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Feeding Ecology of *Acetes intermedius* Omori 1975 (Crustacea, Decapoda, Sergestidae) in Iligan Bay, the Philippines

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Ephrime B. Metillo (2011) Feeding ecology of *Acetes intermedius* Omori 1975 (Crustacea: Decapoda: Sergestidae) in Iligan Bay, the Philippines. *Zoological Studies* **50**(6): 725-736. A multivariate analysis of stomach contents was used to investigate the trophic ecology of nighttime-collected *Acetes intermedius* in 2 adjacent near-shore estuaries in Iligan Bay, northern Mindanao, the Philippines from Feb. 1999 to Jan. 2000. Thirteen diet categories were observed indicating that *A. intermedius* is an omnivorous zooplanktivore with copepods, ostracods, decapod crustacean larvae, gastropod and bivalve veligers, and amorphous materials as dominant food items. Juveniles, however, showed a predominance of amorphous and fine materials. A linear ordination redundancy analysis showed that peak abundances of different dietary items coincided with monthly rainfall and sea surface temperature. The most common prey item of copepod fragments dominated in Mar. to June, months with high rainfall and warmer seas. Other common prey items, ostracods, bivalve and gastropod veligers, decapod crustacean fragments, chaetognaths, and tintinnids were correlated with cooler months from July to Nov. Peaks of most common ingested prey items were associated with dominance of equivalent zooplankton categories. The present study demonstrates that this species occupies an environmentally cued omnivorous feeding niche between lower-trophic-level plankton, particularly mesozooplankton, and higher predators in the pelagic zone of Iligan Bay. http://zoolstud.sinica.edu.tw/Journals/50.6/725.pdf

Key words: *Acetes intermedius*, Trophic ecology, Multivariate analysis.

Recognized as having a major role in global carbon fixation (Piontkovski and Landry 2003, Champalbert et al. 2007), tropical zooplankton communities are known to be one of the most species-diverse and complex in the pelagic zone (Raymont 1983, McGowan and Walker 1985, Wiggert et al. 2005). They include certain micronektonic shrimps of the genus *Acetes* (Omori 1974 1975 1977, Xiao and Greenwood 1993, McLeay and Alexander 1998, Coman et al. 2006a b). These small highly gregarious sergestid shrimps are caught in the < 1-150 m depth range, exhibit spatial-temporal migration patterns, are extremely euryhaline (freshwater to full seawater), and are eurythermal based on their warm-temperate to tropical distribution (Xiao and Greenwood 1993, Omundsen et al. 2000). *Acetes* spp. may be considered the equivalent of “Antarctic krill” in their respective habitats because of their importance to many predators including several species of squid, 151 species of finfish (e.g., whale sharks and commercially important small pelagic species), prawns, young crocodiles, baleen whales, and many peoples of Asia (Omori 1974 1975 1977, Xiao and Greenwood 1993, Deshmukh 1993, McLeay and Alexander 1998). The average annual catch of *Acetes* from Indo-Asia during 1979 to 1989 exceeded 228,850 tons, which was primarily utilized by the bait, shrimp-paste, and feed-meal industries (Xiao and Greenwood 1993). Despite their known ecological and economic importance, a huge gap still remains in basic information from

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tropical waters where most *Acetes* species are found (Xiao and Greenwood 1993).

Acetes species predominantly feed at night and are generally considered selective omnivores upon phytoplankton and zooplankton (Xiao and Greenwood 1993). However, *A. intermedius* in the subtropical neritic waters of the South China Sea showed positive selection for diatoms in summer (Chiou et al. 2005). Likewise, Collins and Williner (2003) reported strong herbivory in *A. paraguayensis* from the Parana River, Argentina. Data from other biotopes and laboratory experiments show a strong preference of *A. sibogae* for zooplankton prey (Xiao and Greenwood 1993, McLeay and Alexander 1998, Coman et al. 2006a).

