

Spatial and temporal patterns of habitat use by three estuarine species of mysid shrimp

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Abstract. The mysids *Rhopalophthalmus egregius*, *Haplostylus dakini* and *Doxomysis australiensis* are abundant yet unstudied omnivorous crustaceans in Australian estuaries. Habitat use and population dynamics were investigated for these species over spring and summer in the Tweed River, Australia, to explore their ecological role in estuarine ecosystems. Overall, mysids were concentrated in shallow unvegetated and deep unvegetated estuarine habitats. *H. dakini* were most abundant in shallow and deep bare habitats at night, whereas *R. egregius* were most abundant in deep bare habitats during the night. *D. australiensis* were present across all habitats in the night, but negligible numbers were present during the day. Significantly greater numbers of *R. egregius* and *D. australiensis* were sampled during the new moon, compared with the full moon. Significantly larger *R. egregius* and *D. australiensis* individuals were present in benthic habitats at night, indicating possible partitioning of habitat for juvenile and adult subpopulations. Adaptive foraging strategies and habitat use facilitates the coexistence of sympatric mysid species, *H. dakini* and *R. egregius*, and within-species habitat partitioning allowed juvenile *R. egregius* to avoid interaction with adult *R. egregius*. The observed dynamics minimize inter- and intra-specific predation between mysids, and by other predators, while optimizing access to key trophic resources.

Additional keywords: diel period, habitat partitioning, lunar period, predation.

Introduction

Estuaries are highly variable environments that contain a range of important habitats, providing both optimal and sub-optimal conditions for various nektonic life-history stages. These dynamic habitats are continually altered by the effects of tides, run-off, season, and anthropogenic disturbances (Hopkinson and Vallino 1995). The value of certain estuarine habitats relative to others can be overstated, especially when nursery value for fish and crustaceans is only considered in terms of animal abundance (Beck *et al.* 2001). The role of aquatic vegetation in providing refuge for estuarine and marine species is of obvious benefit, however, many juvenile fish species taking refuge in vegetation emerge from this protected habitat to forage (Walters and Martell 2004). In these cases growth and survival can be closely linked to effective exploitation of non-vegetated rather than vegetated habitats. The emphasis placed on importance of submerged aquatic vegetation habitats to estuarine fauna is disproportionate to its extent within estuaries (Ruiz *et al.* 1993). In spite of the dominance of non-vegetated habitats in estuarine systems, few studies have focused on the importance of these habitats to estuarine systems and the fauna that reside there.

Mysid species fulfil a major role in estuarine and marine ecosystems (Roast *et al.* 1998; Froneman 2000; Winkler *et al.* 2003, 2007). Mysids are opportunistic omnivores (Mauchline 1980), and facilitate the transfer of carbon from organic detrital material and phytoplankton to zooplankton and teleost fish

in estuaries. Mysids exert significant predation pressure on harpacticoid and cyclopoid copepods (Jerling and Wooldridge 1994), with these prey species also feeding on the smaller size spectrum of organic debris. A strong tendency to make diel-vertical migrations in most species (Kouassi *et al.* 2006) often couples benthic production with pelagic ecosystems (Roast *et al.* 1998). In some circumstances, mysids provide a direct link between detritus and top-level estuarine predators, including financially and ecologically important species such as Australian salmon *Arripis trutta* (Fenton 1996), mulloway *Argyrosomus japonicus* (Griffiths 1997; Taylor *et al.* 2006), flounder *Paralichthys olivaceus* (Tanaka *et al.* 2006), herring *Herklotsichthys castelnaui*, yellowtail scad *Trachurus novaezelandiae*, sand mullet *Myxus elongates*, flounder *Pseudorhombus* sp., flathead *Platycephalus* sp. and whiting *Sillago* sp. (Pease *et al.* 1981). The transfer of carbon from detritus to benthic and pelagic predators is particularly important in Australian estuaries, with detritus based food webs important for carbon transfer in the face of intermittent and characteristically low inorganic nutrient inputs and limited primary productivity (Rochford 1979).

Several species of mysid exist in Australian estuaries. Of these, three are common to estuaries in south-eastern Australia. *Doxomysis australiensis* is a Leptomysinid occurring in estuarine and offshore waters from Sydney, New South Wales, to the Great Barrier Reef (Talbot 1997). *Rhopalophthalmus egregius* and *Haplostylus dakini* are hyperbenthic mysid species common

in temperate Australian estuaries, although they have a smaller geographic range and more southern distribution than *D. australiensis*. Descriptions of life-history and population dynamics of all three species are absent from the literature, in spite of their high abundance in estuarine waters (Dakin and Colefax 1940); however, parallels may exist between these species and congeneric species occurring elsewhere.

The use of habitats by mysids may be related to several factors including susceptibility to predation, proximity to food supply, salinity, use of tidal currents, and diel cycles. Complex habitats are not principally chosen as a refuge from predation in mysid species, with aggregation or swarming a preferred anti-predator strategy (Flynn and Ritz 1999). Swarming in open water may not protect sympatric mysid species from predation by larger conspecifics or other carnivorous mysid species, as observed for *Rhopalophthalmus terranatalis* (Jerling and Wooldridge 1995); however, this may be overcome by partitioning habitat between mysid prey and potential mysid predators during periods of feeding. This paper explores this concept for three species of estuarine mysid by testing the hypotheses of no difference in size or abundance among vegetated and non-vegetated estuarine habitats, and lunar and diel phases.

