

# Monitoring acoustically tagged king prawns *Penaeus (Melicertus) plebejus* in an estuarine lagoon

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**Abstract** Fine-scale movement patterns in penaeid prawns are rarely observed in situ, but are essential in understanding habitat use, foraging, and anti-predator behaviour. Acoustic telemetry was applied to examine the activity, space utilization, and habitat use of the eastern king prawn *Penaeus (Melicertus) plebejus*, at small temporal and spatial scales. Tracking of sub-adult *P. plebejus* ( $n = 9$ ) in Wallagoot Lake (36.789°S, 149.959°E; 23 April–12 May 2009) and calculation of a minimum activity index (MAI) revealed high variation in activity rates across diel periods and in different habitats. Elevated activity rates and movement indicated foraging in unvegetated habitats during the night. Areas within the 95 and 50% space utilization contours averaged  $2,654.1 \pm 502.0$  and  $379.9 \pm 103.9$  m<sup>2</sup>, respectively, and there was a significant negative relationship between these areas and prawn activity rates in unvegetated habitats. This study provides the first estimates of prawn activity rates and space utilization in the field. Application of acoustic telemetry can increase knowledge of prawn movements and their interactions with other marine species in different habitats.

## Introduction

Determining movement at different temporal and spatial scales is fundamental to understanding behaviour in aquatic organisms. Whilst examples exist for many aquatic organisms (e.g. Cote et al. 2004; Taylor et al. 2006b; Afonso et al. 2009), detailed investigation into prawn behaviour and movement at small spatial scales has not yet been attempted due to technological limitations. Evaluation of prawn movement is traditionally limited to genetic markers (Aubert and Lightner 2000), trace element analysis (Courtney et al. 1994; Fry et al. 2003) and external tags such as streamer tags (Montgomery and Gray 1991; Montgomery et al. 1995). Although these approaches can provide information over larger scales, the data are limited to unidirectional movement information between two points, such as, the point of tagging, spawning or a nursery location, and capture location. Resolving in situ prawn movement at smaller temporal and spatial scales will allow the determination of fine-scale dynamics that may be important for understanding habitat use and foraging behaviour in Penaeidae.

Penaeid prawn species fulfil an important role in estuarine and oceanic ecosystems (Dall et al. 1990), mediating the transfer of energy both as primary consumers (Kieckbusch et al. 2004) and key prey of many predatory fish species (e.g. Kyne and Bennett 2002; Nanjo et al. 2008). Penaeids also support capture fisheries of ~1.5 million tonnes worldwide (Houde and Rutherford 1993) and account for the majority of the international prawn aquaculture production of 2.5 million tonnes (Munro and Owens 2007). Many aspects of penaeid biology have been investigated, including trophic ecology (e.g. O'Brien 1994), fisheries (e.g. Glaister et al. 1990; Ives and Scandol 2007) and broad-scale migration (e.g. Glaister

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et al. 1987). Detailed investigation into penaeid behaviour and movement at smaller scales is needed to complete our knowledge of these taxa and aid interpretation of biological and ecological findings, such as fine-scale patterns in habitat use.

The ways in which prawns interact with their habitat, and the stimuli that provoke this behaviour, are of interest to ecologists. Marine species often have specific requirements for habitats that provide refuge from predators, but are also in the vicinity of appropriate food resources (Walters and Martell 2004). This allows effective partitioning of time to achieve optimal food intake and growth whilst minimizing predation risk. Aquarium experiments have shown that penaeid prawns emerge from the sediment at night and can spend almost the entire night feeding (Hill and Wassenberg 1987). Prawns also periodically emerge from sediments during the day, but for much shorter intervals, and display greatly reduced foraging behaviour (Wassenberg and Hill 1987). Penaeids are preyed upon by many estuarine and oceanic teleost species (e.g. Brewer et al. 1995; Taylor et al. 2006a; Ochwada et al. 2009) and predation—habitat relationships are evident for postlarval *Penaeus plebejus* (Ochwada-Doyle et al. 2010). Reduced diurnal emergence and activity patterns may be an example of risk-averse foraging behaviour; however, there are limited examples where this is studied in natural foraging arenas (e.g. Ochwada et al. 2009).

Acoustic telemetry is an important tool in understanding the ecology and behaviour of marine animals, as fine-scale movements of marine invertebrates, fishes, reptiles and mammals can be effectively monitored (e.g. Cote et al. 2004; Stark et al. 2005; Heupel et al. 2006). Active acoustic telemetry involves actively following the movements of a tagged animal from a boat and allows detailed information on movement and habitat use to be collected across diel, tidal and lunar cycles (Taylor et al. 2006b). This technology has previously been applied to invertebrate species such as lobster *Panulirus cygnus* (MacArthur et al. 2008), conch *Strombus gigas* (Glazer and Kidney 2004) and cephalopods such as *Nototodarus gouldi* (Stark et al. 2005); but this technology is yet to be applied to any prawn species.

This study describes the first application of acoustic tags to a penaeid prawn species, to assess movement and space use in the eastern king prawn *Penaeus (Melicertus) plebejus*, hereafter referred to as *Penaeus plebejus* (Flegel 2007). This species occurs along the east coast of Australia, ranging from 21°S in the deeper waters offshore from Mackay, Queensland to 41°S, (George's Bay, Tasmania and the Gippsland Lakes, Victoria) (Montgomery and Winstanley 1982). *Penaeus plebejus* generally reside within estuaries whilst young. They then exit the estuaries and move to lower latitudes to spawn from March to May (Montgomery et al. 2007). The East Australian Current

(EAC) transports the pelagic larvae to higher latitudes, where they recruit back into rivers and coastal lagoons. The species does not appear to mature south of 32°S (Montgomery et al. 2007). The present study tested attachment of small acoustic tags to *P. plebejus* and observed burying of tagged prawns in a laboratory setting. After evaluation of the tagging approach, the study applied acoustic telemetry to *P. plebejus* in the field to address two objectives: (1) compare diel- and habitat-associated differences in movement and activity patterns; (2) quantify patterns in space utilization and any correlation with prawn size, and habitat-specific activity patterns.

