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Feeding ecology of two sympatric species of *Acetes* (Decapoda: Sergestidae) in Panguil Bay, the Philippines

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Abstract. Sergestid shrimps of the genus *Acetes* are important in global shrimp fisheries and nearshore food-webs. The feeding habits of the sympatric species *Acetes erythraeus* and *A. intermedius* from Panguil Bay, Philippines were studied using gut contents and stable isotopes analyses. Both species are omnivorous suspension feeders of plankton, macrophyte detritus, and amorphous particulate organic materials. However, the diet of adults and juveniles differed by prey type. Gut fullness differed over 24 h with a night-time peak in *A. erythraeus* and morning and midnight peaks in *A. intermedius*. Over 1 year gut fullness peaked during July to September for both species, with a minor peak during January for *A. intermedius*. Stable isotope analysis revealed similar $\delta^{15}\text{N}$ values, but both species showed ontogenetic and interspecific separation of $\delta^{13}\text{C}$. *A. erythraeus* seemed to assimilate highly depleted carbon food sources by mangrove-based detrital and plankton trophic pathways, whereas *A. intermedius* relied on plankton and macroalgal and seagrass detrital pathways. These trophic differences may be mechanisms of partitioning the feeding niche, but allotopy in the two species with *A. erythraeus* confined to more brackish waters and *A. intermedius* dwelling in more saline marine waters may indicate that habitat niche segregation underlies these contrasting carbon trophic pathways.

Additional keywords: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotopes, tropical trophic ecology.

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Introduction

Generally regarded as the interface between terrestrial and marine environments, estuaries are among the most productive and bio-diverse systems responsible for the habitat, nursery, feeding, breeding and protective grounds for various life forms (Wolanski *et al.* 2009). Estuaries also support fisheries, transportation and recreational activities, and serve as excellent natural buffer and/or protection of coastal zones against storms and waves as well as for filtering excess nutrient and pollution (Wolanski *et al.* 2009).

Ecological interactions are important in generating and maintaining biodiversity and productivity of many estuarine ecosystems (Bouillon *et al.* 2011). A fundamental theory in ecology is that competing species often partition their ecological niches, usually in the dimensions of feeding, habitat and time, allowing them to coexist sustaining high species diversity (Schoener 1974). Niche partitioning becomes more important if sympatric and/or syntopic (*sensu* Rivas 1964) species are ecologically very similar such as those members of a guild and those taxonomically closely related congeners and conspecifics

(Flock and Hopkins 1992; Duffy 1996). Tropical estuarine mangrove ecosystems are generally species rich but very few studies are conducted on invertebrate macrofauna despite the possible diversity in resource utilisation in highly dynamic mangrove environments (Bouillon *et al.* 2008).

The sergestid shrimps of the genus *Acetes* are extremely euryhaline and often occur in large aggregations in estuarine, shallow tropical, subtropical and temperate waters occupying a rarely studied trophic position that links seston, invertebrate and fish predators (Omori 1975a, 1975b, 1978; Xiao and Greenwood 1993; McLeay and Alexander 1998; Chiou *et al.* 2000; Omundsen *et al.* 2000; Coman *et al.* 2006; Metillo 2011). *Acetes* may be regarded as the ‘Antarctic krill’ of the tropics (Metillo 2011) as it is food to many predators including squids, finfish (e.g. whale sharks and commercially important small pelagic species), prawns, young crocodiles, baleen whales, and many peoples of Asia (Omori 1975a, 1975b, 1978; Deshmukh 1993; Xiao and Greenwood 1993; McLeay and Alexander 1998; Abrantes and Sheaves 2009a). Primarily used in the bait, shrimp

paste, and feed meal industries, *Acetes* is one of the world's most important shrimp fishery resources with its average annual catch exceeding 228 850 tons from Indo-Asia alone during 1979 to 1989 (Xiao and Greenwood 1993).

Among the 14 known species of *Acetes*, only three have been reported from the Philippines: *Acetes erythraeus* in Manila Bay, Paracale Bay (Omori 1975b), and Iligan Bay (Metillo *et al.* 2009), *A. intermedius* in Iloilo, Panay Island (Omori 1975b) and Iligan Bay, Mindanao Island (Metillo *et al.* 2009), and *A. sibogae*, in Manila Bay and Iloilo (Omori 1975b). Of these, *A. erythraeus* has been recorded to coexist with *A. intermedius* in Panguil Bay, a south-western inlet of Iligan Bay (Metillo *et al.* 2009; Metillo 2011). The species are morphologically similar as both belong to the *erythraeus* group (Omori 1975b). A horizontal spatial separation of population assemblages seems apparent with *A. intermedius* occurring mostly in the outer half towards the mouth of Panguil Bay, whereas *A. erythraeus* are found in the inner brackish portion of the Bay (Metillo *et al.* 2009). The two species may be zoogeographically sympatric, but their ecological circumstances match the definition of allotopic species according to Rivas (1964).

Acetes species are primarily omnivorous ingesting a wide variety of suspended food particles including phytoplankton, mesozooplankton, tripton, and animal and plant detritus (Xiao and Greenwood 1993; Chiou *et al.* 2005; Coman *et al.* 2006; Amani *et al.* 2011; Metillo 2011). However, feeding proclivities are common with some species ingesting more plant than animal material (e.g. Collins and Williner 2003; Chiou *et al.* 2005) or *vice versa* (Xiao and Greenwood 1993; McLeay and Alexander 1998; Coman *et al.* 2006; Metillo 2011). Furthermore, temporal variation has been reported in the diet of *A. japonicus* (Amani *et al.* 2011), *A. intermedius* (Metillo 2011) and *A. serrulatus* (Oh *et al.* 2011).

Apart from investigation of stomach contents, and recent fatty acid biomarkers analysis (Boecklen *et al.* 2011) and metagenomic DNA analysis of gut contents (Traugott *et al.* 2013), trophic relationships in marine ecology have been typically studied using the stable isotope ratios of carbon and nitrogen, with the assumption that isotopic signals of the diet are transferred to the consumers following predictable isotopic fractionation (Michener and Kaufman 2007). The primary food source of *A. sibogae australis* in shrimp ponds is zooplankton but stable isotopes analysis identified food sources other than zooplankton (e.g. macroalgae) may also be important (Coman *et al.* 2006). Stable isotopes analysis has indicated that *Acetes* species occupy a carnivorous trophic position (Chew *et al.* 2012), but Tanaka *et al.* (2011) reported species-specific variation between detritivorous and carnivorous trophic levels. Thus, the trophic position of estuarine *Acetes* remains ambiguous.

In this study, we analysed spatial and temporal variations of stomach contents and stable isotopes of carbon and nitrogen to understand the trophic ecology of two sympatric *Acetes* species (*A. intermedius* and *A. erythraeus*) in Panguil Bay, Southern Philippines.

Materials and methods

Study site

A. intermedius and *A. erythraeus* specimens were collected in Panguil Bay, a mangrove-lined estuarine inlet at the south-west

(SW) corner of the bigger Iligan Bay, Northern Mindanao (location: 7°56'–8°04'N, 123°36'–123°46'E), Southern Philippines (Fig. 1). Detailed site description, hydrography and water circulation in Panguil Bay are given in Canini *et al.* (2013). In summary, with an average of 5 m, the depth of Panguil Bay gradually decreases from the mouth to the inner portion, but a narrow and deep lengthwise channel in the middle occupies three-quarters of the total length of the bay. The remaining mangrove forest has an area of 27.3 km² mostly concentrated in the inner parts of the bay. Input from 29 rivers and 46 minor tributaries keeps salinity lower at the inner stations (4–6), whereas higher salinity at stations (1–3) near the mouth is due to marine influence from the adjacent Iligan Bay. Variation of hydrographic parameters is primarily influenced by monsoon. Salinity is generally higher (10–31.7) in the cooler (24–32°C) north-east (NE) monsoon months (from October to March), but lower (3.3–29.7) in the warmer (30–32°C) SW monsoon months of June through to September. Elevated salinity in the bay is also due to strong NE winds that push Iligan Bay marine waters inwards. The opposite happens when SW winds dominate. Higher mean dissolved oxygen values (7.1–7.9 mg L⁻¹) occur in November and August, compared with those (6.5–6.6 mg L⁻¹) in the months of February and May. The pH (8.8–9.2) is typical of normal seawater in February, but slightly acidic, typical of a mangrove estuary, in other months. Dissolved nitrate was generally lower (0.4–0.7 mg L⁻¹) in rainy SW monsoon months compared with the warmer months of February through to May (0.4–0.9 mg L⁻¹). Lowest concentrations of dissolved orthophosphate were recorded in November (0.1–0.2 mg L⁻¹), but higher in rainy months during SW monsoon (0.1–0.4 mg L⁻¹). Chlorophyll-*a* concentrations were higher during SW monsoon (1.4–2.6 µg L⁻¹) than NE monsoon (0.1–1.9 µg L⁻¹), but highest during the calm and warm intermonsoon month of May (0.2–3.6 µg L⁻¹). Heavy rainfall and strong winds during NW monsoon coincided with highest concentrations (0.8–2.9 × 10² mg L⁻¹) of total suspended solids throughout Panguil Bay.

Sampling

For the spatial variation in diet the two *Acetes* species were collected on 24–25 August 2009 at six stations (Stations 1–6; Fig. 1). The six stations covered sharp gradients of depth and salinity with both parameters gradually decreasing from outermost (Station 1) to the innermost (Station 6) portions of the bay: salinity ranges at Stations 1–3 and Stations 4–6 were 25–45 and 15–25 respectively. Temporal diet periodicity in the two species was investigated for 24 h with 3-h interval on 26–27 April 2009, and for 1 year from April 2009 to March 2010. Once per month sampling was done at the most accessible stations (Station 3 for *A. intermedius* and 7 for *A. erythraeus*) at night-time (1900–2400 hours) as abundance and feeding intensity were highest at these times (Xiao and Greenwood 1993; Chiou *et al.* 2003, 2005; Metillo 2011). A triangular push net with a mesh size of 2.0 mm and attached at the bow of a motorised boat was used to collect duplicate samples of *Acetes* per station or per sampling hour and month, and all shrimps were fixed in 10% formalin immediately after capture and were transported to the laboratory for sorting.