Materials and methods

Study site

The present study was conducted in the Tweed River on the far north coast of New South Wales (28.170°S, 153.556°E). The Tweed River catchment (1100 km²) supports primarily sugarcane agriculture, and includes two significant broadwaters, giving a high waterway area of 30 km² relative to river length (26 km). The river contains an extensive area of wetland habitat, is a popular tourist destination, and is an important fish, prawn and oyster fishery (TSC 1996). The high agricultural land use in the river catchment leads to occasional acid sulfate soil problems, which can adversely affect riverine fauna (Sammot 2002).

Sample collection and processing

Sampling was conducted to determine mysid dynamics across a range of conditions, and use of different habitats. Over a 6-month sampling period, samples were collected on the incoming tide on every full and new moon, during the day and night. Three habitats were sampled under each set of conditions: shallow bare, deep bare and shallow vegetated, with three replicate tows undertaken in each habitat. The deep-bare habitat site was in the main river channel ~7 km upstream from the river mouth, and consisted of a sand/silt substrate up to 10.2 m deep. Shallow-bare habitat site was also in the main river channel ~0.5 km downstream from the deep-bare habitat, and consisted of sand/silt substrate up to 4.5 m deep. The shallow-vegetated habitat site was located outside of the main river channel immediately adjacent to the deep-bare habitat site. Vegetation consisted of dense *Zostera capricorni* beds in a water depth of up to 1.5 m.

Sampling was carried out on the Tweed River between 7 October 2006 and 18 March 2007, using an epibenthic sled (480- μ m mesh size, 0.7 m wide, 0.3 m high). The sled was deployed and towed over a random track at each site for up to 5 min (covering <250 m). Samples were collected in a 1-L sample jar connected

to the cod-end of the net, and a GPS waypoint marked at deployment and retrieval of the net (accuracy of 4.5–8.0 m). Samples were fixed in 10% formalin, and salinity, temperature and turbidity measurements recorded for each tow from a Yeo-Kal water quality meter (Yeo-Kal Electronics, Brookvale, NSW, Australia).

Mysid species were sorted from sled samples in the laboratory under low power using a dissecting microscope (Olympus SZ-CTV), and stored in 95% ethanol. Mysids were spread evenly across a glass Petri dish containing a calibration bead, and photographed with a Kodak 5-megapixel digital camera. The size of each mysid was measured automatically using the count/size function in Image Pro Plus v 4.5 (Media Cybernetics, Silver Spring, MD, USA), and then manually checked for errors. The dry weight was then calculated for each mysid using weight-area relationships, developed as follows. Up to 75 individuals for each species of mysid were randomly sampled across different sex, times, locations and size classes of organisms. Organisms were photographed as described above, and images measured for carapace length, total length and surface area using Image Pro Plus v 4.5. Each mysid was air-dried for 2 min to allow the ethanol to evaporate, wet weight was recorded, the sample was lyophilized for 72 h, and then weighed ($\pm 1 \mu$ g) using a Cahn C-33 microbalance (Thermo-Fisher Scientific, Waltham, MA, USA). Regressions were developed for each species using the curve fit function in SPSS (SPSS, Chicago, IL, USA).

Analysis

Abundance and biomass measurements were standardised for tow area calculated from GPS waypoints. Non-normal data were square-root transformed before statistical analysis. Three-factor ANOVAs were conducted on abundance data for each species to test the null hypotheses of no significant difference in mysid abundance among moon (fixed, orthogonal; full and new), diel period (fixed, orthogonal; day and night), and habitat (fixed, orthogonal; shallow, seagrass or deep habitats). Two-factor ANOVAs were carried out on mean biomass measurements of the three mysid species to test the null hypothesis of no difference in mysid size among diel period, and habitat. Hochbergs analysis was used for *a posteriori* pairwise comparisons between factor levels. Significant interaction terms between fixed factors were evaluated using tests of simple main effects, by comparing *A* means at each level of *B* independently. Bray–Curtis dissimilarities were calculated for the day and night density estimates produced for each species, from which a dissimilarity matrix was generated. Clusters were generated using the unweighted pair-groups method using arithmetic averages algorithm (UPGMA). All univariate statistics were undertaken in SPSS and multivariate statistics were carried out in PRIMER v. 5.2.2 (PRIMER-E, Plymouth, UK).

Results

Temperature ($24.7 \pm 0.2^\circ\text{C}$), salinity (29.1 ± 0.2) and turbidity (4.0 ± 0.1 ntu; mean \pm s.e.) were relatively constant among sites during the sampling period (Table 1). Significant mysid weight (mg)–area (mm²) regressions were produced for *Haplostylus dakini* ($Weight = 0.038 \times Area^2 + 0.005 \times Area - 0.007$; $r^2 = 0.93$, d.f. = 108, $P < 0.001$), *Rhopalophthalmus egregius* ($Weight = 0.013 \times Area^2 + 0.003 \times Area + 0.059$; $r^2 = 0.91$,

