

Original Article

Cite this article: Lim KC, Chong VC, Lim P-E, Yurimoto T, Loh KH (2019). Feeding ecology of three sympatric species of stingrays on a tropical mudflat. *Journal of the Marine Biological Association of the United Kingdom* 99, 999–1007. <https://doi.org/10.1017/S0025315418000759>

Received: 24 November 2017

Revised: 11 August 2018

Accepted: 15 August 2018

First published online: 2 October 2018

Key words:

Diet overlap; feeding ground; feeding habits; mudflat; Myliobatiformes; ontogenetic shift

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Feeding ecology of three sympatric species of stingrays on a tropical mudflat

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Abstract

Periodic fish ingressions into intertidal areas during high tide are known to occur on tropical mudflats. This study aimed to elucidate the feeding ground function of coastal mudflats for three common stingray species in the Klang Strait, Malaysia. Stingrays (disc width range from 5.65–54.50 cm) sampled over 17 months using a large barrier net (~2 ha enclosure) at two sampling sites were examined for their diet composition, prey frequency and prey volume according to predator species and maturity. The index of relative importance and Schoener's index of diet overlap were calculated. The three stingray species fed on relatively similar prey items which varied in size and contribution. *Brevitrygon heterura* fed on the widest range of prey taxa (28) whereas *Hemistrygon bennetti* (22) and *Telatrygon biasa* (17) showed higher prey specialization. The Penaeidae (dominantly *Metapenaeus brevicornis* and *M. affinis*) were the most important food item in the stingray diet which also included Actinopterygii, Amphipoda, Brachyura and Calanoida. The stingray diet showed an ontogenetic shift, with young stingrays tending to be generalists whereas the more mature stingrays (except *H. bennetti*) become more specialized in their feeding habits. This shift in feeding strategy reflects the diversity of prey taxa abundantly available to young stingrays on the mudflats, while the larger stingrays adapt to feed on larger prey once they enter deeper waters.

Introduction

There are currently more than 90 published works on the feeding biology of the Myliobatiformes based on the literature review by Jacobsen & Bennett (2013) and 17 additional works reported between 2013 and 2018. This can be considered a dramatic increase considering that about 28% of these works were carried out between 1961 and 2000. However, there are currently only 14 published works on the feeding biology of the Myliobatiformes in regions close to Malaysia; 12 of these are from Australian waters and the other two from Japan. Stingray dietary studies in these areas are hampered by sampling costs, lack of fresh samples or an inability to adequately process frozen samples (Jacobsen & Bennett, 2013). In the Indo-Pacific region, stingray markets tend to be from artisanal fisheries (Blaber *et al.*, 2009; White & Kyne, 2010), although large catches are thought to be unaccounted for due to the pervasive problem of illegal, unreported and unregulated fishing (White & Kyne, 2010).

Current studies on the feeding biology of myliobatoids are quite similar to those prior to 2000, focusing on general diet (Navarro-González *et al.*, 2012; Bornatowski *et al.*, 2014), ontogenetic diet shift (Jacobsen & Bennett, 2012; López-García *et al.*, 2012), spatial and temporal diet variation (some relate this to habitat utilization) (Navia *et al.*, 2011; Woodland *et al.*, 2011; Shibuya & Zuanon, 2013), resource or dietary partitioning (Jacobsen & Bennett, 2012; O'Shea *et al.*, 2013; Varghese *et al.*, 2014) and feeding movement (Corcoran *et al.*, 2013). However, published works up to 2018 covered only 35% of species (80 out of 229 species in Eschmeyer & Fong, 2015) within the Myliobatiformes.

Stingrays in the Indo-Pacific region received even less attention. The few identification texts available such as White *et al.* (2006) and Last *et al.* (2010) have provided some general descriptions of their diet. Nevertheless, the word 'presumably' was commonly used to describe the diet of almost every species indicating the uncertainty or lack of knowledge of stingray food habits in the region. This is unfortunate since understanding their feeding ecology is crucial for conservation given the increasing human threats to critical coastal ecosystems such as mangroves, mudflats and coral reefs, which may serve as essential feeding or nursery areas for these fishes (Chong *et al.*, 1990; Beck *et al.*, 2001; Cerutti-Pereyra *et al.*, 2014). For instance, previous (e.g. Sasekumar *et al.*, 1992) and preliminary work have indicated that juvenile stingrays enter shallow coastal mudflats in waves following tidal inundation.

Coastal mudflats can be very productive habitats as a result of high nutrient inputs from fluvial discharge (Trott & Alongi, 1999; Teoh *et al.*, 2016) and outwelling from adjacent mangrove forests (Tanaka & Choo, 2000; Alongi, 2009). Such mudflats are known feeding grounds of fishes (Chong *et al.*, 2012; Lee *et al.*, 2016), penaeid shrimps (Leh & Sasekumar, 1984; Marsitah & Chong, 2002), mysid shrimps (Ramarn *et al.*, 2015), hermit crabs (Teoh &



