, black to greenish-yellow
5 (4)	Mandibular	dichromatic, black to greenish-yellow
6 (5)	Maxillar	dichromatic, black to greenish-yellow
7 (6)	Maxillipedal	-----
8 (7)	Lateral Intestinal	dichromatic, black to greenish-yellow + scattered red; segment 1 coalesced with 13 below
9 x	Subintestinal	dichromatic, black to greenish-yellow

B	<u>Visceral Group</u>	
10 (8)	Median Gastric	dichromatic, black to greenish-yellow
11 (9)	Precardiac	-----
12(10)	Subcardiac	-----
13(11)	Postcardiac	dichromatic, black to greenish-yellow; coalesced with 8 in 1st abdominal segment

SECONDARY SYSTEM

14 x	Posterior Carapacial	dichromatic, black to greenish-yellow; 3 pairs, often coalesced
15(12)	Posteroventral Carapacial	-----

16 (12)	Lateral Carapacial	dichromatic, black to greenish-yellow
17 x	Dorsal Carapace	
	Spine	- - - - -
18 (13)	Maxillipedal	- - - - -
19 (14)	Optic	dichromatic, black to greenish-yellow
20 (15)	Median Ocular Centre	dichromatic, black to greenish-yellow

NOTE: (1) to (15) numerical status of chromatophores after
Aikawa (1929)

x not included in Aikawa's system

- chromatophore absent

Planes marinus Rathbun, 1915

Planes marinus is one of the two oceanic species of this genus occasionally found among floating debris stranded on the coasts of New Zealand and the Chatham Islands. Twenty-seven ovigerous female crabs with eggs in all stages of development, three males, and a large number of juvenile crabs were found among stalked barnacles attached to a rope-covered glass fishing float washed up at Lyall Bay, Wellington, 3-2-1965.

Eggs freshly laid are dark brownish-purple in colour and measure 0.30 mm x 0.29 mm. Eggs about to hatch measure 0.42 mm x 0.39 mm and the little remaining yolk is coloured light brown. The period of incubation is about six weeks. Female crabs lay more than one batch of eggs each breeding season, as the four female crabs from which larvae were hatched had all deposited a further batch of eggs beneath the abdomen within 12 hours. Mature females of this species occur during February and March, April (Bennett 1964, p. 81 - referred to P. minutus (Linnaeus)), and May (Dell 1963a - referred to Pachygrapsus marinus (Rathbun), see Chace 1966). It is unlikely that these four months define the limits of the breeding period, and Planes marinus may breed in all months of the year as recorded for P. minutus by Lebour (1944).

THE PRE-ZOEAL LARVA

The pre-Zoeal larval cuticle of Planes marinus lacks plumose processes as in Leptograpsus variegatus. The duration of the pre-zoeal stage is 15 to 20 minutes.

THE FIRST STAGE ZOEAL LARVA

Larvae were hatched from four female crabs between 8-2-1965

and 16-2-1965. Two of these females were kept in the laboratory for a further six weeks until the second batch of eggs hatched, thus obtaining an estimate of the incubation period. Larvae survived for only five days and died while still in the first zoeal stage.

Description

The following description is shortened to a comparison with the first stage Zoea larva of Leptograpsus variegatus described previously.

Cephalothorax (Figs 10, 11)

Total length of larva 1.25 mm. Rostral spine 0.24 mm long, straight, and expanded as in Leptograpsus variegatus; dorsal carapace spine equal to rostral spine in length and slightly curved posteriorly; tip of rostral spine to tip of dorsal spine 0.87 mm; lateral carapace spines absent. Cephalothorax similar to that of the stage one Zoea of Leptograpsus variegatus in all remaining characters.

Cephalic Appendages (Figs 12-16)

First antenna (Fig. 12) as in Leptograpsus variegatus described previously.

Second antenna (Fig. 13) similar to that of L. variegatus but considerably shorter: spinous process 0.22 mm long with anterior spines much smaller than in L. variegatus and numbering only seven in longitudinal series.

Mandible (Fig. 14) as in L. variegatus.

First maxilla (Fig. 15) differs from that of the previous species only in the possession of six rather than five plumose setae on the proximal endite.

Planes marinus: Stage 1 Zoea Larva

Fig. 10 Stage 1 Zoea; lateral view

Fig. 11 Stage 1 Zoea; posterior view

Fig. 12 First antenna of left side

Fig. 13 Second antenna of left side

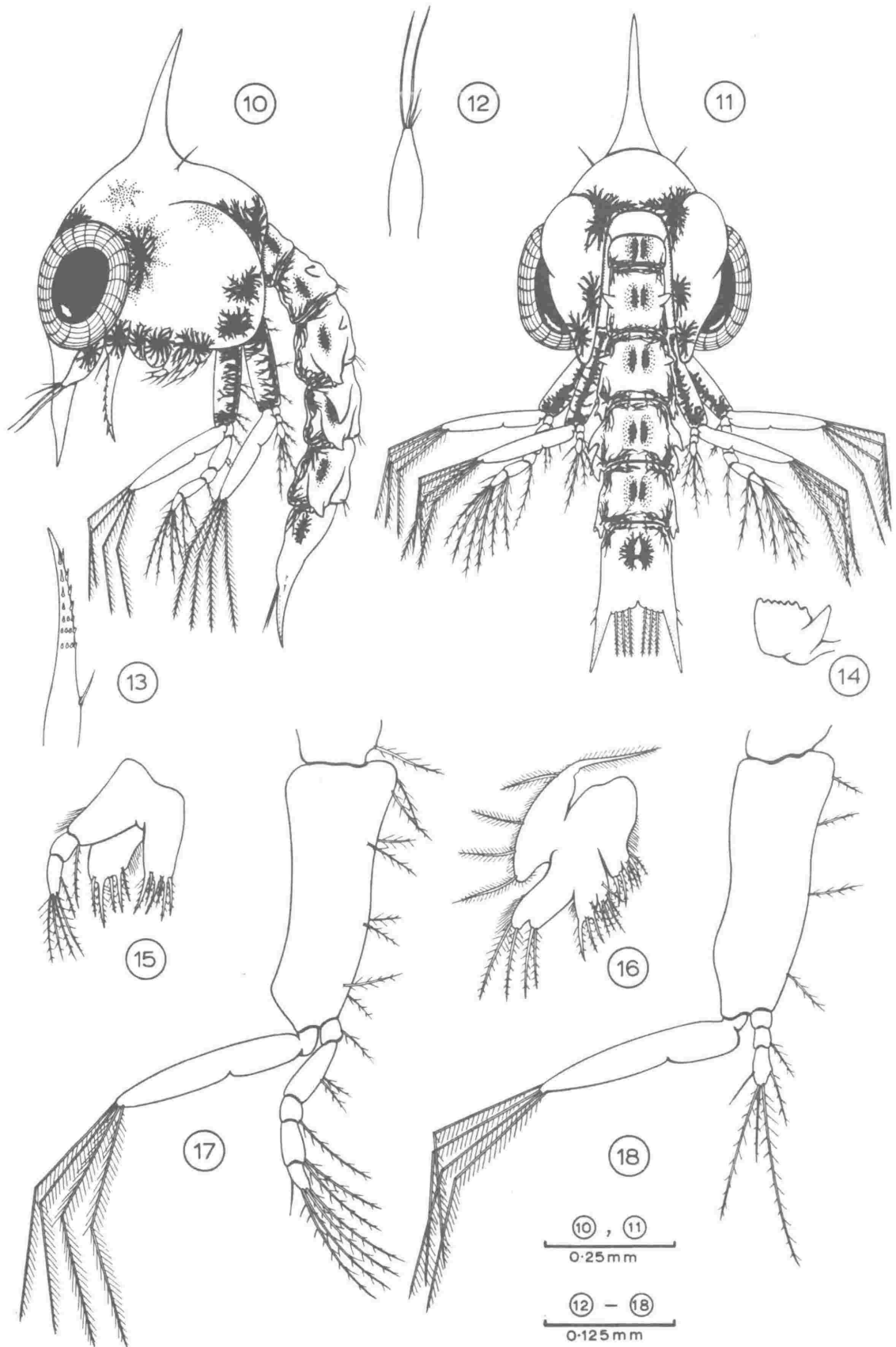
Fig. 14 Mandible of left side

Fig. 15 First maxilla of left side

Fig. 16 Second maxilla of left side

Fig. 17 First maxilliped of left side

Fig. 18 Second maxilliped of left side



Second maxilla (Fig. 16) also similar to that of L. variegatus, but the number of plumose setae borne by the proximal to distal endites is four, two, five, and four arranged as illustrated in Fig. 16.

First maxilliped (Fig. 17) and second maxilliped (Fig. 18) both agree in all details with corresponding appendages described for the first stage Zoea larva of L. variegatus.

Abdomen (Figs 10, 11)

The abdomen differs from that described for L. variegatus only in the form and armature of the telson. Rectangular telson plate 0.17 mm long and slightly wider than that of L. variegatus (0.14 mm); two tiny lateral spines at base of each lateral telson cornu; lateral cornua straight, but slightly curved posteriorly (see Fig. 10).

Chromatophore Pattern (Figs 10, 11, Table 2)

Stage one Zoea larvae of Planes marinus are intensely coloured and appear black or dark grey under low magnification. The colour and distribution of chromatophores is listed in Table 2.

TABLE 2

Planes marinus Rathbun

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

1.	Supracerebral	red or orange-red
2.	Antennular	black
3.	Antennal	black
4.	Labral	black
5.	Mandibular	black
6.	Maxillar	black
7.	Maxillipedal	black, coalesced with 18 below
8.	Lateral Intestinal	dichromatic, black to red; monochromatic black in telson
9.	Subintestinal	black

B. Visceral Group

10.	Median Gastric	dichromatic, black to red
11.	Precardiac	-----
12.	Subcardiac	-----
13.	Postcardiac	red or orange-red

SECONDARY SYSTEM

14.	Posterior Carapacial	black
15.	Posteroventral Carapacial	2 pairs, black, often coalesced
16.	Lateral Carapacial	-----
17.	Dorsal Carapace Spine	-----
18.	Maxillipedal	black, coalesced with 7 above
19.	Optic	black
20.	Median Ocular Centre	black

SUBFAMILY VARUNINAE

Hemigrapsus crenulatus (H. Milne Edwards, 1837)

Balss (1957) included the genus Hemigrapsus Dana together with Heterograpsus Lucas in the genus Brachynotus de Haan. However Hemigrapsus has persisted as the more commonly used generic name for the two New Zealand species (Bennett 1964; Dell 1963; Garth 1957; Richardson 1949).