Stomach content analysis has become a common tool in trophic interaction studies involving marine organisms. Diet analysis provides a very detailed view of an individual's diet. Although effective identification and quantification of stomach contents are a challenge in crustacean macrozooplankton which tend to dismember prey during consumption, a thorough spatiotemporal diet investigation is still particularly useful in trophic analyses (Takahashi and Kawaguchi 1998, Chiou et al. 2005).

Except for information on *Acetes* fishery production (17,260 tons was registered in 1989), no information on the ecology of *Acetes* exists from the Philippines. In this study, the feeding habits of *A. intermedius* in nearshore waters of Iligan Bay were analyzed monthly for 1 yr using multivariate approaches. The specific objectives of the present study were: (i) to examine the variability of different prey items of *A. intermedius* from 2 sampling sites between Feb. 1999 and Jan. 2000, (ii) to assess the importance of selected environmental factors (zooplankton abundance, salinity, temperature, total suspended solids (TSS), rainfall, and tides) to diet variability, and (iii) to infer trophic interactions of *A. intermedius*.

MATERIALS AND METHODS

Collection of *A. intermedius*, mesozooplankton, and seawater

Sampling of *A. intermedius* and measurement of physicochemical conditions were conducted once a month from Feb. 1999 to Jan. 2000 in 2 southern coastal localities of Iligan Bay (Fig. 1). The bay is part of the poorly studied but important Sulu-Sulawesi large marine ecosystem (SSLME) (Sherman and Gold 1990). It is a trapezoidal-shaped bay facing the Mindanao Sea to the north and is contiguous with the smaller Panguil Bay to the southwest. Iligan Bay is located at 8°12'-8°40'N, 123°50'-124°16'E, with an area of 2300 km^2. The 1st sampling location (station 1) was located off Tambacan, Iligan City (8°12'50"N, 124°11'7"E), adjacent to the city port. About 20 km west of St. 1 and close to a reef flat, the 2nd site (St. 2) was located off Larapan, Kauswagan (8°11'58"N, 124°6'20"E). Both sampling sites are estuarine with a characteristic muddy-sand substratum and riverine input.

Sampling was conducted on moonless nights following results that abundances and feeding intensity of *Acetes* peak during this period (Omori 1974 1975 1977, Xiao and Greenwood 1992 1993, Chiou et al. 2003 2005). *A. intermedius* was collected at 22:00-02:00 at depths of 20-45 m using a conical net with a 1-mm mesh and 1-m mouth diameter, which was mounted on the outrigger of a motorized canoe. Three replicates of 15-min subsurface horizontal tows were made parallel to the shore at a speed of 0.4 m/s. Captured *A. intermedius* individuals were immediately fixed in 5% formalin in 0.45-μm Millipore-filtered seawater (Millipore, Billerica, MA, USA).

Immediately following *Acetes* sampling, triplicate samples of zooplankton were collected using a General Oceanics conical plankton net (Miami, FL, USA) with a 275-μm mesh size, 0.3-m mouth diameter, and a flow meter mounted at the center of the mouth. Samples were preserved in 5% formalin in filtered seawater, and the abundance (number/m^3) was estimated by counting a 1-ml Stempel pipette aliquot under a stereomicroscope. A Folsom plankton splitter (Hope, ID, USA) was used to split samples with very high densities. Zooplankton groups were identified using manuals by Newell and Newell (1963) and Yamaji (1982).

Subsurface water temperature, salinity, dissolved oxygen, and TSS were concurrently determined in triplicate respectively using a mercury thermometer, a refractometer, Winkler titration, and gravimetric methods. Rainfall data were obtained from a weather station 0.5 km from the sampling sites, while tidal height values were from tide gauges at each site.

