

## Niche partitioning in two syntopic mudskipper species (Teleostei: Gobiidae: Oxudercinae) in a Singapore mangrove

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**Abstract.** Reportedly segregated in Thai mangroves, *Periophthalmodon schlosseri* (henceforth *Pn. schlosseri*) and *Periophthalmus walailakae* (henceforth *Ps. walailakae*) coexist syntopically in Singapore mangroves. Diet and habitat selection were investigated to ascertain if partitioning exists between these two mudskipper species. Three permanent plots (each measuring 5 × 5 m) were established per mudskipper species to investigate burrow, and site fidelity in a mangrove forest in Lim Chu Kang, Singapore. After determining plot fidelity, mudskippers within the six plots were collected for diet analyses. The microhabitats were assessed for abiotic parameters of canopy cover, sediment organic content, and sediment grain size. Despite twice-daily tidal migrations, *Pn. schlosseri* displayed both burrow, and plot fidelity; *Ps. walailakae* exhibited plot fidelity only. The mean densities ( $\pm$  S.E.) of *Pn. schlosseri* and *Ps. walailakae* in the plots were  $3.3 \pm 0.7$  and  $5.2 \pm 0.2$  individuals per 25 m<sup>2</sup>, respectively. Both mudskipper species are predominantly cannibalistic, with extensive overlaps in the diet niche. Both species demonstrated high Indices of Preponderance for crabs in their diets (*Pn. schlosseri*: 91.3%; *Ps. walailakae*: 81.9%). Results suggest optimal foraging by both mudskippers on the most abundant brachyuran prey species at the sampling site, *Paracleistostoma depressum*. The difference in mudskipper sizes did not result in brachyuran prey size variation: the smaller *Ps. walailakae* was equally capable of preying on similar-sized prey as *Pn. schlosseri*. The diets of *Pn. schlosseri* and *Ps. walailakae* were supplemented with opportunistic ingestion of winged insects and benthic worms, respectively. Temporal partitioning was observed during foraging bouts: *Pn. schlosseri* feeds immediately upon emersion whereas *Ps. walailakae* forages later after tide has fully receded. Competition was further alleviated through spatial partitioning. Multidimensional Scaling of the sampled abiotic parameters showed no clustering effect for either mudskipper species plots but habitat heterogeneity was detected through one-way Analysis of Similarities ( $R = 0.396$ ). Areas occupied by *Pn. schlosseri* were more open-canopied (mean canopy cover:  $64.0 \pm 3.8\%$ ) whereas *Ps. walailakae* occupied shadier habitats ( $84.6 \pm 1.9\%$ ;  $p < 0.05$ ). There was no significant difference in organic content in sampled sediments ( $p = 0.588$ ). Sediment compositions sampled from the mudskipper plots were poorly sorted; *Pn. schlosseri* inhabit areas of coarse siltation (mean sediment grain size:  $66.6 \pm 8.7 \mu\text{m}$ ) while *Ps. walailakae* plots had fine sandy substrates ( $100.7 \pm 14.6 \mu\text{m}$ ). Syntopy in *Pn. schlosseri* and *Ps. walailakae* is achieved through temporal variation in feeding, and spatial exploitation of specific microhabitats.

**Key words.** feeding ecology, habitat selection, brachyuran crabs, *Periophthalmodon schlosseri*, *Periophthalmus walailakae*.

### INTRODUCTION

The term ‘mudskipper’ is commonly applied to ‘oxudercine gobies’ sensu Murdy (1989) of *Periophthalmus* lineage (Agorreta et al., 2013). Many mudskipper species are amphibious; they are found in intertidal areas, principally mangroves and mangrove-associated habitats (Murdy, 1989). Terrestrial adaptations of many mudskipper species intrigued scientists, who have used them as model organisms for physiological studies (e.g., Jew et al., 2013; Sakamoto et al., 2015). With varying degrees of aquaticity (Kok et al., 1998), different mudskipper species are able to exploit

different zones along the intertidal gradient (Polgar & Crosa, 2009). In contrast to the extensive literature on physiology, there is a dearth of literature on the ecology of mudskippers possibly due to the challenging working conditions in mangrove-associated habitats.

Fourteen species of mudskippers were reported from Singapore, including the giant mudskipper, *Periophthalmodon schlosseri* (Pallas, 1770), and the yellow-spotted mudskipper, *Periophthalmus walailakae* Darumas & Tanticodok, 2002 (Larson et al., 2008). Prior to its description, *Periophthalmus walailakae* (henceforth *Ps. walailakae*) was mistaken for juveniles of *Periophthalmodon schlosseri* (henceforth *Pn. schlosseri*) due to the presence of a lateral black stripe in both species (Jaafar et al., 2006). Based on specimens examined by Jaafar et al. (2006), adults of *Pn. schlosseri* (max. SL: 208 mm) are approximately twice as large as those of *Ps. walailakae* (max. SL: 117 mm). Published reports indicate conflicting evidence on the population distribution of these two species. In Thailand, where *Ps. walailakae*

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was first described, these two species were reported to be allopatric; *Ps. walailakae* occurs along the west coast facing the Andaman Sea while *Pn. schlosseri* is distributed along the east coast facing the Gulf of Thailand (Darumas & Tantichodok, 2002). In Singapore (Jaafar et al., 2006) and Peninsular Malaysia (Polgar & Khaironizam, 2008), these two species are sympatric.