Hemigrapsus crenulatus occurs intertidally or semi-terrestrially in estuaries and on mudflats over most of New Zealand excepting in the far north and in the Chatham Islands. The species lives under rocks and occasionally burrows. In most localities H. crenulatus occupies the same ecological niche as Helice crassa Dana, but in some areas where the habitat appears to be suitable, H. crassa is present in abundance but Hemigrapsus crenulatus is inexplicably absent. H. crenulatus also occurs in Chile (Garth 1957).

Ovigerous females were collected from the Mangonui Estuary, North Auckland, 23-10-1964, and from the Hutt River Estuary, Wellington Harbour during 1967. In the Wellington area a few ovigerous females were collected during October, 1967, and by late November, 1967, female crabs carrying eggs in all stages of development were abundant. The precise limits of the breeding season have not been determined. However it is likely that each female crab lays more than one batch of eggs in one season, as ovigerous females frequently possessed gravid ovaries.

Eggs freshly laid are light brownish yellow and measure 0.28 mm x 0.26 mm. When ready to hatch the eggs are almost transparent and measure 0.34 mm x 0.33 mm with remaining yolk coloured light brown.

THE PRE-ZOEA LARVA

The pre-zoeal cuticle covers the body and appendages of the larva but lacks plumose processes as in Leptograpsus variegatus and Planes marinus. Pre-Zoea larvae moult from this cuticle within five or ten minutes of hatching.

THE FIRST STAGE ZOEAL LARVA

Larvae were hatched from two females collected from the Mangonui Estuary, 1964, and six females obtained from the Hutt River Estuary during November and December, 1967. Larvae survived no longer than seven days in the laboratory.

Description

Cephalothorax (Figs 19, 20)

Total length of larva 1.22 mm. Rostral spine 0.29 mm long and straight; dorsal carapace spine 0.41 mm long and curved backwards; tip of rostral spine to tip of dorsal spine 1.05 mm; lateral carapace spines 0.19 mm in length and directed postero-ventrally. Carapace without lateral swellings but with one pair of dorsolateral setae as in the two species previously described; posterior margin of carapace fringed with short stout setae rather than with fine hairs. Eyes sessile but small compared with those of the first stage Zoea larvae of Leptograpsus variegatus and Planes marinus.

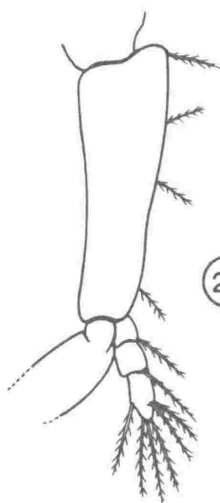
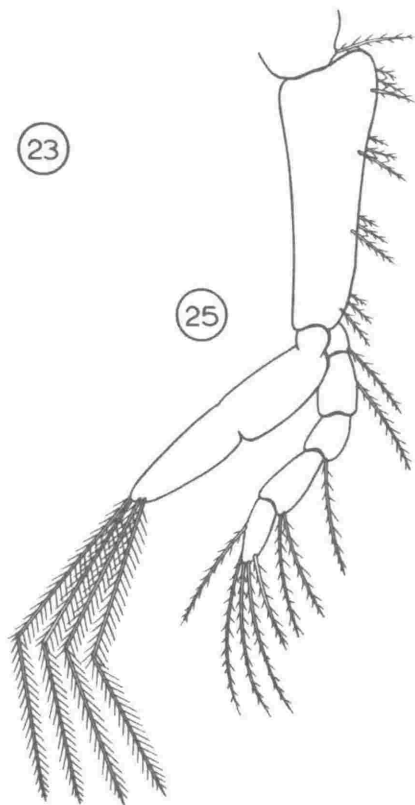
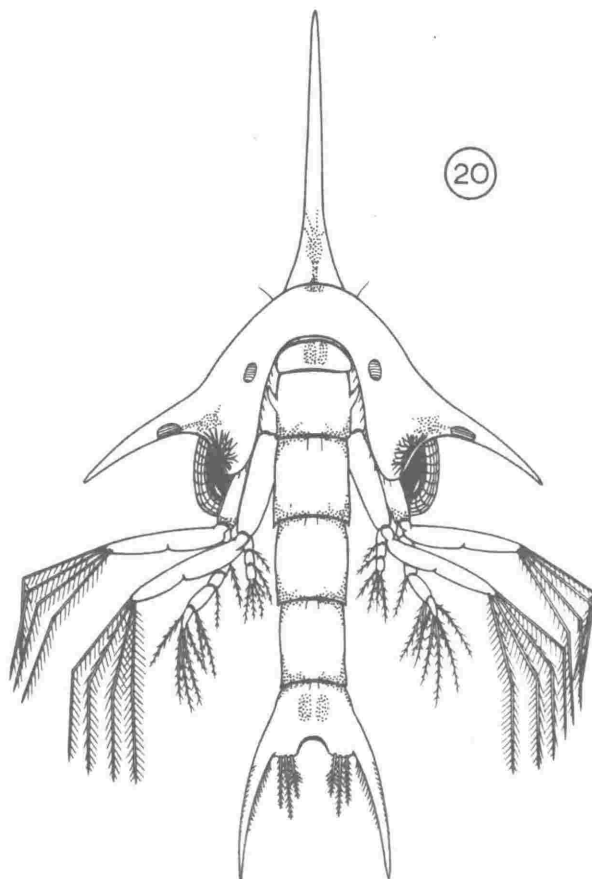
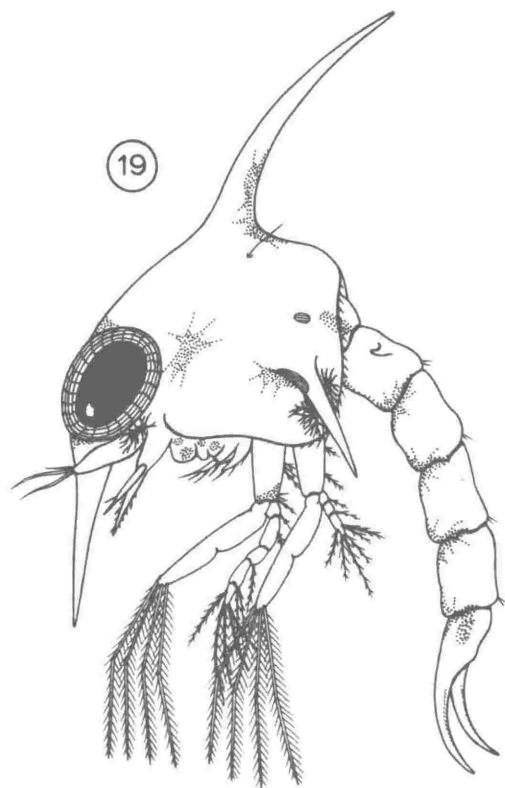
Cephalic Appendages (Figs 21-24)

First antenna (Fig. 21) uniramous with two long aesthaetes and one shorter aesthaete at its tip.

Second antenna (Fig. 22) comprises a spinous process 0.12 mm in length bearing a double row of small spines along its distal half,

Hemigrapsus crenulatus: Stage 1 Zoea Larva

- Fig. 19 Stage 1 Zoea; lateral view
- Fig. 20 Stage 1 Zoea; posterior view
- Fig. 21 First antenna of left side
- Fig. 22 Second antenna of left side
- Fig. 23 First maxilla of left side
- Fig. 24 Second maxilla of left side
- Fig. 25 First maxilliped of left side
- Fig. 26 Second maxilliped of left side
(exopod not represented)



19 , 20
0.25 mm

21 - 26
0.125 mm

and a well developed exopod slightly more than one half the length of the spinous process; exopod with one strong lateral spine arising just below its tip and two small setae in a corresponding position medially.

Mandible similar to that of the two species previously described.

First maxilla (Fig. 23) with palp of three segments having the same number and arrangement of setae as described for Leptograpsus variegatus and Planes marinus; proximal endite with four marginal plumose setae; distal endite with five such setae but inner margin without fringe of fine hairs.

Second maxilla (Fig. 24) with first (proximal), second, third, and fourth (distal) endites bearing four, two, three, and three marginal plumose setae respectively, setae arranged as illustrated in Fig. 24; endites without fine marginal hairs. Palp and scaphognathite similar to those of the two species previously described.

First maxilliped (Fig. 25) with one plumose seta arising from the inner margin of coxa. Basis bearing four groups of three short, sparsely plumose setae spaced along its inner margin. Endopod of five segments: merus, propodus and dactylus all equal in length and each about half the length of the ischium and carpus; ischium with one inner distal seta; merus with one seta mid-way along its inner margin; carpus bearing one long inner distal seta; propodus with two inner distal setae; dactylus with four long terminal setae and one long seta arising mid-way along the outer margin. All setae of endopod are sparsely plumose. Exopod as long as the endopod and bearing four natatory setae as in all described stage one brachyuran Zoea larvae.

Second maxilliped (Fig. 26) with short endopod differing from that of the previous two species only in details of setation: first and second segments each with one inner distal seta; third segment with two inner subterminal setae, one outer subterminal seta, and three rather short terminal setae; all setae are sparsely plumose.

Buds of third maxillipeds, pereopods, and gills absent.

Abdomen (Figs 19, 20)

Abdomen (see Figs 19, 20) comprises five segments of about equal length (0.125 mm) and a telson: first segment without spines or setae; second segment with a paired, forwardly-directed lateral papilla; third to fifth segments without lateral papillae but with short, rudimentary lateral spines; second to fifth segments each with two dorsal setae; pleopod buds absent.

Telson (see Fig. 20) 0.30 mm long, widely forked with long slender rami: lateral cornua curved slightly inwards, strongly curved dorsally, and bearing two dorsolateral rows of short hairs for the greater part of their length; tips of cornua 0.23 mm apart. Median cleft in posterior margin of telson broad and crescent-shaped; three plumose posterior telson setae arising either side of the median cleft; inner pair of setae with three or four pairs of stronger hairs centrally.

Chromatophore Pattern (Figs 19, 20, Table 3)

Living stage one Zoea larvae of Hemigrapsus crenulatus appear transparent to the naked eye, but the very intense yellow chromatophores situated at the base of the dorsal carapace spine and in the lateral carapace spines usually give a yellow tinge to the larvae. The colour and distribution of chromatophores is listed in Table 3. Red chromatophores appear black when contracted.