Diet analysis

Prior to dissection, *Acetes* was identified to species using the key of Omori (1975), and from each monthly sample, 35 adults and, if present, 35 juveniles were sorted out, and the individual total body length was measured using Vernier calipers to an accuracy of 0.01 mm. The stomachs of shrimp were removed under a stereomicroscope, and then graded by the degree of fullness into the following categories: 1 (0%), 2 (1%-25%), 3 (26%-50%), 4 (51%-75%), and 5 (76%-100%). Gut contents of individual shrimp were examined under stereo- and compound microscopes, and all ingested prey items were counted and identified to the lowest taxon possible. Since micronektonic shrimps and most crustaceans macerate captured prey prior to ingestion, individual prey items in the stomachs of *A. intermedius* were enumerated by the weighted points method (Williams 1981, Takahashi and Kawaguchi 1998), using the following the equation:

Percentage weighted points for the *i*th prey =

$$\sum_{j=1}^{n} w_i a_{ij} \times 100 / \sum_{j=1}^{n} \sum_{j=1}^{s} w_j a_{ij}$$

where a_{ij} is number of points of prey item *i* in the foregut of the *j*th shrimp, w_j is the weighting with the value dependent on the class (1-5) of stomach fullness of the *j*th shrimp, *n* is the number of shrimp examined for the diet analysis, and *s* is the number of prey categories.

Analysis of diet overlap between juveniles and adults

Diet overlap between juveniles and adults at a given site was compared using the formula of Schoener (1970):