Table 1. Abiotic measurements taken at each site during the survey period

	Deep bare			Seagrass			Shallow bare		
	Salinity	Temp. (°C)	Turbidity (ntu)	Salinity	Temp. (°C)	Turbidity (ntu)	Salinity	Temp. (°C)	Turbidity (ntu)
Oct-06	28.7	19.6	3.3	28.5	21.3	5.3	29.9	21.1	2.5
Nov-06	28.1	25.4	2.7	28.4	25.1	3.3	29.8	25.0	1.8
Dec-06	29.3	24.0	3.2	28.9	24.1	4.4	32.7	24.2	3.4
Jan-07	29.8	24.2	3.7	29.7	24.6	4.7	32.0	24.5	3.7
Feb-07	28.7	26.7	4.5	28.3	26.7	5.3	31.0	26.9	5.2
Mar-07	26.2	27.8	4.6	26.3	26.6	5.4	28.5	26.8	4.4

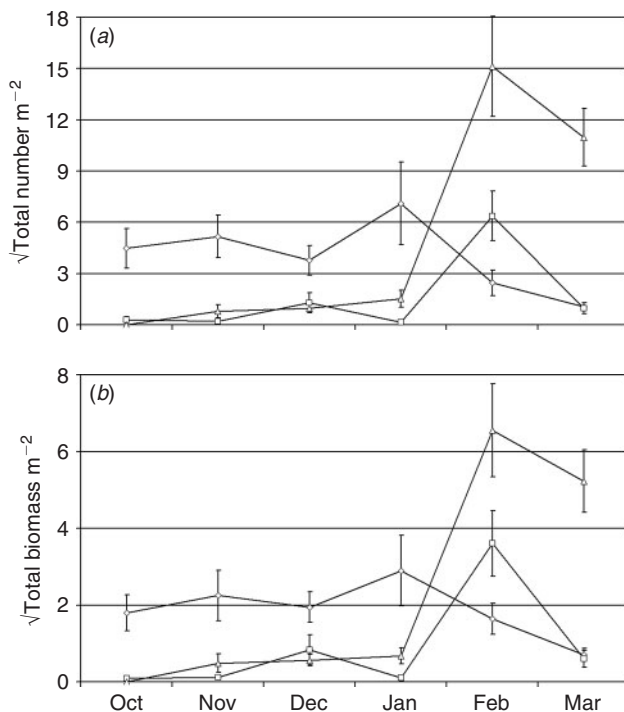


Fig. 1. Mean \pm s.e. abundance (a) and biomass (b) of *Haplostylus dakini* (\diamond), *Rhopalophthalmus egregius* (\triangle) and *Doxomysis australiensis* (\square), by month.

d.f. = 76, $P < 0.001$) and *Doxomysis australiensis* ($Weight = 0.055 \times Area^{1.348}$; $r^2 = 0.93$, d.f. = 77, $P < 0.001$). The high r^2 value of these regressions indicates that the body area–biomass approach developed here produces suitable accuracy for biomass calculations and inferences of population dynamics. *H. dakini* abundance and biomass were relatively stable across spring/summer but began to decline in January when *D. australiensis* and *R. egregius* began to increase (Fig. 1). *D. australiensis* and *R. egregius* abundance and biomass were low for most of spring/summer, but peaked in mid–late summer, with the greatest biomass present in the estuary in February and March (Fig. 1). Total biomass of mysid shrimp within the estuary appeared to peak in mid–late summer, with the greatest biomass present in the estuary in January and February (Fig. 1b).

Three-factor ANOVAs were conducted on abundance data for each species to test the null hypotheses of no significant

difference in mysid abundance between full and new moon, day and night, and shallow bare, seagrass or deep bare habitats (Table 2a). Most of the variation in abundance of *H. dakini* was a result of diel effects ($F_{1,168} = 33.97$, $P < 0.001$), with significantly more mysids present during the night (Fig. 2a). Subjective interpretation of a significant diel \times lunar interaction (Table 2a) showed that the increase in abundance between day and night was much greater during the new moon than the full moon. Hochbergs post-hoc analysis showed significantly greater numbers of *H. dakini* were present in shallow ($P < 0.001$) and deep ($P < 0.001$) habitats than in seagrass habitats (Fig. 2a), but simple main effects of a significant diel \times habitat interaction term (Table 2a) showed that this relationship was not significant for daytime samples ($F_{2,80} = 0.88$, $P = 0.500$).

There was less variation in abundance of *R. egregius* than *H. dakini* (Table 2a), with no significant difference over the diel period ($F_{1,168} = 2.21$, $P = 0.139$). There was a significantly greater abundance of *R. egregius* present in deep water compared with shallow (Hochbergs, $P = 0.001$) and seagrass (Hochbergs, $P = 0.001$) habitats (Fig. 2b), and significantly greater abundance during the new moon ($F_{1,168} = 6.51$, $P = 0.012$; Fig. 3). Abundance of *D. australiensis* was significantly greater during the new moon ($F_{1,168} = 4.08$, $P = 0.045$; Fig. 3), and during the night (Table 2a; $F_{1,168} = 29.27$, $P < 0.001$; Fig. 2c) for all habitats.

Cluster analysis produced groupings based on habitat association by the three species (Fig. 4). *R. egregius* day and night populations and *H. dakini* day populations were concentrated in deep water habitats, whereas *D. australiensis* and *H. dakini* night populations were concentrated in shallow habitats. The daytime *D. australiensis* population was most dissimilar as it was present in negligible numbers across all habitats.