*Periophthalmodon schlosseri* individuals are distributed along the entire intertidal gradient, from banks of creeks, to open mudflats, to within mangrove forests (Takita et al., 1999; Polgar & Crosa, 2009). In comparison, *Ps. walailakae* individuals are more localised in mangrove forests: from along small inlets up to drier landward fringes (Khaironizam & Norma-Rashid, 2005; Polgar & Khaironizam, 2008). Studies on the feeding ecology of *Pn. schlosseri* documented fiddler crabs (*Uca* spp.) as its main prey, switching to insects at night and supplemented with worms throughout the day (Mazlan et al., 2006). Sexual differences in food selection were also detected: females prefer to prey on medaka fish (*Oryzias* sp.) instead of *Uca* spp. favoured by male *Pn. schlosseri* (Zulkifli et al., 2012). Although *Ps. walailakae* has been reported a carnivore (Darumas, 1997), there is little or no published work on foraging ecology, diet, or gut contents, of this species. In various Singapore mangrove forests, the diets of these two mudskippers consisted mainly of small epibenthic mangrove brachyurans in addition to polychaetes, onchidiums and smaller fishes (Su, 2009).

This study attempts to close the knowledge gap on the foraging ecology and niche specifications of these two prominent mudskippers. The ecological niches of *Pn. schlosseri* and *Ps. walailakae* are investigated in terms of diet and habitat preferences. In turn, the niches of these mudskipper species were evaluated for overlap and partitioning for their coexistence in a Singapore mangrove.

## MATERIAL AND METHODS

**Study site.** Lim Chu Kang mangrove is located on the northwestern coast of Singapore (1°26'45"N, 103°42'32"E) consisting of a forest and a mudflat that extends approximately 50 m during ebb spring tide. The area undergoes two ebb tides within a 24-hr cycle, with tidal variation between 0.0–3.2 m. Both *Pn. schlosseri* and *Ps. walailakae* are syntopic and common in this area.

**Baseline study of mudskipper species.** Permanent plots (5 × 5 m each) were established to observe *Pn. schlosseri* (n = 3) and *Ps. walailakae* (n = 3), each plot was at least 5 m apart to ensure no overlap. Each plot was exclusively inhabited only by either species. The permanent plots were demarcated with 4 polyvinyl chloride poles but left unfenced to minimise disturbance to the mudskippers, prey community and the surrounding habitat. Observations were conducted for two hours with the aid of a pair of binoculars (8 × 30, Jenoptik) on sunny days during ebb tides, and at least 1 m away from the permanent plot on a raised platform to

minimise disturbance to mudskippers. Observations were not conducted on rainy days as preliminary studies indicate low mudskipper activity. The relative positions of all concavities on the ground within each plot were recorded during the first field session; each concavity may be a tide pool, an abandoned burrow, or an actively maintained burrow. Occupied burrows and all mudskippers were noted and photographed for identification to ascertain fidelity to plot or burrow. Individual mudskippers were identified using distinctive spots on the faces and torsos. A total of 4 sessions were conducted fortnightly during ebb spring tides from August to October 2010 for each of the permanent plots (n = 24).

**Predator removal and diet analysis.** After the baseline study, all mudskippers within each plot were collected in November 2010 during an ebb spring tide. When the tide has fully receded, mudskippers within the plots were chased into their respective burrows. A burrow trap constructed from recycled metal cans was deployed in every concavity within the plot for 4–6 hours to ensure complete removal of predators. Mudskippers were captured as they exited the burrows for gaseous exchange, burrow maintenance, or feeding. Collected mudskippers were fixed in 10% buffered formalin immediately to arrest digestion and transferred into 75% ethanol after 1 week for long-term preservation. Morphometric measurements of the standard length (snout to caudal peduncle), gape width (lateral distance between left rictus and right rictus) and gape length (anterior-most tip of snout to rictus) of each specimen were taken with a pair of vernier calipers (0.01 mm). All measurements were taken on the left side of the individual. Each specimen was then dried with a paper towel, weighed and dissected ventrally. Relative gut length was recorded by taking the ratio of the gastrointestinal tract to standard length. The gastrointestinal tract was differentiated into distinct regions, i.e., stomach and intestine, and weights (0.01 g) were recorded. The stomachs and intestines were then dissected lengthwise and the contents removed for analysis. Wet weight of the contents was derived from subtracting the weight of emptied stomach or intestinal walls from the weight of the respective gut before content removal. A fullness index (expressed as parts per decimile; see Herbold, 1986) was computed for each portion of the gut using the following formula:

$$\text{Fullness index} = \frac{\text{weight of gut contents} \times 10,000}{\text{weight of fish}}$$

Gut contents were sorted into prey categories under a stereomicroscope. Dietary analyses for fishes are typically confined to the anterior half/third of the alimentary canal due to digestive deterioration of contents posteriorly (see McCormick, 1998). However, as the intestinal food items were equally recognisable and reliable as items from the stomach, the gut contents were pooled for analysis. The volume of each prey category (in mm<sup>3</sup>) was ascertained using a Sedgewick Rafter counting cell. A compound Index of Preponderance (see Natarajan & Jhingran, 1961) can then

be determined for each prey category using the following formulae:

Frequency of occurrence ( $F_i$ ) =

$$\frac{\text{Number of individuals containing prey item } i}{\text{Number of individuals with food items in their gut}}$$

Percentage of occurrence ( $O_i$ ) =

$$\frac{F_i}{\Sigma F} \times 100\%$$

Percentage of volume ( $V_i$ ) =

$$\frac{\text{Volume of prey item } i}{\text{Total volume of prey items in gut}} \times 100\%$$

Index of preponderance ( $I_i$ ) =

$$\frac{O_i V_i}{\Sigma O_i V_i} \times 100\%$$

Encountered crabs were sorted into the lowest possible taxonomic groups. The number of crab individual within a gut was taken as the number of discernible carapaces present (e.g., 5 crab individuals were recorded in a gut containing 7 chelipeds and 5 carapaces) to prevent inflation of prey counts from partial ingestions. Carapace widths of the ingested crabs were measured (to 0.01 mm) whenever possible. The relationship between gape size of both species of predator and the size of their respective prey was investigated.