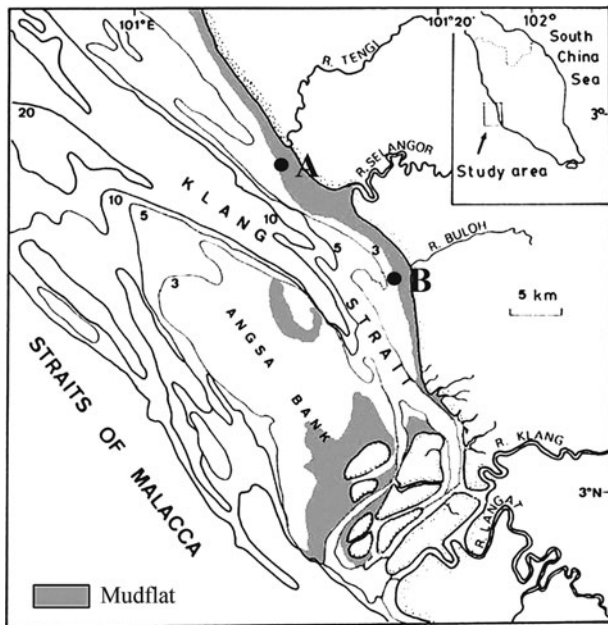


Fig. 1. Selected study sites on Klang Strait mudflat, Peninsular Malaysia. A. Bagan Pasir (BP), B. Sungai Buloh (SB).

Chong, 2015), molluscs (Broom, 1982; Rodelli *et al.*, 1984) and shorebirds (Burger *et al.*, 1997; Backwell *et al.*, 1998). Unfortunately, coastal mudflats particularly in the eastern Asian region are increasingly subject to land reclamations for development (Kao *et al.*, 1998), while coastal development often alters coastline morphology and hydrodynamics resulting in mud and sediment erosion (Łabuz, 2015).

One of the larger and more important mudflats in Peninsular Malaysia is the Klang Strait mudflat (3°21.850'N 101°10.665'E) on the western coast (Figure 1) where the country's largest blood cockle culture beds (5000 ha) are also located. In the Klang Strait, soft-bottom stingrays are commonly encountered in commercial catches although their catches are low. However, scientific works on their ecology are lacking. Three species of stingray that are commonly found in the Klang mudflat include the dwarf whipray (*Himantura walga*), Bennett's stingray (*Dasyatis bennetti*) and sharpnose stingray (*Dasyatis zugei*) (Lim *et al.*, 2014). A recent stingray revision renamed these species as *Brevitrygon heterura*, *Hemitrygon bennetti* and *Telatrygon biasa* respectively (Last *et al.*, 2016). Lim (2016) suggested that the Klang mudflat acts as an important feeding and nursery ground of these coastal stingrays.

In this study, we hypothesize that since stingrays regularly enter the coastal mudflat during high tide, they forage on the coastal mudflat, making it an important feeding ground. Hence, the aim of this study is to elucidate the feeding ground function of the intertidal mudflat for the three major stingray species in Klang Strait; here, we examined feeding habits, food partitioning and ontogenetic shift (if any) in food usage to understand their feeding ecology.

Materials and methods

Stingrays were sampled from the Klang mudflat every month from July 2012 to November 2013. The fishing method used was an artisanal barrier net of 2.5 cm stretched mesh size deployed at two sampling sites located off the fishing villages at Bagan Pasir (BP) (03°22.072'N 101°10.529'E) and Sungai Buloh (SB) (03°17.605'N 101°15.276'E) (Figure 1). The L-shaped barrier net was deployed close to high slack water facing landward. The fish were retained when the tide receded. All batoids caught

Table 1. Simplified classification of maturity stages for male and female stingrays in Klang Strait (adapted from White *et al.*, 2001; Yokota *et al.*, 2012).

Sexes	Maturity stages	Description
Male	Juvenile	Small and non-calcified clasper, length usually not reaching posterior end of pelvic fin. Small and thread like testes. Vas deferens hardly seen.
	Subadult	Slightly enlarged and calcified claspers, approaching or slightly passing posterior end of pelvic fin. Enlarged testes without prominent lobes. Vas deferens with slight coiling.
	Adult	Enlarged and fully calcified claspers. Fully developed testes with prominent lobes. Vas deferens tightly coiled.
Female	Juvenile	Ovaries and uteri thread like. Both uteri similar in size.
	Subadult	Left ovary and uterus beginning to enlarge with small yolked ova.
	Adult	Left ovary fully developed with ripe yolked ova. Uterus well developed, can be flaccid, with developing embryos or having large empty cavity (recently given birth).

were collected. In the case of very large catches, a maximum of 60 fishes were randomly selected for analysis of stomach contents.

Stingrays obtained from each sampling were identified according to Last *et al.* (2010, 2016). The disc width (DW) of each specimen was measured to the nearest mm. The sexual maturity of male and female fish was determined by examining the reproductive tracts after incision of the ventral abdominal wall. In addition, the size and calcification stage of the claspers were examined in males. Fish were then categorized as juvenile, subadult or adult following the descriptions given in Table 1.

The fish's stomach was removed by cutting its anterior end (i.e. before the oesophagus) and posterior end just after the pyloric sphincter. Stomachs were individually placed in separate containers and preserved in 4% formaldehyde until examination of food items. The preserved stingray's stomach was first slit open and all food items were washed into a Petri dish. For large food items such as fish, crab and penaeid shrimp, the water displacement method (Hyslop, 1980) was used to estimate their volume. The small remaining food items were pipetted out into a gridded 1 ml-Sedgewick rafter cell and examined under a compound microscope. The volume of each small food item was estimated from the cover area of each item using the eye estimation method (Chong, 1977). All food items were identified to the lowest possible taxa. The number of prey items was also counted.