Two-factor ANOVAs were carried out on mean biomass measurements of the three mysid species to test the null hypothesis of no difference in mysid size between day and night, and shallow, seagrass or deep habitats (Table 2b). There were no significant differences in *H. dakini* size within diel period; however; significantly larger *R. egregius* ($F_{1,95} = 5.75$, $P = 0.021$) and *D. australiensis* ($F_{1,95} = 24.12$, $P < 0.001$) individuals were present at night (Fig. 5). There were no significant differences in mysid size between habitat for any species of mysid. The trend in mysid size across time provides some evidence for multiple generations of *H. dakini* and *D. australiensis* occurring throughout the sampling period (Fig. 6), with peaks in size occurring in December and February.

Table 2. ANOVA for abundance (a) and mean weight (b) measurements among diel period (day and night), habitat (shallow bare, seagrass and deep bare) and lunar period (full moon and new moon), for species *Haplostylus dakini*, *Rhopalophthalmus egregius* and *Doxomysis australiensis*
MS, mean square; * denotes significant result; ** denotes highly significant result

Source of variation	d.f.	<i>H. dakini</i>			<i>R. egregius</i>			<i>D. australiensis</i>		
		MS	F	P	MS	F	P	MS	F	P
(a) Habitat	2	258.03	8.64	<0.001**	115.11	7.91	0.001**	127.03	1.91	0.151
Diel period	1	1014.60	33.97	<0.001**	32.18	2.21	0.139	1945.94	29.27	<0.001**
Lunar period	1	19.59	0.66	0.419	94.76	6.51	0.012*	271.23	4.08	0.045*
Habitat × diel period	2	112.77	3.78	0.025*	36.17	2.48	0.086	58.73	0.88	0.415
Habitat × lunar period	2	12.56	0.42	0.657	29.25	2.01	0.137	2.02	0.03	0.970
Diel period × lunar period	1	194.06	6.50	0.012*	1.26	0.09	0.769	65.11	0.98	0.324
Habitat × lunar period × diel period	2	89.54	3.00	0.053	9.68	0.67	0.516	24.43	0.37	0.693
Error	168	29.87			14.56			66.49		
(b) Habitat	2	0.05	0.31	0.732	0.01	0.03	0.971	0.03	0.70	0.50
Diel period	1	0.59	3.56	0.062	1.15	5.75	0.021*	1.12	24.12	<0.001**
Habitat × diel period	2	0.24	1.42	0.246	0.20	0.98	0.38	0.04	0.84	0.43
Error	95	0.17			0.20			0.05		

Discussion

The three mysid species investigated here have distinctive diel and lunar migratory behaviours and patterns of habitat use. Overall, mysid abundance was concentrated in non-vegetated estuarine habitats, irrespective of depth, with (sometimes significantly) lower abundance in seagrass. Abundances in seagrass were generally 5–30% of those recorded in bare estuarine habitats under similar conditions. The basis of this preference for non-vegetated areas instead of seagrass is most probably effective trophic use and anti-predator behaviour.

Detritivorous/phytoplanktivorous species of mysid shrimp like *Haplostylus dakini* may derive trophic benefits from exploiting unvegetated over seagrass habitats. Organic detritus tends to accumulate in troughs of sediment ripples within unvegetated estuarine habitat, and detrital load in these environments can be higher than that of vegetated habitats (Iwasaki 1993; Netto and Lana 1997). Detritus accumulation on bare sediments provides a concentrated food supply for these species, possibly within a habitat relatively sheltered from tidal currents. Furthermore, studies have detected greater densities of copepod prey in unvegetated habitats relative to vegetated ones (Iwasaki 1993; Netto and Lana 1997), which indicates improved forage resources for potentially carnivorous mysid species such as *Rhopalophthalmus egregius* in unvegetated habitats as well.

Although there is evidence supporting trophic benefits for mysid species exploiting non-vegetated habitats, the spatial heterogeneity of seagrass habitats may have a greater influence on mysid distribution. Seagrass habitat complexity does have a positive relationship with abundance of some caridean shrimp (Unsworth *et al.* 2007), but potentially interferes with the social organisation (swarming) and anti-predator behaviour of mysid species. Mysids are highly social species that aggregate in swarms or shoals (Ritz 2000), comprising a spatially contiguous group of conspecifics at medium to high densities. This level of organisation has evolved to enhance reproductive success and underpins the key anti-predator behaviour of this taxa (Mauchline 1980). The spatial complexity of seagrass habitats confuses this organisation and makes aggregation difficult.

Consequently the integrity of the swarm is compromised by intrusion of vegetation, thus decreasing the effectiveness of the primary anti-predator response. The efficiency of this type of organisation and distribution is evident in Australian estuaries, with mysids appearing less frequently in the diets of ambush predators (Linke *et al.* 2001).

Seasonal dynamics

Haplostylus dakini showed a pronounced decrease in abundance in late summer, with *Rhopalophthalmus egregius* and *Doxomysis australiensis* showing a marked increase in abundance at this time. *Haplostylus* spp. captured in the English Channel showed the greatest abundances during the spring (Zouhiri *et al.* 1998), and similarly high abundances occurred for *H. dakini* in spring and early summer. Species replacement over temporal scales observed here may be a result of intraguild predation between sympatric predatory *R. egregius*, and non-predatory *H. dakini* and *D. australiensis*, when the former species become more abundant in late summer; however, regular sampling over longer temporal scales is necessary to confirm this. A similar phenomenon has been observed in Gammarid amphipods *Gammarus duebeni celticus* and *G. pulex*, where intraguild predation by *G. pulex* on *G. d. celticus* leads to the rapid replacement of the latter (Dick *et al.* 1999). The mean individual biomass of *H. dakini*, *R. egregius* and *D. australiensis* does not form a continuing relationship with time over the sampling period. Bi- or tri-monthly peaks in mean individual biomass for *H. dakini* and *D. australiensis* indicate that several generations may have been sampled. Weekly sampling over longer temporal periods would also clarify these observations, and also any seasonal effects on the generation time of these mysid populations.