**Abiotic parameters characterising microhabitats.** The microhabitat of each plot was characterised by canopy cover, organic content of the sediment, and sediment particle size. Abiotic factors of burrow water (e.g., pH, salinity and dissolved oxygen) were disregarded as mudskippers are capable of altering these parameters (see Ishimatsu et al., 1998; Randall et al., 2004). Three sampling points were generated randomly for the collection of these abiotic parameters. A concave spherical densiometer was used to determine canopy cover. At each point, an average of readings in the 4 cardinal directions was recorded and converted to percent canopy cover ( $n = 18$ ).

A mangrove sediment sample (approximately 500 g), was also collected at each sampling point ( $n = 18$ ) and stored at  $-20^\circ\text{C}$  in the laboratory prior to analysis to prevent decay. The sediment was first dried at  $90^\circ\text{C}$  to constant weight. Approximately 5 g (to 0.0001 g) was crushed and burned in the furnace at  $350^\circ\text{C}$  for 16 hours to determine the organic content of the sediment using the loss on ignition method (Bale & Kenny, 2005). In the analysis of sediment particle size, the silt and clay was separated from the sand fraction following Bale & Kenny (2005). The grain size composition of the sand fraction was determined by dry sieving through a stack of Wentworth grade sieves (aperture sizes of 2.0 mm, 1.0 mm, 0.5 mm, 0.25 mm, 0.125 mm, 0.063 mm). Full analysis of the silt and clay fraction was conducted via the sedimentation process using Stokes' Law according to Buchanan (1984) for the particle sizes of 0.0625 mm, 0.0312

mm, 0.0156 mm, 0.0078 mm and 0.0039 mm. The weight of each sediment class size (to 0.0001 g) was shown as a percentage of the total weight of the initial dried sediment sample. Organic content and sediment particle size analyses of each sediment sample was replicated thrice and averaged for reliability.

The ordination patterns of the abiotic parameters (canopy cover, organic content, and sediment particle sizes) were analysed with Multidimensional Scaling (MDS, using S17 Bray Curtis similarity with PRIMER 6), to explore habitat heterogeneity between the *Pn. schlosseri* and *Ps. walailakae* plots. A one-way Analysis of Similarities (ANOSIM with PRIMER 6) was carried out to further support these results. Nested one-way Analysis of Variance (ANOVA with MINITAB 17) was performed on the canopy cover and organic content of the sampled sediment independently for the factors 'Plots' (random) nested within 'Species' (fixed) to identify the abiotic factor(s) that differentiate(s) habitat selection between *Pn. schlosseri* and *Ps. walailakae*. Equality of variance was tested using Levene's test and an arcsine transformation was treated to both data sets to cure the heteroscedasticity of percentage data. The percentage by composition of the sediment size classes were further analysed using GRADISTAT 8.0 to determine the mean grain size and sorting of the sediment.

## RESULTS

**Baseline study of predator species.** The mean densities ( $\pm$  S.E.) of *Pn. schlosseri* and *Ps. walailakae* in the permanent plots were  $3.3 \pm 0.7$  and  $5.2 \pm 0.2$  individuals per  $25 \text{ m}^2$  respectively, with little fluctuation throughout the study. The numbers of concavities exceeded the mudskipper individuals in every plot. Burrows constructed by *Pn. schlosseri* can be readily differentiated from those of *Ps. walailakae* through the size of the surface pools: *Pn. schlosseri* burrows are approximately twice larger, with diameters approaching 30 cm. Fidelity to burrow as well as plot were ascertained in *Pn. schlosseri*. However, *Ps. walailakae* individuals were tracked to different established burrows within the same plot, and thus demonstrated plot fidelity only (Fig. 1).

**Predator removal and diet analysis.** In total, nine individuals of *Pn. schlosseri* and 15 *Ps. walailakae* were collected from the plots. The larger mudskipper species, *Pn. schlosseri*, was found to be almost twice the length and four times the weight of *Ps. walailakae* (Table 1). The short relative gut lengths of dissected specimens (*Pn. schlosseri*:  $0.57 \pm 0.04$ ; *Ps. walailakae*:  $0.63 \pm 0.03$ ) indicated that both mudskippers are carnivorous (see Geevarghese, 1983) and the dietary contents confirmed this. Although both species were collected at the same time after the receding tide, stomach contents differed in these two species: *Pn. schlosseri* individuals had more contents in their stomachs (mean stomach fullness index:  $26.6 \pm 8.8$ ) than do *Ps. walailakae* (mean stomach fullness index:  $12.5 \pm 7.3$ ). The majority of *Ps. walailakae* individuals (12 of 15 individuals) had empty stomachs; only three individuals had contents in stomach