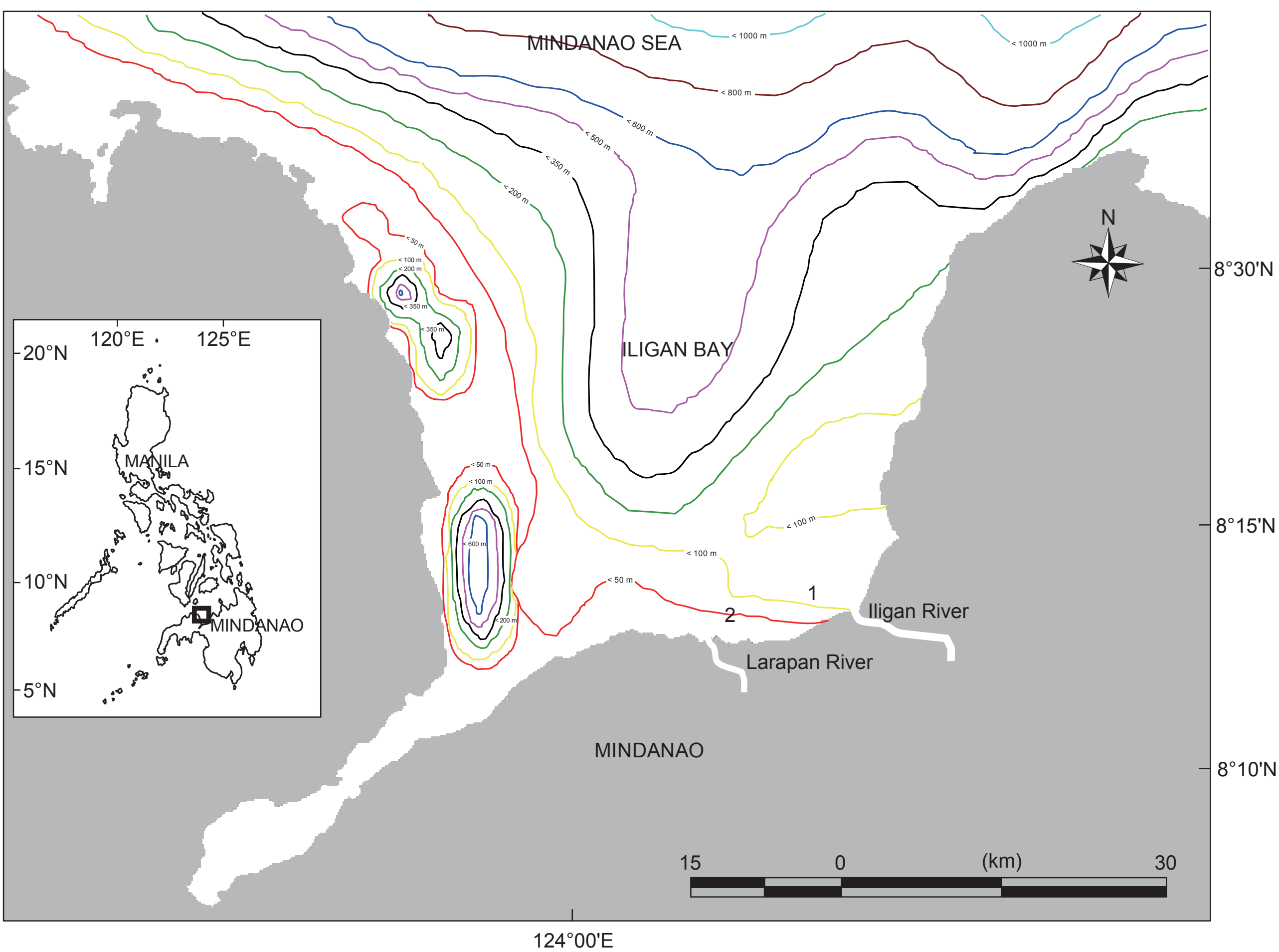

Fig. 1. Sampling localities for *Acetes intermedius* off Tambacan (station 1) and Larapan (St. 2) in Iligan Bay (enclosed in square), northern Mindanao, the Philippines.

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

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 (adults) and y (juveniles).

Statistical analysis

Statistical comparisons of environmental variables, zooplankton abundance, total length, gut fullness, and stomach contents between stations and among months were made by a non-parametric analysis of variance (ANOVA, using the Kruskall-Wallis *H*-test). Shannon's diversity and Pielou's evenness indices of zooplankton samples were computed using the software PRIMER vers. 5.2 (Clarke and Warwick 2001). Potential relationships of categories of stomach contents with environmental variables (physicochemical conditions and zooplankton abundances) were analyzed by a parametric multivariate detrended correspondence analysis (DCA) and linear ordination redundancy analysis (RDA) using the software CANOCO (Canonical Community Ordination) vers. 4.5 (ter Braak and Šmilauer 2002). Data of individual stomach contents were arcsine-transformed as recommended for percentage data (Zar 1996), while environmental variables were standardized. The statistical significance of relationships between diet composition and environmental variables, and the importance of individual environmental variable were evaluated using a Monte Carlo permutation available in the same CANOCO software.

RESULTS

Environmental variables

Values of salinity (H = 2.50, p > 0.11), temperature (H = 6.93, p > 0.05), TSS (H = 0.85, p > 0.36), tide (H = 1.08, p > 0.78), and rainfall (H = 1.04, p > 0.85) were similar between stations, but not among months for salinity (H = 17.51, p < 0.05), temperature (H = 14.69, p < 0.05), TSS (H = 26.25, p < 0.01), tide (H = 12.52, p < 0.001), or rainfall (H = 49.54, p < 0.001) (Table 1). Highest temperatures (28.8-29°C) were noted in Apr., May, and Oct. Low salinities (< 21 ppt) at both sites were recorded in Mar., and July to Sept. A La Niña event began in June 1998 and continued through Mar. and Apr. 1999, resulting in unusually high rainfall values in these normally dry months. Rainfall decreased from Aug. and had returned to normal levels by Dec. 1999. TSS values from both stations remained at > 0.05 g from Mar. to Oct. and were < 0.05 g in other months. High tidal heights were observed from Sept. to Nov., with average ones in Feb. and Apr. to July, and low ones in Dec., Jan., Mar., and Aug.

Only data on zooplankton categories that appeared in the stomachs of *A. intermedius* are presented (Table 2), as these were used in the multivariate analysis. Abundances for all categories were comparable between stations (H = 0.33-6.22, p > 0.20-0.62) and among months (H = 1.98-13.40, p > 0.45-0.99). The most abundant were copepods and decapod crustacean larvae with combined relative abundances of 76.3% at St. 1 and 83.4% at St. 2. The peaks in abundance (dominance) of these 2 categories coincided with low evenness and diversity values recorded from Feb. to July (Table 2).