TABLE 3

Hemigrapsus crenulatus (H. Milne Edwards)

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

1.	Supracerebral	-----
2.	Antennular	dichromatic, black to yellow
3.	Antennal	-----
4.	Labral	2 pairs, red
5.	Mandibular	2 pairs, red
6.	Maxillar	-----
7.	Maxillipedal	-----
8.	Lateral Intestinal	red to yellow (1st abdominal segment and telson only)
9.	Subintestinal	red

B. Visceral Group

10.	Median Gastric	red
11.	Precardiac	-----
12.	Subcardiac	red to yellow; often coalesced with 17 below
13.	Postcardiac	-----

SECONDARY SYSTEM

14.	Posterior Carapacial	yellow (very small)
15.	Posteroventral Carapacial	black
16.	Lateral Carapacial	red + intense yellow in base of lateral carapace spines
17.	Dorsal Carapace Spine	red to intense yellow; often coalesced with 12 above
18.	Maxillipedal	red (1st maxilliped only)

- | | | |
|-----|----------------------|-----|
| 19. | Optic | red |
| 20. | Median Ocular Centre | red |
-

Note: Yellow chromatophores represented by parallel shading

Hemigrapsus edwardsi (Hilgendorf, 1882)

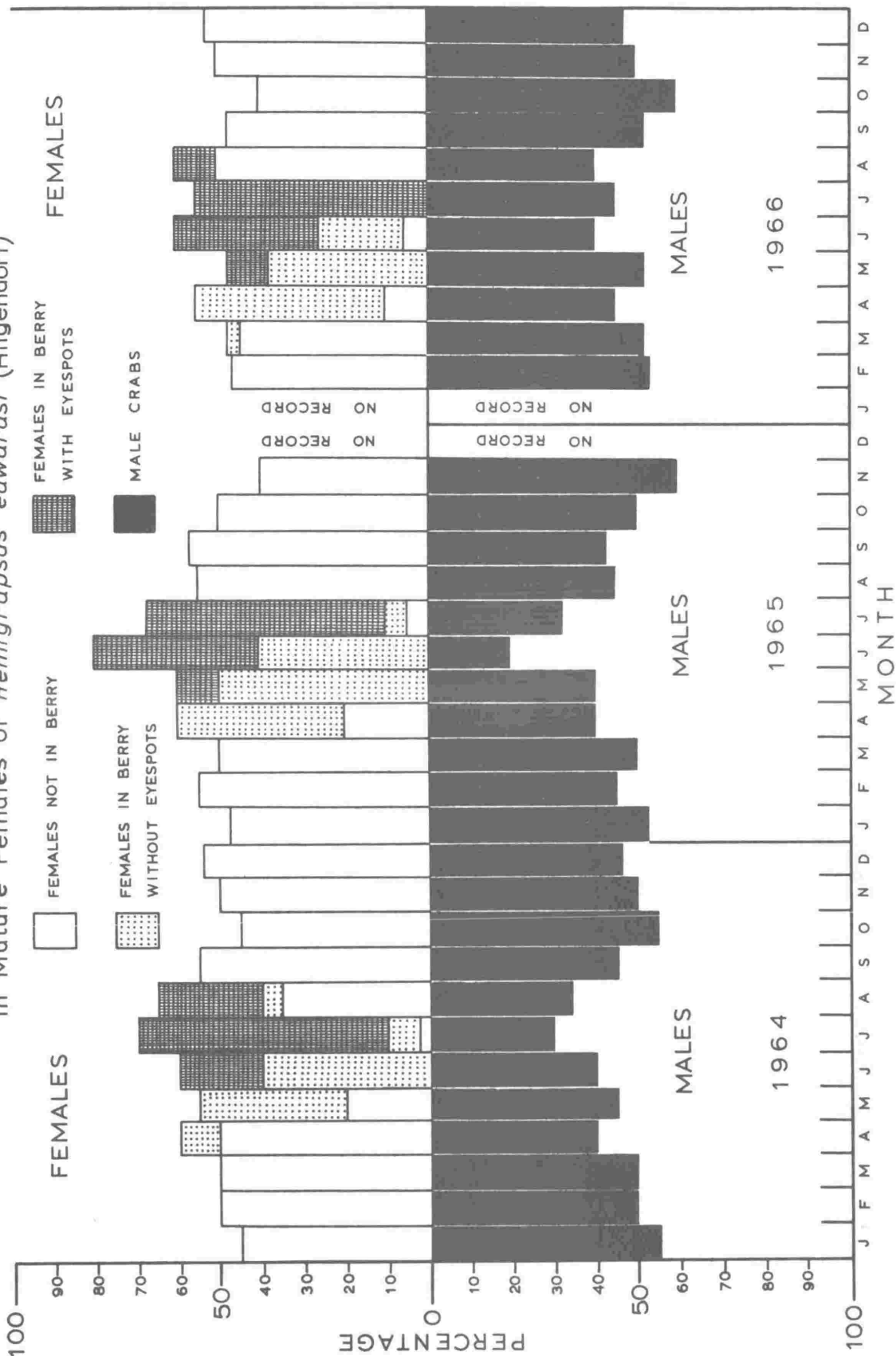
Hemigrapsus edwardsi is endemic to New Zealand, but does not occur in the Chatham Islands or islands to the south of New Zealand. The species is common throughout the mainland, excepting in the far north, and occupies a variety of intertidal habitats in mud, gravel and among rocks. It generally occurs in relatively sheltered conditions.

Ovigerous females were collected from Portobello (Dunedin), 13-12-1964 and from Island Bay (Wellington). A readily accessible colony of this species occurring at Island Bay was kept under observation during 1964-66 to determine the limits of the breeding season (Fig. 27). A random sample of 100 mature crabs was collected during the first or second week of each month over this period.

In each of the three years "berried" females occurred in late autumn and winter (April to July). There was no evidence of a summer breeding period. Eggs were incubated for about six weeks and female crabs incubate only one batch of eggs per year. A few females in early berry occurred in May 1966, and in 1964 and 1966 the egg-bearing period extended in to August (Fig. 27). The peak of the breeding season occurred during June and July when usually more than 50% of mature female crabs were ovigerous. During the egg-bearing season in each year, females were more abundant than males in the upper tidal zone, with mainly males present towards the mid-tide area. The overall sex ratio was about equal over the extent of its range at other times of the year.

Fig. 27 Sex Ratio and Seasonal Reproductive
Condition in Mature Females of
Hemigrapsus edwardsi (Hilgendorf)

Sex Ratio and Seasonal Reproductive Condition in Mature Females of *Hemigrapsus edwardsi* (Hilgendorf)



The smallest ovigerous female collected possessed a carapace width of 16.0 mm, but the majority of females are not mature until the carapace width exceeds 19.0 mm. The number of eggs carried by each crab has been estimated as 26,000 (Bennett 1964, p.83). Eggs freshly laid measure 0.37 mm x 0.33 mm (0.35 mm x 0.35 mm) and are light brown in colour, becoming darker as incubation progresses. Eggs about to hatch are almost transparent, but the little remaining yolk is dark brown. Eggs measure 0.42 mm x 0.39 mm at this time.

THE PRE-ZOEAL LARVA

The pre-Zoea larva of this species differs little from that of H. crenulatus. The duration of the pre-zoeal stage is about 15 minutes.

THE FIRST STAGE ZOEAL LARVA

Larvae were hatched from five females collected from the Wellington area, and one female from Portobello. The stage one Zoea larva of H. edwardsi (attributed to Heterograpsus sexdentatus Milne Edwards) was figured by Thomson and Anderton (1921, p.100) but not fully described.

Description

The following description has been shortened to a comparison with the first stage Zoea larva of Hemigrapsus crenulatus described previously.

Cephalothorax (Figs 28, 29)

Total length of larva 1.47 mm. Rostral spine 0.25 mm long and straight; dorsal carapace spine 0.50 mm long, curved posteriorly at its base but slightly recurved anteriorly in its distal half; tip of

Hemigrapsus edwardsi: Stage 1 Zoea Larva

Fig. 28 Stage 1 Zoea; lateral view

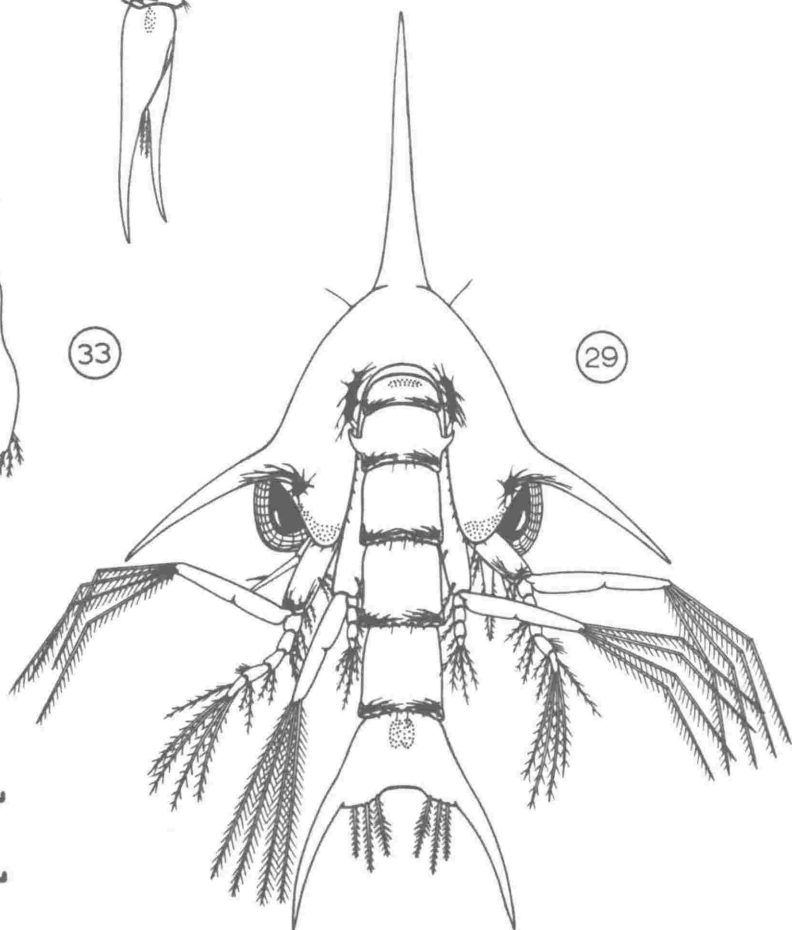
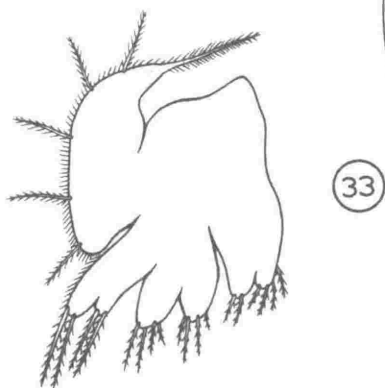
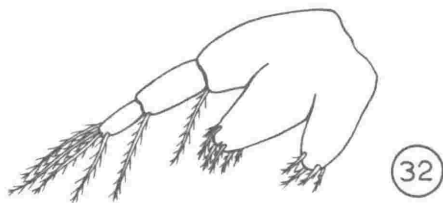
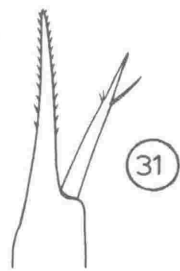
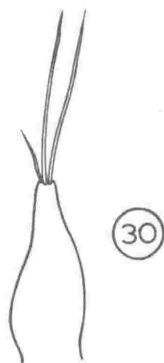
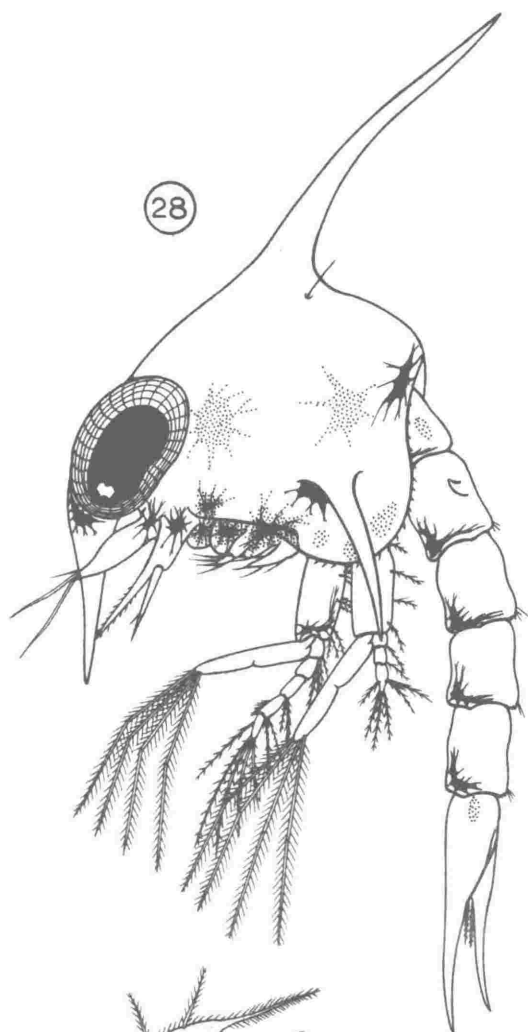
Fig. 29 Stage 1 Zoea; posterior view