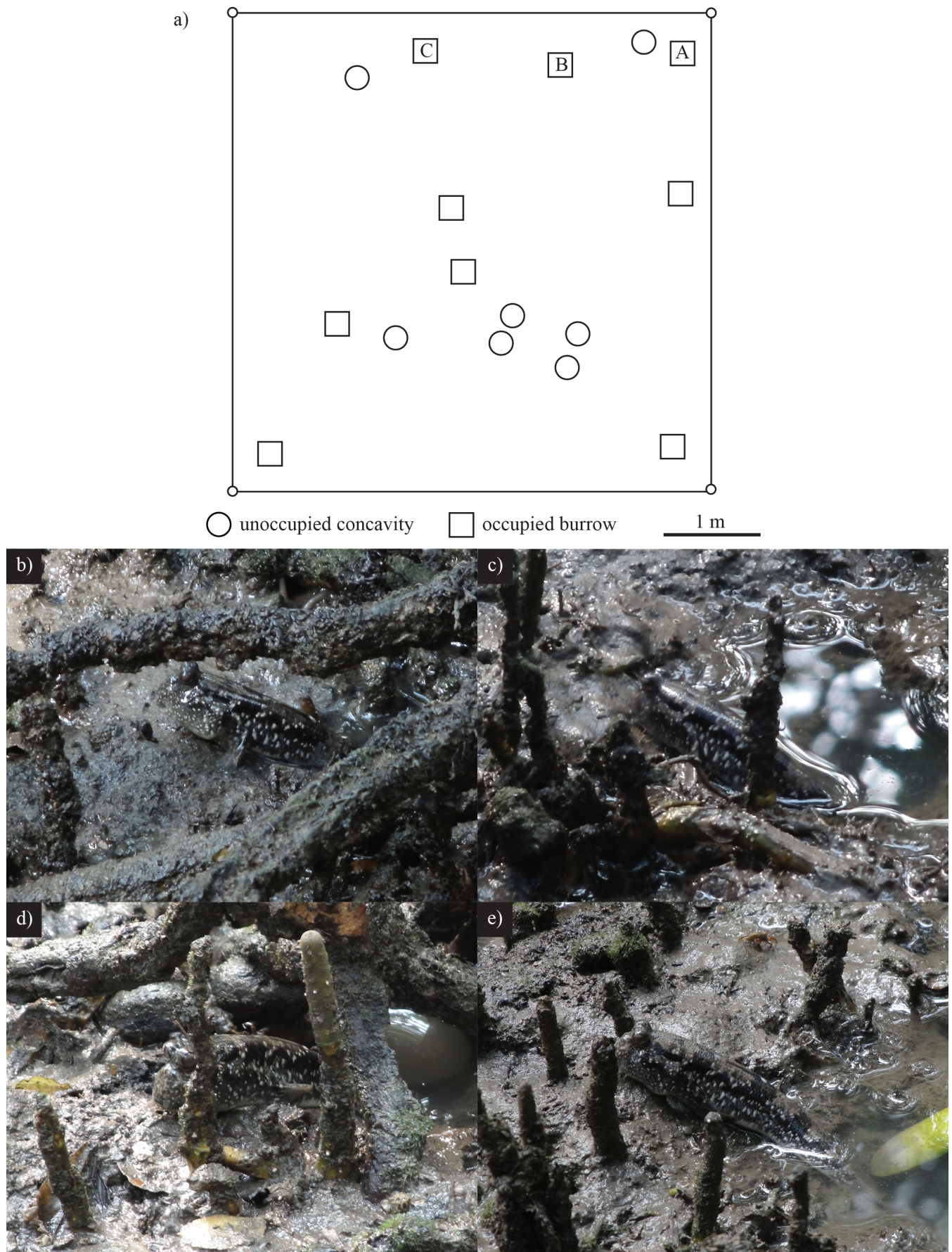


Fig. 1. Plot fidelity exhibited by a *Periophthalmus walailakae* individual monitored over four spring tides—(a) relative positions of concavities in permanent plot, (b) 30 August 2010: individual in burrow A, (c) 12 September 2010: individual in burrow B, (d) 27 September 2010: individual in burrow C, (e) 11 October 2010: individual in burrow B.



Table 1. Morphometric measurements and gut content weights (to 2 decimal places) of *Periophthalmodon schlosseri* and *Periophthalmus walailakae*.

	<i>Periophthalmodon schlosseri</i>		<i>Periophthalmus walailakae</i>	
	Mean $\pm$ S.E.	Range	Mean $\pm$ S.E.	Range
Standard length (mm)	180.09 $\pm$ 2.12	174.26–195.85	102.79 $\pm$ 4.62	61.92–126.46
Gape width (mm)	27.32 $\pm$ 0.62	24.41–30.82	15.27 $\pm$ 0.87	9.18–20.05
Gape length (mm)	18.10 $\pm$ 0.65	15.19–21.71	10.33 $\pm$ 0.54	6.42–13.35
Total weight (g)	93.47 $\pm$ 2.97	83.74–109.28	21.67 $\pm$ 2.53	3.82–35.67
Stomach contents (g)	0.31 $\pm$ 0.10	0.03–0.86	0.04 $\pm$ 0.02	0–0.29
Intestine contents (g)	0.58 $\pm$ 0.17	0–1.38	0.12 $\pm$ 0.03	0–0.55