## Materials and methods

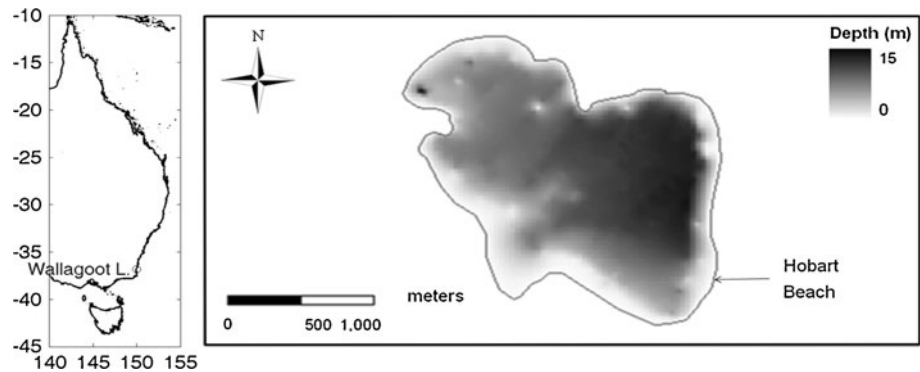
### Study area

The field component of this study was undertaken in Wallagoot Lake (36.789°S, 149.959°E), a landlocked estuarine lagoon on the south-eastern coast of Australia (Fig. 1). The lake is fed from a catchment 35 km<sup>2</sup> in size consisting of primarily national park, with minimal residential and agricultural land use. Wallagoot Lake has a waterway area of 4 km<sup>2</sup>, contains extensive shallow sand flats and is intermittently opened to the ocean. The lake bottom consists primarily of bare sandy substrate and *Zostera* sp., *Halophila* sp. and *Ruppia* sp., which have a combined coverage of approximately 0.8 km<sup>2</sup>. The lake contains an assemblage of predatory fish including fortescue (*Centropogon australis*), dasytid rays, and occasionally bream (*Acanthopagrus* sp.) and snapper (*Pagrus auratus*). The present study focused on the southeastern shore of the lake (Hobart Beach), where large *P. plebejus* are frequently captured by recreational anglers (Fig. 1). Temperature and salinity within the lake generally range between 15–25°C and 33–37, respectively.

### Attachment of acoustic tags to *Penaeus plebejus*

Eastern king prawns were collected in May 2008 using dip nets from Wallagoot Lake and transported by road in a 1,300-l aerated transporter to Sydney Institute of Marine Science (SIMS). At SIMS, prawns were placed into a covered 1,000-l tank containing a sand substrate 10 cm deep, on a flow-through aquarium system supplied with 5-l min<sup>-1</sup> fresh seawater (14.6 ± 0.1°C, salinity of 35.2 ± 0.1, Mean ± SE) from Sydney Harbour. Prawns were left to acclimatize for 7 days, and were fed 1–2 g diced, frozen pilchard (*Sardinops neopilchardis*), per prawn at 11:00 h each day. After 2 days, prawns were observed emerging from the sediment and feeding after pilchards were added to the tank.

**Fig. 1** Location of Wallagoot Lake on east coast of Australia, and bathymetric map of estuary at time of sampling



The tagging method was developed in the laboratory, where tagged prawns could be observed after tagging. Twelve eastern king prawns ( $32.7 \pm 0.7$  mm carapace length, mean  $\pm$  SE) were removed from the holding tank using a dip net and placed into three smaller 20-l aerated holding tanks. Individual prawns were removed from the holding tank, weighed on digital scales and then placed on a dissecting board where carapace length was measured. For tagging, each prawn was held gently between the thumb and index finger with the abdomen resting between the palm of the hand and the dissecting board (Appendix 1 of ESM). The carapace was dried with a tissue before a 1-cm line of cyanoacrylate gel (Loctite<sup>®</sup>) was applied along the dorso-carapace, and a Sonotronics<sup>®</sup> PT-1 transmitter (16 mm length, 7.1 mm diameter, 1.25 g in air, dummy transmitter with no internal circuitry) immediately immersed in the gel and held for 10 s. The PT-1 transmitter accounted for  $9.3 \pm 0.9\%$  (mean  $\pm$  SE) of the total body mass of the prawn in both the aquarium and the field experiments and never exceeded 13.9% of total body mass. The prawn was then placed in a 20-l aerated recovery tank for 10 min, before being placed in the 1,000-l tank (the water in the recovery tank was exchanged after each individual was added).

Prawns were observed daily in the SIMS aquarium (under ambient light conditions without artificial illumination) for 7 days. At 11:00 h, tags and prawns visible within the tank were classified as “buried, tag exposed”, “not buried, tagged”, “not buried, untagged” and “deceased”, with “tag” referring to the PT-1 tag. Prawns were then fed 1–2-g diced, frozen pilchard per prawn, and after 10 min the prawns were again classified as above. Observations were repeated every 10 min for an hour, without disturbing the tank or cover. Any detached tags were removed after the daily observation period, and PT-1 tag numbers recorded.

#### Tracking of *Penaeus plebejus*

Nine juvenile eastern king prawns ( $28.8 \pm 0.7$  mm carapace length, mean  $\pm$  SE, Table 1) were tagged and tracked at Wallagoot Lake over two periods: 23–28 April (tag numbers 4, 17, 49, 50, 51, 52, 53); and 7–12 May 2009 (tag numbers 1 and 2). Prawns were collected using dip nets, held in aerated 80-l tanks for approximately 24 h, tagged with active PT-1 tags (as described above) and then monitored in an aerated holding tank for 2 h. Each PT-1 tag was programmed to transmit a signal on a unique

**Table 1** Biometric and movement information for tagged *Penaeus plebejus* in Wallagoot Lake

Tag number	Mass (g)	CL (cm)	Number of detections	Total distance (m)	# days monitored	MAI $\pm$ SE (m h <sup>-1</sup> )	50% area (m <sup>2</sup> )	Aquatic macrophyte (50%)	95% area (m <sup>2</sup> )	Aquatic macrophyte (95%)	50:95 ratio	Core areas
1	16	3.0	102	1,324	5	54.9 $\pm$ 4.8	190	59	2,173	21	0.09	1
2	11	2.7	12	259	2	23.8 $\pm$ 2.2	416	7	2,123	51	0.20	1
4	16	2.9	31	2,330	3	131.9 $\pm$ 44.1	150	0	2,164	0	0.07	6
17	9	2.6	39	1,798	4	83.2 $\pm$ 48.3	276	100	2,372	58	0.12	1
49	19	2.9	55	1,626	6	53.5 $\pm$ 18.2	184	100	1,289	89	0.14	1
50	17	3.1	66	2,902	6	57.6 $\pm$ 8.3	231	0	1,996	5	0.12	3
51	11	2.8	62	2,529	6	85.7 $\pm$ 24.6	293	2	2,084	7	0.14	7
52	11	2.8	42	915	6	44.3 $\pm$ 23.1	1,144	13	6,441	86	0.18	2
53	21	3.2	57	2,020	6	40.3 $\pm$ 8.0	535	30	3,245	16	0.17	7

The 50% area and 95% area represent the area within 50 and 95% space utilization contours, respectively. Aquatic macrophyte (50%) and aquatic macrophyte (95%) indicate the proportion of vegetated habitat within 50 and 95% space utilization contours, respectively. Aquatic macrophyte is primarily *Zostera* sp

frequency of 73 – 83 kHz, which comprised a unique series of short bleeps separated by a 3-s pause. The series of coded bleeps transmitted continuously for the life of the tags (6 days). After tagging, the prawns were transported by boat and released at the site of capture. Moulting stage was not determined prior to tag attachment in this study.