Fig. 30 First antenna of left side

Fig. 31 Second antenna of left side

Fig. 32 First maxilla of left side

Fig. 33 Second maxilla of left side



28 , 29
 0.25mm
 30 - 33
 0.125mm

dorsal spine 1.20 mm; lateral carapace spines 0.25 mm long and curved posteroventrally. Carapace otherwise similar to that of H. crenulatus.

Cephalic Appendages (Figs 30-34)

First antenna (Fig. 30) with two long aesthaetes and one shorter aesthaete at its tip.

Second antenna (Fig. 31) with spinous process 0.20 mm long and bearing two rows of short spines as in H. crenulatus; exopod slightly more than one half the length of spinous process, subterminal setae present as in H. crenulatus.

Mandible similar to that of the three species previously described.

First maxilla (Fig. 32) as described for H. crenulatus except that the basal palp segment here lacks fine marginal hairs.

Second maxilla (Fig. 33) with distal pair of endites each bearing four marginal plumose setae; maxilla otherwise similar to that of H. crenulatus.

Thoracic Appendages

First maxilliped (see Figs 28, 29) differs from that of H. crenulatus only in the setation of the endopod; ischium with two inner distal setae; merus with two setae mid-way along its inner margin; carpus bearing two inner distal setae; propodus with two inner distal setae and an outer tuft of fine hairs; dactylus with four long terminal setae and one long seta arising mid-way along its outer margin. All setae of endopod are sparsely plumose.

Second maxilliped (see Figs 28, 29) with armature of setae the same as that of H. crenulatus.

Abdomen (Figs 28, 29)

Abdominal segments each about 0.14 mm long; third to fifth segments with fine dorsal denticles along the posterior margin, but otherwise the same as in H. crenulatus.

Telson (see Fig. 29) 0.35 mm long, very widely forked with slender rami; lateral cornua curved slightly inwards, only slightly curved dorsally and without dorsolateral hairs; tips of cornua 0.38 mm apart. Posterior margin of telson not deeply indented, median cleft poorly differentiated; three plumose posterior telson setae present as in H. crenulatus.

Chromatophore Pattern (Figs 28, 29, Table 4)

Stage one Zoea larvae of Hemigrapsus edwardsi are transparent under low magnification, but black centres of colouration impart a greenish tinge to living larvae. The colour and distribution of chromatophores is listed in Table 4.

LATER LARVAL STAGES

Three stage two Zoea larvae were obtained by moult from the first stage seven days after hatching. These differed mainly in the possession of six natatory setae on the exopods of the first and second maxillipeds, the presence of small buds of the third maxillipeds and of the first and second pereopods, and the possession of rudimentary pleopod buds.

A probable third zoeal stage is briefly described by Thomson and Anderson (1921, p. 100).

TABLE 4

Hemigrapsus edwardsi (Hilgendorf)

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

1.	Supracerebral	-----
2.	Antennular	black
3.	Antennal	black
4.	Labral	2 pairs, dichromatic black to red
5.	Mandibular	dichromatic, black to red
6.	Maxillar	dichromatic, black to red
7.	Maxillipedal	-----
8.	Lateral Intestinal	red (1st abdominal segment and telson only)
9.	Subintestinal	dichromatic, black to yellow

B. Visceral Group

10.	Median Gastric	orange-red to yellow
11.	Precardiac	-----
12.	Subcardiac	-----
13.	Postcardiac	orange-red to yellow

SECONDARY SYSTEM

14.	Posterior Carapacial	black
15.	Posteroventral Carapacial	2 or 3 red
16.	Lateral Carapacial	black, extending into lateral carapace spines as deep yellow
17.	Dorsal Carapace Spine	-----
18.	Maxillipedal	black (1st maxilliped only)
19.	Optic	-----
20.	Median Ocular Centre	black

SUBFAMILY SESARMINAE

Cyclograpsus lavauxi (H. Milne Edwards, 1853)

Cyclograpsus lavauxi is restricted to the New Zealand mainland and occurs from the Bay of Islands in the north to the Otago Peninsula in the south. The species occupies the upper part of the tidal zone, often occurring in supra-littoral rocky habitats among stones and loose pebbles. C. lavauxi is a common species and widely distributed in suitable habitats¹ (Bennett 1964, p. 85).

Ovigerous females are commonly found during the months of October, November, and December. Occasional berried females were collected during September 1967 and January 1964, but the peak of the annual egg-bearing period occurs from October to December inclusive. Ovigerous females showed no signs of regenerating ovaries and only one batch of eggs each year is therefore probable.

Eggs freshly laid measure 0.32 mm x 0.31 mm and are coloured dark purple. This colour becomes lighter during incubation. Eggs ready to hatch measure 0.38 mm x 0.35 mm, and are transparent with strong black eyespots.

THE PRE-ZOEA LARVA

The pre-Zoea larva of Cyclograpsus lavauxi has no plumose processes and differs little from this stage of species described

¹ Cyclograpsus insularum which has been clearly separated by Campbell and Griffin (1966) occurs very sporadically in northern New Zealand, with at least one small population established in a restricted locality at Whakatane (Dell and Marshall 1967).

previously in this paper. The duration of the pre-zoeal stage is from five minutes to 15 minutes.

THE FIRST STAGE ZOEAL LARVA

Larvae on which the following description is based were hatched from four females collected from the Wellington area, two from Castle Point, and two from Whakatane.

Description

First stage Zoea larvae of Cyclograpsus lavauxi are very similar to those of Hemigrapsus crenulatus and H. edwardsi (Varuninae). The following description is therefore shortened to a comparison with these species.

Cephalothorax (Figs 33, 34)

Total length of larva 1.13 mm. Rostral spine 0.25 mm long and straight, or occasionally curved slightly backwards at its tip; dorsal carapace spine 0.40 mm long, curved posteriorly at its base, but slightly recurved anteriorly in its distal half as in Hemigrapsus edwardsi; tip of rostral spine to tip of dorsal spine 0.95 mm; lateral carapace spines 0.18 mm long, almost straight, but depressed and directed posteriorly. Cephalothorax otherwise similar to that of H. crenulatus and H. edwardsi.

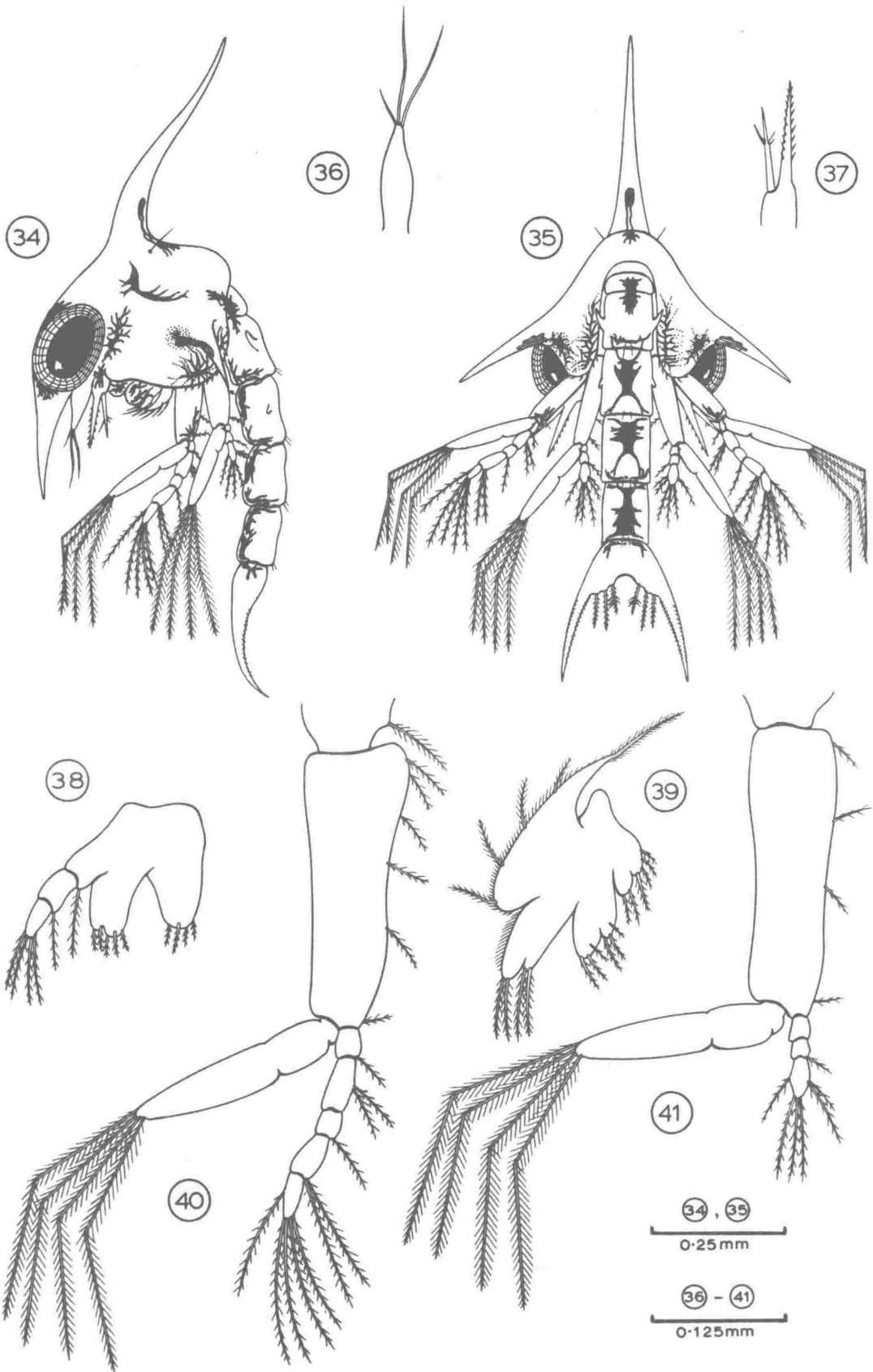
Cephalic Appendages (Figs 36-39)