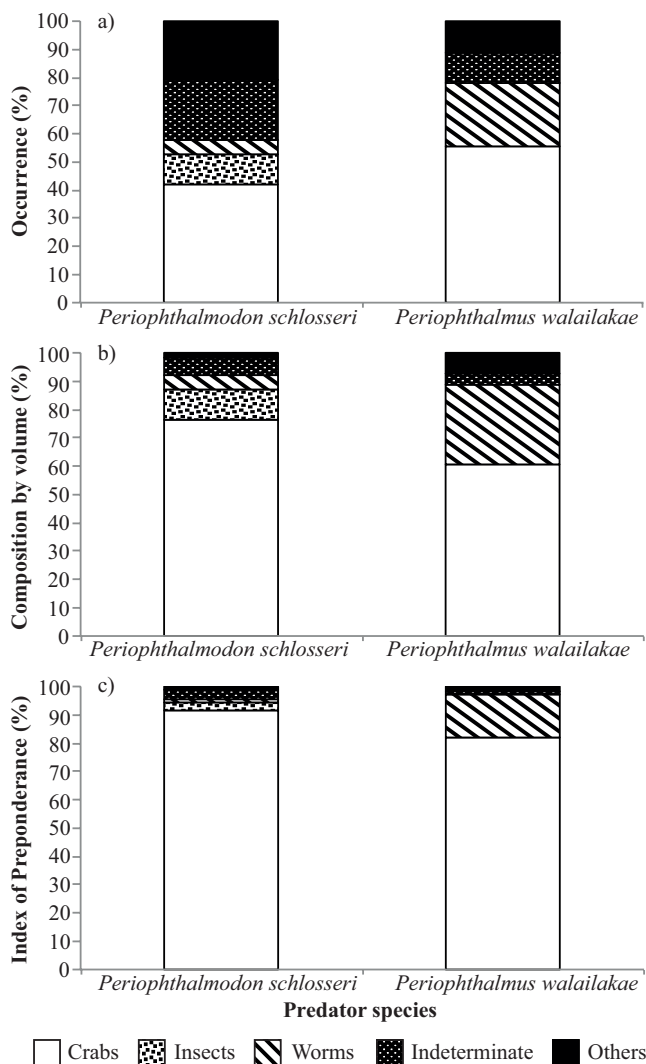


Fig. 2. Contents of dissected guts of *Periophthalmodon schlosseri* and *Periophthalmus walailakae* sorted to prey categories: (a) occurrence, (b) composition by volume and (c) Index of Preponderance. Indeterminate—items digested beyond recognition, Others—prey of low encounter rates (e.g., snails, onchidiums, and mussels).

when collected. In contrast, the intestinal fullness indices in the two mudskippers were similar (*Pn. schlosseri*:  $58.4 \pm 19.7$ ; *Ps. walailakae*:  $50.4 \pm 11.5$ ).

Overall, the dietary contents of *Pn. schlosseri* and *Ps. walailakae* overlapped extensively with three main prey categories: brachyuran crabs, insects and worms. Crabs made up the majority of the diet, occurring in approximately half of the sampled individuals and represented by 60% of prey volume in both mudskippers (Figs. 2a, b). The composite Index of Preponderance showed a high dominance of crabs in their diet, at 91.3% and 81.9% for *Pn. schlosseri* and *Ps. walailakae*, respectively (Fig. 2c). Crabs removed from the gut were not intact; appendages were mostly detached from carapaces (Figs. 3a–c). Winged insects (Insecta: Hymenoptera; Fig. 3d) were exclusively found in the gut contents of *Pn. schlosseri*, but with a low preponderance of 3.3%. All other prey categories reflected low dominance in diet of *Pn. schlosseri*. Worms ranked second, at 15%, in prey category for *Ps. walailakae* (Fig. 2c); worms encountered included sipunculids (Sipunculidae; Fig. 3e) and polychaetes (Polychaeta; Fig. 3f). The category ‘Others’ consisted of prey with low encounter rates such as red cherry snails, onchidiums, and mussels. Items that were digested beyond recognition were accorded the category ‘Indeterminate’.

Three crab species were identified from all available brachyuran prey parts: *Paracleistostoma depressum* De Man, 1895, *Baruna trigranulum* (Dai & Song, 1986), and *Haberma nanum* Ng & Schubart, 2002. *Paracleistostoma depressum* (Fig. 3a) had the highest occurrence in the gut contents of both *Pn. schlosseri* and *Ps. walailakae*—eight (out of nine) *Pn. schlosseri* ingested 51 individuals while seven (out of 15) *Ps. walailakae* ingested eight individuals. The latter two crab species were rare: only one *B. trigranulum* (Fig. 3b) was counted in each mudskipper species, and one *H. nanum* (Fig. 3c) was recorded in one *Ps. walailakae* specimen. There was no relationship between gape width (Fig. 4a) or gape length (Fig. 4b) of the predators, and the ingested brachyuran prey size.