Cumulative prey curves were constructed by species, maturity stage, sex and site to evaluate whether the number of sampled stomachs was sufficient to elucidate the diet of stingrays on tropical mudflats. The number of stomachs examined can be considered sufficient if the slope is less than 0.1 (Soberón & Llorente, 1993). This analysis involved randomizing the sample order 999 times and plotting the mean number of prey categories present against the number of stomachs analysed using PRIMER v6 software (Clarke & Gorley, 2006).

The index of relative importance (IRI) (Pinkas *et al.*, 1971) of prey item for each maturity stage and species of stingray was calculated using the modified formula of Cortés (1997): $IRI = (\%V + \%N) \times \%F$, where $\%V = V_i n^{-1} \times 100\%$, given V_i is the total volume of prey of a particular taxon i and n is the total volume of all prey in all stomachs; $\%N = N_i n^{-1} \times 100\%$, given N_i is the total number

of prey of a particular taxon i and n is the total number of all prey identified in all stomachs examined; $\%F = F_i n^{-1} \times 100\%$, given F_i is the number of stomachs containing a particular prey taxon i and n is the total number of stomachs with any prey. The percentage of IRI (%IRI) was then calculated by dividing the IRI of each prey taxon by the total IRI, multiplied by 100%.

Schoener's index of diet overlap (Schoener, 1970) was calculated using the formula: $C_{AB} = 1.0 - 0.5 (\sum |I_{A,i} - I_{B,i}|)$, where I is the index of relative importance of prey i in the diets of stingray species A and B. Stingray feeding strategies were analysed graphically following Amundsen *et al.*'s (1996) two-dimensional scatterplot by using both prey specific abundance (P_i) and frequency of occurrence (%F) data. Prey specific abundance was calculated using the formula: $P_i = (\sum S_i / \sum S_{ii}) \times 100$, where P_i is the prey specific abundance of prey i , S_i is the number of prey item i and S_{ii} is the total number of prey items in the stomach that contain prey i .

Further comparison of the diet of stingrays was achieved using non-metric multi-dimensional scaling (nMDS) ordination and analysis of similarity (ANOSIM) in PRIMER v6 (Clarke & Gorley, 2006). ANOSIM was first performed on the non-pooled dataset (V , N and F) to determine whether there were significant differences between site or sex for each species. If there were no significant differences, the datasets were combined to reduce the number of factors and increase the sample size. As suggested by Pardo *et al.* (2015), partially pooled data provide a better representation and partitioning of the variation among species in multivariate analysis.

More refined analyses based on partially pooled data were carried out only if the sample size was sufficiently large (i.e. based on the cumulative prey curve slope criterion). Similarity matrices were constructed using the Bray–Curtis dissimilarity coefficient calculated from partially pooled data. These data (% V , % N , % F and %IRI) were square-root transformed after being individually pooled by randomly combining 3–10 stomachs to increase the number of prey categories per stomach following Pardo *et al.* (2015). The obtained similarity matrices were used in nMDS ordination to visualize the variation among the stingrays. The similarity percentage analysis (SIMPER) of non-pooled data (V , N and F) was performed to identify the most important contributors to the variation in diet among the stingrays. For testing for spatial (site) differences in diet, the ANOSIM test was applied to only the juveniles of *B. heterura* which had sufficient sample sizes at both BP and SB sites.

In addition, the mean and range of number of prey taxa consumed by each stingray according to species and maturity were calculated. Kruskal–Wallis ANOVA was conducted on non-pooled data to compare the significant difference among the number of prey taxa consumed by the stingray species on the Klang mudflat. The volume of the largest prey item (PV_{max}) found in each stomach was also recorded so as to determine its relationship with predator (stingray) size (disc width) by using type I linear regression (Zar, 1999). Both variables were subject to natural logarithmic (\log_e) transformation in the regression analysis to linearize the essential length-weight (volume) relationship.

Results

A total of 540 specimens of the three dominant stingrays were obtained from the two sites during the 17-month study. These included 349 *B. heterura*, 102 *H. bennetti* and 89 *T. biasa*. The initial ANOSIM test on non-pooled data, however, indicated no significant difference between sexes ($P > 0.05$); hence, data were then pooled without consideration of sex. Similarly, ANOSIM test showed no significant diet difference between subadult and adult fish ($P > 0.05$), and these maturity stages were then also pooled.

Only the sample sizes of juvenile *B. heterura* were sufficiently large (i.e. cumulative prey curve achieving its asymptote) to allow diet comparison between sites (Figure S1). The cumulative prey curves for juvenile *H. bennetti* achieved its asymptote when site datasets were combined. However, despite data pooling, the diet results of juvenile *T. biasa*, subadult and adult *H. bennetti*, *B. heterura* and *T. biasa* may be considered as preliminary due to their small sample sizes ($N = 17$ –38). The detailed information on number of stomachs examined and the number of empty stomachs according to species and maturity stage are given in Table S1.

Twenty-nine prey taxa were identified by stomach content analysis (Table 2). The 'Unknown' category that formed part of the stomach content was partially digested prey items that could not be fully identified. Generally, the Penaeidae with eight identified species were dominated by *Metapenaeus affinis* (up to 56.2% IRI) and *M. brevicornis* (up to 68.9%IRI) as the most important prey items. Other important identifiable prey taxa with more than 10%IRI value included Amphipoda (59.7%IRI), Brachyura (39.7%IRI), Calanoida (20.5%IRI) and Actinopterygii (19.4%IRI).

