

Comparative morphology of the feeding appendages of four mesozooplankton species in the Sundays River estuary

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The morphology of feeding appendages of the coexisting estuarine copepods, *Pseudodiaptomus hessei* and *Acartia longipatella*, and mysids, *Rhopalophthalmus terranatalis* and *Mesopodopsis wooldridgei*, were examined and compared as an aid in elucidating dietary differences. The robust mandibles of *P. hessei* copepodids compared to the more pointed and slender teeth with no molar region, of *A. longipatella* suggest that the latter species relies on more fragile food particles. Mandible edge indices indicate, however, omnivorous feeding by both species. No clear dietary differences could be deduced from the dimensions of the second maxillae of these copepods. Mandible edge indices calculated for the mysid species suggest a more herbivorous feeding mode in *M. wooldridgei* and a more carnivorous one in *R. terranatalis*, supporting previous studies on their diets. No interspecific differences between the mysid size classes were evident from edge indices. Significant increments in setae and setule lengths and spacing with increasing mysid size class were evident, reflecting differences in food particle sizes utilized. The morphological differences in the feeding apparatus could reflect differences in the diets between species and indicate differences in food particle sizes utilized by the various developmental stages within species. These differences in diet should reduce inter- and intraspecific competition.

Die morfologie van die voedingsapparaat van die kopepoda-spesies, *Pseudodiaptomus hessei* en *Acartia longipatella* en mysidacea-spesies, *Rhopalophthalmus terranatalis* en *Mesopodopsis wooldridgei* is ondersoek en vergelyk as 'n hulpmiddel om verskille in dieet toe te lig. Die robuuste kake van *P. hessei* in vergelyking met die meer gepunte en delikate tande, sonder enige maaltand-gedeelte, van *A. longipatella*, dui op die verbruik van meer delikate voedseldeeltjies deur laasgenoemde. Kaak-indekse dui egter op 'n omnivoriese voedingswyse deur beide spesies. Dieetverskille tussen die twee kopepoda-spesies word nie deur afmetings van die sekondêre maksilla geïllustreer nie. Kaak-indekse vir die mysidacea-spesies dui op 'n meer herbivoriese voedingswyse vir *M. wooldridgei* in vergelyking met 'n meer karnivoriese voedingswyse in *R. terranatalis*, wat steun verleen aan vorige studies. Geen interspesifieke verskille tussen die kaak-indekse van die mysidacea grootte-klasse is gevind nie. Betekenisvolle toenames in die lengtes en spasiëring van setae en sekondêre setae is gevind met 'n toename in mysidacea grootte-klasse, wat dui op verskille in die grootte van voedseldeeltjies gebruik. Bogenoemde morfologiese verskille kan dui op dieetverskille tussen spesies, asook verskille in grootte van voedseldeeltjies verbruik deur verskillende ontwikkelingsstadia van 'n bepaalde spesie. Hierdie dieetverskille behoort inter- en intraspesifieke kompetisie te verminder.

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Mesozooplankton in the Sundays River estuary is dominated by the mysids, *Rhopalophthalmus terranatalis* and *Mesopodopsis wooldridgei* (formerly *M. slabberi*, Wittmann 1992), and the calanoid copepods, *Pseudodiaptomus hessei* and *Acartia longipatella* (Wooldridge & Bailey 1982). Since these species have overlapping distributions in the estuary (Wooldridge & Bailey 1982), it can be hypothesized that they utilize different food resources to reduce competition and this may be reflected in structural differences in the morphology of their respective feeding appendages. To quote Schoener (1982) '... data on morphological differences between species, traditionally considered inferior to data on resource use itself, could in fact be superior for estimating the degree of competition between species. ...; if morphological adaptations constitute a genetic memory of such competition, they will more accurately reflect its ecological importance.' It is also possible that the morphology of the mouthparts differs between the various instars of the same species, implying changes in diet during growth and development. The objective of the present study was to compare mouthpart morphology of the dominant mesozooplankton species and their instars or size classes occurring in the Sundays River estuary, thereby elucidating differences and similarities that might aid

interpretation of their feeding ecology. For this comparison emphasis was placed on the structure of (a) the mandibular cutting edges of mysids and copepods, (b) the second maxillae of copepods and (c) the thoracic legs of mysids. These appendages were chosen for the following reasons:

(a) The denticulate cutting edge of copepod mandibles is known to differ between species with different feeding modes (Anraku & Omori 1963; Itoh 1970). Size and structure of mysid mandibles may also reflect dietary differences (Mauchline 1980, Webb & Wooldridge 1989).

(b) The second maxillae of copepods were traditionally thought to play an important role in the sieving of food particles from the water (Anraku & Omori 1963; Gauld 1966; Boyd 1976; Nival & Nival 1976). Since the studies of Alcaraz, Paffenhöfer & Strickler (1980) and Koehl & Strickler (1981), using microcinematography, the filtering abilities of the second maxillae have been questioned, although their importance in particle capture is still recognized (Cowles & Strickler 1983; Vanderploeg & Paffenhöfer 1985; Paffenhöfer & Stearns 1988).

(c) The thoracic legs of euphausiids function as a feeding basket to filter food particles (Mauchline & Fisher 1969). Inter-setule mesh size determines the filtering efficiency of this

basket (McClatchie & Boyd 1983). Although Canon & Manton (1927) attribute filtration in the mysid *Hemimysis lamornae* to the maxillae, the thoracic legs and their setae also appear to be prominent appendages used for the capturing and filtration of food particles by mysids (Siegfried & Kopache 1980; Webb & Wooldridge 1989; Schabes & Hamner 1992).

Methods

Copepods

Light and scanning electron microscope (SEM) studies were made of the mandibles of nauplii, copepodid and adult stages of *Acartia longipatella* and *Pseudodiaptomus hessei*. Mandibles were dissected from animals preserved in 5% formalin.

Preserved animals were prepared for SEM micrographs by gradually dehydrating specimens using ethanol. Mandibles were dissected out, critical-point dried and sputter coated with gold. SEM micrographs were made with a Joel JSM 840 scanning electron microscope (E.M. Unit, Rhodes University, Grahamstown).

A morphological comparison was made of the second maxillae of the two copepod species. Setal and setule (secondary seta) measurements were determined from specimens preserved in 5% formalin. Measurements were made using light microscopy with the aid of a camera lucida and a stage micrometer. Measurements taken included setal lengths and intersettle spacing of each seta and representative setules on each seta for the different copepod instars. The areas covered by the second maxillae setae of adults of the two copepod species were measured and compared.

Mysids

The mandibles of three mysid classes, (juveniles, immatures and adults; Mauchline 1980) of *Mesopodopsis wooldridgei* and *Rhopalophthalmus terranatalis* were examined with the aid of SEM and light microscopy. The methods were similar to those described above.

Pereopods 2–7 were also removed from mysids and the merus, carpus and propodus segments examined and compared in terms of setae and setule arrangements and lengths. Measurements were done on intersettle spacing and setal length on each segment. One seta representative of every pair of setae on each segment of pereopods 2–7 was measured in each mysid size class. Representative setules on each pair of setae were also measured to determine intersettle spacing and setule length.

Results and Discussion

Copepods

Nauplii

Pseudodiaptomus hessei and *Acartia longipatella* nauplii possess strong masticatory processes on the coxa and basis of the antenna. Development of these processes is progressive, from a strong spine on the basal segment in the first nauplius stage to three spines in nauplius N6 (Jerling & Wooldridge 1989). Gauld (1958) attributed food collection by nauplii to the mandibular setae while the masticatory processes retain the food collected.