**Abiotic parameters characterising microhabitats.** The abiotic parameters in all sampled plots showed no clustering in the MDS plot (Fig. 5a). Sample points partially overlapped, with evidence of distinction between the plots of each mudskipper species (One-way ANOSIM:  $R = 0.396$ ,  $p <$

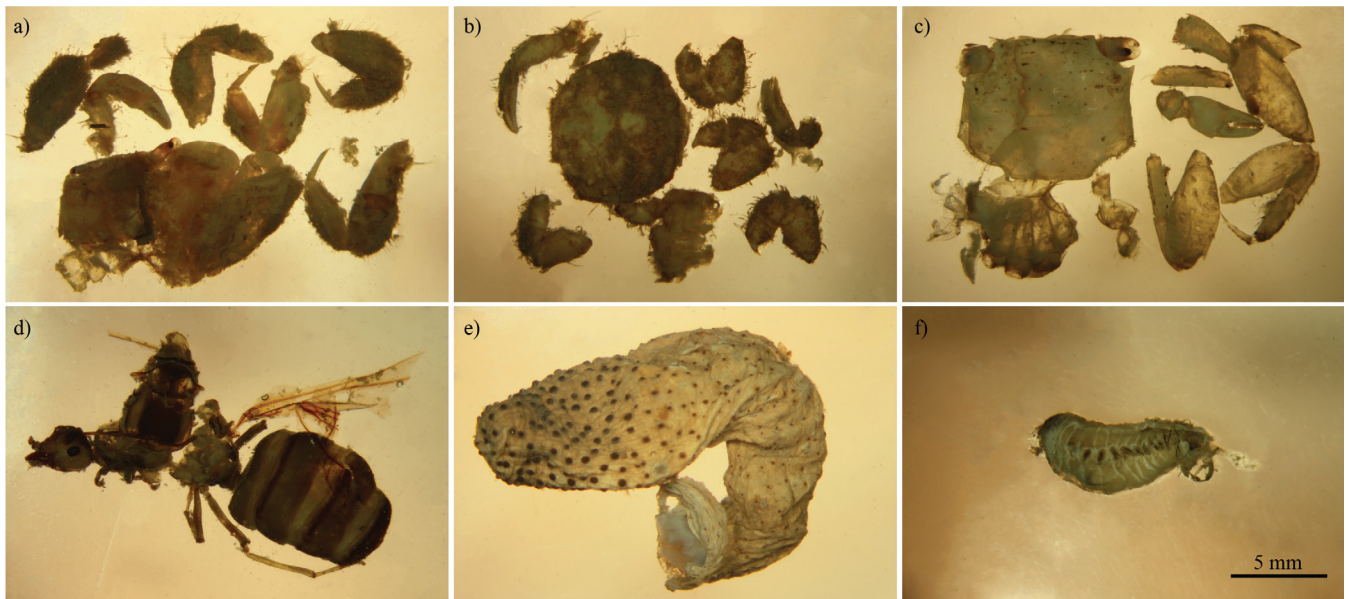


Fig. 3. Prey items encountered in *Periophthalmodon schlosseri* and *Periophthalmus walailakae*: (a) *Paracleistostoma depressum*, (b) *Baruna trigranulum*, (c) *Haberma nanum*, (d) winged insect, (e) sipunculid worm and (f) polychaete worm.

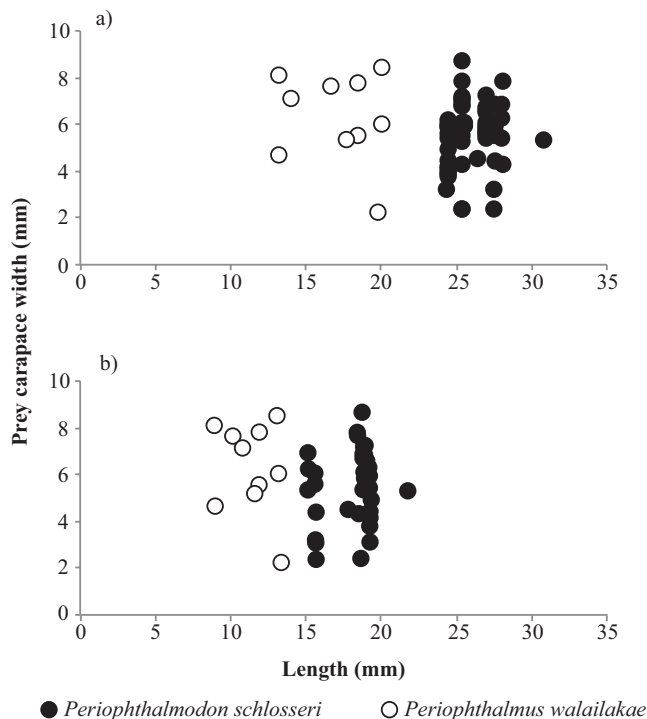


Fig. 4. The influence of (a) gape width and (b) gape length of *Periophthalmodon schlosseri* and *Periophthalmus walailakae* on the maximum size of ingested brachyuran prey.

0.05; where  $0 < R < 1$ ,  $R = 0$  suggests habitat homogeneity,  $R = 1$  suggests habitat heterogeneity). Significant differences existed in canopy cover readings between *Pn. schlosseri* and *Ps. walailakae* plots (nested ANOVA:  $F_{1,4} = 8.04$ ,  $p = 0.047$ ): *Pn. schlosseri* was more exposed (mean canopy cover:  $64.0 \pm 3.8\%$ ) while *Ps. walailakae* plots had denser canopy cover (mean canopy cover:  $84.6 \pm 1.9\%$ ) (Fig. 5b). No difference was detected in the sediment organic content from either mudskipper species plots (nested ANOVA:  $F_{1,4} = 0.35$ ,  $p = 0.588$ ); both *Pn. schlosseri* and *Ps. walailakae* were found in plots with similar sediment organic content