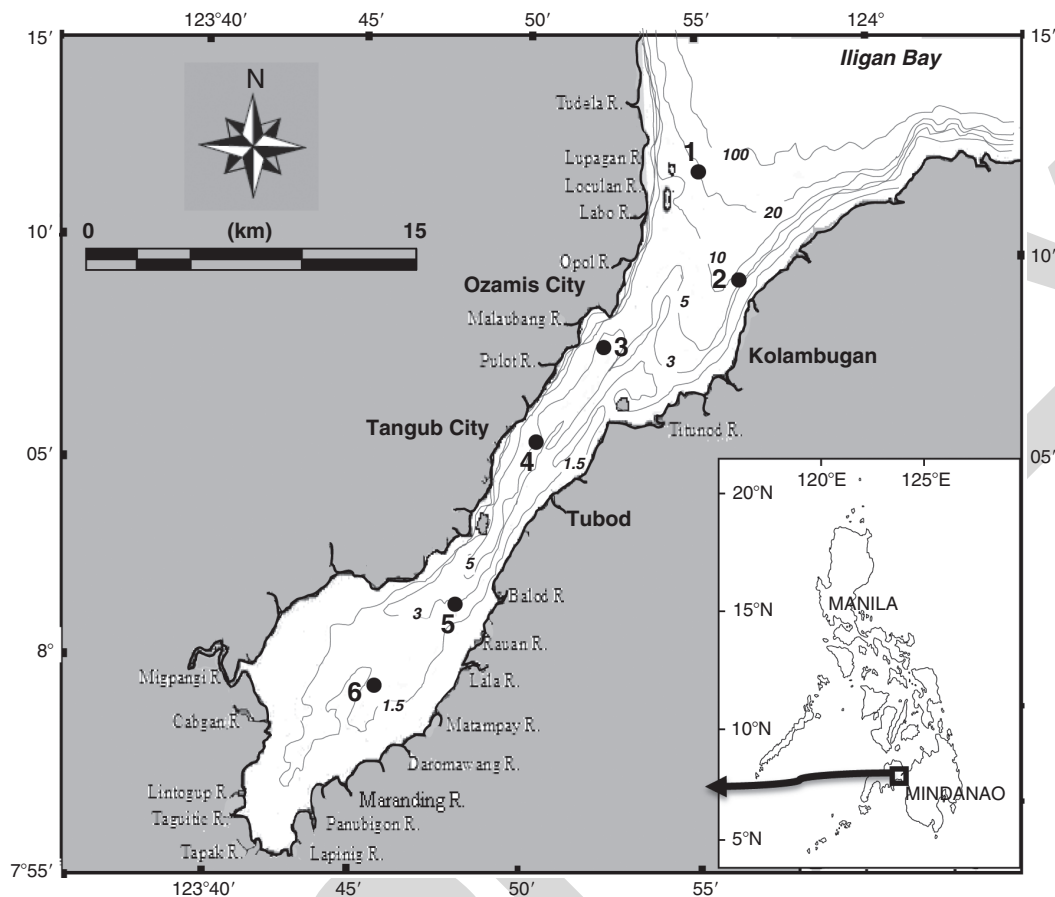


Fig. 1. Location of the sampling stations in Panguil Bay, Northern Mindanao, Philippines.

Sampling for the stable isotopes analysis was made at Stations 2 and 3 for *A. intermedius* and Stations 4 and 5 for *A. erythraeus* on 2–9 February 2014 using the same push net. Potential food sources (microphytobenthos from sediments, phytoplankton, zooplankton, particulate organic matter (POM), fresh seagrass, fresh macroalgae, fresh and decomposing mangrove) were also collected at these sampling stations. Freshly caught *Acetes* were placed in plastic bags and kept in ice, and sorted in the laboratory into juveniles, and adult males and females under a dissecting microscope within 6 h of collection. Microphytobenthos from the top 5 mm of surface sediment cores were collected during low tide using a PVC pipe (diameter 10 cm). Phytoplankton were collected by filtering 20 L of water samples onto 60- μ m sieve and the filtrate further filtered using pre-combusted (450°C, 3 h) GF/F filters. For zooplankton, collections were made by 3-min horizontal tows using a conical plankton net (mouth diameter 0.5 m, mesh size 135 μ m), and samples were stored in a cooler on ice and sorted in the laboratory within 6 h of collection. For POM samples a 5-L Niskin sampler (General Oceanics, Miami, FL, USA) was used to collect 20 L of water between 0 and 1.5 m. Water samples were immediately filtered on board and suspended particles passing through a 335- μ m sieve but those retained on a 60- μ m sieve were regarded as POM. Fresh and decaying leaves of the mangroves *Bruggiera* sp. (Stations 4 and 5) and *Rhizophora* sp.

(Stations 2 and 3), fresh thalli of the macroalgae *Hormophysa* sp., and fresh epiphyte-free leaves of the seagrass *Halodule uninervis* were collected for macrophyte samples. These macrophyte species are dominant at the *Acetes* sampling sites in Panguil Bay (Jimenez *et al.* 1996). *Acetes* and potential food sources were prepared in triplicate samples, and immediately after collection, all samples were dried in an oven at 60°C for 24 h, and stored in a dessicator before carbon and nitrogen stable isotopes analysis.

Diet analysis

Prior to diet analysis, pooled duplicate samples were transferred to 95% ethanol and individuals of the two species were sorted into categories of juvenile and adult male and female. Sexes were determined by the presence and absence of the clasping spine on the lower antennular flagellum and the petasma on the first pleopod (Omori 1975b). Taxonomic descriptions of Omori (1975b) were used for species identification of the *Acetes*.

Stomach contents were analysed according to Metillo (2011). In brief, 35 adult individuals of each species were randomly picked from the preserved sample. The carapace length was obtained on each individual by measuring the dorsal distance from the apex of the rostrum to the posterior median

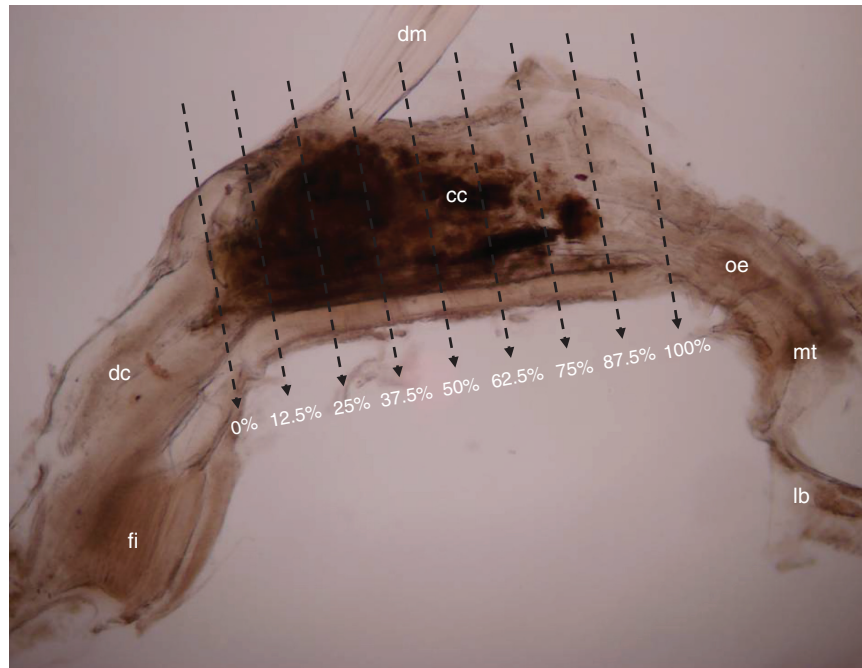


Fig. 2. Lateral view of *Acetes erythraeus* foregut showing the basis of percent gut fullness. Foregut parts shown from the most anterior: labium (lb), mouth (mt), oesophagus (oe), cardiac chamber (cc) with stomach contents, dorsal median muscle (dm), pyloric chamber dorsal channel (dc) and ventral filtration chamber (fi).

edge of the carapace using a vernier caliper (± 0.01 mm). The entire stomach with intact oesophagus and a portion of the intestine (both parts minimise spillage of stomach contents) (Fig. 2; anatomical nomenclature after Icely and Nott 1992) was carefully removed from the dorsal portion of the cephalothorax and placed onto a clean glass slide with a drop of glycerol. The fullness of the cardiac stomach was estimated and expressed as percent gut fullness (Fig. 2). The mid-dorsal cardio-pyloric region of the stomach was then slit open and all the contents were emptied onto the slide and covered with a glass coverslip. If present, 35 juvenile individuals were randomly sorted out from the sample and their diet analysed. Diet of juveniles was separately analysed as their stomach contents contrasted with those of adults (Xiao and Greenwood 1993; Metillo 2011). Prey categories used were as described by Metillo (2011, table 4), but ostracod fragments, echinoderm larvae, and chaetognaths, which were rare in this study, were fused and placed under the 'others' category. Plant fragments and silt were added as new categories as these were very common dietary items. Percentage weighted points for each prey was computed following the formula used by Metillo (2011). Diet overlap between species among sampling sites and across time was computed using the formula of Schoener (1970):

$$R_o = 100(1 - \sum |px_i - py_i|/2)$$

where R_o is the overlap index expressed as percentage, and px_i and py_i are the relative importance (ratio of the points) of each food item i in the stomachs of predator x (*A. erythraeus*) and y (*A. intermedius*).

Stable isotopes analysis

We analysed stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) in adult male, female and juvenile *Acetes*; bulk zooplankton (retained in $>135\text{-}\mu\text{m}$ mesh net); POM; microphytobenthos on sediment, phytoplankton; decaying and fresh mangrove leaves, macroalgae and seagrasses, to examine the relative trophic position of *Acetes* and potential prey and/or food source in isotope space. Except for *Acetes* that were sorted into juveniles and adults, all other samples are bulk samples. All dried samples were ground to a fine powder and analysed using a Thermo Elemental Analyzer coupled to a ThermoFinnigan DELTAplus XP stable isotope ratio mass spectrometer (ThermoFisher Scientific, Waltham, MA, USA) by a ConFlo-III (Thermo Electron Corp., Bremen, Germany) continuous flow interface (measurement error -0.3%). All *Acetes* and zooplankton samples were acidified with drops of 0.1N HCl without rinsing to remove calcium carbonate and chitin (Jacob *et al.* 2005) and re-dried in the oven for 48 h at 60°C and packed in tin capsules. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures were measured in at least three replicates, and 1.0–2.0 mg (dry weight) of tissue was used from each sample. Lipids were not removed from zooplankton samples before stable isotopic analysis because biomass values were generally low, and other studies have shown that lipid extraction results in overestimates in $\delta^{15}\text{N}$ (Bodin *et al.* 2007). Based on the atomic C : N ratios, which were measured simultaneously with the analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, we corrected the $\delta^{13}\text{C}$ of zooplankton samples for lipids following the mass balance model equation for zooplankton recommended by Smyntek *et al.* (2007, eqn 5), because increases in lipids can alter carbon isotope ratios by selecting the

lighter carbon isotope (C^{12}) over the heavier (C^{13}). The $\delta^{13}C$ and $\delta^{15}N$ values were obtained in parts per thousand (‰) relative to the standard, according to the following formula:

$$\delta^{13}C \text{ or } \delta^{15}N = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$$

- 5 To obtain atomic C : N ratios of the samples, L-alanine was used to calibrate the quantification of carbon and nitrogen. A laboratory standard was used for every 12 experimental samples in sequence. By convention standards of Pee Dee Belemnite (PDB) for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$ are used to express delta values.