First antenna (Fig. 36) similar to that described for H. crenulatus and H. edwardsi.

Second antenna (Fig. 37) with spinous process 0.14 mm long and an endopod slightly more than half this length, but appendage is in other details similar to that of H. crenulatus and H. edwardsi.

Cyclograpsus lavauxi: Stage 1 Zoea Larva

- Fig. 34 Stage 1 Zoea; lateral view
- Fig. 35 Stage 1 Zoea; posterior view
- Fig. 36 First antenna of left side
- Fig. 37 Second antenna of right side
- Fig. 38 First maxilla of left side
- Fig. 39 Second maxilla of left side
- Fig. 40 First maxilliped of left side
- Fig. 41 Second maxilliped of left side



Mandible, and first maxilla (Fig. 38) as described for H. edwardsi.

Second maxilla (Fig. 39) with the same armature of fine hairs and fringing marginal setae as in H. crenulatus.

Thoracic Appendages (Figs 40, 41)

First maxilliped (Fig. 40) with only six plumose setae spaced along inner margin of basis; endopod with one plumose seta arising from inner margin of both the ischium and carpus, two such setae arising mid-way along the merus and from the inner distal margin of propodus; first maxilliped otherwise possesses the same number and arrangement of setae as described for this appendage in H. crenulatus and H. edwardsi.

Second maxilliped (Fig. 41) provided with the same setation as that of H. edwardsi.

Abdomen (Figs 34, 35)

Abdominal segments each about 0.12 mm in length; third segment with a small pair of posteriorly directed dorsolateral papillae. Telson (see Fig. 35) 0.28 mm long and widely forked; tips of cornua 0.24 mm apart. Other structural details of the abdomen and telson agree with Hemigrapsus crenulatus.

Chromatophore Pattern (Figs 34, 35, Table 5)

First stage Zoea larvae of Cyclograpsus lavauxi are transparent or light green under low magnification. Black centres of colouration show clearly. The colour and distribution of chromatophores is listed in Table 5.

TABLE 5

Cyclograpsus lavauxi (H. Milne Edwards)

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

1.	Supracerebral	-----
2.	Antennular	-----
3.	Antennal	dichromatic, black to yellow
4.	Labral	dichromatic, black to yellow
5.	Mandibular	2 pairs, dichromatic, black to yellow
6.	Maxillar	-----
7.	Maxillipedal	-----
8.	Lateral Intestinal	dichromatic, black to yellow (1st abdominal segment only)
9.	Subintestinal	dichromatic, black to yellow

B. Visceral Group

10.	Median Gastric	dichromatic, black to yellow
11.	Precardiac	-----
12.	Subcardiac	dichromatic, black to yellow; coalesced with 17 below
13.	Postcardiac	dichromatic, black to yellow

SECONDARY SYSTEM

14.	Posterior Carapacial	-----
15.	Posteroventral Carapacial	dichromatic, black to red
16.	Lateral Carapacial	dichromatic, black to red + yellow in base of lateral carapace spines
17.	Dorsal Carapace Spine	dichromatic, black to yellow; coalesced with 12 above
18.	Maxillipedal	dichromatic, black to yellow (1st maxilliped only)
19.	Optic	dichromatic, black to yellow
20.	Median Ocular Centre	dichromatic, black to yellow

Helice crassa Dana, 1851

Helice crassa occurs throughout New Zealand excepting in the far north, and is restricted to the mainland. The species lives intertidally, often semi-terrestrially, burrowing in mud or earth fringing estuaries or mangrove swamps. H. crassa is mainly gregarious, and occurs abundantly in suitable habitats.

Ovigerous females were collected from the following localities: Mangonui Estuary, North Auckland, 23-10-1964; the Wellington area during 1964 and 1967; Avon River Estuary, Christchurch, 23-8-1964; Portobello, Dunedin 14-12-1964. Mature female crabs incubate eggs during November and December of each year, but occasional ovigerous females were found in late August, September, October, and early January. The majority of female crabs incubate more than one batch of eggs each year. Two females kept in the laboratory hatched one brood of larvae, then relaid eggs immediately and incubated these through to hatching in six weeks without a second contact with a male. The incubation period under natural conditions is not known.

When freshly laid, eggs are brownish yellow in colour and measure 0.26 mm x 0.26 mm. Eggs about to hatch are transparent or light grey-green with black eyespots and chromatophores clearly visible under low magnification. At this time eggs measure 0.32 mm x 0.31 mm.

THE PRE-ZOEAL LARVA

Plumose pre-zoeal processes are lacking as in other species so far described. The first stage Zoea larva moults from the pre-zoeal cuticle within ten minutes of hatching.

THE FIRST STAGE ZOEAL LARVA

Description

The following description is based on larvae hatched from two females collected from each of the four localities listed previously. Only the diagnostic characters which distinguish this larva from that of Cyclograpsus lavauxi are described in detail.

Cephalothorax (Figs 42, 43)

Total length of larva 1.10 mm. Rostral spine 0.19 mm long and straight; dorsal carapace spine 0.35 mm long and curved posteriorly; tip of rostral spine to tip of dorsal spine 0.90 mm; lateral carapace spines 0.15 mm long, directed slightly posteriorly and curved downwards; posterior and ventral margins of carapace fringed with short fine hairs rather than setae; cephalothorax similar in other details to that of Cyclograpsus lavauxi.

Cephalic Appendages (Figs 44-48)

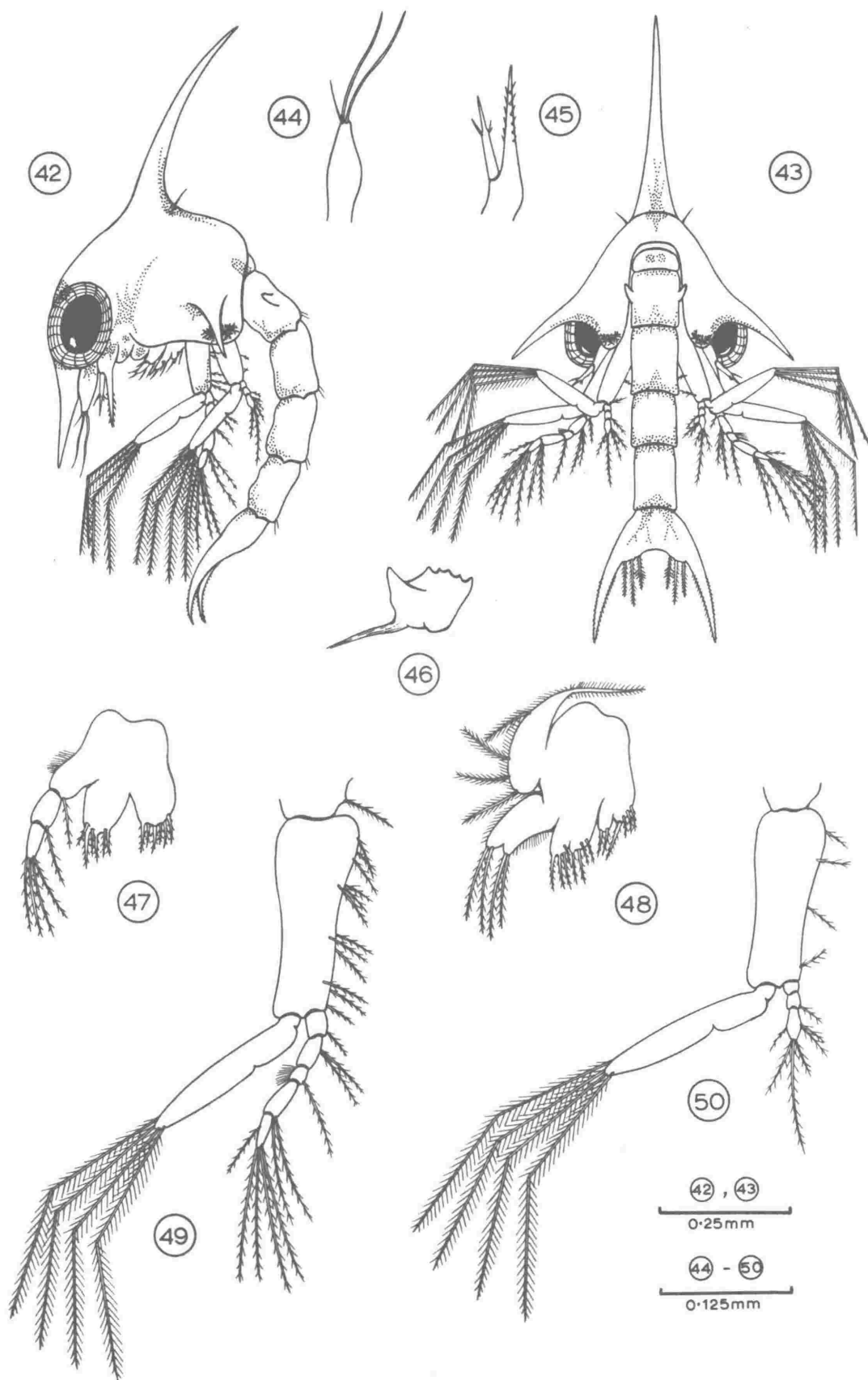
First antenna (Fig. 44), second antenna (Fig. 45) and mandible (Fig. 46) similar to those of C. lavauxi in all details of proportion and armature.