Mandibular gnathobases were only evident from the N4 stage onward, suggesting the possibility of ingesting larger and more robust particles as naupliar development proceeds. The mandibles of the last nauplius stage (N6) of *P. hessei* and *A. longipatella* differ markedly (Figure 1). The mandible in nauplii N6 of *P. hessei* possesses a cutting edge composed of three sharp teeth of 3 to 5 μm from cusp to tip whereas the mandible of *A. longipatella* nauplii is blunt. This would suggest that the N6 nauplius stage of *P. hessei* is more able to pierce and break particles than the N6 stage of *A. longipatella*.

Copepodids

A significant morphological change in the structure of the mandibular edge occurs after molting from N6 to C1 in both *Pseudodiaptomus hessei* and *Acartia longipatella*. More teeth are present on the mandibular cutting edge (Figure 1) and the second maxillae are also well developed (Jerling & Wooldridge 1989). This morphological change reflects a change in diet as the copepod develops from N6 to C1 (Marshall & Orr 1972).

Apart from the addition of setae and general enlargement, little morphological change takes place in the feeding apparatus during copepodid development of *P. hessei* (Jerling & Wooldridge 1989). An increase in mandibular size is likely to enable later developmental stages to ingest larger particles or cells compared to younger copepodid stages.

Mandibles. The mandibles of *P. hessei* adults consist of six strong tricusped incisor teeth and a section with two molars (Figure 2). The last molar often possesses a pointed membrane-like structure; this structure is not present on all mandibles. Light microscope observations showed that the molar process is still undeveloped in C1 although six teeth are also present (Figure 1). Teeth present on the mandibles of *A. lon-*

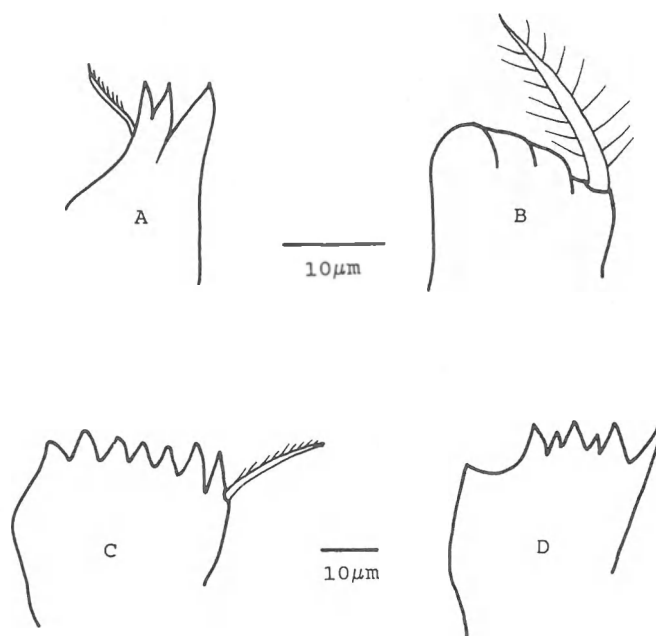


Figure 1 Diagrammatic presentation of naupliar and copepodid mandible denticulate edges in *Pseudodiaptomus hessei*: A = N6, C = C1; and *Acartia longipatella*: B = N6, D = C1.