Data analysis

- All statistical comparisons of total lengths, gut fullness, specific category of gut contents between the two species and life stages (adults and juveniles) and between stations, over 24 h and among sampling months were made by the non-parametric analysis of variance Kruskal–Wallis H test and comparison of means by Mann–Whitney U -test using the software SPSS ver. 11 (SPSS 2002). Comparison of mean $\delta^{13}C$ and $\delta^{15}N$ values between *Acetes* species and life stages, and between potential food sources were made using Student's homoscedastic two-tailed t -test also available in the software SPSS ver. 11 (SPSS 2002).

- The combination of feasible food sources of both *Acetes* species were calculated using the IsoSource linear mixing model of Phillips and Gregg (2003). It correctly estimates the proportions of diet due to a few sources, even when all sources are not utilised (Phillips 2001). Potential food sources were categorised into phytoplankton, zooplankton, POM, dead mangrove leaves, seagrass, and macroalgae. Mean $\delta^{13}C$ and $\delta^{15}N$ values were calculated for each food source and the two *Acetes* species, and these mean values were corrected for fractionation per trophic level using 0.8‰ for $\delta^{13}C$ (McCutchan *et al.* 2003; Bouillon *et al.* 2011) and 2.8‰ for $\delta^{15}N$ (Michener and Kaufman 2007; Tanaka *et al.* 2011) for micronektonic shrimps. The IsoSource method analyses all possible combinations of each food source potential contribution (0–100%) in 1% increments and mass balance tolerance of 0.2%. Results are reported as median contribution and 1–99 percentile of frequency distribution of proportions for each food source.

Results

Total lengths, gut fullness and gut contents among stations

- Acetes* samples from Stations 1–3 were composed only of *A. intermedius* whereas Stations 4–6 contained only *A. erythraeus*. Total lengths were similar in adult and juvenile specimens of both species in these stations (Table 1). Mean gut fullness that ranged from 30 to 55% in adults and 25 to 45% in juveniles in both species are comparable across stations ($H = 12.20$, d.f. = 6, $P > 0.19$) (Table 1). For both species, stomach contents observed in adults were mostly zooplankton, whereas those found in juveniles were mainly amorphous materials (41–71%). For instance, the major stomach contents of adult *A. intermedius* were decapod crustacean fragments and copepod individuals and fragments, amorphous materials, macrophyte fragments, and dinoflagellate cells (Fig. 3a). However adult *A. erythraeus* primarily ingested

copepod individuals and fragments, and few decapod crustacean fragments, amorphous materials, gastropod and bivalve veliger individuals and fragments and macrophyte materials (Fig. 3a). Apart from amorphous materials, juvenile *A. intermedius*, as with adults, predominantly ingested decapod crustacean fragments, gastropod and bivalve veliger individuals and fragments, macrophyte fragments, and silt. Juvenile *A. erythraeus*, like adults, also ingested large amounts of copepod individuals and fragments, bivalve veliger individuals and fragments, and macrophyte fragments (Fig. 3b).

Total lengths, gut fullness, and gut contents over time

Sizes were similar in all individuals examined over 24 h for *A. erythraeus* adults ($H = 10.30$, d.f. = 7, $P > 0.17$) and juveniles ($H = 8.24$, d.f. = 5, $P > 0.14$), and *A. intermedius* adults ($H = 9.61$, d.f. = 7, $P > 0.21$) and juveniles ($H = 7.43$, d.f. = 5, $P > 0.07$) (Table 1). However, diel periodicity was observed in the gut fullness in *A. erythraeus* adults ($H = 28.45$, d.f. = 7, $P < 0.001$) and juveniles ($H = 21.30$, d.f. = 7, $P < 0.01$), and *A. intermedius* adults ($H = 29.64$, d.f. = 7, $P < 0.001$) and juveniles ($H = 22.55$, d.f. = 7, $P < 0.01$) (Table 1). Mean gut fullness of *A. intermedius* adults ranged from 20 to 65%, but highest values were observed at 0900 and 2100–2400 hours. In contrast, highest values were noted from 2100 to 2330 hours in *A. erythraeus* gut fullness that ranged from 25 to 55% (Table 1). Decapod fragments, amorphous materials, macrophyte fragments, silt, and few bivalve veliger individuals and fragments filled the stomachs of *A. intermedius* (Fig. 4a) whereas copepod individuals and fragments, gastropod and bivalve veliger individuals and fragments, amorphous materials, few silt and macrophytes fragments comprised the contents in *A. erythraeus* (Fig. 4c). Notably, more macrophyte fragments were observed in *A. intermedius* than in *A. erythraeus*. The gut fullness of the juveniles of both species showed similar periodicity patterns as those in adults, but variability in values in juveniles rendered this periodicity pattern apparent (Table 1). A similar trend was shown with *A. erythraeus* juveniles ingesting more copepods than juvenile *A. intermedius* that ingested more decapod crustaceans than the former (Fig. 4b, d). In general, amorphous materials dominated the stomach content in juveniles of both species.

Total lengths of dissected adults of *A. erythraeus* ($H = 87.34$, d.f. = 11, $P < 0.001$) and *A. intermedius* ($H = 117.41$, d.f. = 11, $P < 0.001$) differed significantly among months (Table 1). Largest individuals of *A. erythraeus* were observed in April and May, whereas those of *A. intermedius* in September and October. Monthly gut fullness differed significantly among months in adult *A. erythraeus* ($H = 59.57$, d.f. = 11, $P < 0.001$) and *A. intermedius* ($H = 25.45$, d.f. = 11, $P < 0.01$), but both species showed similar trends with highest values observed during SW monsoon months from June to September (Table 1). Again, *A. erythraeus* ingested more copepod individuals and fragments than decapod crustacean fragments whereas *A. intermedius* showed the reverse (Fig. 5a, c). Most intense consumption of these animal prey occurred during the SW monsoon, particularly in August and September in *A. erythraeus* and June for *A. intermedius*. Other food items ingested in substantial amounts in other months by *A. erythraeus* were amorphous materials and macrophyte fragments and a small amount of

Table 1. Average carapace length (CL) \pm standard deviation (s.d.; mm), number of individuals examined (N), and average percent gut fullness (%GF \pm s.d.) of adult (among stations, 24 h and from April 2009 to March 2010) and juvenile (among stations, 24 h and from July 2009 to February 2010) *Acetes intermedius* and *A. erythraeus*

<i>Acetes intermedius</i>				<i>Acetes erythraeus</i>			
	CL	N	%GF		CL	N	%GF
<i>Adults</i>				<i>Adults</i>			
Station 1	0.36 \pm 0.05	35	43 \pm 27	Station 4	0.66 \pm 0.05	35	38 \pm 13
Station 2	0.49 \pm 0.07	35	55 \pm 25	Station 5	0.67 \pm 0.08	35	54 \pm 21
Station 3	0.39 \pm 0.02	35	42 \pm 15	Station 6	0.71 \pm 0.08	35	30 \pm 22
<i>Juveniles</i>				<i>Juveniles</i>			
Station 1	0.20 \pm 0.03	35	42 \pm 23	Station 4	0.30 \pm 0.07	35	38 \pm 24
Station 2	0.25 \pm 0.02	35	24 \pm 15	Station 5	0.37 \pm 0.06	35	29 \pm 25
Station 3	0.27 \pm 0.04	35	24 \pm 21	Station 6	0.45 \pm 0.05	35	39 \pm 21
<i>Adults</i>				<i>Adults</i>			
0830–0900 hours	0.37 \pm 0.05	35	59 \pm 22		0.69 \pm 0.08	35	21 \pm 14
1130–1200 hours	0.38 \pm 0.04	35	22 \pm 19		0.74 \pm 0.07	35	36 \pm 30
1430–1500 hours	0.40 \pm 0.06	35	32 \pm 24		0.71 \pm 0.09	35	48 \pm 23
1730–1800 hours	0.37 \pm 0.05	35	48 \pm 25		0.67 \pm 0.07	35	43 \pm 24
2030–2100 hours	0.42 \pm 0.08	35	60 \pm 22		0.63 \pm 0.07	35	55 \pm 25
2330–2400 hours	0.42 \pm 0.05	35	62 \pm 21		0.60 \pm 0.06	35	51 \pm 18
0230–0300 hours	0.36 \pm 0.05	35	28 \pm 22		0.64 \pm 0.09	35	27 \pm 17
0530–0600 hours	0.40 \pm 0.06	35	35 \pm 27		0.63 \pm 0.12	35	23 \pm 28
<i>Juveniles</i>				<i>Juveniles</i>			
0830–0900 hours	0.29 \pm 0.02	35	57 \pm 40		0.27 \pm 0.06	35	20 \pm 20
1130–1200 hours	0.40 \pm 0.01	35	30 \pm 42		0.32 \pm 0.02	35	15 \pm 07
1430–1500 hours	0.32 \pm 0.01	35	20 \pm 32		0.29 \pm 0.07	35	30 \pm 14
1730–1800 hours	0.29 \pm 0.01	35	40 \pm 35		0.37 \pm 0.02	35	30 \pm 17
2030–2100 hours	0.31 \pm 0.01	35	58 \pm 21		0.34 \pm 0.04	35	50 \pm 26
2330–2400 hours	0.31 \pm 0.01	35	40 \pm 15		0.34 \pm 0.02	35	40 \pm 35
0230–0300 hours	0.29 \pm 0.01	35	17 \pm 21		0.34 \pm 0.06	35	13 \pm 06
0530–0600 hours	0.32 \pm 0.02	35	25 \pm 22		0.32 \pm 0.02	35	20 \pm 17
<i>Adults</i>				<i>Adults</i>			
April 2009	0.36 \pm 0.05	35	42 \pm 27		0.86 \pm 0.07	35	34 \pm 17
May	0.39 \pm 0.02	35	55 \pm 24		0.87 \pm 0.06	35	34 \pm 27
June	0.50 \pm 0.05	35	42 \pm 28		0.69 \pm 0.09	35	55 \pm 14
July	0.44 \pm 0.12	35	68 \pm 27		0.73 \pm 0.07	35	38 \pm 24
August	0.44 \pm 0.11	35	69 \pm 09		0.70 \pm 0.08	35	54 \pm 30
September	0.52 \pm 0.06	35	69 \pm 24		0.68 \pm 0.08	35	77 \pm 15
October	0.54 \pm 0.06	35	46 \pm 23		0.74 \pm 0.07	35	40 \pm 24
November	0.44 \pm 0.05	35	49 \pm 33		0.82 \pm 0.06	35	48 \pm 20
December	0.53 \pm 0.07	35	52 \pm 25		0.72 \pm 0.09	35	22 \pm 19
January 2010	0.42 \pm 0.11	35	60 \pm 25		0.61 \pm 0.07	35	23 \pm 14
February	0.34 \pm 0.04	35	52 \pm 22		0.61 \pm 0.09	35	31 \pm 28
March	0.36 \pm 0.05	35	45 \pm 24		0.73 \pm 0.08	35	36 \pm 23
<i>Juveniles</i>				<i>Juveniles</i>			
July 2009	0.20 \pm 0.02	35	90 \pm 25		0.39 \pm 0.01	35	47 \pm 15
August	0.25 \pm 0.02	35	60 \pm 20		0.45 \pm 0.02	35	63 \pm 15
September	0.23 \pm 0.04	35	100 \pm 21		0.37 \pm 0.01	35	70 \pm 17
December	0.33 \pm 0.03	35	90 \pm 10		0.43 \pm 0.03	35	75 \pm 11
January 2010	0.32 \pm 0.02	35	100 \pm 14		0.35 \pm 0.03	35	56 \pm 16
February	0.31 \pm 0.02	35	70 \pm 15		0.39 \pm 0.04	35	50 \pm 18