Tracking commenced at 20:00 h on the evening of release and continued 24 h day<sup>-1</sup> for up to 6 days. Active acoustic tracking was undertaken as described by Taylor et al. (2006b), using a Sonotronics<sup>®</sup> USR-96 acoustic receiver, a DH-4 directional hydrophone (immersed at a depth of ~0.6 m off the starboard bow) mounted in a forward facing direction and Koss<sup>®</sup> PRO-4AA headphones. The receiver scanned relevant frequencies whilst the boat manoeuvred around the tracking area at four knots, and signals detected by the receiver were interpreted auditorily through the headphones. When a signal was detected, it was followed until an abrupt decrease in signal strength indicated that the boat passed over the transmitter. The boat was immediately turned around and a waypoint marked using a GPS76 (Garmin), where the signal was strongest. Tags were located sequentially every 0.5–3.0 h at a positional accuracy of  $3.0 \pm 0.8$  m (mean  $\pm$  SE, calculated using a moored transmitter as described by Taylor et al. 2006b). Briefly, positional accuracy was determined by attaching a pinger to a submerged mooring in 4 m of water and locating the pinger six times using the tracking technique described above. Accuracy of the GPS during the tracking period was typically ~3 m. Waypoints were downloaded into Mapsource<sup>®</sup> v. 5.4 (Garmin), and distances and time elapsed between successive waypoints calculated. Activity rates were expressed as a minimum activity index (*MAI*, m h<sup>-1</sup>) by dividing the distance moved between waypoints by the time elapsed during this movement.

Space utilization distribution was calculated for each prawn with a Fixed Kernel Density Estimator (ArcGIS v. 9.3 with Hawth's Tools Extension). This approach used likelihood cross-validation (Cvh) as the smoothing factor (which is recommended where sample size is less than or equal to 50, Horne and Garton 2006). To reflect the majority and core space utilization distribution for tracked prawns, 95 and 50% contours were chosen, respectively, and the ratio of 50–95% contour areas (50:95) was used as an indicator of the level of residency in the core area (Parsons et al. 2003; Taylor et al. 2006b).

#### Statistical analyses

Homogeneity of variance was evaluated using Levene's test (Levene 1960), normality assessed by visual inspection of a normal probability plot, and data log<sub>10</sub> transformed where necessary. Each waypoint was assigned to a particular habitat type (unvegetated or aquatic macrophyte) using

existing habitat data for the tracking area. Each individual prawn was considered as the replicate unit of observation for all analyses.

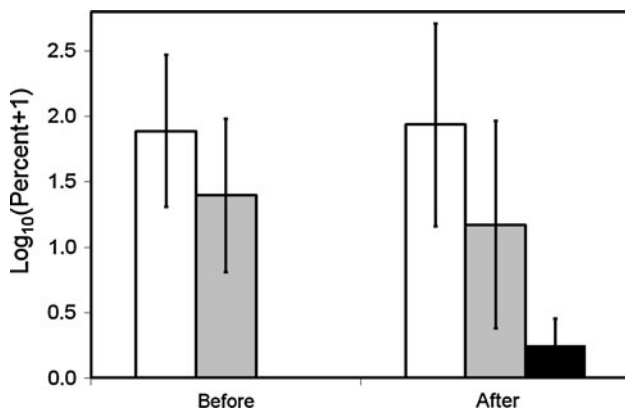
Two dependent variables, activity rates (*MAI*) and distance moved, were calculated from tracking data and used to assess objective one. Differences in these variables across the diel period (two levels; night, 1800–0600 h and day 0600–1800 h) and in different habitats (two levels; unvegetated or aquatic macrophyte) were evaluated using two-factor ANOVA. Prawns 1 and 2 (Table 1) were excluded from ANOVA analyses, as they were tracked over a different moon phase (full moon).

Objective two was assessed by correlating prawn size (mass, g) with the area within core (50%) and majority (95%) space utilization contours using simple linear regression. The relationship between prawn size and the 50:95% ratio described above was also tested using simple linear regression. Stepwise multiple linear regression and model selection (Akaike's Information Criterion, Bozdogan 1987) were used to evaluate the relative influence of activity rates in different habitats on the observed patterns of space utilization. Two models regressed the area within the core (50%) and majority (95%) space utilization contours against activity rates in unvegetated habitat (mean *MAI* in unvegetated) and activity rates in vegetated habitat (mean *MAI* in aquatic macrophyte). All statistical analyses were undertaken using PASW Statistics v. 18.0 (SPSS Inc, Chicago, Illinois, USA) with the exception of regression analyses, which were undertaken in R v. 2.7.2 (Ihaka and Gentleman 1996).

## Results

### Attachment of acoustic tags to *Penaeus plebejus* and post-tagging observations in the laboratory

All eastern king prawns survived the tag attachment and the observation period, and there were minimal differences in burying and emergence of tagged prawns before and after the introduction of food (Fig. 2). All prawns were buried prior to the introduction of food; however, prawns occasionally emerged from the sediment to feed within the 1-h observation period. The diced pilchard was completely consumed by the time of the following observation period on the following day. A maximum of ~40% of PT-1 tagged prawns buried with their tags exposed over the course of the experiment, and the number of exposed tags appeared to decrease after the introduction of food to the tank, possibly as a result of sediment disturbance as the prawns emerged. All PT-1 tags remained attached to tagged prawns through the experimental period, with the exception of one tagged prawn that shed its exoskeleton along with the tag on day seven.