Population structure and habitat partitioning

Haplostylus dakini abundance was significantly greater during the night than day. Although no published research exists on this species, other Gastrosaccinidae show strong diel vertical migration (DVM, e.g. Macquartmoulin and Maycas 1995;

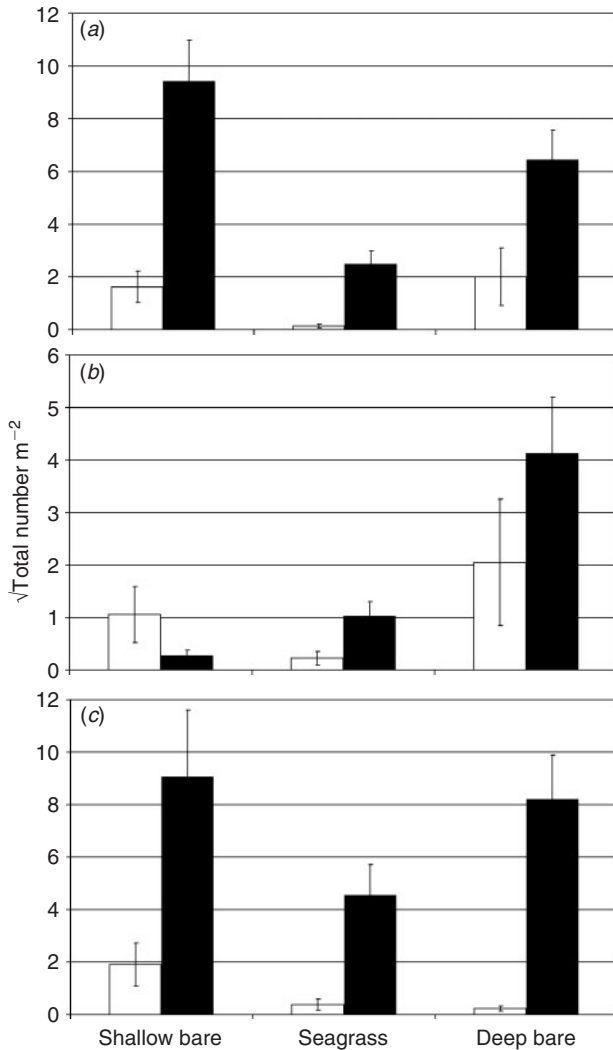


Fig. 2. Mean \pm s.e. abundance of *Haplostylus dakini* (a), *Rhopalophthalmus egregius* (b) and *Doxomysis australiensis* (c) by habitat and diel period (day, white bars; night, black bars).

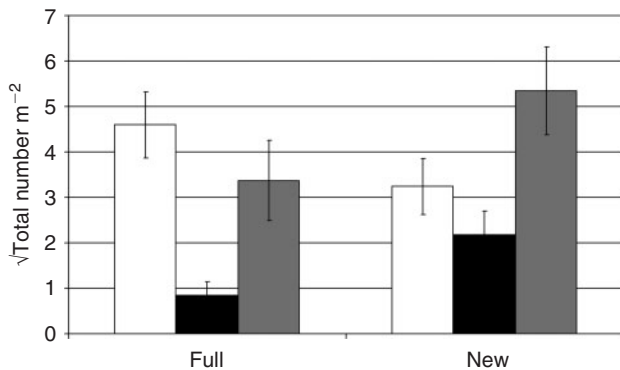


Fig. 3. Mean \pm s.e. abundance of *Haplostylus dakini* (white bars), *Rhopalophthalmus egregius* (black bars) and *Doxomysis australiensis* (grey bars) by lunar period.

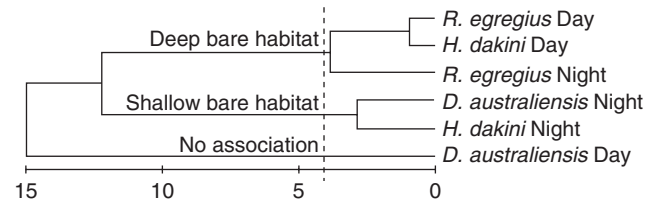


Fig. 4. Dendrogram from cluster analysis of square-root transformed abundance data for *Haplostylus dakini*, *Rhopalophthalmus egregius* and *Doxomysis australiensis* during the day and night. The vertical line indicates the level of dissimilarity used to separate groups by habitat association.

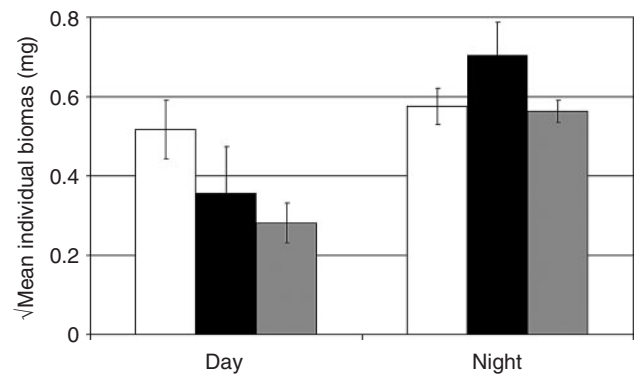


Fig. 5. Mean \pm s.e. individual biomass of *Haplostylus dakini* (white bars), *Rhopalophthalmus egregius* (black bars) and *Doxomysis australiensis* (grey bars) by diel period.