dinoflagellate and diatom cells and fragments, bivalve and gastropod veliger individuals and fragments, and silt. Throughout the year similar amounts of amorphous materials, bivalve and gastropod veligers, macrophyte fragments, dinoflagellates cells and fragments, and silt were observed. Absent in the *A. erythraeus* stomachs, tintinids were dietary items of *A. intermedius* during NE monsoon months, and pteropod fragments during SW monsoon months of June and September.

Sufficient numbers of juveniles of both species were only obtained for 6 months (from July to September and December–February). Mean lengths of *A. erythraeus* juveniles differed ($H = 7.43$, d.f. = 5, $P > 0.07$) with largest individuals analysed in August and December. Similarly, mean lengths of *A. intermedius* juveniles differed among months ($H = 7.43$, d.f. = 5, $P > 0.07$) with larger sizes dissected in December through to February (Table 1). Gut fullness was similar in both species

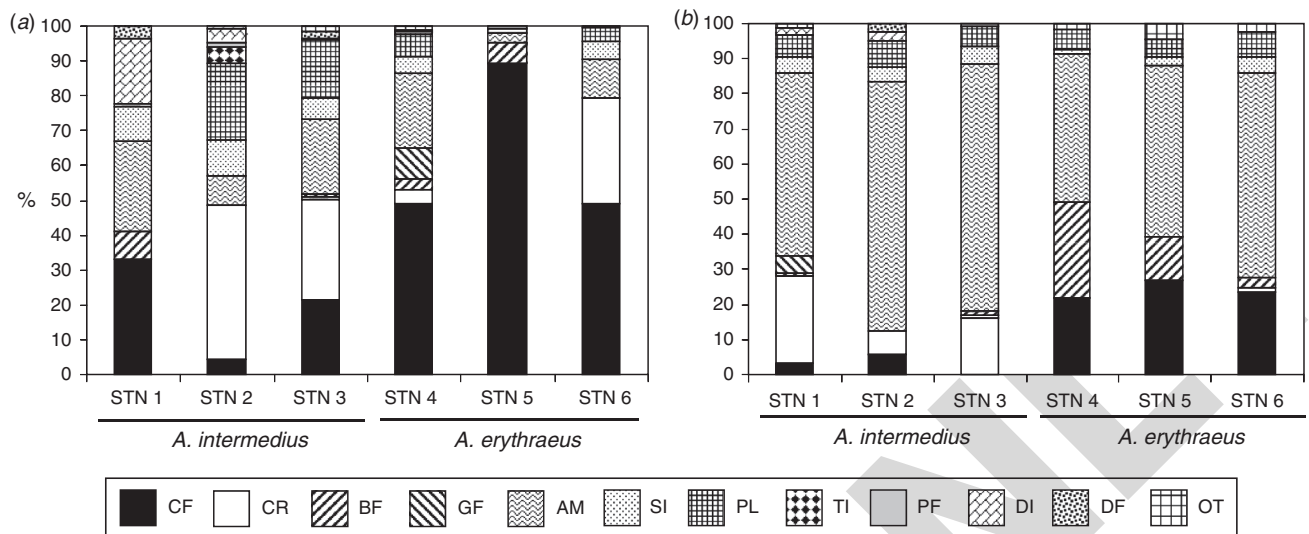


Fig. 3. Percentage contribution of stomach contents in adults (a) and juveniles (b) of *A. intermedius* (Stations [STN] 1–3) and *A. erythraeus* (Stations 4–6) from six sampling stations in Panguil Bay, Philippines. Stomach contents: AM: amorphous materials; BF: bivalve veliger individuals and fragments; CF: copepod individuals and fragments; CR: decapod crustacean fragments; DF, diatom cells and fragments; DI, dinoflagellate cells and fragments; GF: gastropod veliger individuals and fragments; OT, other rare food items; PF, pteropod fragments; PL, macrophyte fragments; SI, silt; TI, tintinnids.

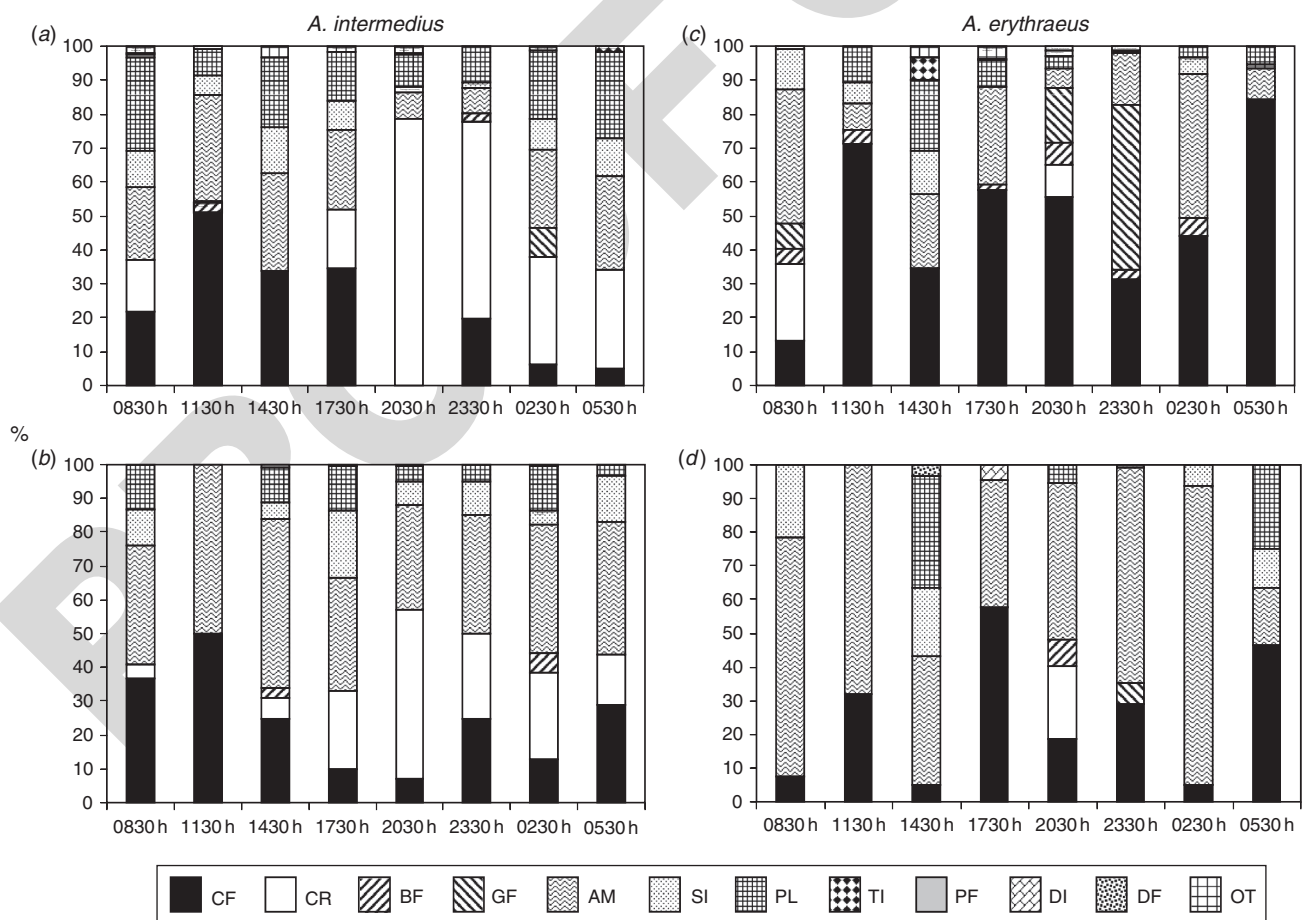


Fig. 4. Diel variations in percentage contribution of stomach contents in *A. intermedius* adults (a) and juveniles (b), and *A. erythraeus* adults (c) and juveniles (d) from Panguil Bay, Philippines. Stomach contents legends as in Fig. 3.