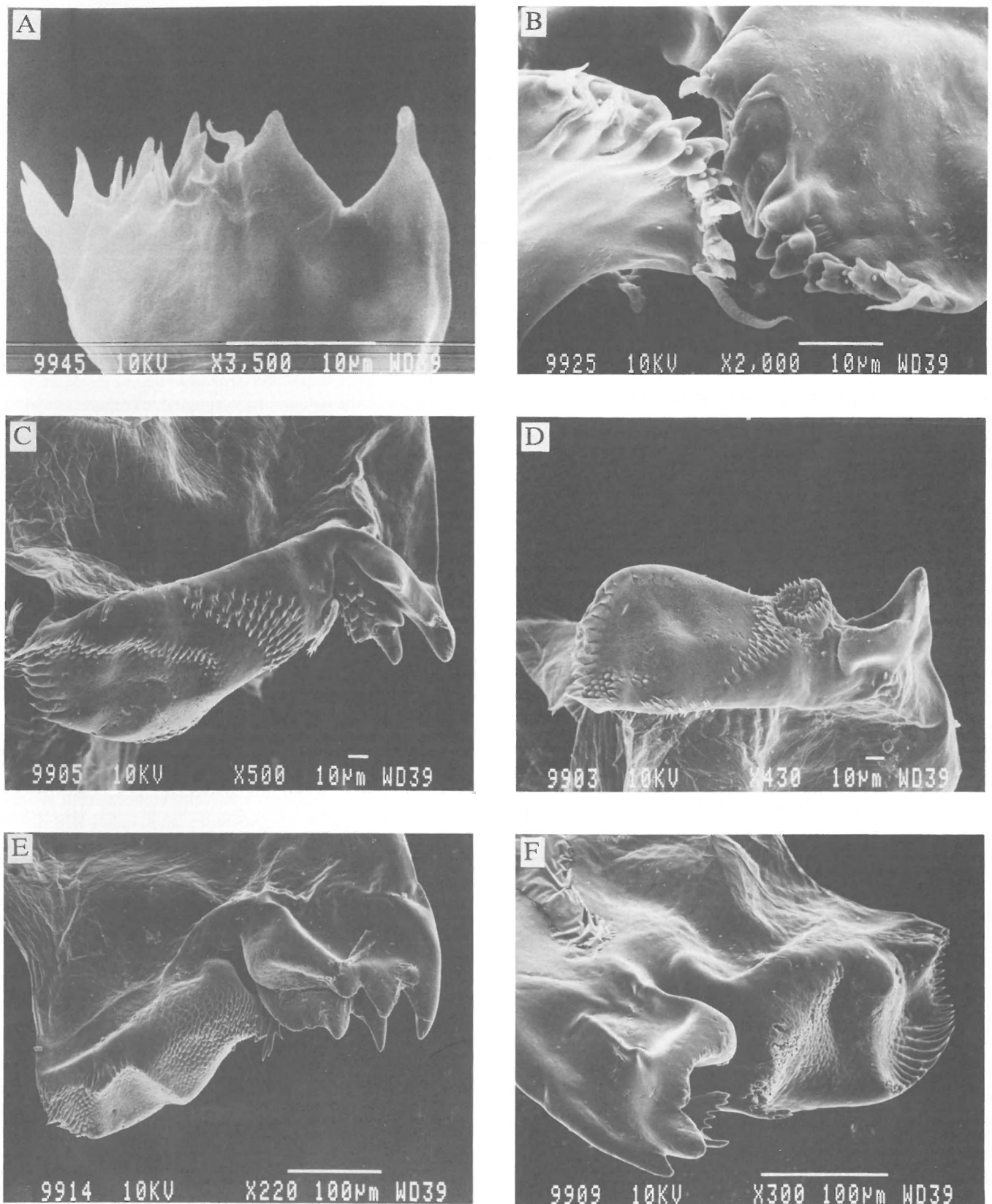


Figure 2 Mandibles of adult females: A = *Acartia longipatella*, B = *Pseudodiaptomus hessei*, C and D = left and right mandibles of *Mesopodopsis wooldridgei* respectively, E and F = left and right mandibles of *Rhopalophthalmus terranatalis* respectively.

gipatella increase in number from seven in C1 to 10 in adults. The general mandibular edge structure of *A. longipatella* differs markedly from that of *P. hessei*, sharply pointed teeth without any region resembling a molar section being present (Figure 2).

Grinding teeth, i.e. more rounded and less sharp, as described for *Calanus finmarchicus*, would be an indication of herbivory. Sharp, strong teeth (*Tortanus discaudatus*) are characteristic of carnivorous feeding. Omnivorous copepods have mandibular cutting edges between these two types

(Anraku & Omori 1963). Herbivory in the case of *Calanus finmarchicus* implies feeding on diatoms (Anraku & Omori 1963; Marshall & Orr 1972) where the mandibles are used to crush the rigid silica frustules. The microplankton of the Sundays estuary is dominated by flagellates. Diatoms are also present but usually at very low concentrations (Hilmer 1990).