Zouhiri *et al.* 1998), burying in the sediments during the day and emerging to feed at night (Kibirige *et al.* 2003).

Rhopalophthalmus egregius individual mean biomass was four times greater during the night; however, there was no significant difference in abundance between day and night. This suggests there may be a juvenile and adult subpopulation partitioning their distribution, with juveniles using the hyperbenthos during the day and adults at night. This explains the surprising lack of a diel relationship for numbers of *R. egregius*, which was also observed in congeneric *Rhopalophthalmus terrantalis* (Wooldridge and Bailey 1982). *Rhopalophthalmus* spp. adults are cannibalistic (Wooldridge and Bailey 1982), and adults and juveniles have been known to segregate to minimize cannibalistic interactions (Mauchline 1980). Kouassi *et al.* (2006) found DVM and diurnal feeding behaviour in congeneric *Rhopalophthalmus africana*, with numbers of juvenile mysids at the surface peaking during the night, and adult numbers peaking during the day. In aquarium experiments, juvenile *R. africana* required a specific ingestion rate up to ten times that of adults, and the ingestion rate was five times more dependent on zooplankton concentration for juveniles, which indicates lower capture efficiency and greater handling time for juveniles. DVM of copepod prey shows that a greater concentration of zooplankton are present near the bottom during the day (Leising *et al.* 2005; Morgado *et al.* 2006; Thorisson 2006), when juvenile *R. egregius* are near the bottom. These relationships show the *R. egregius* population may be partitioning habitat to increase juvenile survival, by both minimizing intraspecific predation of adults on juveniles, and allowing the exploitation of this niche foraging

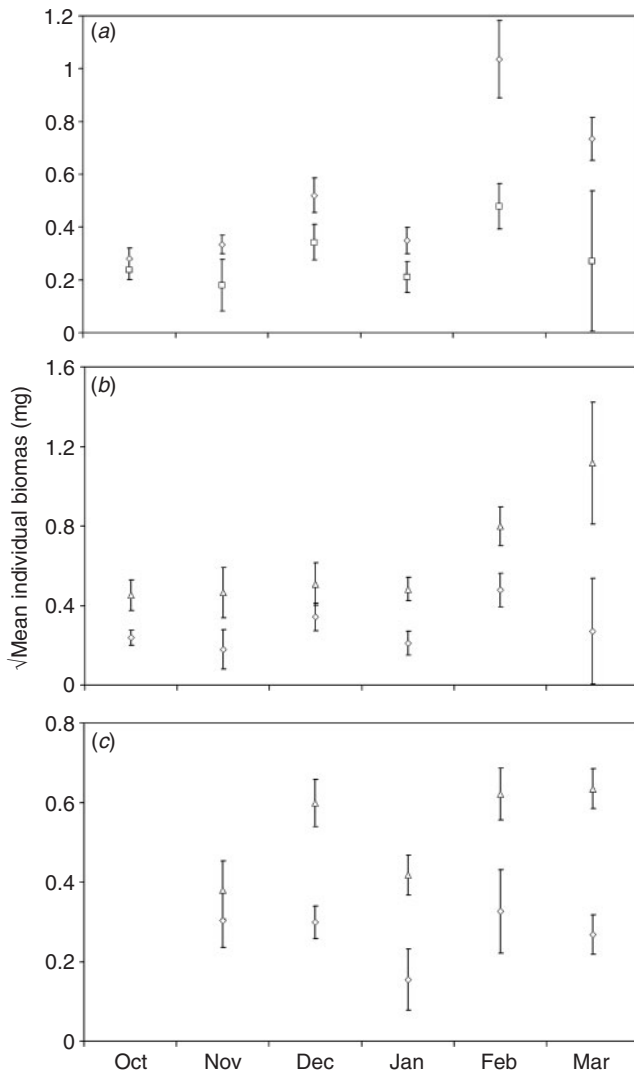


Fig. 6. Mean \pm s.e. individual biomass of day (\diamond) and night (\triangle) samples for *Haplostylus dakini* (a), *Rhopalophthalmus egregius* (b) and *Doxomysis australiensis* (c), by month.

environment by juveniles at optimal prey abundance to enhance growth. The mechanisms behind the phenomena described above for *R. egregius* are the subject of research presently underway in the Georges River.

Only taxonomic information exists for *D. australiensis*; quantitative studies on the ecology of this species are lacking, as is the case for many mysid species (Wooldridge 1986). Few studies exist on members of Leptomysini in general, but other members of the tribe have been shown to be detritivorous and phytoplanktivorous (Mauchline 1980). The structure of the maxillary apparatus in this species suggests it would be good for sweeping detritus into the mouth, as well as grasping phytoplankton (S. Talbot, Australian Museum, pers. comm.). The *D. australiensis* estuarine population sampled in the present study comprised two size classes, with day samples characterised by negligible numbers of small mysids ($0.5 \text{ mysids m}^{-3}$), and night samples being dominated by high numbers of large mysids

($\sim 50 \text{ mysids m}^{-3}$). The drop in numbers and biomass of *D. australiensis* in March indicates a decline of the estuarine population towards the end of summer. The ubiquitous distribution of this species across estuarine, coastal and reef habitats indicates that the species may use the estuary for a limited period only, possibly to exploit a particular trophic niche, such as a summer estuarine phytoplankton bloom. This is supported by the lack of habitat preference or partitioning exhibited by *D. australiensis* relative to the other resident species, *H. dakini* and *R. egregius*.