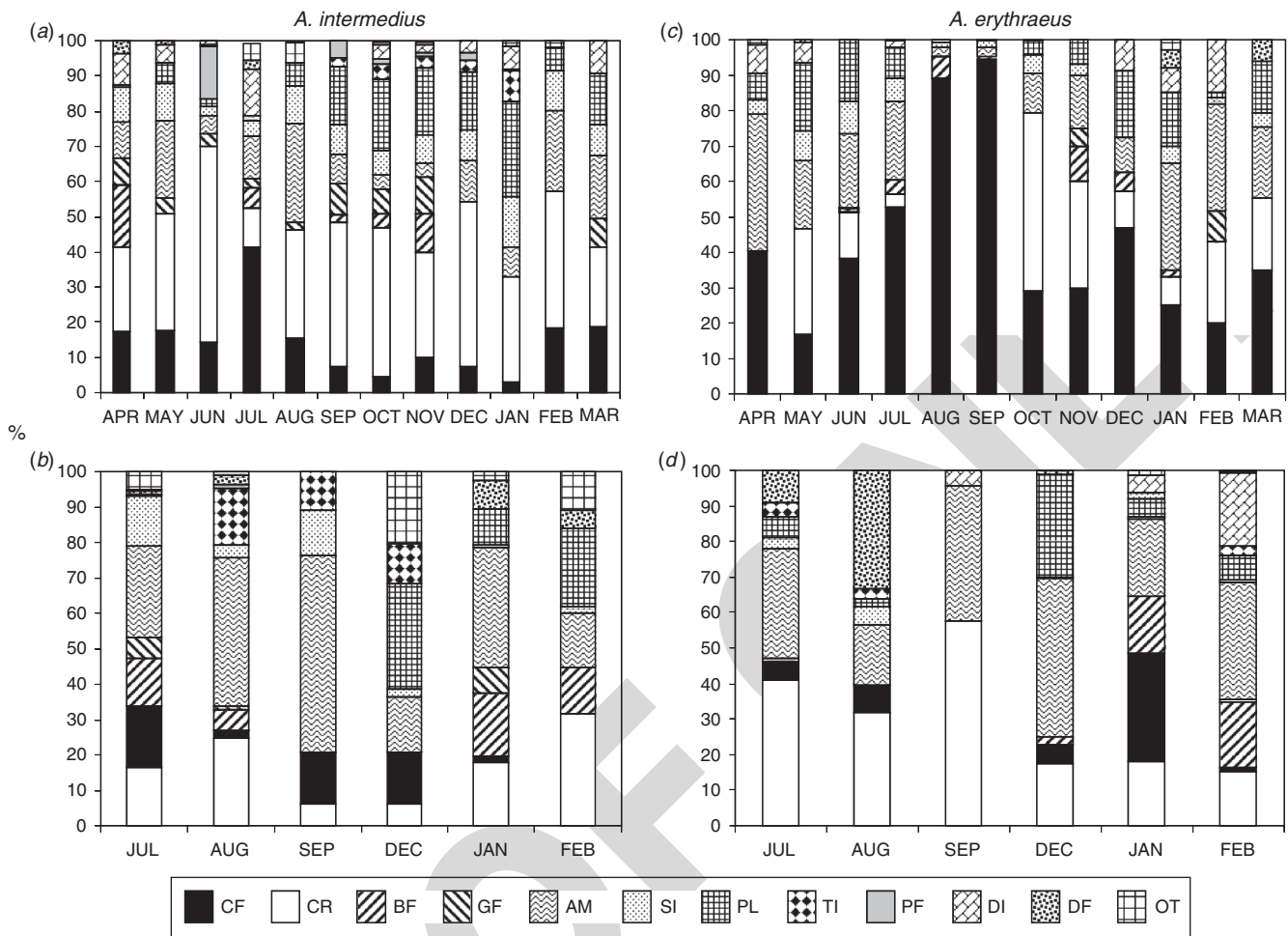


Fig. 5. Monthly variations in percentage contribution of stomach contents in *A. intermedius* adults (a) and juveniles (b), and *A. erythraeus* adults (c) and juveniles (d) from Panguil Bay, Philippines. Stomach contents legends as in Fig. 3.

among months (Table 1). More copepod fragments were found in the stomachs of *A. erythraeus* than in *A. intermedius*, with greatest values observed during SW monsoon months from July to September (Fig. 5b, d). Both species ingested comparable amounts of amorphous materials, gastropod and bivalve veliger individuals and fragments, and macrophyte fragments, but more diatom and dinoflagellate cells and fragments were respectively observed in July and August, and January and February in *A. erythraeus*. Decapod crustacean fragments, tintinids, silt and other rare food materials were more common in *A. intermedius* than in the other species.

Feeding niche overlap between species

Apart from the two comparisons among adults that yielded low values (25 and 30%), adults and juveniles of both species generally shared (>35%) dietary items among stations with the highest of 76% between juveniles from Stations 2 and 6 (Fig. 6). Except for the low overlap values of 21 and 13% respectively at 2030 and 2330 hours, values were high ranging from 40 to 92% in adult and juveniles of both species over 24 h. Ingested food by adults and juveniles of the two species also overlapped by 40–85% across months.

Stable isotopes values of two Acetes species and potential food items

Stable isotope analysis showed that $\delta^{15}\text{N}$ values in *A. erythraeus* were similar between adult males and females (d.f. = 5, $P > 0.61$), between adult male and juveniles (d.f. = 5, $P = 0.19$) and between adult female and juveniles (d.f. = 5, $P > 0.22$) (Fig. 7). Similarly, $\delta^{15}\text{N}$ values in *A. intermedius* were similar between adult males and females (d.f. = 5, $P > 0.77$), between adult males and juveniles (two-tailed t -test, d.f. = 5, $P > 0.21$), and adult females and juveniles (d.f. = 5, $P > 0.26$). In contrast, a clear separation of $\delta^{13}\text{C}$ levels was shown between *A. erythraeus* adult females and juveniles (two-tailed t -test, d.f. = 5, $P < 0.03$), and between adult males and juveniles (two-tailed t -test, d.f. = 5, $P < 0.01$). Adults showed more depleted $\delta^{13}\text{C}$ than juveniles. However, adult males and females of *A. erythraeus* (d.f. = 5, $P > 0.62$) and *A. intermedius* (d.f. = 5, $P = 0.56$) were isotopically similar for $\delta^{13}\text{C}$. Similarly, more depleted $\delta^{13}\text{C}$ levels in juveniles differed significantly from *A. intermedius* males (d.f. = 5, $P < 0.03$) and females (d.f. = 5, $P < 0.02$). Surprisingly, it was the opposite in *A. erythraeus* with adults having more depleted $\delta^{13}\text{C}$ than juveniles. Overall, *A. erythraeus* individuals had more depleted $\delta^{13}\text{C}$ values than in *A. intermedius*.

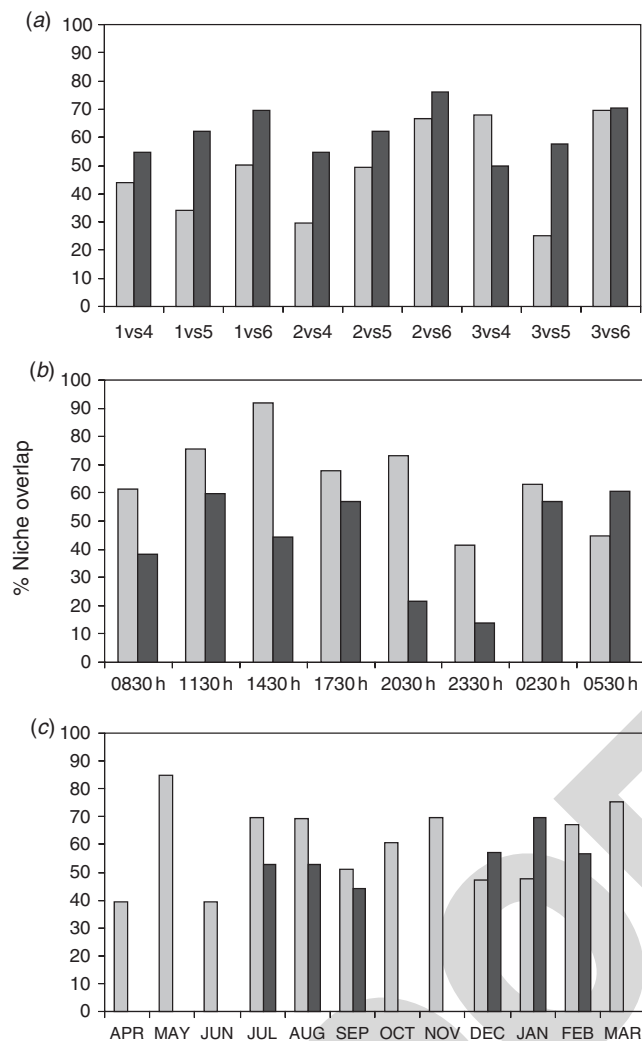


Fig. 6. Diet overlap values between *A. intermedius* and *A. erythraeus* across sampling stations (a), over 24 h (b), and over 12 months (c) from Panguil Bay, Philippines. Solid bars, juveniles; grey bars, adults.

(d.f. = 5, $P < 0.0001$), but *A. erythraeus* $\delta^{15}\text{N}$ values were more enriched than those in *A. intermedius* (d.f. = 5, $P < 0.03$).

As for the potential food, POM had significantly lower values of $\delta^{15}\text{N}$ than those of *A. erythraeus* ($P < 0.04$ for all), but a large variation rendered POM and *A. intermedius* having indistinguishable values ($P > 0.06$ for all) (Fig. 7). Except for the much depleted $\delta^{13}\text{C}$ values for adult *A. erythraeus* ($P < 0.03$ for both), values for *A. intermedius* and *A. erythraeus* juveniles are similar to the POM values ($P > 0.08$ for both). Zooplankton values were generally lower in $\delta^{15}\text{N}$ for both species, but statistically the same in $\delta^{13}\text{C}$ with juvenile *A. intermedius* (d.f. = 5, $P > 0.98$), lower in adult *A. intermedius* ($P < 0.02$ for both), and higher than all *A. erythraeus* stages ($P < 0.03$ for all). Phytoplankton $\delta^{15}\text{N}$ values were significantly lower than those of both *Acetes* species, but more depleted $\delta^{13}\text{C}$ values of phytoplankton were very similar with those of *A. erythraeus* adult males (d.f. = 5, $P > 0.18$) and females (d.f. = 5, $P > 0.68$). Values of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for both *Acetes* species were much higher than the most depleted values of decaying and fresh

mangrove leaves and twigs. Both *Acetes* species showed higher $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ values than the seagrass (*H. uninervis*) leaves (d.f. = 5, $P < 0.0001$). Values of $\delta^{13}\text{C}$ were different for both *Acetes* species and the highly enriched seaweed (*Hormophysa* sp.), but $\delta^{15}\text{N}$ values were statistically the same for the macroalgae and both *Acetes* species ($P > 0.96$ for all). Microphytobenthos values were lower in $\delta^{15}\text{N}$ for both *Acetes* species, but were the same ($P > 0.46$) in $\delta^{13}\text{C}$ of inner station samples with *A. intermedius*.

