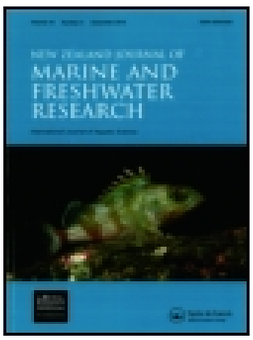

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LIFE-HISTORY STUDIES ON NEW ZEALAND BRACHYURA

3. FAMILY OCYPODIDAE. FIRST STAGE ZOEA LARVA OF *HEMIPLAX HIRTIPES* (JACQUINOT, 1853)

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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).

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 × 0.24 mm when freshly laid and are dark brown in colour. Eggs ready to hatch measure 0.28 mm × 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, 1968, and in press).

LARVAL DEVELOPMENT

THE PRE-ZOEA 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). First stage Zoea larvae moult from the pre-zoeal cuticle within 5 or 10 minutes from the time of hatching.

FIRST STAGE ZOEA 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 8 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, straight; dorsal carapace spine 0.46 mm long, 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). Carapace with a pair of dorsolateral setae situated just behind the dorsal carapace spine; posterior margins fringed with fine, very 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.

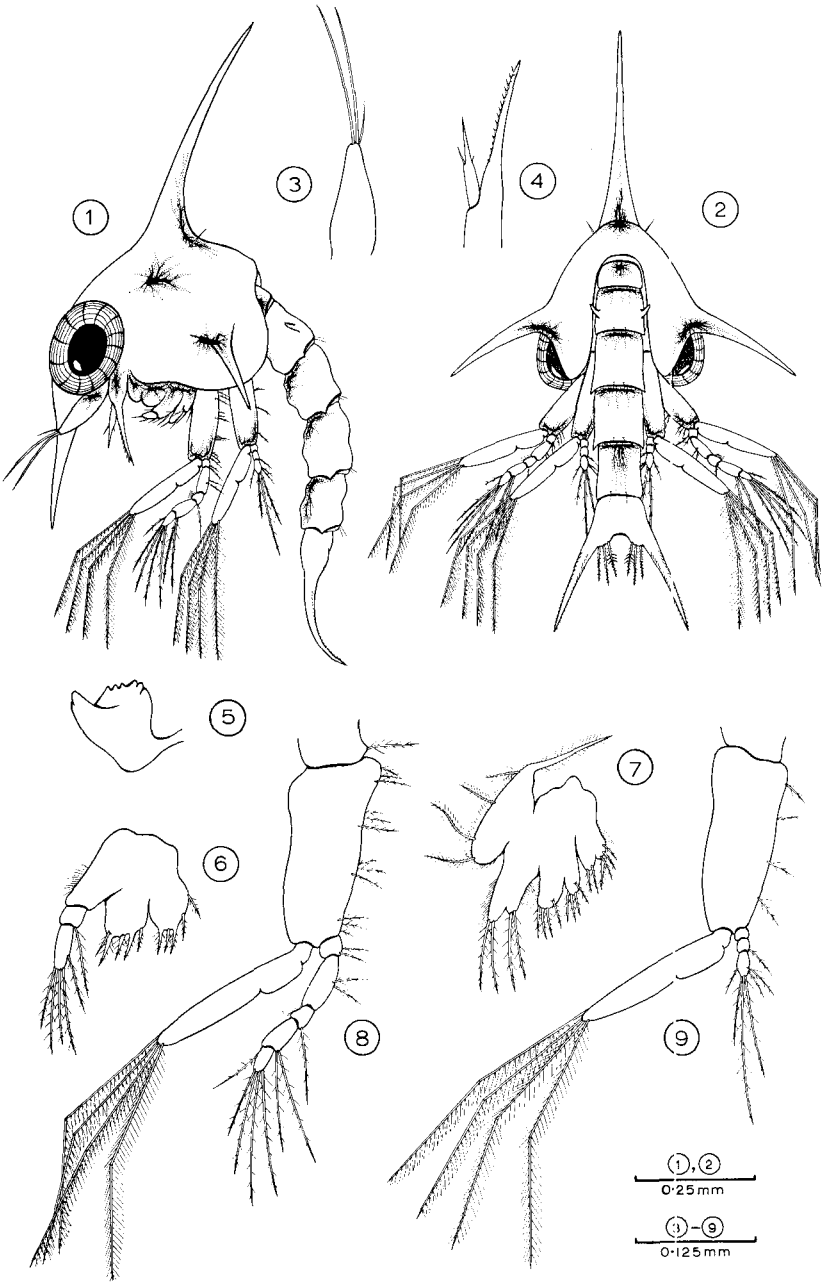
Second maxilliped (Fig. 9) similar to the first, but with a much shorter endopod of three segments. Coxa without setae. Basis with four short, sparsely plumose setae spaced along its inner margin. Endopod only one third the length of endopod of first maxilliped: first segment without setae; second segment 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, pereiopods, or 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 segment with a paired lateral papilla or protuberance as in all known brachyuran larvae; second to fifth segments with a pair of rudimentary ventrolateral 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)