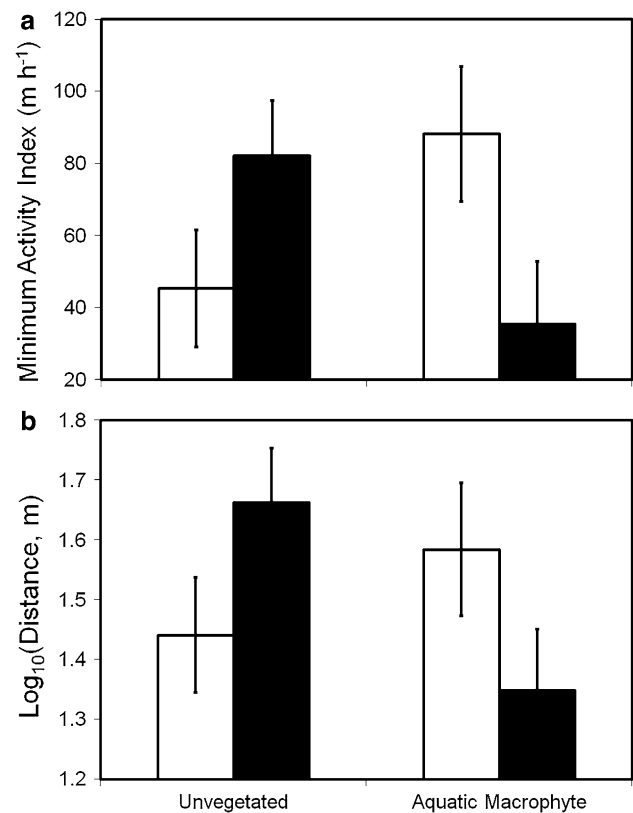
**Fig. 2** Mean  $\pm$  SE per cent burying in tagged prawns before and after provision of food, showing per cent of tagged prawns completely buried in sediment (*open bars*), per cent of tagged prawns buried in sediment but with tags exposed (*shaded bars*) and per cent of tagged prawns not buried in sediment (*black bars*). Data were averaged across 7 days of observation, and  $\log_{10}(x + 1)$  transformed to allow representation of small data values

#### *Penaeus plebejus* activity and space utilization

All eastern king prawns survived the capture and tagging procedure and commenced moving after release back into the wild. The maximum MAI calculated was  $840 \text{ m h}^{-1}$ , and up to 1,600 m was covered in a 24-h period. Activity rates for each individual prawn averaged over the course of the tracking period are indicated in Table 1.

There were no significant differences in eastern king prawn activity rates (MAI) between diel periods (day or night) and habitats (unvegetated or aquatic macrophyte); however, there was a significant diel period  $\times$  habitat interaction term ( $F_{(1,26)} = 6.98$ ,  $P = 0.014$ , Fig. 3a). The two-factor interaction term was interpreted by comparing MAI in different habitats separately for day and night, with the  $F$ -value for each pairwise comparison calculated using the mean-square error from the full two-factor ANOVA model (analysis of simple main effects, Quinn and Keough 2002). Whilst there was no significant difference in MAI between unvegetated or aquatic macrophyte habitats during the day ( $F_{(1,12)} = 2.97$ ,  $P = 0.120$ ), activity rates were significantly greater in unvegetated habitats during the night ( $F_{(1,14)} = 4.07$ ,  $P = 0.050$ , Fig. 3a). Similar relationships were detected in the total distance moved between diel periods and in different habitats. A significant diel period  $\times$  habitat interaction term ( $F_{(1,26)} = 5.14$ ,  $P = 0.032$ , Fig. 3b) was interpreted as no difference in the total distance moved through unvegetated and aquatic macrophyte habitats during the day ( $F_{(1,12)} = 0.93$ ,  $P = 0.353$ ), but significantly greater movement in unvegetated habitats during the night ( $F_{(1,14)} = 5.26$ ,  $P = 0.038$ , Fig. 3b).

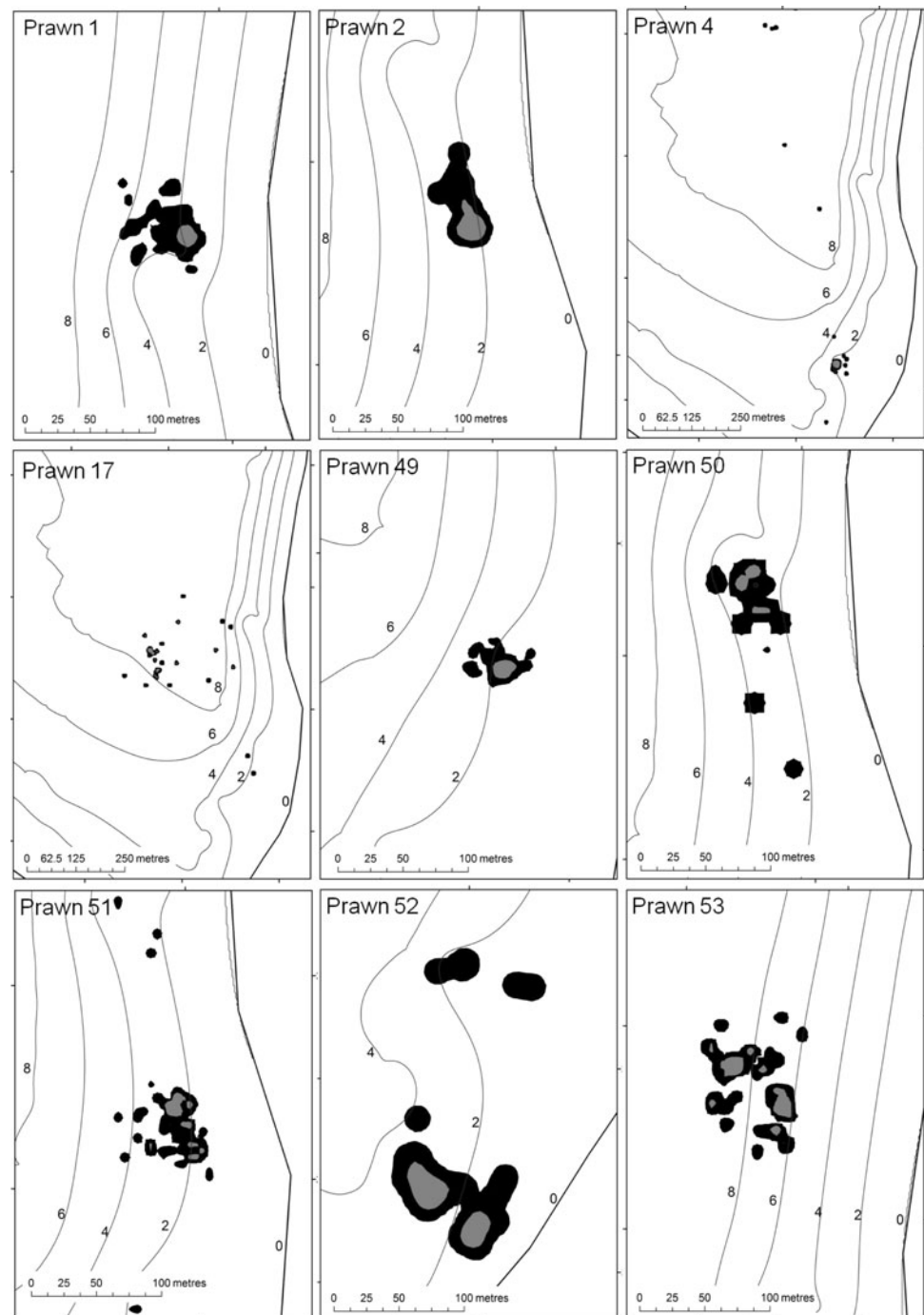
The area within majority (95%) and core (50%) space utilization contours were as large as 6,441 and 1,144  $\text{m}^2$ ,