Total length, individuals with stomach contents, and gut fullness

Adult total lengths between stations were similar (H = 0.46, p > 0.49), but varied among months (H = 200.04, p < 0.0001) with the smallest individuals observed in Apr. and the largest ones in Nov. (Table 3). Sizes of juveniles were similar between stations (H = 39.28, p > 0.48), but differed among months (H = 77.32, p < 0.0001), with the smallest and largest individuals recorded in Sept. and June, respectively. Of 35 individuals dissected per month, 17-35 of the adults and 23-35 of the juveniles had stomach contents (Table 3). Ranges of gut fullness of adult individuals were comparable between the 2 stations (H = 61.53, p > 0.06); similar observations were seen in juveniles (H = 49.50, p > 0.30) (Table 3). Gut fullness in both adults (H = 276.82, p < 0.001) and juveniles (H = 317.82, p < 0.0001) differed among months with highest values recorded in May for adults and in May and Aug. for juveniles.

Gut contents and temporal changes in the diet composition of adults and juveniles

In total, 13 food categories (see descriptions in Table 4) were identified from foregut contents. Monthly diet data for adults were pooled because these were similar between stations (H = 0.25,

$p > 0.60$). Copepods were the most common prey item contributing 19% (July) to 77% (Apr.) (Fig. 2A). Bivalve veligers ranged 0% (Jan.) to 30% (May). Gastropod veligers ranged 0.3% (Jan.) to a peak of 24% (Dec.). Ostracods ranged 1.1% (June) to 56% (Aug.). Brownish amorphous materials, probably of animal origin, were highest (26%) in Feb. Decapod crustacean larvae ranged 0%-7%, peaking in Jan., while chaetognath spines accounted for 0%-4.5% with a peak observed in Oct. Remains of pteropods and tintinnids peaked in Sept. with respective contributions of 1.1% and 8.2%. Very few diatoms were ingested (0.3% in Apr. and 0.4% in Sept.), and more dinoflagellates (0.8% in June) were ingested than diatoms. Echinoderm larvae were only observed in July (2.1%) and Aug. (0.7%).

Monthly diet data for juveniles were also pooled since these were similar between stations ($H = 0.78$, $p > 0.78$). Brownish-green amorphous material dominated (25% in May to 42% in Aug.) the diets of juveniles (Fig. 2B). Copepod fragments contributed 7%-39% and peaked in June. Bivalve and gastropod veligers respectively peaked in Oct. (17%) and July (4.3%). Ostracods (7.5%) and echinoderm larvae (1.7%) were only found in July, and chaetognaths (1.1%) were only seen in Oct. Decapod crustacean fragments and tintinids respectively peaked in Oct. (18%) and Aug. (16%). Small amounts of pteropod fragments were recorded only in June (0.1%) and July (0.2%). Dinoflagellates were most common in May (15%), while diatoms were mostly found in July (4.6%).

Diet niche overlap between adults and juveniles

Strong diet overlap was commonly observed with > 50% values obtained in May, June, July, and Oct. (Table 5). Overlap was weak (< 50%) in the months of Aug. and Sept. when relatively more

Table 1. Average (± standard deviation) physicochemical values over the entire sampling period from the 2 sampling stations, Iligan Bay, northern Mindanao, the Philippines. Multivariate analysis codes of physicochemical conditions are in brackets