Juvenile stingrays were found to exhibit different feeding habits (Table 2). They fed primarily on penaeids (*M. affinis* and *M. brevicornis*) with both *B. heterura* and *H. bennetti* more frequently eating *M. brevicornis* (41.1%IRI and 61.4%IRI respectively) while *T. biasa* consumed *M. affinis* (56.2%) more often. The presence of amphipods (33.2%IRI) and calanoid copepods (11.5%IRI) in the *B. heterura* diet indicated a different diet from *H. bennetti*. The diet of *B. heterura* showed site differences with individuals from BP feeding primarily on *M. brevicornis* (68.9%IRI) while individuals from SB mainly fed on amphipods (59.7%) and calanoid copepods (20.5%). Amphipods and calanoid copepods formed a minor part of the diet of *B. heterura* in BP (10.1% and 3.7%), and *H. bennetti* (8.3% and 1.3%). The high percentages of small-sized prey items were due to either the higher number (% N) or higher occurrence (% F) of such prey. For instance, at SB, amphipods and calanoids represented 37.5% N (78.2% F) and 28.8% N (57.3% F) of the diet of *B. heterura* respectively.

For the subadult and adult stingrays, the results showed a potential ontogenetic diet shift (Table 2). *Telatrygon biasa* ($N = 38$) which showed more specialized feeding behaviour, fed almost entirely on penaeid shrimps (>95%IRI). Another species of similar size, *B. heterura*, showed less specialization with increased predation on brachyurans and fish but reduced predation on penaeid shrimps, amphipods and calanoids. Diet shift in *H. bennetti* was similar to *B. heterura*; subadult and adult stingrays consumed more fish and brachyurans in place of the penaeids and amphipods consumed by juvenile stingrays.

The numbers of prey taxa found in each species of stingray by maturity stage were different, with *B. heterura* feeding on the widest range of prey followed by *H. bennetti* and *T. biasa* (Table S2). Moreover, the number of prey taxa found in individual stomachs varied between stingray species with maxima of 10, 8 and 4 prey taxa for *B. heterura*, *H. bennetti* and *T. biasa* respectively (Table S2). Results from Kruskal–Wallis ANOVA test showed that the number of prey taxa consumed was significantly different among the three stingray species, with *T. biasa* taking the least prey ($P < 0.05$). In addition, the number of prey taxa consumed by juvenile *B. heterura* in Bagan Pasir was significantly higher than juvenile *B. heterura* in Sungai Buloh ($P < 0.05$). Other maturity comparisons showed no significant differences ($P > 0.05$).

The volume of the largest prey item (PV_{max}) ingested was positively correlated ($r = 0.77$, $P < 0.01$) with stingray size (Figure 2). The mean PV_{max} of juveniles of the small sized stingray *B. heterura* from Bagan Pasir (average disc width 8.46 cm) was 35.13 mm³ (maximum 1000 mm³) while that of the subadults or adults of the large-sized stingray *H. bennetti* (average disc width 31.09 cm) was 2326.71 mm³ (maximum 15,000 mm³).

Table 2. Index of relative importance (%IRI) of the prey taxa recorded from stomach content analysis of three stingray species

Taxa	Abbreviation	<i>Brevitrygon heterura</i>			<i>Hemitrygon bennetti</i>		<i>Telatrygon biasa</i>	
		J-BP (N = 156)	J-SB (N = 124)	SA (N = 33)	J (N = 58)	SA (N = 17)	J (N = 23)	SA (N = 38)
Actinopterygii	Acti	0.1	0.0	6.1	0.3	19.4	0.1	0.3
Peneaeidae								
<i>Kishinouyepeneaeopsis maxillipedo</i>	Kmax		0.0					
<i>Metapenaeus affinis</i>	Maff	0.0	0.2	10.7	11.3	45.5	56.2	53.4
<i>Metapenaeus brevicornis</i>	Mbre	68.9	9.0	20.0	61.4	0.7	0.8	43.1
<i>Metapenaeopsis stridulans</i>	Mstr	0.0						
<i>Parapenaeopsis coromandelica</i>	Pcor	0.3		0.6				1.1
<i>Parapenaeopsis hardwickii</i>	Phar		0.0	0.1	0.0			
<i>Penaeus indicus</i>	Pind	0.1		0.4		0.6		
<i>Penaeus merguensis</i>	Pmer				0.1	2.3		
Unidentified species	Pen	0.0	0.8	1.6	1.5	0.3		0.4
Caridae	Cari	0.0		0.9				
Alpheidae	Alph			0.1				
Sergestidae	Serg	0.1	0.0	0.2	0.0		2.0	0.1
Upogebiidae	Upog			0.0	0.1	0.2		
Paguroidea	Pagu	0.8	0.0	2.9	0.1		0.1	0.3
Brachyura	Brac	3.7	3.3	39.7	0.3	24.9	0.1	0.3
Stomatopoda	Stom	0.0	0.0	0.2		0.2	1.0	1.0
Mysidacea	Mysi	0.1	0.2	4.2	0.3	0.3		0.1
Cumacea	Cuma	0.6	0.0		0.0	0.2		
Amphipoda	Amph	10.1	59.7	5.0	8.3		29.8	
Isopoda	Isop	0.0	0.0	0.1	0.0			
Ostracoda	Ostr	0.0	0.1		0.4		0.1	
Calanoida	Cala	3.7	20.5	1.6	1.3		0.8	
Cyclopoida	Cycl	0.0	0.0	0.0				
Harpacticoida	Harp	0.0					4.0	0.1
Gastropoda	Gast	6.4		0.1	4.0			
Bivalvia	Biva	0.2	0.0	4.6	2.3	3.3	0.1	
Polychaeta	Poly	1.0	0.0	0.1	0.3	2.2	0.5	
Unknown	Unkn	4.0	6.1	0.7	8.1		4.4	0.1

Samples were pooled by sex, site and/or maturity except those indicated by their specified abbreviations. Site abbreviations (BP, Bagan Pasir, SB, Sungai Buloh), maturity abbreviations (J, juvenile, SA, subadult and adult).