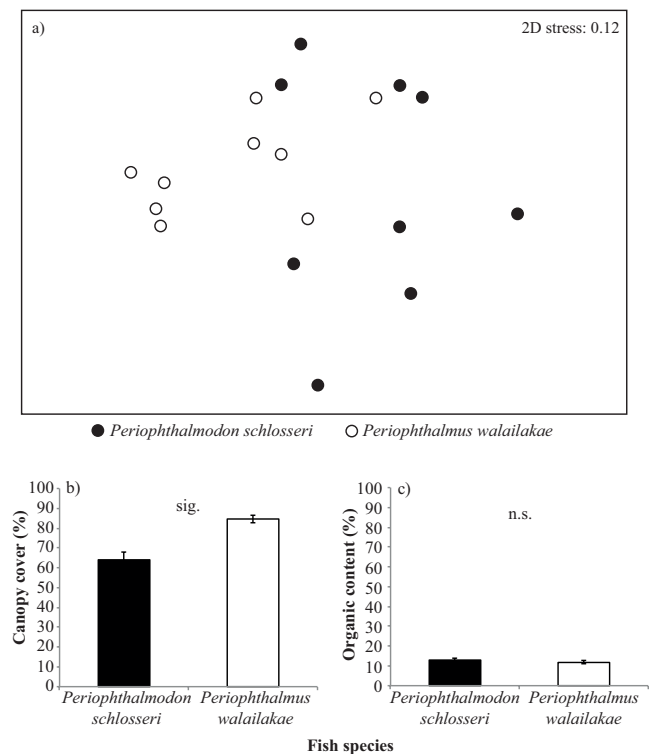


Fig. 5. Abiotic characterisation of the demarcated permanent plots ( $n = 18$ ): (a) two-dimensional MDS on canopy cover, sediment organic content and sediment particle sizes, (b) mean canopy cover and (c) mean organic content of the sediment. sig.—significant; n.s.—not significant; error bars—standard error.

(*Pn. schlosseri*:  $12.9 \pm 1.2\%$ ; *Ps. walailakae*:  $11.7 \pm 0.9\%$ ) (Fig. 5c). Computational GRADISTAT analysis of sediment composition revealed further distinction—*Pn. schlosseri* plots had smaller mean sediment grain size (*Pn. schlosseri* plots:  $66.6 \pm 8.3 \mu\text{m}$ ; *Ps. walailakae* plots:  $100.7 \pm 14.6 \mu\text{m}$ ). Both predator habitats contained poorly sorted sediments; those of *Pn. schlosseri* had very coarse silt while those of *Ps. walailakae* had very fine sand.



## DISCUSSION

The mean densities within the plots of these mudskipper species differed significantly. The mean densities of *Pn. schlosseri* plots were lower than those of *Ps. walailakae*. As *Pn. schlosseri* is twice the size, and four times the weight of *Ps. walailakae*, this result may be indicative of the carrying capacity of the plot with respect to resource availability.

Both *Pn. schlosseri* and *Ps. walailakae* exhibit high site fidelity and homing behaviour; plot densities showed low fluctuations despite both species undergoing twice-daily tidal migrations (see Chua, 2009). In addition, *Pn. schlosseri* exhibited high burrow fidelity based on in-situ individual recognition observations. Burrows of *Pn. schlosseri* are typically 125 cm deep tunnels, filled with hypoxic water, and ends with a horizontal expansion into a dome-shaped chamber for active air-phase maintenance (Ishimatsu et al., 1998). The dome-shaped chamber is critical for aerial deposition and incubation for eggs during reproduction (Clayton, 1993; Ishimatsu et al., 2009). In contrast, little is known about the architecture of *Ps. walailakae* burrows although they are reportedly similar to those of *Pn. schlosseri* (see Darumas, 1997). Burrow integrity is maintained during ebb tide. Mudskippers achieve this by transporting the mud within their mouths from the burrow bottom to the burrow surface, resulting in distinctive “mud pellets” near the burrow opening. The amount of energy expended in burrow construction and maintenance suggests counter-intuitiveness for a mudskipper to have multiple burrows. Yet, *Ps. walailakae* does not exhibit burrow fidelity. A possible explanation is that *Ps. walailakae* burrows may not be as deep or large, lowering the energetic costs in their construction and maintenance. Densities of concavities within the plots always exceed the mudskipper densities as surface pools may persist despite burrow collapse or burrow abandonment. A method to distinguish a burrow that is actively in use is to locate one with mud pellets surrounding the burrow opening.

The lengths of mudskipper species collected in this study are similar to those of Jaafar et al. (2006) with the exception of a slight increase in record for the length of *Ps. walailakae* (126.10 mm SL). Individuals of *Pn. schlosseri* collected are hypothesised to be less than one year old, an age extrapolated by the standard length-age relationship proposed by Mazlan & Rohaya (2008). No similar study had been carried out on *Ps. walailakae*, thus their age cannot be estimated.