**Fig. 3** *Penaeus plebejus* **a** Minimum activity index (MAI), and **b** distance moved ( $m$ ) between day (*white bars*) and night (*black bars*), in unvegetated and aquatic macrophyte habitats within Wallagoot Lake

respectively, during the period eastern king prawns were tracked (Table 1). Movement was usually concentrated in a single core area, but some prawns used a large number of small habitat patches (Table 1; Fig. 4). There was no relationship between prawn mass ( $g$ ) and the area within majority ( $\log_{10}b = 0.008$ ,  $t = 0.51$ ,  $P = 0.625$ ) or core ( $\log_{10}b = 0.004$ ,  $t = 0.19$ ,  $P = 0.859$ ) space utilization contours. The 50:95 area ratio was low (Table 1,  $0.14\% \pm 0.01$ , mean  $\pm$  SE), which suggests that core areas made up a small proportion of the total space used in a relative sense, and this was not significantly related to prawn mass ( $\log_{10}b = -0.003$ ,  $t = 0.27$ ,  $P = 0.798$ ). The area within the core (50%) space utilization contour decreased with increasing prawn activity rates in unvegetated habitat ( $\log_{10}b = -0.84$ ,  $t = -6.07$ ,  $P < 0.010$ , Fig. 5a), but there was no relationship with activity rates in aquatic macrophyte habitat ( $\log_{10}b = 0.20$ ,  $t = 1.28$ ,  $P = 0.249$ , Fig. 5a). Similarly, the area within the majority (95%) space utilization contour decreased with increasing prawn activity in unvegetated habitats ( $\log_{10}b = -0.45$ ,  $t = -2.48$ ,  $P = 0.048$ , Fig. 5b). There was no relationship between the area within the majority (95%) space utilization contour, and activity rates in

**Fig. 4** *Penaeus plebejus* 50% (grey) and 95% (black) space utilization contours in Wallagoot Lake. Bathymetry contours labelled in m. Prawn numbers correspond with those listed in Table 1



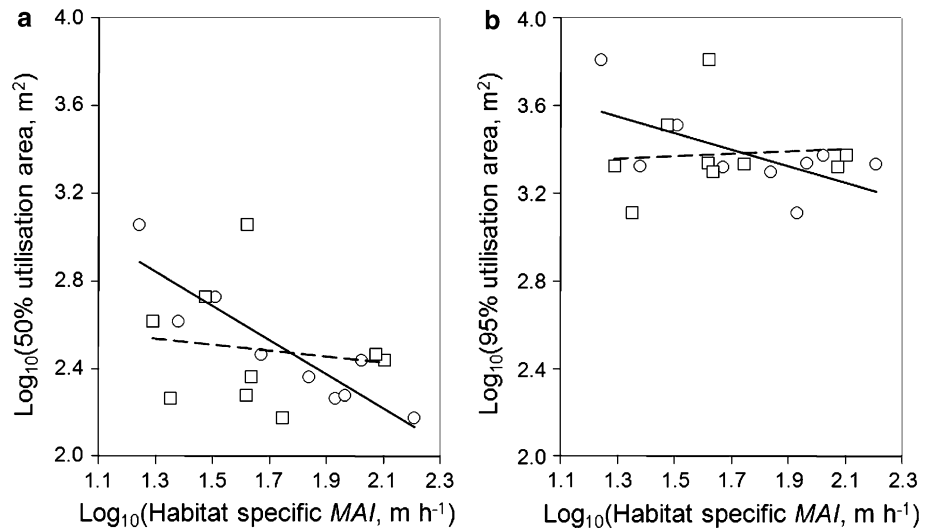
aquatic macrophyte habitat ( $\log_{10}b = 0.24$ ,  $t = 1.15$ ,  $P = 0.296$ , Fig. 5b).

## Discussion

This is the first study to tag prawns with acoustic transmitters and track their movements over fine temporal and spatial scales. The attachment of a 1.25 g PT-1 tag to the dorso-carapace did not result in any appreciable changes in

the ability of *P. plebejus* to bury during the period of attachment. The ability to bury in the sediment is a key anti-predator response common amongst most Penaeidae (e.g. Ruello 1973; Moller and Jones 1975). In a tank environment, penaeid prawns usually remained buried for the majority of the diel period. Emergence periods range from minutes to hours, depending on the degree of hunger and the handling and search time required to effectively forage on the available resources (Ruello 1973; Hill and Wassenberg 1987). Although *P. plebejus* rarely emerged

**Fig. 5** Relationship between transformed minimum activity index (*MAI*) measurements in unvegetated (*open circle; solid lines*) and aquatic macrophyte habitats (*open square; dashed lines*) and area within **a** core (50%), and **b** majority (95%) space utilization contours



during the observation period, the food introduced into the tank was consumed before the next observation period, most likely after dusk. Whilst there were no obvious effects of the tag on the ability of *P. plebejus* to bury, future research should consider how the presence and mass burden of the transmitter might affect the bioenergetics and movement rates of tagged and untagged prawns.

Moulting occurs throughout the penaeid lifecycle and is dependent on a range of factors including prawn size and temperature (Passano 1960). This may create problems when applying acoustic tags to prawns, or when interpreting variation in movement. First, the tag is attached to the exoskeleton and will remain attached to the shed exuviate at the end of the moulting process (Wassenberg and Hill 1984). This was observed for a single *P. plebejus* in the laboratory study on the seventh day after tagging, where the tag was found attached to the carapace exuviate after ecdysis. Ecdysis occurs on a ~20-day cycle in penaeids (for example, a *Penaeus esculentus* moult cycle ranges from 14 to 34 days, Hill and Wassenberg 1992). This far exceeds the current six-days battery life of small acoustic tags such as the PT-1; however, the moulting process can lead to altered behaviour for up to 5 days before and after the night of ecdysis (Wassenberg and Hill 1984). Altered behaviour may include a decrease in feeding time, the complete absence of feeding on the night of ecdysis (Hill and Wassenberg 1992) and an altered emergence pattern (Wassenberg and Hill 1984). Inspection of the exoskeleton to determine the approximate stage of the moult cycle prior to tagging could verify that only prawns sufficiently early in the moult cycle are tagged. This would both ensure that the tag expires prior to ecdysis and allow the stage of the moult cycle to be considered when evaluating results from experimental subjects. Alternatively, acoustic telemetry will allow novel in situ observations of

prawn behaviour to complement laboratory studies (e.g. Wassenberg and Hill 1984), by applying tags to target specific periods of the moult cycle.