FIGS 1–9—*Hemiplax hirtipes:* Stage 1 Zoea larva.

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

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 coloration 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 1968, and in press).

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. 525–6).

Zoea larvae of 14 species belonging to the family Ocypodidae have been described. These species cover the three subfamilies Ocypodinae, Scopimerinae, and Macrophthalminae, and 7 of the 18 extant genera recognised by Balss (1957) are represented. Balss (1957, pp. 1663–5) grouped these seven genera as follows:

SUBFAMILY OCYPODINAE

Ocypode	Weber
Uca	Leach

SUBFAMILY SCOPIMERINAE

Dotilla	Stimpson
Ilyoplax	Stimpson
Scopimera	de Haan

SUBFAMILY MACROPHTHALMINAE

Hemiplax	Heller
Macrophthalmus	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 ZOEA LARVAE OF THE FAMILY OCYPODIDAE

	AUTHOR
1. Lateral carapace spines absent	
(1) 4th abdominal segment expanded laterally	
(a) Antennal exopod reduced:	
Uca annulipes (Latreille) = *Gelasimus annulipes* Latreille	Chhapger 1956
(b) Antennal exopod not reduced: (no known larvae)	
(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 blanfordi Alcock	RajaBai 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 (Forskäl)	Ramadan 1940; Gohar & Al-Kholy 1957

(2) 5th abdominal segment not expanded

(a) Antennal exopod reduced:

Ilyoplax pusillus (de Haan) = *Tympanomerus pusillus* de Haan	Aikawa 1929
Ocypode gaudichaudii M. E. & Lucas	Crane 1940
Ocypode platytarsis Milne Edwards	Rajabai 1951
Scopimera globosa de Haan	Aikawa 1929

(b) Antennal exopod not reduced:

Hemiplax hirtipes (Jacquinot)	Wear, present paper

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 Grapsidae (Wear, in press), 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, pp. 525–6), and this distinctive larval group can now be extended to include *Dotilla sulcata* (Forskäl) 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 the brachyrhynchous 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) and this 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 RajaBai (1959) possesses no lateral carapace spines, has a well developed antennal exopod, and shows larval affinities closer to the Sesarminae and Varuninae (Wear, in press) than to *D. sulcata*. The marked differences between larvae of the two species of *Dotilla* suggest 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), and is formed by three species and 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 *Ilyoplax 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).

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*The most convincing evidence I have found of this apparent relationship is in the first Zoea of *Mictyris longicarpus* Latreille (Mictyridae) described by Cameron (1965) which shows remarkably close affinities with larvae of the hymenosomid genus *Halicarcinus* from New Zealand. *Mictyris longicarpus* Zoeae lack both lateral and dorsal carapace spines thereby supporting Balss' (1957) listing of *Mictyris* as comprising a family distinct from the Ocypodidae.

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 desiccation, wave action, and sand abrasion 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 brachyrhynchous 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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