The rounded teeth of *P. hessei* suggest the ability to feed on particles such as diatoms. The slender, but sharper teeth of *A. longipatella* could suggest a diet of small delicate cells such as the flagellates. The lack of particularly large, strong and sharp teeth (e.g. in *Tortanus discaudatus*; Anraku & Omori 1963), in both *P. hessei* and *A. longipatella* suggests that predation or carnivory does not form a major part of the feeding strategy in these two species.

Itoh (1970, as quoted by Parsons & Takahashi 1973), compared differences in copepod feeding using an 'Edge index, EI' (formula provided in Parsons & Takahashi 1973). EI values of < 500 and with more than 10 teeth on the cutting edge are indicative of a predominantly herbivorous feeding habit; an EI value of 500–900 with approximately 5–10 teeth indicate a mostly omnivorous diet while EI values above 900 with less than seven teeth are calculated for more carnivorous species (Figure 42B in Parsons & Takahashi 1973). Edge indices were calculated for three copepodid developmental stages in *P. hessei* and *A. longipatella* (Table 1). There was a slight decrease in the EI value with each successive copepodid developmental stage. However, most stages in both *P. hessei* and *A. longipatella* fall within the omnivore class, or, in the case of *P. hessei* C3 and adult stages, on the border between the omnivore and herbivore classes.

Second maxillae. The spacing and lengths of setae and setules of the second maxillae in *P. hessei* and *A. longipatella* are given in Table 2. Although smaller and more slender in body size, *A. longipatella* possesses significantly longer setae and setules on the 2nd maxillae than *P. hessei* (Mann-Whitney *U* test, $\alpha = 0,05$). The intersetule distances were also greater for *A. longipatella* (Mann-Whitney *U* test, $\alpha = 0,05$). The area covered by the setae on the 2nd maxillae in adult *P. hessei* ($15614 \pm 3074 \mu\text{m}^2$, $\bar{X} \pm 1\text{SD}$) is, however, not significantly larger ($p = 0,58$; $n = 9$) than that in adult *A. longipatella* ($14868 \pm 2580 \mu\text{m}^2$, $\bar{X} \pm 1\text{SD}$).

Nival & Nival (1976) used intersetule distance on the second maxillae to determine particle sizes filtered by *Acartia clausi*. Vanderploeg & Ondricek-Fallscheer (1982), however,

Table 2 Mean setae and setule spacing (d) and length (l) on the 2nd maxillae of adult and copepodid (C1) *Pseudodiaptomus hessei* and *Acartia longipatella*. Values are in μm with ranges in brackets

Species	Setae		Setule	
	d	l	d	l
<i>P. hessei</i>				
C1	3,9 (1–7)	50,8 (50–55)	2,1 (1,5–3)	1,9 (1,5–3)
Adult	3,5 (1–5)	115,9 (90–130)	4,3 (2–10)	5,1 (2–10)
<i>A. longipatella</i>				
C1	2,4 (1–4)	82,5 (75–90)	4,1 (2,–5)	5,4 (4–8)
Adult	2,4 (1–4)	170,0 (135–195)	7,1 (2–11)	10,6 (7–14)

argued that intersetule distances are a poor predictor of particle-retention efficiency in *Diaptomus sicilis*. The latter authors suggested that the seining motion of the second maxillae, used by *Acartia* for filtering, may explain the discrepancy. Koehl & Strickler (1981) calculated that it is not possible for water to flow between setae, owing to boundary layers around them, and filtration would therefore be impossible. In contrast water flow between setae of the 2nd maxillae of *Eucalanus elongatus* has been observed (Price & Paffenhöfer 1986) even though the calculated boundary layers suggest the opposite. The latter authors however regard setule spacing as unimportant in determining retention efficiency. They observed some cells to stick to the setae but the majority of particles were 'funnelled' towards the mouth and not filtered out by the setae. The role of intersetule distance in the diet of copepods is thus not clear.