First maxilla (Fig. 47) with proximal and distal endites each bearing six stout plumose setae; palp with lateral tuft of hairs arising from the proximal segment.

Second maxilla (Fig. 48) with first (proximal), second, third, and fourth (distal) endites bearing four, two, four, and four marginal plumose setae respectively; palp with fine hairs fringing both its inner and outer margins.

Helice crassa: Stage 1 Zoea Larva

- Fig. 42 Stage 1 Zoea; lateral view
- Fig. 43 Stage 1 Zoea; posterior view
- Fig. 44 First antenna of left side
- Fig. 45 Second antenna of right side
- Fig. 46 Mandible of left side
- Fig. 47 First maxilla of left side
- Fig. 48 Second maxilla of left side
- Fig. 49 First maxilliped of left side
- Fig. 50 Second maxilliped of left side



Thoracic Appendages (Figs 49, 50)

First maxilliped (Fig. 49) with four groups of three setae arising from inner margin of basis; carpus of endopod with a small tuft of hairs.

Second maxilliped (Fig. 50) differs little from this appendage of species previously described in this paper; three terminal setae of endopod all unequal in length.

Abdomen (Figs 42, 43)

The only significant detail distinguishing the abdomen of Helice crassa from that of Cyclograpsus lavauxi is the absence of dorsolateral papillae on the third abdominal segment. The larval telson of each of these two species are not readily separable.

Chromatophore Pattern (Figs 42, 43, Table 6)

The first stage Zoea larvae of Helice crassa are transparent or light yellow-green under low magnification. The colour and distribution of larval chromatophores are listed in Table 6.

LATER LARVAL STAGES

Larvae in the second zoeal stage possess six natatory setae on the exopods of the first and second maxillipeds and all other characters noted in the second stage Zoea larvae of Hemigrapsus edwardsi. Larvae representing two more advanced stages were obtained from the plankton of the Wellington area. Hence there are at least four zoeal stages in life-history of Helice crassa, but the morphological sequence of larval characters does not suggest more than five zoeal stages.

TABLE 6

Helice crassa Dana

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

1.	Supracerebral	-----
2.	Antennular	red
3.	Antennal	red
4.	Labral	2 pairs, red
5.	Mandibular	red
6.	Maxillar	-----
7.	maxillipedal	-----
8.	Lateral Intestinal	red (1st abdominal segment only)
9.	Subintestinal	red to yellow

B. Visceral Group

10.	Median Gastric	red
11.	Precardiac	-----
12.	Subcardiac	red to yellow; extending into dorsal carapace spine
13.	Postcardiac	-----

SECONDARY SYSTEM

14.	Posterior Carapacial	-----
15.	Posteroventral Carapacial	black
16.	Lateral Carapacial	red to yellow; extending into lateral carapace spines
17.	Dorsal Carapace Spine	-----
18.	Maxillipedal	red to yellow (1st maxilliped only)
19.	Optic	red
20.	Median Ocular Centre	red

NOTE: Red chromatophores may appear black when contracted.

SUBFAMILY PLAGUSIINAE

Plagusia chabrus (Linnaeus, 1764)

Plagusia chabrus or the "red rock crab" occurs throughout the north island of New Zealand and in the northern part of the south island, but does not occur in the Chatham Islands or islands to the south of the mainland. Overseas records include Australia, Tasmania, South Africa, Chile, Juan Fernandez, and the Tongan or Friendly Islands (Garth 1957).

The usual habitat is exposed rocky coasts or wave-washed reefs. The species occurs intertidally, but is more abundant subtidally in shallow water where it occupies deep crevices often shared by the spiny lobster Jasus edwardsii (Hutton). The crabs are alert, fast-running, and rarely captured, but are often observed by skindivers or caught in baited lobster pots. P. chabrus rarely leaves the water excepting at night when specimens may be captured while foraging over rock platforms at low tide. Adult crabs are larger than those of other New Zealand grapsid species, and are difficult to keep in captivity, as a constant flow of cool, turbulent seawater is required for survival.

One ovigerous female was collected at Whakatane 5-12-1967, and returned alive to the Victoria University Marine Laboratory at Wellington where the larvae hatched 16-12-1967. Ovigerous females were also collected during the months of November, December, January, and February 1965-68, from Castle Point, the Wellington area, and Kaikoura. All but two of these specimens died before the larvae hatched. Eggs freshly laid measure 0.39 mm x 0.39 mm and

are dull orange or brick red in colour. Eggs ready to hatch measure 0.47 mm x 0.45 mm with the larval chromatophores present giving these a light green colour. Black larval eyespots and chromatophores often give mature eggs a blue iridescence in daylight. The period of incubation is not known, but ovigerous females collected during November and December frequently possessed gravid ovaries.

THE PRE-ZOEAL LARVA

The pre-zoeal cuticle lacks plumose processes as in the species described previously. Molt from the pre-zoeal cuticle occurs almost immediately after hatching.

THE FIRST STAGE ZOEAL LARVA

Description

The following description is based on larvae hatched from the one female collected at Whakatane, and two females obtained from Island Bay, Wellington, during February, 1968.

Cephalothorax (Figs 51-57)

Total length of larva 1.56 mm. Rostral spine 0.53 mm long, straight, curved slightly forwards through its distal half and bearing a variable number of small tubercles; dorsal carapace spine smooth, straight, and usually 0.60 mm long, but may be as short as 0.35 mm, commonly malformed with multispinous tip if shorter than 0.60 mm (see Figs 53-57); tip of rostral spine to tip of dorsal spine 1.56 mm; lateral carapace spines 0.22 mm long and slightly depressed, provided with a few basal hairs and a number of small tubercles irregularly arranged. Carapace with one median frontal tubercle anterior to

base of dorsal carapace spine; posterolateral regions of carapace extended ventrally as a conspicuous lobe; carapace margins without hairs or setae; one pair of dorsolateral setae situated just behind dorsal carapace spine. Eyes large and sessile.

Cephalic Appendages (Figs 58-62)

First antenna (Fig. 58) with two long aesthaetes, one shorter aesthaete, and one fine hair arising from its tip.

Second antenna (Fig. 59) comprises a robust spinous process and a reduced exopod; spinous process 0.37 mm long, often curved posteriorly, and bearing two rows of 10 or 11 small spines along its distal two-thirds; exopod 0.06 mm in length and produced distally into one long aesthaete and two very small setae.

Mandible (Fig. 60) with bicuspid incisor process and a strongly ridged molar surface.

First maxilla (Fig 61) with proximal and distal endites bearing four and five stout plumose setae respectively; cleft separating these endites fringed with fine hairs; palp provided with six setae as in species previously described.

Second maxilla (Fig. 62) with four endites each bearing five stout plumose setae arranged as illustrated in Fig. 62. Appendage otherwise similar to that of the previous six species, but margins here provided with fine hairs in regions where setae do not occur.

Thoracic Appendages (Figs 63, 64)

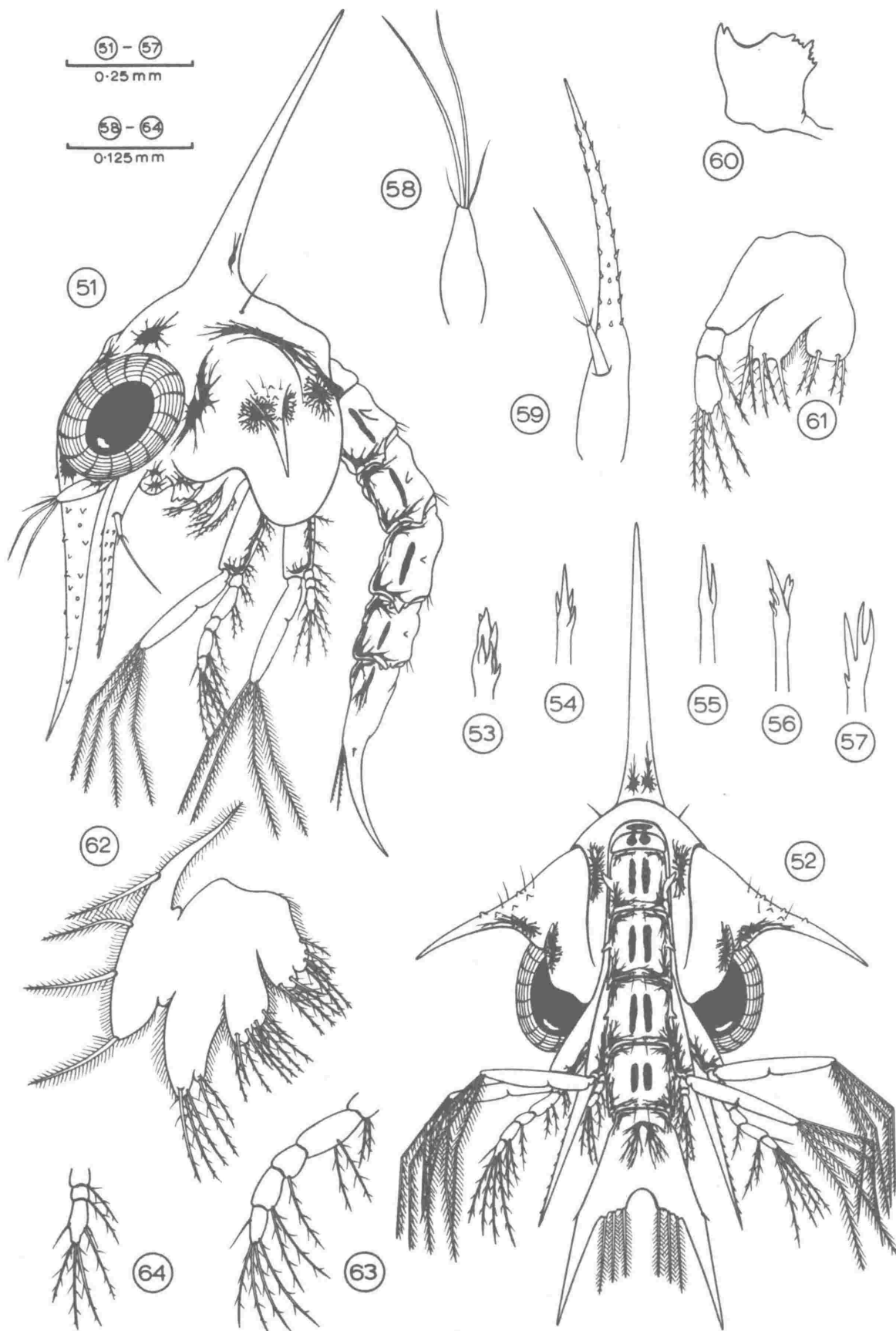
First and second maxillipeds (see Figs 51, 52) differ from those of species earlier described only in details of setation. Endopod of first maxilliped (Fig. 63) with ischium bearing two inner plumose setae; dactylus with one smooth hair-like seta arising mid-way along