In general, juveniles of *B. heterura* showed a generalized feeding strategy involving a wide range of prey taxa that were consumed at low numbers and frequency (Figure 3A). However, the larger *B. heterura* shifted to larger prey, consuming more abundantly or more frequently softer bodied prey (crustaceans) as compared with hard shelled prey (molluscs). Similarly, the juveniles of both *H. bennetti* (Figure 3B) and *T. biasa* (Figure 3C) fed more abundantly although less frequently on a variety of small prey taxa. However, the larger *T. biasa* tended to feed frequently and abundantly on penaeids. Both juvenile and adult *H. bennetti* also appeared to feed more frequently and abundantly on penaeids. Although less frequently consumed, polychaetes and crabs could be ingested abundantly by adult *H. bennetti*, and similarly, stomatopods were ingested by adult *T. biasa*.

Figure 4 shows the nMDS ordinations derived from four measurements of prey items (%V, %N, %F and %IRI with square-root transformation). The results show that none of the measured

variables separated all three stingray species, indicating diet overlap. For instance, juvenile *B. heterura* and *H. bennetti* were clustered together indicating shared prey taxa between them. The diet of juvenile *T. biasa* (grey circles) was more different to these two species; this was clearly observed for all variables except %F. Also, except for %F, subadult and adult stingrays were separated from the juveniles regardless of the species, indicating an ontogenetic diet shift. Subadult and adult diets of the three species overlapped to some degree, except *T. biasa* in a separate cluster if based on %V and %F. The diet of juvenile *B. heterura*, the only species of stingray that could be compared between sites, showed some degree of spatial difference.

ANOSIM results showed that there were substantial differences among the stingray by species, maturity and sites (for juvenile *B. heterura*) with *R*-statistic value of about 0.3 for non-pooled data which increased to greater than 0.7 when the data were partially pooled. These differences were highly significant based on their

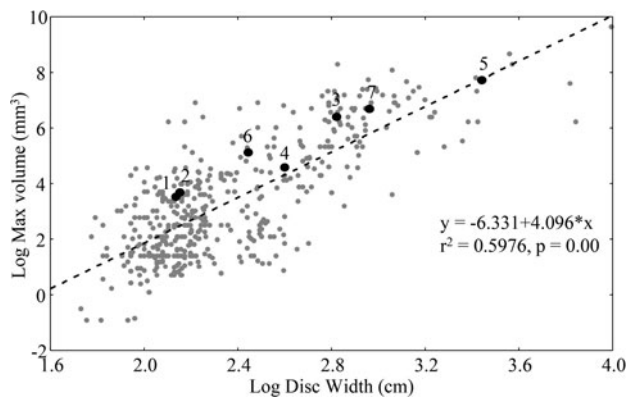


Fig. 2. Linear regression of logarithmic-transformed volume of the largest prey item (PV_{max}) and stingray (predator) size (Disc Width). Grey dots represent individual stomachs; black dots labelled 1–7 represent the mean of regressed variables for the stingray species by maturity stage. Labels: 1 = J-BP, 2 = J-SB, 3 = SA (*B. heterura*); 4 = J, 5 = SA (*H. bennetti*); 6 = J, 7 = SA (*T. biasa*); see Table 2 for further explanation.

P-value (<0.01) for all four diet variables except the comparison between *H. bennetti* and *T. biasa* for partially pooled data (Table 3).

SIMPER analysis showed relatively similar results for the three diet measurements used (*V*, *N*, *F*) (Table S3) which is consistent with the nMDS results. Generally *M. brevicornis* and amphipoda were the most important prey taxa that ranked among the top three prey items in the comparisons. Larger sized *M. affinis* contributed more by volume while small-sized calanoid copepods contributed more by numbers and frequency of occurrence. The calculated Schoener's index of diet overlap (%SI) which ranged from 6.4 to 60.0 (Table 4) indicated low to moderately overlapped diets among the three species of stingray by maturity. The %SI for the juveniles of *B. heterura* from Bagan Pasir and Sungai Buloh was 30.4.

Discussion

This study reveals differences in feeding behaviour among the three species of stingrays in terms of their diet composition and number of prey taxa. Subadult and adult *T. biasa* ingest few prey taxa but feed very frequently and abundantly on penaeid shrimps (Figure 3C), which suggests that the species, on maturity, becomes specialized in its food habits. On the other hand, the large number of prey taxa consumed by *B. heterura* indicates that this species is more of a generalist, consuming a wide range of prey taxa, each in lower quantity and less frequently (Figure 3A). However, several studies have shown that stingray diets can be affected by prey availability from various habitats, where some stingray species consume acorn worms and/or polychaetes more frequently than crabs and stomatopods, as in *D. chrysonota* (Ebert & Cowley, 2003) and *Neotrygon* species (Jacobsen & Bennett, 2012). Our study seems to support this possibility of prey availability affecting diet as for instance, the difference in diet of juvenile *B. heterura* that lived on the different mudflat sites. We do caution that the lesser number of prey taxa observed in *H. bennetti* and *T. biasa* (compared with *B. heterura*) could result from their smaller sample sizes even though the stingrays were sampled over a 17-month period.