Although the differences in intersetule spacing between *A. longipatella* and *P. hessei* are significant, this difference is less than $3 \mu\text{m}$ with the ranges being similar (Table 2). Inter-setule distances in this case should therefore not exert a large influence on the planktonic food particles captured by these copepods, falling predominantly in the nano- and microplankton size range. No clear dietary differences between *A. longipatella* and *P. hessei* are therefore reflected in the morphology of the 2nd maxillae.

Mysids

Mandibles. The incisor processes of the mandibles are used to bite into large masses of food; portions bitten off are pushed onto the molar processes and ground before entering the oesophagus (Grossnickle 1982).

The left and right mandibles of *Mesopodopsis wooldridgei* (Figure 2) are asymmetric. A *lacinia mobilis* is present between the *pars incisiva* and *pars molaris* regions on the left mandible. This position on the right mandible is occupied by a circle of spines. The cutting edges and cusps and valleys on grinding areas of opposing mandibles fit into each other, allowing for maximum contact between the *pars molaris* surfaces. Spine rows occur on the proximal and a row of teeth on the distal *pars molaris* margins of both mandibles. In *Rhopal-*

Table 1 Mandible edge indices, EI (Itoh 1970), calculated for instars of *Pseudodiaptomus hessei* and *Acartia longipatella*

Copepod instar	EI	Number of teeth
<i>P. hessei</i>		
C1	588	7
C3	460	8
Adult	437	8
<i>A. longipatella</i>		
C1	675	7
C3	592	10
Adult	554	10

ophthalmus terranatalis both left and right mandibles possess a *lacinia mobilis*, which are more prominent with more teeth on the right mandible. The *pars incisiva* of the right mandible fits between the cutting edges of the *pars incisiva* on the left mandible (Figure 2). The incisor teeth are strong and pointed, more so than those in *M. wooldridgei*. Cusps and valleys on the *pars molaris* regions of the opposing mandibles fit together bringing the grinding surfaces in close contact. On the distal margin of the *pars molaris* a row of teeth are prominent. Sharp teeth also occur on the proximal margin of the *pars molaris*.

A mandibular edge index was developed for euphausiids (Nemoto 1977) relating mandible structure to diet. Direct comparison between euphausiids and mysids is not possible, but generally the large *pars molaris* in euphausiids indicates herbivory and this may also be true for many mysid species (Mauchline 1980). Edge indices were calculated for the size classes of both species (Table 3). No significant differences were evident between juveniles and adults within a species (ANOVA, $\alpha = 0,05$). The differences between corresponding size classes of *M. wooldridgei* and *R. terranatalis* were however significantly different (Mann-Whitney *U* test, $\alpha = 0,05$). *M. wooldridgei* tends more towards herbivory with its relatively large *pars molaris* while the lower index calculated for *R. terranatalis* suggests a more carnivorous diet. This is in agreement with previous studies on these mysid species (Wooldridge & Bailey 1982; Wooldridge & Webb 1988).

Although Webb & Wooldridge (1989) suggest that 'the sharp, cusped denticulate edges' of the mandibles of *M. wooldridgei* 'are better suited for cutting soft material than piercing and grinding prey', the present study shows a relatively large *pars molaris*, suitable for grinding food particles (Mauchline 1980).

Thoracic legs. The endopods of thoracic legs two to seven of both mysid species are prominent, extending forward, forming a cone-shaped feeding basket. Setae on the merus, carpus and propodus segments of the endopods are arranged in V-shaped pairs, directed anteriorly and slightly inwards. Water flows into the feeding basket and particles trapped are moved anteriorly by medially projecting setae on the basipodites (Schabes & Hamner 1992).