This is a first report to document the temporal partitioning in feeding detected in *Pn. schlosseri* and *Ps. walailakae* in situ. Stomach and intestine content analyses showed that *Pn. schlosseri* fed almost immediately once the mangrove forest is exposed (approximately 1.7 m tidal height), whereas most *Ps. walailakae* had empty stomachs. This was consistent with field observations: *Pn. schlosseri* alternated between burrow maintenance and feeding upon emersion while *Ps. walailakae* individuals emerged only after the tide has fully receded (lowest tidal level, approximately 0.5 m during spring tides). However, the integrity of intestinal contents in *Ps. walailakae* permitted a representative analysis of the prey

diversity. The presence of intestinal food items in individuals with empty stomachs also provided information on the gut passage time of *Pn. schlosseri* and *Ps. walailakae*. Feeding activities are highest during diurnal low tides (Mazlan et al., 2006). With tidal migration along the water edge (Polgar & Crosa, 2009) and minimal high tide feeding, benthic prey items in the intestines must be from the previous low tide, confirming a gut passage time exceeding 12 hours. This information corroborated the results of Mazlan et al. (2004), which estimated the Gastric Emptying Time (time taken from satiation to return of its appetite) for *Pn. schlosseri* at 18 hours. More effort, particularly in situ manipulative work, is required to provide unambiguous evidence for the gut passage evacuation time of items specific to the natural diet of the mudskippers. The low amount of ‘Indeterminate’ content and the ability to discriminate between intestinal prey items, in addition to the long gut passage time, are suggestive of an inefficient digestion system in these fishes.

Both mudskipper species were largely cancrivorous. High encounter rates of *P. depressum* in the guts of both *Pn. schlosseri* and *Ps. walailakae* indicated it as a preferred prey choice, suggestive of optimal foraging. This crab species occurred in highest densities in the plots (unpublished data) and were preyed on indiscriminately. Comparatively, the second most abundant crab species within the plots, *H. nanum*, was rarely encountered in the gut contents of *Pn. schlosseri* and *Ps. walailakae*. Prey behaviour, speed, and escape tactics, when facing predation threat may factor heavily in this observation (Su & Lim, 2016). In contrast to existing literature, neither *Uca* spp. nor fish were encountered in the *Pn. schlosseri* diet analysis (see Mazlan et al., 2006; Zulkifli et al., 2012). Also, the mentioned prey species were not represented in the prey assemblage available to these predators at this mangrove (Su, 2016), suggesting diet variation in different habitats.

Despite differential gape sizes, the smaller predator, *Ps. walailakae*, is equally capable of ingesting similar-sized crabs when compared with *Pn. schlosseri*. The sizes of the ingested brachyuran crabs challenged current paradigm of correlation between prey and predator size (see Nielsen, 1980; Juanes, 1994). Through ontogeny, larger prey gets incorporated in the diet without the loss of small prey items. The range of prey sizes expands as a predator increases in size, resulting in asymmetric patterns in the distributions of predator and prey size (Scharf et al., 2000). Competition was demonstrated between different-sized predators; prey sizes of smaller predators were generally depicted as a subset of that in larger predators (Brooks & Dodson, 1965; Wilson, 1975). However, competition was neither observed in this study, nor is the diet of *Ps. walailakae* a subset of *Pn. schlosseri*. The retention of small prey items in the diet of *Pn. schlosseri* may be due to increased vulnerability, higher relative abundance, and shorter handling time of small prey (see Su, 2016). On the opposite spectrum of the prey size, the maximum ingestible food size was not represented in this instantaneous diet snapshot of *Pn. schlosseri*, and possibly *Ps. walailakae*. *Periophtalmodon schlosseri* was observed to feed opportunistically on a tree climbing crab,

*Episesarma* spp. (approximately 5 cm), circumventing prey-size constraints by tearing up the prey item like the crab-eating snake, *Fordonia leucobalia* (Polgar, G., pers. comm.; see Jayne et al., 2002). Absence of larger prey consumption in this study suggests high abundance of small prey in Lim Chu Kang mangrove (see Su, 2016). It is evident that the diet niches of *Pn. schlosseri* and *Ps. walailakae* overlap extensively in the dominance of crab species, specifically *P. depressum*, with the ingestion of similar-sized prey. Diet partitioning was only demonstrated temporally. Supplementations to the diet were opportunistic inclusion of winged insects in *Pn. schlosseri* and polychaete and sipunculid worms in *Ps. walailakae*, due to their low preponderance.

Through the abiotic characterisation of plots inhabited by *Pn. schlosseri* and *Ps. walailakae*, habitat heterogeneity was established. Plots with *Pn. schlosseri* are characterised by higher siltation, and less dense canopy cover. In contrast, *Ps. walailakae* exhibited greater terrestriality, inhabiting areas of higher canopy cover and dense mangrove vegetation. An open canopy is likely correlated with fewer or smaller pneumatophores. This, together with the smaller sediment size in *Pn. schlosseri* plots, may translate to ease in burrow excavation, and partially account for the large burrow sizes. With this information on spatial partitioning, mudskippers like *Pn. schlosseri* and *Ps. walailakae* may be regarded as potential biomonitors for coastline health assessment, permitting the examination of seaward and landward impacts (see Polgar, 2009; Al-Behbehani & Ebrahim, 2010).

The segregation of *Pn. schlosseri* and *Ps. walailakae* in Thailand indicates an overlapping niche but their syntopy in Singapore suggests two realised niches that are overlapping but yet distinct enough for coexistence. This is possible through temporal variation in feeding and spatial exploitation of different microhabitats. To gain a holistic understanding on habitat partitioning, it is pertinent to examine a community at different trophic levels. Habitat characteristics that allow recruitment and settlement of prey may in turn affect predator distribution and colonisation. These factors are exemplified in this study; comprehensive understanding of the synecologies of *Pn. schlosseri* and *Ps. walailakae*, and within the trophic system, can only be achieved when discussed in tandem with resident brachyuran prey community (see Su, 2016).

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