Finally, lunar-related trends in abundance exhibited by *R. egregius* and *D. australiensis* have been observed previously in mysid shrimp. Changes in abundance during different moon phases are the result of decreased migration during moonlit phases (full moon). Kouassi *et al.* (2006) propose that this may be a response to avoid predation by fish.

This first study into the ecology and dynamics of mysid shrimp in Australian estuaries has shown potential habitat zonation and adaptive foraging strategies facilitating the coexistence of sympatric mysid species, *H. dakini* and *R. egregius*. Within-species habitat partitioning may allow juvenile *R. egregius* to minimize predation by adult *R. egregius*. Although the present study has examined dynamics in the context of the ecology of related species, future research should endeavour to establish the trophic linkages between these three species and their food using stable isotope analysis. In addition, research should also examine interactions between the three species under controlled laboratory conditions, to determine the extent of intraspecific and intraguild predation.

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References

- Beck, M. W., Heck, K. L., Jr, Able, K. W., Childers, D. L., Eggleston, D. B., *et al.* (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* **51**, 633–641. doi:10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2
- Dakin, W., and Colefax, A. (1940). 'The Plankton of the Australian Coastal Waters off New South Wales, Part 1.' (Australasian Medical Publishing Company: Glebe.)
- Dick, J. T. A., Montgomery, W. I., and Elwood, R. W. (1999). Intraguild predation may explain an amphipod replacement: evidence from laboratory populations. *Journal of Zoology* **249**, 463–468. doi:10.1111/J.1469-7998.1999.TB01216.X
- Fenton, G. E. (1996). Production and biomass of *Tenagomysis tasmaniae* Fenton, *Anisomysis mixta australis* (Zimmer) and *Paramesopodopsis rufa* Fenton from south-eastern Tasmania (Crustacea: Mysidacea). *Hydrobiologia* **323**, 23–30.
- Flynn, A. J., and Ritz, D. A. (1999). Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. *Journal of the Marine Biological Association of the United Kingdom* **79**, 487–494. doi:10.1017/S0025315498000617