M. wooldridgei possess setules on the endopods of the tho-

Table 4 Mean setae and setule length (l) and spacing (d) on the thoracic legs of *Mesopodopsis wooldridgei* and *Rhopalophthalmus terranatalis*. Values are in μm with ranges in brackets

Species	Setae		Setules	
	l	d	l	d
<i>M. wooldridgei</i>				
Juveniles	127 (40–210)	26 (15–45)	23 (10–40)	8 (3–12)
Immatures	224 (125–350)	35 (15–55)	27 (10–50)	7 (5–15)
Adults	302 (20–470)	44 (10–70)	34 (10–80)	9 (2–15)
<i>R. terranatalis</i>				
Juveniles	97 (30–240)	22 (10–70)	–	–
Immatures	174 (50–365)	34 (10–100)	–	–
Adults	269 (70–500)	49 (15–125)	–	–

racic legs. Intersetal spacing increases with increasing body size (Table 4, significant at $\alpha = 0,05$, Tukey test). Intersetule spacing was significantly different between adults and immatures but not between immatures and juveniles (Table 4, Tukey test, $\alpha = 0,05$). Similar to Cooper & Goldman's (1980) observations on *Mysis relicta*, prey in *R. terranatalis* is captured by closing the endopods of the thoracic legs over the prey, pushing it towards the mouthparts. No setules (secondary setae) are present. Setae length and intersetal spacing increased significantly with increasing body size (Table 4, Tukey test, $\alpha = 0,05$).

Although boundary layers around setae and setules could preclude water movement through the intersetal or setule spaces (Koehl & Strickler 1981), setule spacing is important for retaining small particles and may determine the minimum size of particle that can be retained (McClatchie & Boyd 1983). *M. wooldridgei* should accordingly be able to feed on smaller particles than any of the *R. terranatalis* size classes, owing to the presence of setules in the feeding basket of the former. The setal spacing (Table 4) of *M. wooldridgei* and *R. terranatalis* size classes suggests more efficient capturing of smaller particles by juveniles than by adults.

Summary and Conclusion

Although the food resources exploited by the mesozooplankton species in the Sundays River estuary probably overlap, the results from this study support the possibility of inter- and intraspecific dietary differences.

Differences in diet may be due to intraspecific morphological changes as well as interspecific differences. In the former category, the change in mandible structure between nauplii and copepodid stages suggests different food and feeding modes used by instars. An increase in the size of the feeding appendages with growth would allow later instars of copepods and mysid size classes to utilize larger food particles.

Table 3 *Pars molaris* to *pars incisiva* ratios (pm/pi) in the left mandible of juvenile, immature and adult *Mesopodopsis wooldridgei* and *Rhopalophthalmus terranatalis*, pm = width of *pars molaris*, pi = length of *pars incisiva*

Species	n	pm/pi \pm SD
<i>M. wooldridgei</i>		
Juvenile	5	1,39 \pm 0,22
Immature	5	1,33 \pm 0,17
Adult	4	1,37 \pm 0,15
<i>R. terranatalis</i>		
Juvenile	5	0,76 \pm 0,05
Immature	4	0,82 \pm 0,16
Adult	5	0,79 \pm 0,06

With respect to interspecific differences, the mandibles of *Pseudodiaptomus hessei* naupliar stage N6 are more prominent than those of the same stage of *Acartia longipatella*. Mandibles of the adults of the two copepod species also differ markedly; *P. hessei* possesses more robust mandibles with a molar region, and this is in contrast to the mandibles of *A. longipatella* which have sharp, more fragile teeth with no molar area. No clear reflection of dietary differences could, however, be extrapolated from the morphology of the second maxillae.

Mandible edge indices calculated for the mysid species suggest a more herbivorous feeding mode for *M. wooldridgei*, and more carnivorous feeding in *R. terranatalis*. Intersestule spacings on the thoracic endopod setae of *M. wooldridgei*, compared to the absence of any setules in *R. terranatalis*, imply the ability of the former to capture small particles more effectively.

These morphological differences could therefore reflect differences in diets between species and indicate differences in food particle sizes utilized by the various developmental stages within species. This should reduce the occurrence of inter- and intraspecific competition.

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