Month	Salinity (ppt) [SAL]	Temperature (water, °C) [TEMP]	Total suspended solids (g dry weight/L) [TSS]	Tidal height (m) [TIDE]	Rainfall (mm) [RAIN]
Tambacan (station 1)					
Feb. 1999	24.75 ± 0.35	26.00 ± 0.00	0.03 ± 0.01	0.80 ± 0.0	546.00 ± 5.66
Mar.	17.00 ± 0.00	28.25 ± 0.35	0.20 ± 0.01	-0.05 ± 0.0	347.00 ± 0.71
Apr.	15.50 ± 0.71	28.00 ± 0.71	0.21 ± 0.00	0.95 ± 0.01	319.50 ± 0.71
May	17.50 ± 0.71	29.00 ± 0.00	0.24 ± 0.00	0.81 ± 0.01	343.00 ± 1.41
June	18.00 ± 0.00	27.90 ± 0.14	0.27 ± 0.04	0.74 ± 0.01	209.50 ± 0.71
July	10.25 ± 0.35	26.00 ± 0.00	0.19 ± 0.01	0.70 ± 0.0	203.00 ± 2.83
Aug.	20.50 ± 0.71	28.00 ± 0.00	0.23 ± 0.00	0.31 ± 0.01	116.00 ± 1.41
Sept.	11.00 ± 0.00	28.00 ± 0.00	0.22 ± 0.00	1.22 ± 0.01	93.80 ± 0.28
Oct.	11.50 ± 0.71	29.00 ± 0.00	0.20 ± 0.00	1.53 ± 0.02	244.35 ± 5.16
Nov.	21.50 ± 0.71	28.00 ± 0.00	0.11 ± 0.13	1.62 ± 0.01	548.05 ± 1.34
Dec. 1999	24.75 ± 0.35	27.75 ± 1.09	0.09 ± 0.09	0.42 ± 0.01	105.00 ± 9.90
Jan. 2000	28.00 ± 0.00	27.25 ± 0.35	0.15 ± 0.19	0.37 ± 0.01	116.15 ± 5.44
Larapan (station 2)					
Feb. 1999	20.50 ± 0.71	28.75 ± 0.35	0.03 ± 0.00	0.62 ± 0.01	534.00 ± 2.83
Mar.	11.25 ± 0.35	28.00 ± 0.00	0.19 ± 0.01	-0.02 ± 0.00	345.50 ± 2.12
Apr.	30.50 ± 0.71	28.80 ± 0.28	0.22 ± 0.02	0.93 ± 0.01	321.00 ± 1.41
May	29.00 ± 0.00	29.00 ± 0.00	0.21 ± 0.02	0.48 ± 0.01	341.50 ± 0.71
June	25.00 ± 0.00	28.50 ± 0.71	0.19 ± 0.01	0.74 ± 0.01	219.00 ± 1.41
July	25.25 ± 0.35	28.50 ± 0.71	0.23 ± 0.02	0.66 ± 0.00	212.50 ± 2.12
Aug.	20.50 ± 0.71	28.00 ± 0.00	0.21 ± 0.02	0.23 ± 0.00	136.00 ± 1.41
Sept.	23.00 ± 0.00	28.00 ± 0.00	0.21 ± 0.02	1.08 ± 0.00	90.70 ± 0.14
Oct.	27.00 ± 0.00	28.00 ± 0.00	0.25 ± 0.06	1.47 ± 0.04	235.85 ± 0.21
Nov.	29.50 ± 0.71	28.00 ± 0.00	0.11 ± 0.04	1.45 ± 0.16	518.05 ± 1.34
Dec. 1999	25.50 ± 0.71	26.75 ± 0.35	0.05 ± 0.05	0.78 ± 0.45	96.35 ± 0.21
Jan. 2000	28.50 ± 0.71	29.00 ± 0.00	0.11 ± 0.09	0.05 ± 0.39	115.15 ± 4.03