Feasible food sources mixture of two *Acetes* species

The contribution of food sources to the nutrition of both *Acetes* species differed within and between species (Fig. 8). For all stages of *A. intermedius*, POM (69–74%) was the top food source followed by macroalgae (57–64%). Surprisingly, juveniles showed a lower value (57%) for macroalgae than those in adults. Zooplankton contribution ranked third (52–55%) with juveniles showing the highest value. Seagrass ranked fourth (42–46%) in contribution with the lowest value shown by juveniles. Detrital mangrove leaves showed similar values for adults (25–27%), but those for juveniles were higher (31%). Phytoplankton contribution was similar for all stages and showed next to the lowest in contribution (25–27%). The lowest contribution came from sediments (6–11%). In *A. erythraeus*, POM was the highest contributor, which was up to 90% shown by adult females (Fig. 8). The second highest was zooplankton with the highest value of up to 41% recorded in juveniles. Decomposing mangrove leaves ranked third because of the high value in adults (21–24%). Surprisingly, juveniles only had a maximum of 17%. Macroalgae ranked fourth in adults (19–23%), but the value for juveniles was large (up to 36%). Seagrass (12–17%) and phytoplankton (12–16%) followed, whereas microphytobenthos contributed the lowest (4–10%) to the nutrition of *A. erythraeus* adults and juveniles.

Discussion

The number of categories of stomach contents did not vary in space and time (24 h and 1 year) for the two *Acetes* species in Panguil Bay. This was supported by the generally high values of diet overlap index for both species collected from different sites, and over 24 h and for 1 year. Unlike the predominantly herbivorous *A. paraguayensis* (Collins and Williner 2003) and *A. intermedius* (Chiou *et al.* 2005) from Taiwan coastal waters, stomach contents analysis in *A. erythraeus* and *A. intermedius* from Panguil Bay showed omnivory with a predilection for zooplankton-based diet. The 12 diet categories were more than those identified for *A. sibogae australis* (Xiao and Greenwood 1993; McLeay and Alexander 1998; Coman *et al.* 2006), *A. japonicus* (Amani *et al.* 2011) and *A. serrulatus* (Oh *et al.* 2011), but comparable to those observed in *A. intermedius* populations of the nearby Iligan Bay (Metillo 2011). As in the present study, the Madagascan *A. erythraeus* showed strong preference for animal prey (Le Reste 1970).

However, the relative proportions of each stomach item were variable between species, and between adult and juveniles within species. Large amount of copepods were ingested by *A. erythraeus* whereas *A. intermedius* had highest amounts of decapod crustacean fragments. Ontogenetic differences were

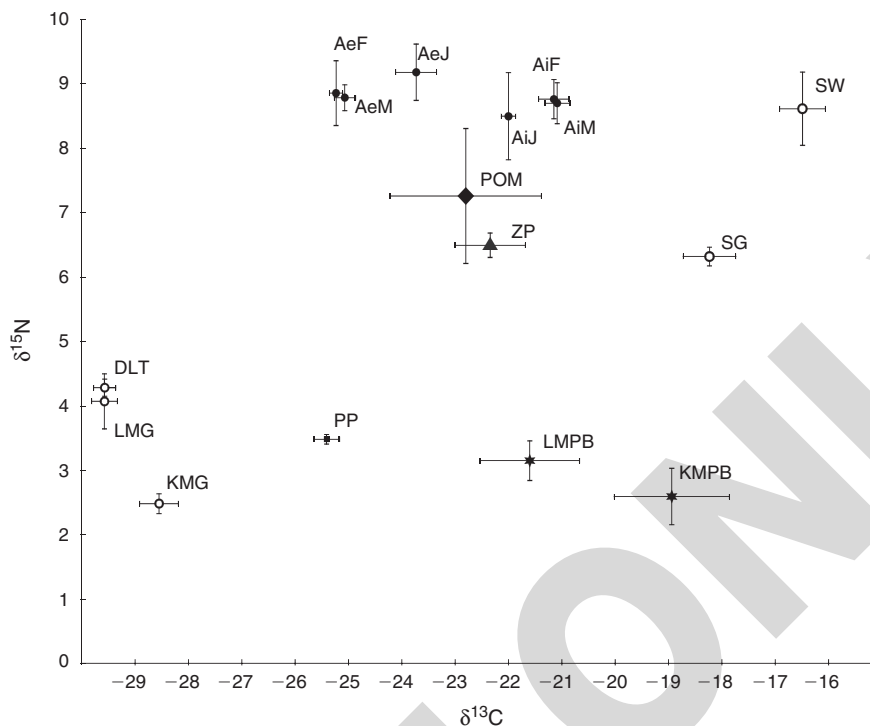


Fig. 7. Biplot of unadjusted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of *A. intermedius* (Ai) and *A. erythraeus* (Ae) adult female (F) and male (M) and juveniles (J), and various primary producers (fresh *Rhizopora* sp. [KMG] and *Bruggiera* sp. [LMG] and decomposing leaves of *Bruggiera* sp. [DLT], zooplankton (ZP), phytoplankton [PP], fresh seagrass *Halodule uninervis* [SG], and fresh macroalgae *Hormophysa* sp. [SW]), particulate organic matter (POM), and Stations 2 (KMPB) and 5 (LMPB) microphytobenthos from Panguil Bay, Philippines.

shown with amorphous materials being more abundant in the stomachs of juveniles than in the adults in both *Acetes* species. Furthermore, temporal changes in feeding intensity was observed for the adults of both *Acetes* species with a night-time unimodal gut fullness for the adults *A. erythraeus* and a bimodal (one night-time and one daytime) for *A. intermedius*. In contrast, Chiou *et al.* (2005) observed a single peak of around midnight feeding mainly on phytoplankton in the case of Taiwan population of *A. intermedius*.

Furthermore, the monthly diet variation coincided with changes in monsoonal seasons in Panguil Bay with April and May as the hot intermonsoon months, from June to October as the wet SW monsoon months, and November to March as NE monsoon months (Han *et al.* 2009; Villanoy *et al.* 2011).

A. erythraeus showed single intense zooplanktivorous feeding from July to September, but *A. intermedius* appeared to have two, one from June to August and a minor peak from January to March. Temporal variations have been observed in *A. intermedius* (Metillo 2011) and *A. japonicus* (Amani *et al.* 2011) in that zooplankton were mostly ingested in the warmer month of March in both species. Bimodal peaks in zooplankton ingestion in September and March were observed for *A. serrulatus* (Oh *et al.* 2011). July to September is rainy SW monsoon season in Panguil Bay, which seems to similarly influence feeding peaks as in *Acetes* species in Malaysian waters (Amani *et al.* 2011; Oh *et al.* 2011).

Stable isotopes showed several interesting aspects of *Acetes* feeding ecology. We provide unequivocal evidence of separation of carbon source for two coexisting species of *Acetes*. *A. erythraeus* showed substantial reliance of more depleted carbon source that could either be traced to direct feeding of mangrove-derived particulate detritus as suggested by Isosource results for POM and decomposing mangrove leaves or by feeding on zooplankton and phytoplankton that is fueled by mangrove-derived dissolved ^{13}C (Abrantes and Sheaves 2009a). *A. intermedius*, however demonstrated greater reliance on macroalgae as POM or as those particles assimilated by suspension-feeding zooplankton and decapod larvae. The carbon source of the juveniles of both species was quite unexpected. Interestingly, ontogenetic shifts in carbon source was demonstrated by the two species with the juveniles of *A. erythraeus* tend to include more macroalgal particles whereas the juveniles of *A. intermedius* relying more on mangrove particulate matter. It is also possible that the carbon depletion in *A. intermedius* juveniles could be due to ingestion of zooplankton that ingest phytoplankton with highly depleted carbon from decomposing mangrove materials (Abrantes and Sheaves 2009a; Bouillon *et al.* 2011). Nevertheless, these clear differences in carbon source in the two *Acetes* species reflect specialisations that concur with findings in penaeid shrimps (Abrantes and Sheaves 2009b) and oceanic sergestids (Flock and Hopkins 1992). Hence, it is very important to take into account the feeding