The type and contribution of consumed prey reiterates the benthic feeding behaviour of stingrays with the exception of larger stingrays which also feed on bony fish. The present finding agrees with Jacobsen & Bennett (2013) that most dasytid stingrays feed primarily on decapods (Penaeidae in the present study). However, the present study also shows the importance of other prey taxa consumed by stingrays during ontogeny. Based on our preliminary findings, *H. bennetti* shows a trend of decreased ingestion of penaeid shrimps and increased ingestion of crabs and fish as they

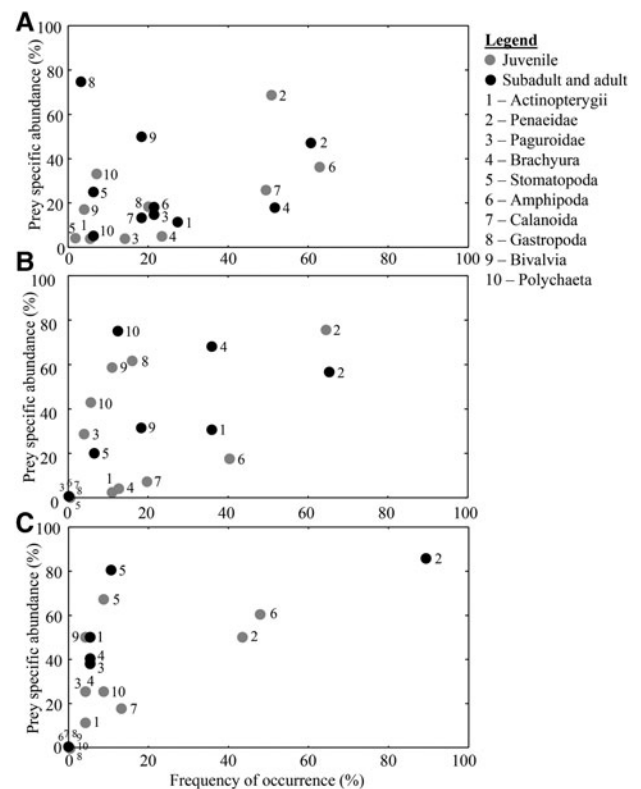


Fig. 3. Scatterplots of prey specific abundance against frequency of occurrence in the diet of three species of stingray. (A) *B. heterura*, (B) *H. bennetti* and (C) *T. biasa*. Grey symbols = juvenile, black symbols = subadult and adult.

grow larger. Both *B. heterura* and *T. biasa* show reduced ingestion of amphipods and copepods that are replaced by penaeid shrimps, crabs and/or fish as they grow. Recent studies on the ontogenetic diet shift in the Dasytidae show, however, that the contribution of penaeid and caridean shrimps becomes less important when brachyuran, polychaete and/or stomatopodean prey are also consumed as the fish develops (Ismen, 2003; Jacobsen & Bennett, 2011, 2012; López-García *et al.*, 2012). For stingrays of larger body size (e.g. *Hypanus longus* with a maximum disc width of 158 cm), bony fishes can constitute an important portion of their diet (López-García *et al.*, 2012). Similar studies on skates have also shown diet shift related to body size. For instance, the diet of *Dipturus innominatus* in New Zealand shifted from small crustaceans to larger crustaceans and fish when body size increased (Forman & Dunn, 2012). Six species of skates in south-eastern Australia all showed size-related changes in diet, in which four small-bodied species (*Dentiraja cerva*, *D. confusa*, *D. lemprieri* and *Spiniraja whitleyi*) living on the continental shelf preyed mostly on caridean shrimps, while a larger-bodied species (*Dipturus canutus*) living on the continental slope showed an ontogenetic diet shift from anomurans to brachyurans (Treloar *et al.*, 2007). The same authors also reported that another large-bodied species (*Dipturus gudgeri*) living on the slope preyed on teleosts irrespective of body size.

The contribution of copepods in the diet of stingrays has not been documented except for *D. chrysonota* (Ebert & Cowley, 2003). No other studies on the food of juvenile or small stingrays have recorded copepods in their diet (Ismen, 2003; Raju, 2003; Jacobsen & Bennett, 2011, 2012). Our study shows, however, that the contribution of copepods in juvenile *B. heterura* (3.7% IRI in Bagan Pasir and 20.5% IRI in Sungai Buloh) were substantially higher than in *D. chrysonota* (<1% IRI) as reported by Ebert & Cowley (2003). Moreover, full stomachs that were filled with only copepods (up to 149 copepods in a stomach) were observed