- Froneman, P. W. (2000). Feeding studies on selected zooplankton in a temperate estuary, South Africa. *Estuarine, Coastal and Shelf Science* **51**, 543–552. doi:10.1006/ECSS.2000.0700
- Griffiths, M. H. (1997). Feeding ecology of South African *Argyrosomus japonicus* (Pisces: Sciaenidae), with emphasis on the Eastern Cape surf zone. *South African Journal of Marine Science* **18**, 249–264.
- Hopkinson, C. S., and Vallino, J. J. (1995). The relationships among mans' activities in watersheds and estuaries – a model of runoff effects on patterns of estuarine community metabolism. *Estuaries* **18**, 598–621. doi:10.2307/1352380
- Iwasaki, N. (1993). Distribution of meiobenthic copepods from various habitats in Pauatahanui Inlet, New-Zealand. *New Zealand Journal of Marine and Freshwater Research* **27**, 399–405.
- Jerling, H. L., and Wooldridge, T. H. (1994). Comparative morphology of the feeding appendages of 4 mesozooplankton species in the Sundays River Estuary. *South African Journal of Zoology* **29**, 252–257.
- Jerling, H. L., and Wooldridge, T. H. (1995). Feeding of 2 mysid species on plankton in a temperate South African estuary. *Journal of Experimental Marine Biology and Ecology* **188**, 243–259. doi:10.1016/0022-0981(95)00007-E
- Kibirige, I., Perissinotto, R., and Nozais, C. (2003). Grazing rates and feeding preferences of the mysid shrimp *Gastrosaccus brevifissura* in a temporarily open estuary in South Africa. *Marine Ecology Progress Series* **251**, 201–210. doi:10.3354/MEPS251201
- Kouassi, E., Pagano, M., Saint-Jean, L., and Sorbe, J. C. (2006). Diel vertical migrations and feeding behavior of the mysid *Rhopalophthalmus africana* (Crustacea: Mysidacea) in a tropical lagoon (Ebrie, Cote d'Ivoire). *Estuarine, Coastal and Shelf Science* **67**, 355–368. doi:10.1016/J.ECSS.2005.10.019
- Leising, A. W., Pierson, J. J., Cary, S., and Frost, B. W. (2005). Copepod foraging and predation risk within the surface layer during nighttime feeding forays. *Journal of Plankton Research* **27**, 987–1001. doi:10.1093/PLANKT/FBI084
- Linke, T. E., Platell, M. E., and Potter, I. C. (2001). Factors influencing the partitioning of food resources among six fish species in a large embayment with juxtaposing bare sand and seagrass habitats. *Journal of Experimental Marine Biology and Ecology* **266**, 193–217. doi:10.1016/S0022-0981(01)00356-2
- Macquartmoulin, C., and Maycas, E. R. (1995). Inshore and offshore diel migrations in European benthopelagic mysids, genera *Gastrosaccus*, *Anchialina* and *Haplostylus* (Crustacea, Mysidacea). *Journal of Plankton Research* **17**, 531–555. doi:10.1093/PLANKT/17.3.531
- Mauchline, J. (1980). The biology of mysids and euphausiids. In 'Advances in Marine Biology'. (Eds J. Blaxter, F. Russell and M. Yonge.) pp. 1–263. (Academic Press: London.)
- Morgado, F. M., Pastorinho, M. R., Quintaneiro, C., and Re, P. (2006). Vertical distribution and trophic structure of the macrozooplankton in a shallow temperate estuary (Ria de Aveiro, Portugal). *Scientia Marina* **70**, 177–188.
- Netto, S. A., and Lana, P. C. (1997). Intertidal zonation of benthic macrofauna in a subtropical salt marsh and nearby unvegetated flat (SE, Brazil). *Hydrobiologia* **353**, 171–180. doi:10.1023/A:1003090701675
- Pease, B., Bell, J., Burchmore, J., Middleton, M., and Pollard, D. (1981). The ecology of fish in Botany Bay: Biology of commercially and recreationally valuable species. State Pollution Control Commission, BBS 23B, Sydney.
- Ritz, D. A. (2000). Is social aggregation in aquatic crustaceans a strategy to conserve energy? *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 59–67. doi:10.1139/CJFAS-57-S3-59
- Roast, S. D., Thompson, R. S., Widdows, J., and Jones, M. B. (1998). Mysids and environmental monitoring: A case for their use in estuaries. *Marine and Freshwater Research* **49**, 827–832. doi:10.1071/MF97099
- Rochford, D. J. (1979). Nutrient status of the oceans around Australia. CSIRO Division of Fisheries and Oceanography Report 1977–1979, CSIRO, Hobart.
- Ruiz, G. M., Hines, A. H., and Posey, M. H. (1993). Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Marine Ecology Progress Series* **99**, 1–16. doi:10.3354/MEPS099001
- Sammut, J. (2002). Associations between acid sulfate soils, estuarine acidification, and gill and skin lesions in estuarine and freshwater fish. *Dissertation Abstracts International Part B: Science and Engineering* **63**, 1097.
- Talbot, M. S. (1997). *Doxomysis acanthina*, a new leptomysinid (Crustacea: Mysidacea) from the northern Great Barrier Reef, Australia, with extensions to the known distributions of *D. australiensis* W.M. Tattersall, 1940 and *D. spinata* Murano, 1990, and a key to the genus *Doxomysis*. *Proceedings of the Biological Society of Washington* **110**, 426–438.
- Tanaka, Y., Yamaguchi, H., Tominaga, O., Tsusaki, T., and Tanaka, M. (2006). Relationships between release season and feeding performance of hatchery-reared Japanese flounder *Paralichthys olivaceus*: In situ release experiment in coastal area of Wakasa Bay, Sea of Japan. *Journal of Experimental Marine Biology and Ecology* **330**, 511–520. doi:10.1016/J.JEMBE.2005.09.022
- Taylor, M. D., Fielder, D. S., and Suthers, I. M. (2006). Spatial and ontogenetic variation in the diet of wild and stocked mulloway (*Argyrosomus japonicus*, Sciaenidae) in Australian estuaries. *Estuaries and Coasts* **29**, 785–793.
- Thorisson, K. (2006). How are the vertical migrations of copepods controlled? *Journal of Experimental Marine Biology and Ecology* **329**, 86–100. doi:10.1016/J.JEMBE.2005.08.011
- TSC (1996). Upper Tweed Estuary Management Plan. Tweed Shire Council, Tweed Heads.
- Unsworth, R., De Grave, S., Jompa, J., Smith, D., and Bell, J. (2007). Faunal relationships with seagrass habitat structure: a case study using shrimp from the Indo-Pacific. *Marine and Freshwater Research* **58**, 1008–1018. doi:10.1071/MF07058
- Walters, C. J., and Martell, S. (2004). 'Fisheries Ecology and Management.' (Princeton University Press: Princeton.)
- Winkler, G., Dodson, J. J., Bertrand, N., Thivierge, D., and Vincent, W. F. (2003). Trophic coupling across the St. Lawrence River estuarine transition zone. *Marine Ecology Progress Series* **251**, 59–73. doi:10.3354/MEPS251059
- Winkler, G., Martineau, C., Dodson, J. J., Vincent, W. F., and Johnson, L. E. (2007). Trophic dynamics of two sympatric mysid species in an estuarine transition zone. *Marine Ecology Progress Series* **332**, 171–187. doi:10.3354/MEPS332171
- Wooldridge, T. (1986). Distribution, population dynamics and estimates of production for the estuarine mysid, *Rhopalophthalmus terranatalis*. *Estuarine, Coastal and Shelf Science* **23**, 205–223. doi:10.1016/0272-7714(86)90055-7
- Wooldridge, T., and Bailey, C. (1982). Euryhaline zooplankton of the Sundays Estuary and notes on trophic relationships. *South African Journal of Marine Science* **17**, 151–163.
- Zouhiri, S., Vallet, C., Mouny, P., and Dauvin, J. C. (1998). Spatial distribution and biological rhythms of suprabenthic mysids from the English Channel. *Journal of the Marine Biological Association of the United Kingdom* **78**, 1181–1202.

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