Motile activity and foraging patterns of prawns, and diel variation in these patterns, are usually measured in aquaria using actual observations or recorded footage (Hill and Wassenberg 1987, 1992). Such studies are useful for observations under controlled conditions, but there are obvious experimental artefacts, such as observational disturbances or tank size effects (Bergstrom and Englund 2004). Acoustic telemetry complements such controlled experiments by monitoring prawns in their natural environment in the presence of natural biotic and abiotic (i.e. predator, prey, light and habitat) stimuli. Such field studies, though, are also subject to a different set of experimental limitations in addition to those associated with the moulting cycle. In general, research on organism movements using acoustic telemetry often suffers from low statistical power when detecting small effect sizes, which arises from several factors over and above the financial cost of the tags. Only a limited number of tags can be effectively monitored without collisions due to a limited range of frequencies across which standard acoustic telemetry tags transmit (usually 69–83 kHz), although other telemetry systems use technology to overcome this. In addition, there is often a necessity to average observations to address statistical assumptions such as sample independence, which reduces the degrees of freedom available for statistical comparisons. Considering the effect sizes and variability in movement rates from existing laboratory studies and the present in situ study will be useful in designing future field experiments.

The approach in the current study is a useful way of tracking movements of several individuals simultaneously over a specified time period, and the minimum activity

index (*MAI*) is a practical way to express these activity patterns (Connolly et al. 2002; Taylor et al. 2006b). It should be noted, however, that the tracking approach calculates movement as a straight-line between two points and does not account for variation in this straight-line distance (such as circular or meandering movement patterns). Consequently, data presented in this study may underestimate both distance moved and activity rates. This limitation may be addressed in future studies by complementing manual tracking with occasional continuous monitoring of individual organisms throughout the tracking period. Nonetheless, data presented here indicate that *MAI* of a *P. plebejus* can reach up to  $860 \text{ m h}^{-1}$  in the absence of tidal currents. Considering *MAI* as a minimum index the actual rate of movement may be even greater and may also be amplified by a favourable current. These estimates of movement over smaller spatial scales complement existing quantitative measurements of movement for streamer-tagged *P. plebejus* over larger scales, which indicate movement rates up to  $240 \text{ m h}^{-1}$  when averaged over longer periods (calculated from Montgomery 1990). These values highlight the differences in movement rates within a complex estuarine environment, relative to migrations over latitudinal scales.

*Penaeus plebejus* are thought to be amongst the most responsive of Australian penaeid species to light (Wassenberg and Hill 1994) and typically bury in the sediment in response to this stimulus. This is supported indirectly by decreases in recreational CPUE using dip nets during the summer full moon (Griffiths 1999), when nocturnal light levels are highest. It is thought that foraging is undertaken during these periods of nocturnal emergence when the risk of predation by visual predators is lowest (Benfield and Minello 1996; Ochwada et al. 2009). In our study, activity rates appeared slightly greater during the night; however, diel period was not a significant main effect in the ANOVA model. The significant interaction term and inverse relationship of both *MAI* and distance moved between factor combinations partially explain this result. *Penaeus plebejus* movement (collectively *MAI* and distance moved) is greater in aquatic macrophytes during the day and greater in unvegetated habitat during the night; however, only the latter difference was significant. In New South Wales, *P. plebejus* preys on organisms such as estuarine mysid shrimp (Suthers 1984), which are significantly more abundant in unvegetated benthic habitats during the night (Taylor 2008). The partitioning of movement between habitats and diel periods observed here also supports previous findings regarding nocturnal emergence from predation refuge and foraging over unvegetated substrates in the western king prawn *Penaeus latissulcatus* (Tanner and Deakin 2001).

This study provides the first ever field measurements of small-scale space utilization for a species of penaeid prawn. The lack of similar estimates for other organisms of similar mass or behaviour makes comparison difficult. The area within the 95% space utilization contour ( $2,654.1 \pm 502.0 \text{ m}^2$ , mean  $\pm$  SE of all individuals in Table 1) was relatively similar to home range measurements for the larger decapod *Homarus americanus* (Watson et al. 2009)  $>62 \text{ mm CL}$  ( $1,002.4 \pm 195.7 \text{ m}^2$ ), but much smaller than leafy seadragon *Phycodurus eques* ( $12,912.5 \pm 4,975.5 \text{ m}^2$ ), which are potentially of similar size and swimming ability to *P. plebejus* (Connolly et al. 2002). The small area within the core (50%) space utilization contour ( $379.9 \pm 103.9 \text{ m}^2$ , mean  $\pm$  SE of all individuals in Table 1) for *P. plebejus* indicates that movement is highly concentrated within a discrete area (which can be calculated to represent a circle of diameter approximately 13 m) and implies that prawns may principally rely on forage resources over a small spatial area and in the direct vicinity of their predation refuge. There was no relationship detected between body mass and space utilization. This conflicts with current models which show strong allometric scaling of space use (e.g. Mysterud 1998; Taylor et al. 2006b), but this may be due to the small size range analysed here.

The 50:95 space utilization ratio is an indicator of how evenly animals utilize space. If animals use space in a homogenous fashion, then the ratio is  $\sim 0.50$  (Parsons et al. 2003; Taylor et al. 2006b). The low ratio of  $\sim 0.14$  observed for *P. plebejus* indicates that over a short observation periods (up to 6 days), the prawns spent most of their time in a small portion of the total area that they used. Prawn 4 displayed unusual behaviour, utilizing a large number of small patches intensively with very little movement in the areas between them. This behaviour was evident in Prawn 53 to a lesser extent, and potentially relates to the use of deeper water by these individuals, where a lower abundance of primary consumer prey (e.g. Clark et al. 2003) may require an alternative foraging strategy. For most prawns with multiple 50% space utilization contours, each contour was similar in size and shape; although there was high variability in size and shape of 50% contours amongst individuals. The factors contributing to this variability cannot be determined from this data set but may relate to the type and quality of prey available in each habitat (Hill and Wassenberg 1987, 1992) or simply individuality in foraging behaviour (Tinker et al. 2008).