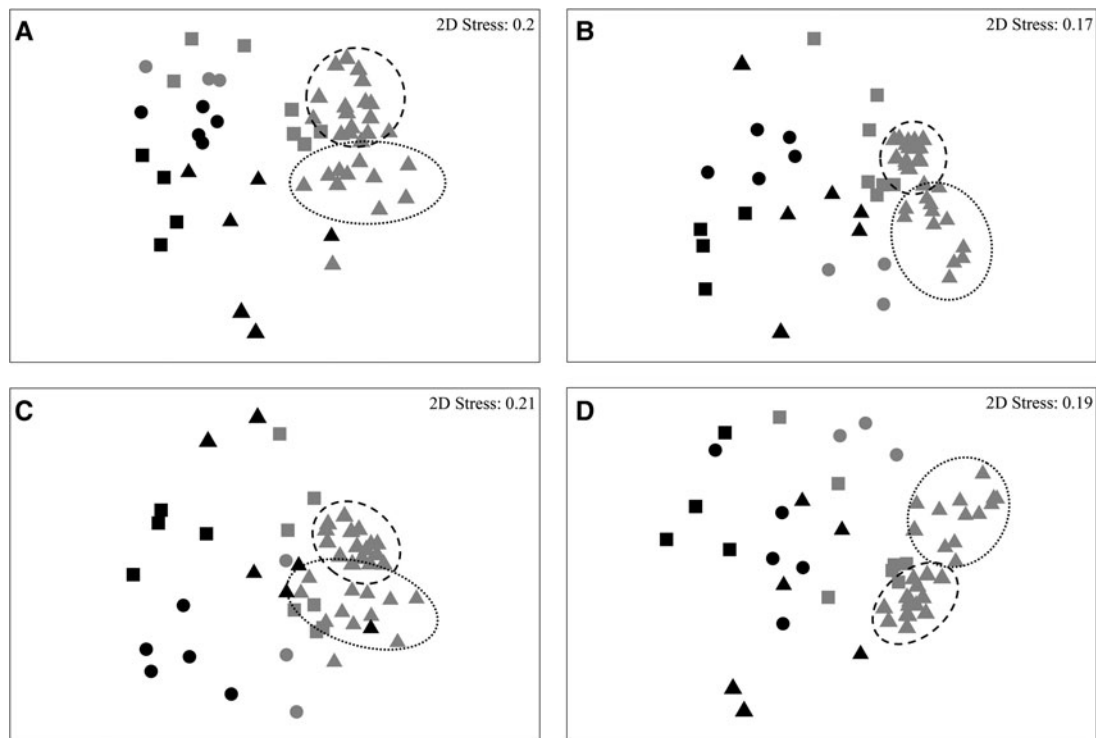


Fig. 4. Non-metric multidimensional scaling ordination of three sympatric species of stingray by maturity based on partially pooled data of food items measured using (A) %V, (B) %N, (C) %F and (D) %IRI. Species: triangle = *Brevitrygon heterura*, square = *Hemitrygon bennetti*, circle = *Telatrygon biasa*; Maturity: grey symbols = juvenile, black symbols = subadult and adult; Only juveniles of *B. heterura* are enclosed by drawn ellipses to show site differences (dashed line ellipse = Bagan Pasir, dotted line ellipse = Sungai Buloh).

Table 3. *R*-statistic values in the ANOSIM test (non-pooled/ partially-pooled) for global and pairwise comparisons among stingray groups

	%V	%N	%F	%IRI
Global test	0.309**/0.764**	0.321**/0.804**	0.319**/0.719**	-/0.823**
Pairwise tests				
Bhe × Hbe	0.192**/0.411**	0.208**/0.373**	0.21**/0.424**	-/0.35**
Bhe × Tbi	0.297**/0.654**	0.315**/0.647**	0.347**/0.706**	-/0.582**
Hbe × Tbi	0.033*/0.119	0.034*/0.076	0.04**/0.247*	-/0.045
Bhe J × Bhe SA	0.393**/0.799**	0.384**/0.730**	0.398**/0.522**	-/0.765**
Hbe J × Hbe SA	0.237**/0.526**	0.244**/0.823**	0.242**/0.722**	-/0.78**
Tbi J × Tbi SA	0.169**/0.846*	0.158**/0.938*	0.159**/0.595*	-/0.897*
Bhe J BP × Bhe J SB	0.202**/0.679**	0.203**/0.856**	0.168**/0.723**	-/0.911**

Bhe, *B. heterura*; Hbe, *H. bennetti*; Tbi, *T. biasa*; J, juvenile; SA, subadult and adult; BP, Bagan Pasir; SB, Sungai Buloh.

*Significant at $P < 0.05$.

**Significant at $P < 0.01$.

in our *B. heterura* specimens. This is the first record of copepods being heavily consumed by a stingray. Consumed crabs belonging to the family Sesamiidae is also an interesting observation of the present study. According to Tan & Ng (1988) and Ng (1998), these crabs are commonly found inhabiting mangroves and muddy areas, yet they had not been recorded on the mudflat area during sampling. Hence, it is likely that the stingrays forage deep into the adjacent mangrove forest during spring flood tide. Despite the large bed area of cultured blood cockles on the Sungai Buloh mudflat, this study shows negligible intake of this hard-shelled bivalve as food by the stingrays, similar to other Dasyatidae (Jacobsen and Bennett, 2013; Pardo *et al.*, 2015). The dasyatids have small weak teeth unlike durophagous myliobatids which have strong tooth plates for crushing hard shells (Ajemian & Powers, 2012; Kolmann *et al.*, 2015).