Plagusia chabrus: Stage 1 Zoea Larva

- Fig. 51 Stage 1 Zoea; lateral view
- Fig. 52 Stage 1 Zoea; posterior view
- Figs 53 Dorsal carapace spine; some variations
to 57 in length and form of its tip
- Fig. 58 First antenna of left side
- Fig. 59 Second antenna of left side
- Fig. 60 Mandible of left side
- Fig. 61 First maxilla of left side
- Fig. 62 Second maxilla of left side
- Fig. 63 Endopod of first maxilliped of left side
- Fig. 64 Endopod of second maxilliped of left side

51 - 57
0.25 mm

58 - 64
0.125 mm



its outer margin. Endopod of second maxilliped (Fig. 64) with one smooth hair-like seta arising mid-way along outer margin of terminal segment.

Abdomen (Figs 51, 52)

First abdominal segment 0.10 mm long and without spines, setae, or papillae; second segment 0.11 mm long and bearing a pair of forwardly directed dorsolateral papillae and two small dorsal hairs; third, fourth and fifth segments each 0.14 mm long and provided with a pair of small posteriorly directed dorsolateral papillae and two small dorsal hairs; second and third segments with short lateral spines usually bilobed; those of fourth and fifth segments trilobed.

Telson (see Fig. 52) more or less triangular, 0.43 mm in length, with 0.33 mm separating the tips of the lateral cornua; telson plate 0.16 mm long; lateral cornua slender and not curved inwards, bearing one tiny lateral spine basally; cornua without longitudinal rows of hairs or setae. Median cleft in posterior margin of telson relatively deep and crescent-shaped; three pairs of posterior plumose setae all about equal in length; inner setae without strong hairs centrally.

Chromatophore Pattern (Figs 51, 52, Table 7)

Stage one Zoea larvae of Plagusia chabrus are intensely coloured and appear black or very dark green under low magnification. The chromatophore pattern is listed in Table 7.

TABLE 7

Plagusia chabrus (Linnaeus)

Chromatophore Pattern of Stage One Zoea Larva

PRIMARY SYSTEM

A. Neural Group

- | | | |
|----|--------------------|--|
| 1. | Supracerebral | dichromatic, black to yellow |
| 2. | Antennular | dichromatic, black to yellow |
| 3. | Antennal | ----- |
| 4. | Labral | 2 pairs, dichromatic, black to yellow |
| 5. | Mandibular | dichromatic, black to yellow |
| 6. | Maxillar | ----- |
| 7. | Maxillipedal | dichromatic, black to yellow; often
coalesced with 18 below |
| 8. | Lateral Intestinal | dichromatic, black to yellow;
segment 1 coalesced with 13 below |
| 9. | Subintestinal | dichromatic, black to yellow |

B. Visceral Group

- | | | |
|-----|----------------|---|
| 10. | Median Gastric | dichromatic, black to yellow |
| 11. | Precardiac | ----- |
| 12. | Subcardiac | ----- |
| 13. | Postcardiac | dichromatic, black to yellow;
coalesced with 8 in 1st abdominal
segment |

SECONDARY SYSTEM

- | | | |
|-----|---------------------------|---|
| 14. | Posterior Carapacial | dichromatic, black to yellow |
| 15. | Posteroventral Carapacial | ----- |
| 16. | Lateral Carapacial | 2 pairs, dichromatic, black to yellow |
| 17. | Dorsal Carapace Spine | 2 pairs, dichromatic, black to yellow |
| 18. | Maxillipedal | dichromatic, black to yellow; often
coalesced with 7 above |
| 19. | Optic | dichromatic, black to yellow |
| 20. | Median Ocular Centre | dichromatic, black to yellow |

DISCUSSION

Breeding and Incubation

All New Zealand grapsid crabs breed in late spring and summer with the exception of Hemigrapsus edwardsi which incubates eggs during late autumn and winter (Fig. 27). In this species there was no evidence of a summer breeding period, which has been suggested by Bennett (1964, p. 83). The tendency for ovigerous females of H. edwardsi to live around the upper limits of its intertidal range is even more marked in Helice crassa. In H. crassa females bearing mature eggs were commonly found living in burrows around spring high water level, with the majority of males and non-ovigerous females occurring lower down the intertidal zone. This feature was noted by Bennett (1964).

Evidence obtained during this study suggests that Planes marinus, Hemigrapsus crenulatus, Helice crassa, and Plagusia chabrus incubate more than one batch of eggs during a breeding season.

Detailed work on the breeding season of Leptograpsus variegatus in Chile has been published by Antezana, Fagetti, and Lopez (1965). These authors found that ovigerous females occurred from October through to February, with the majority of females bearing eggs during October, November, and December. Compared with the November to January incubation period noted here for New Zealand specimens, the breeding period in Chile is about one month earlier and extends over a longer period of time (Antezana, Fagetti, and Lopez 1965, pp. 46-7).

Number of Zoea Larval Stages

All evidence suggests that New Zealand grapsid crabs possess at least four, and possibly five zoeal stages in their life-histories.

The absence of buds of the third maxillipeds, pereopods, and pleopods in stage one suggests that more than two zoeal stages exist. The rudimentary nature of these appendages in stage two Zoea larvae reared from the eggs of Hemigrapsus edwardsi and Helice crassa further supports this claim. Three zoeal stages are rare among grapsid crabs, and this number is known only in Sesarma reticulatum Say (Costlow and Bookhout 1962). All remaining species described possess four or five stages, with the first stage Zoea larva of each species being as far advanced in development as those hatched from New Zealand species which bear eggs of similar size. Larvae of Hemigrapsus edwardsi and Helice crassa belonging to third, fourth, and possibly fifth zoeal instars were obtained from the Wellington plankton.

Larval Migration to the Chatham Islands

Knowledge of the larval life-histories of New Zealand Grapsidae throws little further light on the absence of this family from suitable habitats at the Chatham Islands about 450 miles east of New Zealand (Dell 1960). Occasional specimens of the oceanic genus Planes occur (Bennett 1964, p. 81) but these probably arrive as juveniles or adults attached to flotsam. Since four or five zoeal stages and a Megalopa larval stage probably occur in New Zealand grapsid crabs, the length of planktonic larval life would be about 30 to 40 days as in Cyclograpsus cinereus Dana (Costlow and Fagetti 1967).

Surface currents flow almost directly eastwards from New Zealand to the Chatham Islands. Based on drift card releases, Brodie (1960, p. 246) calculated the most rapid rate of drift around the New Zealand coastline as 10.2 miles per day over a distance of 22 miles. At this rate planktonic larvae would travel only from 300 miles to 400 miles if entirely favourable conditions persisted from the

time of hatching to the time of metamorphosis to the first juvenile crab stage. The quickest recoveries of drift cards from the Chatham Islands after release from the east coast of New Zealand are 7-11-1953 to 24-3-1954 (137 days), and 25-8-1953 to 19-1-1954 (147 days) (E. W. Dawson, pers. comm.). All other recorded release to recovery times were considerably longer. Hence the possibility of grapsid larvae from the New Zealand mainland reaching the Chatham Islands within six weeks appears remote, especially since brachyuran larvae are most likely unable to prolong planktonic life until a suitable substrate is found (Wear 1967).

Dell (1960) noted that every brachyuran species recorded from the Chatham Islands is also known from the mainland between Cook Strait and Banks Peninsula. The faunal list includes species with five Zoea larval stages (Cancer novaezelandiae (Jacquinot)), and others with only two Zoea larval stages (Notomithrax peroni (Milne Edwards), N. ursus (Herbst), Eurynolambrus australis Milne Edwards and Lucas). (Wear, unpublished data). Two further species present (Pilumnus lumpinus Bennett, P. novaezelandiae Filhol) have direct development, with planktonic life almost completely abbreviated (Wear 1967). Hence the presence or absence of brachyuran species in the Chatham Islands fauna is apparently unrelated to the length of planktonic larval life and larval dispersal. However, Leptograpsus variegatus and Plagusia chabrus are widely distributed geographically, and occur in areas separated by extensive oceans. The absence of these two species from the Chatham Islands fauna is surprising and unexpected (Dell 1960).

Affinities of the Larvae

Zoea larvae hatched from New Zealand grapsid crabs fall into three distinct groups following the grouping of adult genera into the

subfamily Grapsinae (Leptograpsus, Planes), the subfamilies Varuninae and Sesarminae (Cyclograpsus, Helice, Hemigrapsus), and the subfamily Plagusinae (Plagusia).

The Zoea larvae of Leptograpsus variegatus and Planes marinus are almost inseparable from those of Planes minutus (Linnaeus) (Hyman 1924; Lebour 1944), Pachygrapsus marmoratus (Fabricius) (Hyman 1924; Bourdillon-Casanova 1960), and P. transversus (Gibbes) (Lebour 1944). These all show close affinities with larvae of the genera Grapsus (Aikawa 1937; Gohar and Al-Kholy 1957) and Metopograpsus (RajaBai 1961) in the subfamily Grapsinae, and all form a distinct group among grapsid larvae. Outside the family Grapsidae, this group of larvae also share many distinctive characters with larvae of genera of the family Ocypodidae (Wear, in press, b).

Zoea larvae of New Zealand crabs belonging to the genera Cyclograpsus, Helice, and Hemigrapsus differ only in minor larval characters. These larvae show close relationship with larvae previously described from genera in the subfamilies Varuninae and Sesarminae, especially those of Chasmagnathus (Boschi, Scelzo, and Goldstein 1967), Cyclograpsus (Costlow and Fagetti 1967), Hemigrapsus (Aikawa 1929; Hart 1935), and Heterograpsus (Aikawa 1929) described from elsewhere. Among larvae of other brachyrhynchous crabs they show the closest affinities with those of genera in the families Ocypodidae (Wear in press, b) and Gecarcinidae (Cabrera 1966).