The negative relationship between the area within the core (50%) space utilization contour and *P. plebejus* activity rates over unvegetated habitat is the converse of a positive relationship between area and movement that may be expected on the assumption that a greater rate of movement is required to cover a wider area. Considering



risk-averse foraging behaviour (Clark et al. 2003; Walters and Martell 2004), foraging is likely undertaken close to resting and refuge habitat, and this is evident in the relatively small core areas observed here. Previous studies have shown that both sedimentary (Ruello 1973) and epibenthic food availability (Wassenberg and Hill 1987) affect the distribution of eastern Australian penaeids, but prawns and other crustaceans also have specific requirements for burying such as appropriate sediment grain size (e.g. Sanders 1958). An optimal habitat would facilitate risk-averse foraging by including sediment appropriate for burying in the vicinity of appropriate forage items (McTigue and Zimmerman 1998). Specific requirements for foraging and refuge habitats may explain the use of small habitat patches for the bulk of prawn activity. Assuming juvenile and adult *P. plebejus* individuals prefer unvegetated habitats for foraging, as is the case for *Mellicertus latisulcatus* (Tanner and Deakin 2001), the negative relationship between activity and space utilization may reflect plasticity in foraging strategy amongst individuals. The relationship observed in the current study may represent a trade-off between area and activity, where prawns appear to forage over a wider area relatively slowly, or a smaller area faster. Covering a greater range may improve the chance of encountering prey, whereas covering a smaller area more thoroughly may improve access to more cryptic or less abundant organisms. Also, if a high density patch of preferred prey is encountered, movement may be concentrated over this area for a period of time. This behaviour likely depends on the type and availability of food within a habitat patch (Sih 1982), and future studies should investigate prey abundance and quality in relation to space utilization by prawns.

This study demonstrates that monitoring of fine-scale prawn movements using telemetry is appropriate for evaluating prawn behaviour and movement in the context of microhabitats and short time periods. Future studies could be improved by determining prawn moult stage at the time of tagging, quantifying the effects of the tag burden on swimming ability of the prawn, undertaking simultaneous measurements of prawn densities, diet and prey distribution, and microhabitat variables (such as substrate type and sediment grain size); and monitoring total movement of prawns alongside the minimum activity index. In *P. plebejus*, acoustic tagging has revealed high activity rates over small spatial scales and intensive use of small habitat patches by prawns. These data contribute to our understanding of the intricacies of movement and behaviour in Penaeidae and provide a basis for future evaluation of predator–prey and species–habitat interactions.

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## References

- Afonso P, Fontes J, Holland K, Santos R (2009) Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally *Pseudocaranx dentex*, and their implications for marine reserve design. *Mar Ecol Prog Ser* 381:273–286
- Aubert H, Lightner DV (2000) Identification of genetic populations of the Pacific blue shrimp *Penaeus stylirostris* of the Gulf of California, Mexico. *Mar Biol* 137:875–885
- Benfield MC, Minello TJ (1996) Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. *Environ Biol of Fishes* 46:211–216
- Bergstrom U, Englund G (2004) Spatial scale, heterogeneity and functional responses. *J An Ecol* 73:487–493
- Bozdogan H (1987) Model selection and Akaike's Information Criterion: the general theory and its analytical extensions. *Physcometrika* 52:345–370
- Brewer DT, Blaber SJM, Salini JP, Farmer MJ (1995) Feeding ecology of predatory fishes from Groote Eylandt in the Gulf of Carpentaria, Australia, with special reference to predation on penaeid prawns. *Estuar Coast Shelf Sci* 40:577–600
- Clark KL, Ruiz GM, Hines AH (2003) Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats. *J Exp Mar Biol Ecol* 287:37–55
- Connolly RM, Melville AJ, Preston KM (2002) Patterns of movement and habitat use by leafy seadragons tracked ultrasonically. *J Fish Biol* 61:684–695
- Cote D, Moulton S, Frampton P, Scruton D, McKinley R (2004) Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. *J Fish Biol* 64:665–679
- Courtney AJ, Die DJ, Holmes MJ (1994) Discriminating populations of the eastern king prawn, *Penaeus plebejus*, from different estuaries using ICPMS trace–element analysis. *Atomic Spectrosc* 15:1–6
- Dall W, Hill B, Rothlisberg P, Sharples D (1990) The biology of the Penaeidae. *Adv Mar Sci* 27:1–488
- Flegel TW (2007) The right to refuse revision in the genus *Penaeus*. *Aquaculture* 264:2–8
- Fry B, Baltz DM, Benfield MC, Fleegeer JW, Gace A, Haas HL, Quinones-Rivera ZJ (2003) Stable isotope indicators of movement and residency for brown shrimp (*Farfantepenaeus aztecus*) in coastal Louisiana marshscapes. *Estuaries* 26:82–97
- Glaister JP, Lau T, McDonall VC (1987) Growth and migration of tagged eastern Australian king prawns, *Penaeus plebejus* Hess. *Aust J Mar Freshw Res* 38:225–241
- Glaister JP, Montgomery SS, McDonall VC (1990) Yield-per-recruit analysis of eastern king prawns *Penaeus plebejus* Hess, in eastern Australia. *Aust J Mar Freshw Res* 41:175–197
- Glazer RA, Kidney JA (2004) Habitat associations of adult queen conch (*Strombus gigas* L.) in an un-fished Florida keys back reef: applications to essential fish habitat. *Bull Mar Sci* 75: 205–224
- Griffiths SP (1999) Effects of lunar periodicity on catches of *Penaeus plebejus* (Hess) in an Australian coastal lagoon. *Fish Res* 42:195–199

- Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Mar Freshw Res* 57:1–13
- Hill BJ, Wassenberg TJ (1987) Feeding behavior of adult tiger prawns, *Penaeus esculentus*, under laboratory conditions. *Aust J Mar Freshw Res* 38:183–190
- Hill BJ, Wassenberg TJ (1992) Preferences and amount of food eaten by the prawn *Penaeus esculentus* over the molt cycle. *Aust J Mar Freshw Res* 43:727–735
- Horne JS, Garton EO (2006) Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *J Wildl Manage* 70:641–648
- Houde ED, Rutherford ES (1993) Recent trends in estuarine fisheries—predictions of fish production and yield. *Estuaries* 16:161–176
- Ihaka R, Gentleman R (1996) R: a language for data analysis and graphics. *J Comp Graph Stat* 5:299–314
- Ives MC, Scandol JP (2007) A Bayesian analysis of NSW eastern king prawn stocks (*Melicertus plebejus*) using multiple model structures. *Fish Res* 84:314–327
- Kieckbusch DK, Koch MS, Serafy JE, Anderson WT (2004) Trophic linkages among primary producers and consumers in fringing mangroves of subtropical lagoons. *Bull Mar Sci* 74:271–285
- Kyne PM, Bennett MB (2002) Diet of the eastern shovelnose ray, *Aptychotrema rostrata* (Shaw and Nodder, 1794), from Moreton Bay, Queensland, Australia. *Mar Freshw Res* 53:679–686
- Levene H (1960) Robust tests for equality of variances. In: Olkin I, Hotelling H (eds) *Contributions to probability and statistics*. Stanford University Press, Palo Alto, pp 278–292
- MacArthur LD, Babcock RC, Hyndes GA (2008) Movements of the western rock lobster (*Panulirus cygnus*) within shallow coastal waters using acoustic telemetry. *Mar Freshw Res* 59:603–613
- McTigue TA, Zimmerman RJ (1998) The use of infauna by juvenile *Penaeus aztecus* (Ives) and *Penaeus setiferus* (Linnaeus). *Estuaries* 21:160–175
- Moller TH, Jones DA (1975) Locomotory rhythms and burrowing habits of *Penaeus semisulcatus* (De Haan) and *P. monodon* (Fabricius) (Crustacea, Penaeidae). *J Exp Mar Biol Ecol* 18:61–77
- Montgomery SS (1990) Movements of juvenile eastern king prawns, *Penaeus plebejus*, and identification of stock along the east-coast of Australia. *Fish Res* 9:189–208
- Montgomery SS, Gray CA (1991) Effects of sizes of streamer tags on mortality and growth of juvenile eastern king prawns *Penaeus plebejus*. *Mar Ecol Prog Ser* 76:33–40
- Montgomery S, Winstanley RH (1982) Prawns (east of Cape Otway). Fish situation report no. 6. CSIRO Marine Laboratories, Cronulla
- Montgomery SS, Brett PA, Blount C, Stewart J, Gordon GNG, Kennelly SJ (1995) Loss of tags, double-tagging and release methods for eastern king prawns, *Penaeus plebejus* (Hess): laboratory and field experiments. *J Exp Mar Biol Ecol* 188:115–131
- Montgomery SS, Courtney AJ, Blount C, Stewart J, Die DJ, Cosgrove M, O'Neill MF (2007) Patterns in the distribution and abundance of female eastern king prawns, *Melicertus plebejus* (Hess, 1865), capable of spawning and reproductive potential in waters off eastern Australia. *Fish Res* 88:80–87
- Munro J, Owens L (2007) Yellow head-like viruses affecting the penaeid aquaculture industry: a review. *Aquac Res* 38:893–908
- Mysterud A (1998) The relative roles of body size and feeding type on activity time of temperate ruminants. *Oecologia* 113:442–446
- Nanjo K, Kohno H, Sano M (2008) Food habits of fishes in the mangrove estuary of Urauchi River, Iriomote Island, southern Japan. *Fish Sci* 74:1024–1033
- Obrien CJ (1994) Ontogenetic changes in the diet of juvenile brown tiger prawns *Penaeus esculentus*. *Mar Ecol Prog Ser* 112:195–200
- Ochwada F, Loneragan N, Gray C, Suthers I, Taylor M (2009) The influence of habitat complexity on habitat preference and predation mortality in postlarval eastern king prawn *Penaeus plebejus*: implications for stock enhancement. *Mar Ecol Prog Ser* 380:161–171
- Ochwada-Doyle F, Loneragan N, Gray C, Taylor M (2010) Using experimental ecology to understand stock enhancement: comparisons of habitat-related predation on wild and hatchery-reared *Penaeus plebejus* Hess. *J Exp Mar Biol Ecol* 390:65–71
- Parsons D, Babcock R, Hankin R, Willis T, Aitken J, O'Dor R, Jackson G (2003) Snapper *Pagrus auratus* (Sparidae) home range dynamics: acoustic tagging studies in a marine reserve. *Mar Ecol Prog Ser* 262:253–265
- Passano LM (1960) Moulting and its control. In: Waterman TH (ed) *The physiology of crustacea: metabolism and growth*, vol I. Academic Press, New York, pp 473–536
- Quinn G, Keough M (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Port Melbourne
- Ruello NV (1973) Burrowing, feeding, and spatial distribution of the school prawn *Metapenaeus macleayi* (Haswell) in the Hunter River region, Australia. *J Exp Mar Biol Ecol* 13:189–206
- Sanders HL (1958) Benthic studies in Buzzards Bay. 1. Animal-sediment relationships. *Limnol Oceanogr* 3:245–258
- Sih A (1982) Optimal patch use: variation in selective pressure for efficient foraging. *Am Nat* 120:666–685
- Stark K, Jackson G, Lyle J (2005) Tracking arrow squid movements with an automated acoustic telemetry system. *Mar Ecol Prog Ser* 299:167–177
- Suthers IM (1984) Functional-morphology of the mouthparts and gastric mill in *Penaeus plebejus* Hess (Decapoda, Penaeidea). *Aust J Mar Freshw Res* 35:785–792
- Tanner JE, Deakin S (2001) Active habitat selection for sand by juvenile western king prawns, *Melicertus latisulcatus* (Kishinouye). *J Exp Mar Biol Ecol* 261:199–209
- Taylor MD (2008) Spatial and temporal patterns of habitat use by three estuarine species of mysid shrimp. *Mar Freshw Res* 59:792–798
- Taylor MD, Fielder DS, Suthers IM (2006a) Spatial and ontogenetic variation in the diet of wild and stocked mullet (*Argyrosomus japonicus*, Sciaenidae) in Australian estuaries. *Estuar Coast* 29:785–793
- Taylor MD, Laffan SD, Fielder DS, Suthers IM (2006b) Key habitat and home range of mullet (*Argyrosomus japonicus*) in a south-east Australian estuary: finding the estuarine niche to optimise stocking. *Mar Ecol Prog Ser* 328:237–247
- Tinker MT, Bentall G, Estes JA (2008) Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proc Nat Acad Sci* 105:560–565
- Walters CJ, Martell S (2004) *Fisheries ecology and management*. Princeton University Press, Princeton
- Wassenberg TJ, Hill BJ (1984) Molting behavior of the tiger prawn *Penaeus esculentus* (Haswell). *Aust J Mar Freshw Res* 35:561–571
- Wassenberg TJ, Hill BJ (1987) Natural diet of the tiger prawns *Penaeus esculentus* and *Penaeus semisulcatus*. *Aust J Mar Freshw Res* 38:169–182
- Wassenberg TJ, Hill BJ (1994) Laboratory study of the effect of light on the emergence behavior of 8 species of commercially important adult penaeid prawns. *Aust J Mar Freshw Res* 45:43–50
- Watson WH, Golet W, Scopel D, Jury S (2009) Use of ultrasonic telemetry to determine the area of bait influence and trapping area of American lobster, *Homarus americanus*, traps. *New Zeal J Mar Freshw Res* 43:411–418