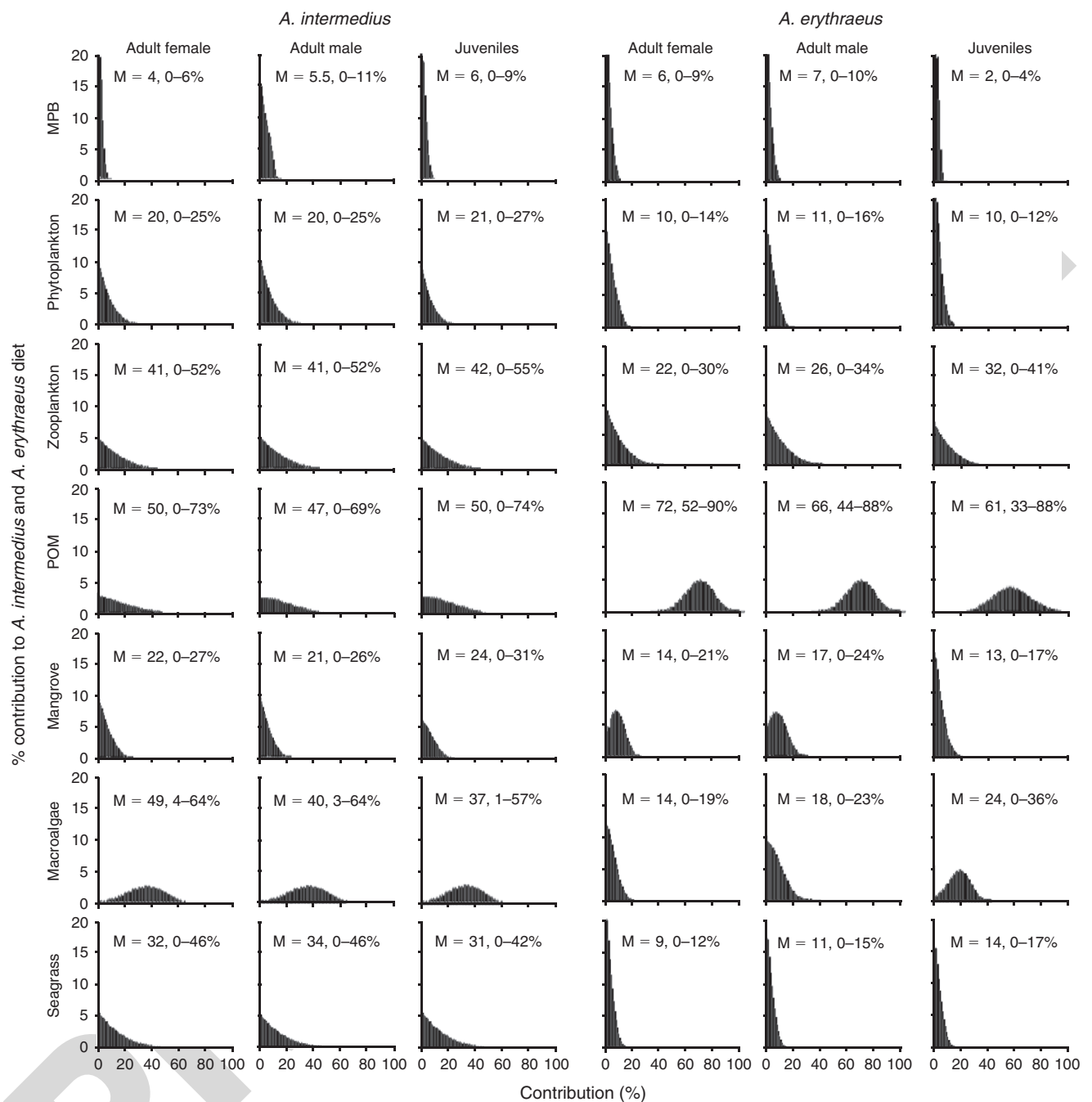


Fig. 8. Distribution of feasible contributions of five food sources to nutrition of *A. intermedius* and *A. erythraeus* based on fractionation-adjusted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. M, median; range, 1–99 percentiles. MPB: microphytobenthos; POM: particulate organic matter.

ecology of each *Acetes* species as each has different carbon isotopic signatures that would then be reflected in their predators.

It would be interesting to further trace carbon source and biochemical pathways by stable isotopes, DNA, and fatty acids biomarkers analyses (Boecklen *et al.* 2011; Traugott *et al.* 2013). For instance, different macroalgal taxa show distinct stable isotopes and fatty acid biomarkers that could be traced in food-webs (Alfaro *et al.* 2006; Elsdon 2010). Coman *et al.*

(2006) examined *A. sibogae* from artificial shrimp ponds and suggested there might be a greater dependence on macroalgae within these systems, and that zooplankton are not the only food source. The finding that adult *A. intermedius* and juveniles of *A. erythraeus* can source their body carbon from macroalgae suggests another possible food chain in tropical estuary, i.e. macroalgal-based chain, which was omitted in the models of Abrantes and Sheaves (2009a) and Chew *et al.* (2012), but recognised by Bouillon *et al.* (2011). In this study, both

sympatric but allotopic congeners of omnivorous suspension feeding crustaceans *Acetes*, can at least show differences in carbon sources, perhaps as a mechanism of partitioning their feeding niche in the estuary as a means of alleviating or minimising competition as noted in micronektonic deep sea sergestids (Flock and Hopkins 1992) and in shallow-water temperate mysids (Metillo *et al.* 2007).

Alternatively, because our sampling of the two *Acetes* species seems to suggest that both inhabit different habitats, the two species need not partition their feeding niche as both may have little chance to meet, hence little competition. Considering the obvious horizontal gradients of depth, salinity, and pH in Panguil Bay, and the fact that *A. erythraeus* are able to tolerate environmental parameters in the inner muddy portions of the bay, whereas *A. intermedius* populations are well suited in more saline and deeper portion of the bay (Metillo *et al.* 2009), these two species may also be partitioning the habitat niche. In fact, it is in this ecological context that we used the term 'allotopy', which, according to Rivas (1964), is 'to be used in reference to two or more related species which do not occupy the same macro-habitat, and are presumably not in close proximity, cannot interbreed, and do not occur together in the same locality although they may have the same geographic distribution (sympatric)'. The spatial differences in diet can be attributed to the two species inhabiting contrasting habitats as noted in monospecific *A. sibogae* populations occurring in salinity and sandy to muddy substrate gradients (Xiao and Greenwood 1992). It is also likely that the two species feed non-selectively, i.e. they fed on any food items that were present in their habitat non-selectively. The observed difference in their stomach contents might simply reflect the difference in composition of organic materials in their environment (near mouth v. inner area of the bay), as a parsimonious hypothesis. For a test of this possibility, it would be necessary to examine the composition of potential food particles in the environment, which has not been done in this study and in many other *Acetes* and micronektonic shrimps trophic studies (e.g. Xiao and Greenwood 1992; Collins and Williner 2003; Chiou *et al.* 2005; Metillo 2011). However, until an accurate picture on the distribution of the two *Acetes* species in Panguil Bay becomes available, we can only surmise separation in the habitat niche dimension of both species. Especially because *A. erythraeus* is known to tolerate a much wider salinity range of 1.5–35 (Le Reste 1970; Omori 1975b) than *A. intermedius*, which has a narrower salinity tolerance of 15–33 (Chiou *et al.* 2003; Arshad *et al.* 2007), there is still the possibility that populations of the two species will mix and occupy overlapping habitats and possibly compete for food.

In conclusion, both *A. erythraeus* and *A. intermedius* are zooplanktivorous omnivores based on stomach content and carbon and nitrogen stable isotopes analysis. A clear separation in carbon sources was shown with *A. intermedius* depending more on macroalgae-based detritus food chain whereas *A. erythraeus* exploiting the mangrove-based detritus food chain. Ontogenetic difference on the carbon source was also shown with *A. intermedius* juveniles incorporating food from mangrove-detrital food chain, whereas *A. erythraeus* juveniles ingesting less depleted macroalgal-based detrital source. Diel and monthly differences in feeding intensity, preponderance to specific prey types, ontogenetic changes, and habitat

preferences may minimise competition between the two species, thus allowing the two species to coexist in Panguil Bay. Hence, stomach contents and stable isotopes analyses identified two coexisting *Acetes* species as an important component of the Panguil Bay food-web most likely as an intermediary between fish predators and seston, which comprises primarily zooplankton and mangrove and macroalgal detritus, but least on phytoplankton.

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References

- Abrantes, K., and Sheaves, M. (2009a). Food web structure in a near-pristine mangrove area of the Australian Wet Tropics. *Estuarine, Coastal and Shelf Science* **82**, 597–607. doi:10.1016/J.ECSS.2009.02.021
- Abrantes, K., and Sheaves, M. (2009b). Sources of nutrition supporting juvenile penaeid prawns in an Australian dry tropics estuary. *Marine and Freshwater Research* **60**, 949–959. doi:10.1071/MF08269
- Alfaro, A. C., Thomas, F., Sergent, L., and Duxbury, M. (2006). Identification of trophic interactions within an estuarine food web (northern New Zealand) using fatty acid biomarkers and stable isotopes. *Estuarine, Coastal and Shelf Science* **70**, 271–286. doi:10.1016/J.ECSS.2006.06.017
- Amani, A. A., Amin, S. M. N., and Arshad, A. (2011). Stomach contents of sergestid shrimp *Acetes japonicus* from the Estuary of Tanjung Dawai, Peninsular Malaysia. *Journal of Fisheries and Aquatic Science* **6**, 771–779. doi:10.3923/JFAS.2011.771.779
- Arshad, A., Amin, S. M. N., Siraj, S. S., and Japar, S. B. (2007). New distribution records of sergestid shrimp, *Acetes intermedius* (Decapoda: Sergestidae) from Peninsular Malaysia with notes on its population characteristics. *The Journal of Biological Sciences* **7**, 1305–1313. doi:10.3923/JBS.2007.1305.1313
- Bodin, N., Le Loc'h, F., and Hily, C. (2007). Effect of lipid removal on carbon and nitrogen stable isotope ratios in crustacean tissues. *Journal of Experimental Marine Biology and Ecology* **341**, 168–175. doi:10.1016/J.JEMBE.2006.09.008
- Boecklen, W. J., Yarnes, C. T., Cook, B. A., and James, A. C. (2011). On the use of stable isotopes in trophic ecology. *Annual Review of Ecology Evolution and Systematics* **42**, 411–440. doi:10.1146/ANNUREV-ECOLSYS-102209-144726
- Bouillon, S., Connolly, R. M., and Lee, S. Y. (2008). Organic matter exchange and cycling in mangrove ecosystems: Recent insights from stable isotope studies. *Journal of Sea Research* **59**, 44–58. doi:10.1016/J.SEARES.2007.05.001
- Bouillon, S., Connolly, R. M., and Gillikin, D. P. (2011). Use of stable isotopes to understand food webs and ecosystem functioning in estuaries. In 'Treatise on Estuarine and Coastal Science'. (Eds E. Wolanski and D. S. McLusky.) pp. 143–173. (Academic Press: Waltham, MA, USA)
- Canini, N. D., Metillo, E. B., and Azanza, R. V. (2013). Monsoon-influenced phytoplankton community structure in a Philippine mangrove estuary. *Tropical Ecology* **54**, 329–341.
- Chew, L. L., Chong, V. C., Tanaka, K., and Sasekumar, A. (2012). Phytoplankton fuel the energy flow from zooplankton to small nekton in turbid mangrove waters. *Marine Ecology Progress Series* **469**, 7–24. doi:10.3354/MEPS09997