The first stage Zoea of Plagusia chabrus differs from those of P. dentipes de Haan (Aikawa 1937) and Percnon gibbesi (Milne Edwards) (Lebour 1944) only in detail. The larvae of these three species show no clear affinities with other grapsid Zoea larvae or with larvae of other brachyrhynchous crabs, and together they form a relatively distinct group.

Bourdillon-Casanova (1960, pp. 187-8) summarised the characters of all grapsid Zoea larvae described, discussed larval affinities, and grouped these larvae according to the following key:

1. Lateral carapace spines absent
 - (1) Antennal exopod rudimentary
Telson cornua broad, lateral spines present:
Pachygrapsus, Planes
 - (2) Antennal exopod developed
Telson cornua slender, lateral spines absent:
Sesarma, Grapsus, Gaetice
2. Lateral carapace spines present
 - (1) Antennal exopod rudimentary:
Percnon
 - (2) Antennal exopod developed
 - a. Lateral protuberances on abdominal segments
2 or 2 and 3:
Brachynotus, Heterograpsus, Hemigrapsus
 - b. Lateral protuberances on abdominal segments
2, 3 and 4:
Eriocheir, Plagusia

The above key, based on ten genera and 19 species, conforms only in part with the classification of adults listed by Balss (1957, pp. 1665-70). In some cases Bourdillon-Casanova has used minor characters to separate larvae which are better grouped on overall similarities. For example the Zoea of Percnon gibbesi and that of Plagusia dentipes both possess long, straight rostral, dorsal and

armed lateral carapace spines, a similarly shaped abdomen and telson, and basically the same type of antenna. However, Bourdillon-Casanova separated these two species on a small difference in the degree of development of the antennal exopod. General similarities between the larva of Eriocheir japonicus de Haan (Aikawa 1929) and those of Brachynotus, Hemigrapsus, and Heterograpsus clearly suggest that Eriocheir more properly belongs with the latter three genera, than with Plagusia as suggested by Bourdillon-Casanova (1960).

Since the above (1960) summary, larvae have been described from four additional genera and the following nine species:

	<u>AUTHOR</u>
<u>Chasmagnathus granulata</u> Dana	Boschi, Scelzo, & Goldstein 1967
<u>Cyclograpsus cinereus</u> Dana	Costlow & Fagetti 1967
<u>Grapsus strigosus</u> Herbst	Gohar & Al-Kholy 1957
<u>Metasesarma rousseauxii</u> A. Milne Edwards	RajaBai 1961
<u>Metopograpsus messor</u> (Forskäl)	RajaBai 1961
<u>Plagusia depressa squamosa</u> (Herbst) - pre-Zoea only	RajaBai 1961
* <u>Sesarma cinereum</u> (Bosc)	Costlow & Bookhout 1960
* <u>Sesarma reticulatum</u> Say	Costlow & Bookhout 1962
<u>Sesarma tetragonum</u> (Fabricius)	RajaBai 1961

* Previously described by Hyman (1924)

Larvae of a further two genera and seven species are described in this paper.

The 33 species from which Zoea larvae are now known comprise 17 genera, which is 41% of the 39 grapsid genera recognised by Balss (1957). These larvae readily separate into four groups according

to the key tabulated below. In this key, several characters are used to define each of the four major groups in order to emphasise similarities of larvae within each group. The only apparent anomalies lie in the Zoea of Plagusia dentipes in which the presence of a distinct posterolateral carapace lobe is uncertain (Aikawa 1937, p. 135, Fig. 35a), and in Grapsus grapsus (Aikawa 1937, p. 131, Fig. 31) which possesses all characters common to other known larvae of the subfamily Grapsinae except the present of distinctive posterolateral ridges on the third to fifth abdominal segments.

A KEY TO MAJOR GROUPS OF ZOEAE

LARVAE WITHIN THE FAMILY GRAPSIDAE

1. Lateral carapace spines absent; dorsal carapace spine short and stout
 - (a) Antennal spinous process robust, exopod rudimentary or less than one third the length of spinous process; telson more or less rectangular with cornua short and stout, usually with 1 or 2 short lateral setae.
 - x Abdominal segments 3 to 5 with lobed posterolateral ridges:

Grapsus strigosus, Leptograpsus (1 sp.),
Metopograpsus (1 sp.), Pachygrapsus (2 spp.),
Planes (2 spp.).
 - o Abdominal segments 3 to 5 without posterolateral ridges:

Grapsus grapsus.
 - (b) Antennal spinous process small, exopod developed to about half the length of spinous process; telson widely forked with cornua long and slender, lateral telson setae absent:

Gaetice (1 sp.), Metasesarma (1 sp.),
Sesarma (5 spp.).

2. Lateral carapace spines present; dorsal carapace spine long and slender

- (a) Lateral carapace spines curved downwards and without hairs or tubercles; dorsal carapace spine curved; posterolateral carapace margins not expanded ventrally; antennal exopod about half the length of spinous process:

Brachynotus (1 sp.), Chasmagnathus (1 sp.),
Cyclograpsus (2 spp.), Eriocheir (2 spp.),
Helice (1 sp.), Hemigrapsus (5 spp.),
Heterograpsus (2 spp.).

- (b) Lateral carapace spines straight and bearing hairs or prominent tubercles; dorsal carapace spine straight; posterolateral carapace margins expanded ventrally as a conspicuous lobe; antennal exopod less than one quarter the length of spinous process:

Percnon (1 sp.), Plagusia (2 spp.).

The four groups of genera based on Zoea larval characters given here agree well with the separation of adult genera into subfamilies (Balss 1957). Groups 1(a), 2(a), and 2(b), are each distinct, but genera making up group 1(b) share larval characters of those included in groups 1(a) and 2(a).

Group 1(a) above comprises only larvae of the subfamily Grapsinae, group 2(a) includes larvae of genera belonging to the subfamilies Varuninae (Brachynotus, Hemigrapsus, Heterograpsus, Eriocheir) and Sesarminae (Chasmagnathus, Cyclograpsus, Helice), and group 2 (b) comprises the two genera at present making up the subfamily Plagusiinae. The affinities these groups of larvae show with larvae of other brachyuran families have been previously

discussed (p.255). Group 1 (b) also includes larvae of genera from the subfamilies Varuninae (Gaetice) and Sesarminae (Metasesarma, Sesarma). These Zoea larvae lack carapace spines as in the Grapsinae (group 1 (a)), but all other diagnostic larval characters agree with those of genera placed in group 2(a). Hence known Zoea larvae of the subfamilies Varuninae and Sesarminae are divided into two related groups separated by the presence or absence of lateral carapace spines and the form of the dorsal carapace spine.

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ABSTRACT

1. Abbreviated or direct development is described in Pilumnus novaezelandiae Filhol, 1886 and P. lumpinus Bennett, 1964 (Xanthidae, Pilumninae) from New Zealand. Embryonic development is separated into Nauplius, Metanauplius, and embryonic Zoea stages. In P. novaezelandiae, larvae hatch at a Megalopa stage and are retained beneath the pleon of the female crab. The Megalopa larva and first five juvenile crab stages are described. In P. lumpinus emergent larvae are advanced, much-modified, and non-natatory Zoeae which are not retained by the parent. The Zoea and Megalopa larvae of this species are described. Abbreviated development has little phylogenetic significance among Brachyura, and has probably evolved as a response to habitat requirements of adult crabs.

2. A brief account is given of the systematics and distribution of the New Zealand xanthid crabs Heterozius rotundifrons A. Milne Edwards, 1867, Ozius truncatus H. Milne Edwards, 1834, and of Heteropanope (Pilumnopeus) serratifrons (Kinahan, 1856). Keys are given to the Zoea larvae of New Zealand xanthid Brachyura and to the Megalopa larvae of Heterozius rotundifrons and Ozius truncatus. Notes are given on the seasonal breeding cycle of Heterozius rotundifrons, and the pre-Zoea larva, two Zoea larval stages, and the Megalopa larva reared in the laboratory are described. Ozius truncatus possesses a pre-Zoea larva, four Zoea larval stages, and a Megalopa larva. These have been reared and are described. A key is given for the separation of the Zoea larval stages. The pre-Zoea larva and first stage Zoea larva of Heteropanope (Pilumnopeus) serratifrons are described. There are probably four zoeal stages in the larval development of this species.

3. The characters of Zoea larvae of the family Xanthidae described up to the present time are critically analysed and considered in relation to the status of currently accepted adult genera and species, the generic groupings used by Monod (1956), and the generic composition of the subfamilies proposed by Balss (1957). Xanthid Zoea larvae fall into two natural groups of genera based on larval characters, the most important being the length of the antennal exopod in relation to that of the spinous process. The first group is equivalent to the subfamily Xanthinae as reconstituted by Balss (1957), but there is no larval evidence suggesting that the "Panopean" genera should be separated from the "Xanthian" genera as suggested by Monod (1956). A second natural group is formed by larvae of the subfamily Menippinae as in Balss (1932, 1957), the subfamily Pilumninae of Balss (1957), and the genus Geryon. Larvae of genera in the subfamily Trapeziinae Miers should be removed from the section Hyperolissa and included in this second natural group. Zoea larvae described from the genera Heteropanope and Pilumnopeus form a separate branch of the second group. Zoea larval evidence does not support Monod's (1956) separation of Eriphia from the "Menippian" group of genera.
4. The first stage Zoea larva of Hemiplax hirtipes (Jacquinot, 1853) is described, and present knowledge concerning larvae of crabs of the family Ocypodidae is summarized and discussed. No diagnostic character is common to all ocypodid Zoea larvae, but affinities are shown with those of the families Hymenosomidae, Pinnotheridae, and Grapsidae.
5. Pre-Zoea and first stage Zoea larvae hatched from the grapsid crabs Leptograpsus variegatus (Fabricius, 1793), Planes marinus Rathbun, 1915, Hemigrapsus crenulatus (H. Milne Edwards, 1837), H. edwardsi (Hilgendorf, 1882), Cyclograpsus lavauxi H. Milne Edwards, 1853, Helice crassa Dana, 1851, and Plagusia chabrus (Linnaeus, 1764) from New Zealand are described. A key is

given for the separation of these larvae. Known Zoea larvae of the family Grapsidae show close affinities with those of the brachyrrhynchous families Ocypodidae and Gecarcinidae, and fall into four groups based on larval characters. This system of larval classification agrees with the present arrangement of adult genera into subfamilies except for a division among larvae of the subfamilies Varuninae and Sesarminae. The length of larval life and larval dispersal probably has no bearing on the presence or absence of certain New Zealand species at the Chatham Islands.