Species competition for food in the same feeding ground can be reduced if stingrays have different diel feeding activity (Cortés, 1997), occupy the habitat at different times (Bangley & Rulifson, 2017), share only a small fraction of their feeding niche (Navia *et al.*, 2007; Ruocco & Lucifora, 2016), adapt with some degree of resource partitioning (Treloar *et al.*, 2007), partition their habitat space (O'Shea *et al.*, 2013), or if the shared food resource is abundant (Laptikhovskiy *et al.*, 2001). On the Klang mudflat, stingrays certainly display considerable diet overlap between species compared at both juvenile and mature stages (Table 4). In most cases, diet overlaps (%SI) between species were significant, varying from 26.3 to 60 for juvenile stage, and from 32.8 to 47.2 for mature stage. Notwithstanding the observed ontogenetic diet shift, diet overlaps (15.9–55.6) were also evident between juvenile and mature stages of all species which compete

Table 4. Schoener's index of diet overlap for the stingray groups

	Bhe J	Hbe J	Tbi J	Bhe SA	Hbe SA	Tbi SA
Bhe J	–	**	**	**	**	**
Hbe J	60.0	–	*	**	**	*
Tbi J	36.7	26.3	–	*	*	*
Bhe SA	33.2	42.7	18.9	–	n.s.	**
Hbe SA	6.4	15.9	47.1	47.1	–	**
Tbi SA	42.3	55.5	55.6	32.8	47.2	–

Bhe, *B. heterura*; Hbe, *H. bennetti*; Tbi, *T. biasa*; J, juvenile; SA, subadult and adult.
*Significant at $P < 0.05$, **significant at $P < 0.01$, n.s., not significant.

for rather similar prey items (Figure 3). Interestingly, the penaeid shrimps are the prey item mostly and regularly exploited by both juvenile and mature stingrays of all three species (Figure 3). Thus, penaeid shrimps may represent a common shared resource known to be very abundant on the Klang mudflat which serves as their nursery area (Chong *et al.*, 1990; Sasekumar *et al.*, 1992; Marsitah & Chong, 2002). Lim (2016) reported that different species of stingrays have different recruitment peaks on the Klang mudflat due to different peak breeding periods. Hence, temporal partitioning in the use of the mudflat as a feeding area could further reduce species competition for food and space.

This study shows a positive relationship between predator size (disc width) and the maximum prey volume (Figure 2). The prey eaten by small stingrays (juveniles of *B. heterura* and *T. biasa* that averaged 8.75 cm DW) included amphipods, copepods, fish larvae and postlarval to small juvenile shrimps with variable prey volumes of up to 1000 mm³. Medium-sized stingrays (juvenile of *H. bennetti*, subadult/adult of *B. heterura* and *T. biasa* that averaged 16.01 cm DW) are hypothesized to be capable of chasing their prey, at least more efficiently than small-sized stingrays (Carlson *et al.*, 2004). Their prey including larger-sized shrimps and crabs had variable volumes of up to 4000 mm³. Large-sized stingrays (subadult/adult *H. bennetti* that averaged 31.09 cm DW) in the present study are presumably the most efficient in capturing large prey such as fish (volume of up to 15,000 mm³) which are protein-rich food. However, the energy required for stingrays to prey on fish may be costly, which could explain the lesser contribution of fish as prey, as for instance, 19.4%IRI for subadult/adult *H. bennetti* in the present study. This hypothesis, however, needs verification from further work given the insufficient sample size in the present study, though the low contribution of prey fish (16.5%IRI) in the Myliobatiformes has also been reported in Jacobsen & Bennett (2013).

Given the large stock of penaeid shrimps shared as food by the three stingray species on Klang mudflat, it would be interesting to evaluate the stingray predation pressure and its ecological implication, if any. The mean density (\pm SE) of stingrays were 11 (\pm 3) ind. ha⁻¹ and 24 (\pm 11) ind. ha⁻¹ (Lim, 2016) at Sungai Buloh and Bagan Pasir respectively, while the mean stock density (\pm SE) of penaeid shrimps estimated at Sungai Buloh and Bagan Pasir in the same period of study was 1203 (\pm 866) ind. ha⁻¹ and 1011 (\pm 218) ind. ha⁻¹, respectively (Lee, personal communication). On average, 43% and 39% of the stingrays were found to consume penaeid shrimp, at a rate of \sim 11 and 24 shrimps per fish in Sungai Buloh and Bagan Pasir respectively. Thus, the average predation pressure (\pm SE) on the shrimp stock by stingrays on the mudflat is estimated to be about 10% (\pm 5) at Sungai Buloh and 15% (\pm 8) at Bagan Pasir respectively. However, the predation pressure is considered much lower since the barrier net which also sampled the penaeid shrimps had a mesh size (2.5 cm) that excluded most of the smaller shrimps fed on largely by stingrays.

Notwithstanding the low predation pressure due to the low stingray density and high shrimp density, the overall predation pressure on shrimps is considered high in coastal mudflats since shrimp predation by many teleosts is also well reported in several studies (Ong & Sasekumar, 1984; Chong *et al.*, 2012; Leh *et al.*, 2012).

In conclusion, three major species of dasyatid stingrays make regular high-tide invasions of the coastal mudflats of Klang which serve as their feeding and nursery area. The largely young stingrays exploit the vast benthic resources of penaeid shrimps (eight species) including 19 other prey taxa, displaying low diet overlap and some degree of diet specialization with ontogenetic growth. However, benthic copepods as a major diet for juvenile stingrays (*B. heterura*) is recorded for the first time. Given the importance of coastal mudflats as a productive area of living food resources, this study supports the protection of coastal mudflats which are relentlessly subjected to land-claims for development as well as heavy fishing activities.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315418000759>

Financial support. This work was supported by the Japan International Centre for Agricultural Sciences (JIRCAS) under Grant [57-02-03-1005] given to VCC; and UM IPPP Grant under Grant [PG103-2012B] given to KCL.

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