- Chiou, W.-D., Wu, C.-Z., and Cheng, L.-Z. (2000). Spatio-temporal distribution of sergestid shrimp *Acetes intermedius* in the coastal waters of southwestern Taiwan. *Fisheries Science* **66**, 1014–1025. doi:10.1046/J.1444-2906.2000.00163.X
- 5 Chiou, W.-D., Cheng, L.-Z., and Chen, C.-T. (2003). Effects of lunar phase and habitat depth on vertical migration patterns of the sergestid shrimp *Acetes intermedius*. *Fisheries Science* **69**, 277–287. doi:10.1046/J.1444-2906.2003.00618.X
- Chiou, W.-D., Hwang, J.-J., Cheng, L.-Z., and Chen, C.-T. (2005). Food and feeding habit of Taiwan mauxia shrimp *Acetes intermedius* in the coastal waters of Southwestern Taiwan. *Fisheries Science* **71**, 361–366. doi:10.1111/J.1444-2906.2005.00988.X
- Collins, P. A., and Williner, V. (2003). Feeding of *Acetes paraguayensis* (Nobili) (Decapoda: Sergestidae) from the Parana River, Argentina. *Hydrobiologia* **493**, 1–6. doi:10.1023/A:1025474614248
- 15 Coman, F. E., Connolly, R. M., Bunn, S. E., and Preston, N. P. (2006). Food sources of the sergestid crustacean, *Acetes sibogae*, in shrimp ponds. *Aquaculture* **259**, 222–233. doi:10.1016/J.AQUACULTURE.2006.05.038
- 20 Deshmukh, V. D. (1993). Status of non-penaeid prawn fishery of India and stock assessment of *Acetes indicus* Milne Edwards off Maharashtra. *Indian Journal of Fisheries* **40**, 50–62.
- Duffy, J. E. (1996). Resource-associated population subdivision in a symbiotic coral-reef shrimp. *Evolution* **50**, 360–373. doi:10.2307/2410807
- 25 Elsdon, T. S. (2010). Unraveling diet and feeding histories of fish using fatty acids as natural tracers. *Journal of Experimental Marine Biology and Ecology* **386**, 61–68. doi:10.1016/J.JEMBE.2010.02.004
- Flock, M. E., and Hopkins, T. L. (1992). Species composition, vertical distribution, and food habits of the sergestid shrimp assemblage in the eastern Gulf of Mexico. *Journal of Crustacean Biology* **12**, 210–223. doi:10.2307/1549076
- 30 Han, W., Moore, A., Levin, J., Zhang, B., Arango, H. G., Curchitser, E., Lorenzo, E. D., Gordon, A. L., and Lin, J. (2009). Seasonal surface ocean circulation and dynamics in the Philippine Archipelago region during 2004–2008. *Dynamics of Atmospheres and Oceans* **47**, 114–137. doi:10.1016/J.DYNATMOCE.2008.10.007
- 35 Icely, J., and Nott, J. A. (1992). Digestion and absorption: digestive system and associated organs. In 'Microscopic Anatomy of Invertebrates, vol. 10, Decapod Crustacea'. (Eds F. W. Harrison and A. G. Humes.) pp. 147–201. (Wiley-Liss: London, UK.)
- Jacob, U., Mintenbeck, K., Brey, T., Knust, R., and Beyer, K. (2005). Stable isotope food web studies: a case for standardized sample treatment. *Marine Ecology Progress Series* **287**, 251–253. doi:10.3354/MEPS287251
- 45 Jimenez, C. R., Tumanda, M. I. Jr, and Laurden, A. J. (1996). Post-resource and ecological assessment monitoring and training project in Panguil Bay. Terminal Report. Mindanao State University-Naawan, Naawan, Philippines.
- 50 Le Reste, L. (1970). Biologie de *Acetes erythraeus* (Sergestidae) dans une baie du N.W. de Madagascar (Baie d'Ambaro). *Cahiers O.R.S.T.O.M. Office de la Recherche Scientifique et Technique Outre-Mer Oceanographique* **8**, 35–56.
- McCutchan, J., Lewis, W., Kendall, C., and McGrath, C. (2003). Variation in trophic shift for stable isotope ratios in carbon, nitrogen, and sulphur. *Oikos* **102**, 378–390. doi:10.1034/J.1600-0706.2003.12098.X
- 55 McLeay, L., and Alexander, C. G. (1998). The mechanisms of active capture of animal food by the sergestid shrimp *Acetes sibogae australis*. *Journal of the Marine Biological Association of the United Kingdom* **78**, 497–508. doi:10.1017/S0025315400041588
- 60 Metillo, E. B. (2011). Feeding ecology of *Acetes intermedius* Omori 1975 (Crustacea, Decapoda, Sergestidae) in Iligan Bay, the Philippines. *Zoological Studies* **50**, 725–736.
- Metillo, E. B., Ritz, D. A., and Swadling, K. (2007). *In situ* feeding rate and diet selectivity in Tasmanian mysid species (Crustacea, Mysidacea). *Hydrobiologia* **589**, 207–218. doi:10.1007/S10750-007-0732-4
- Metillo, E. B., Romarate, R. A., Bagaloyos, J. B., Canini, N. D., and Cadelinia, E. M. (2009). Population dynamics and feeding habits of two coexisting species of *Acetes* (*A. erythraeus* and *A. intermedius*) (Decapoda: Sergestidae) in Panguil Bay, northern Mindanao, Philippines. In 'Proceedings of the 4th Vietnam Academy of Science and Technology (VAST)–Japan Society for the Promotion of Science (JSPS) Workshop on Coastal Marine Science'. (Eds. T. D. Thanh, N. Miyazaki, T. Arai, K. Inoue, Y. Fukuyo, S. Kawaguchi, K. Matsuura, S. Nishida, Y. Shirayama, and T. Yanagi.) p. 112. (Vietnam Academy of Science and Technology: Hai Phong, Vietnam). [Abstract only].
- Michener, R. H., and Kaufman, L. (2007). Stable isotope ratios as tracers in marine aquatic food webs. In 'Stable Isotopes in Ecology and Environmental Science'. (Eds K. Lajtha and R. H. Michener.) pp. 238–282. (Blackwell: London, UK.)
- 15 Oh, S. Y., Arshad, A., Japar, S. B., Nor Azwady, A. A., and Amin, S. M. N. (2011). Diet composition of sergestid shrimp *Acetes serrulatus* from the coastal waters of Kukup, Johor, Malaysia. *Journal of Fisheries and Aquatic Sciences* **6**, 809–815. doi:10.3923/JFAS.2011.809.815
- 20 Omori, M. (1975a). The biology of pelagic shrimps in the ocean. *Advances in Marine Biology* **12**, 233–324. doi:10.1016/S0065-2881(08)60459-9
- Omori, M. (1975b). The systematics, biogeography, and fishery of epipelagic shrimps of the genus *Acetes* (Crustacea, Decapoda, Sergestidae). *Bulletin of the Ocean Research Institute of the University of Tokyo* **7**, 1–91.
- 25 Omori, M. (1978). Zooplankton fisheries of the world: a review. *Marine Biology* **48**, 199–205. doi:10.1007/BF00397145
- 30 Omundsen, S. L., Sheave, M. L., and Molony, B. W. (2000). Temporal population dynamics of the swarming shrimp, *Acetes sibogae australis*, in a tropical near-shore system. *Marine and Freshwater Research* **51**, 249–254. doi:10.1071/MF98138
- Phillips, D. L. (2001). Mixing models in analyses of diet using multiple stable isotopes: a critique. *Oecologia* **127**, 166–170. doi:10.1007/S004420000571
- 35 Phillips, D. L., and Gregg, J. W. (2003). Source partitioning using stable isotopes: coping with too many sources. *Oecologia* **136**, 261–269. doi:10.1007/S00442-003-1218-3
- Rivas, L. R. (1964). A reinterpretation of the concepts 'sympatric' and 'allopatric' with proposal of the additional terms 'syntopic' and 'allo-topic'. *Systematic Zoology* **13**, 42–43. doi:10.2307/2411436
- 40 Schoener, T. W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**, 408–418. doi:10.2307/1935376
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* **185**, 27–39. doi:10.1126/SCIENCE.185.4145.27
- 45 Smyntek, P. M., Teece, M. A., Schulz, K. L., and Thackeray, S. J. (2007). A standard protocol for stable isotope analysis of zooplankton in aquatic food web research using mass balance correction models. *Limnology and Oceanography* **52**, 2135–2146. doi:10.4319/LO.2007.52.5.2135
- 50 SPSS (2002). SPSS for Windows version 11. (SPSS Inc.: Chicago, IL.)
- Tanaka, K., Hanamura, Y., Chong, V. C., Watanabe, S., Man, A., Kassim, F. M., Kodama, M., and Ichikawa, T. (2011). Stable isotope analysis reveals ontogenetic migration and the importance of a large mangrove estuary as a feeding ground for juvenile John's snapper *Lutjanus johnii*. *Fisheries Science* **77**, 809–816. doi:10.1007/S12562-011-0396-X
- 55 Traugott, M., Kamenova, S., Ruess, L., Seeber, J., and Plantegenest, M. (2013). Empirically characterising trophic networks: what emerging DNA-based methods, stable isotope and fatty acid analyses can offer. In 'Advances in Ecological Research', Vol. 49. (Eds G. Woodward and D. A. Bohan.) pp. 177–224. (Elsevier Ltd.: London, UK.)
- 60 Villanoy, C. L., Cabrera, O. C., Yñiguez, A., Camoying, M., de Guzman, A., David, L. T., and Flament, P. (2011). Monsoon-driven coastal upwelling

off Zamboanga Peninsula, Philippines. *Oceanography* **24**, 156–165. doi:10.5670/OCEANO.2011.12

Wolanski, E., Brinson, M. M., Cahoon, D. R., and Perillo, G. M. E. (2009). Coastal wetlands: a synthesis. In 'Coastal Wetlands: An Integrated Ecosystem Approach'. (Eds G. M. E. Perillo, E. Wolanski, D. R. Cahoon, and M. M. Brinson.) pp. 1–62. (Elsevier B.V.: Amsterdam.)

Xiao, Y., and Greenwood, J. G. (1992). Distribution and behaviour of *Acetes sibogae* Hansen (Decapoda, Crustacea) in an estuary in relation to tidal and diel environmental changes. *Journal of Plankton Research* **14**, 393–407. doi:10.1093/PLANKT/14.3.393

Xiao, Y., and Greenwood, J. G. (1993). The biology of *Acetes* (Crustacea: Sergestidae). *Oceanography and Marine Biology – an Annual Review* **31**, 259–444.