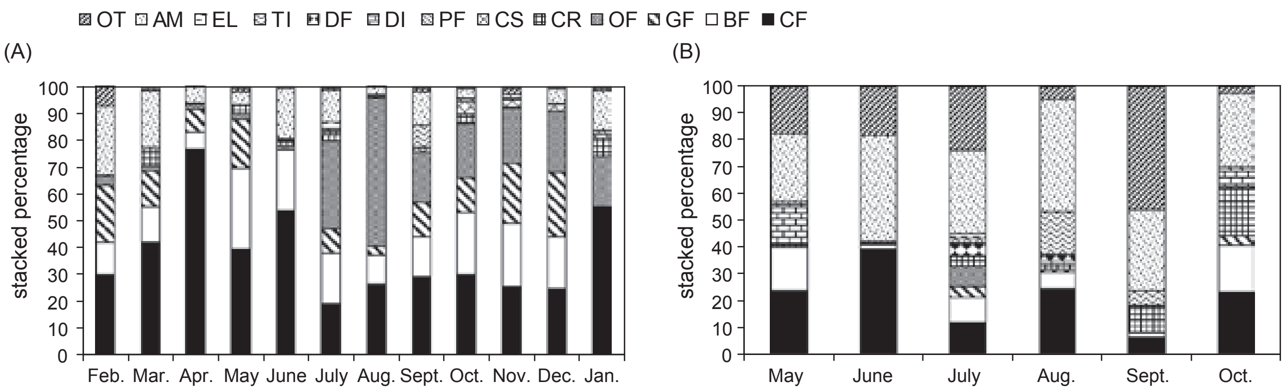

Fig. 2. Monthly mean percentage contributions by volume of the different stomach contents in adult (A) and juvenile (B) *Acetes intermedius*. (see Table 4 for codes and descriptions of stomach contents).

Table 2. Zooplankton average density ± standard deviation (individuals/m^3), relative percent abundance, Pielou's evenness (*J'*), and Shannon-Wiener (*H'*) diversity indices recorded in Iligan Bay from Feb. 1999 to Jan. 2000. Category codes in parenthesis are used in the multivariate redundancy analysis

Tambacan (Station 1)

	Copepods (COP)	Gastropod Veliger (GAV)	Bivalve Veliger (BIV)	Decapod Crustacea (DCR)	Chaetognaths (CHA)	Echinoderm Larvae (ECH)	Ostracods (OST)	Tintinnids (TIN)	*J'*	*H'*
Feb.	1280.0 ± 226.3	0.0 ± 0.0	320.0 ± 113.1	782.0 ± 169.7	66.7 ± 94.3	40.0 ± 56.6	13.3 ± 18.9	0.0 ± 0.0	0.73	2.08
Mar.	1885.0 ± 214.5	200.0 ± 282.8	150.0 ± 212.1	2273.7 ± 1840.8	223.3 ± 61.3	31.7 ± 2.4	33.3 ± 47.1	143.3 ± 33.3	0.64	2.00
Apr.	1466.7 ± 330.0	533.3 ± 47.1	250.0 ± 70.7	1423.3 ± 23.6	216.7 ± 70.7	40.0 ± 56.6	16.7 ± 23.6	283.3 ± 117.9	0.70	2.01
May	1016.7 ± 94.3	175.0 ± 35.4	33.3 ± 23.6	200.7 ± 23.6	58.3 ± 11.8	0.0 ± 0.0	25.0 ± 35.4	0.0 ± 0.0	0.77	1.92
June	866.7 ± 56.6	186.7 ± 37.7	0.0 ± 0.0	41.0 ± 15.0	0.0 ± 0.0	33.3 ± 9.4	33.3 ± 9.3	0.0 ± 0.0	0.72	1.83
July	1388.3 ± 181.5	116.7 ± 66.0	221.7 ± 115.5	567.0 ± 49.5	35.0 ± 49.5	11.7 ± 16.5	58.3 ± 16.5	0.0 ± 0.0	0.73	2.12
Aug.	903.3 ± 174.4	115.0 ± 21.2	173.3 ± 61.3	149.2 ± 189.7	55.0 ± 7.1	16.7 ± 23.6	33.3 ± 23.6	0.0 ± 0.0	0.74	2.13
Sept.	758.3 ± 148.5	128.3 ± 16.5	256.7 ± 165.0	484.3 ± 132.0	58.3 ± 16.5	46.7 ± 33.0	11.7 ± 16.5	140.0 ± 99.0	0.80	2.51
Oct.	941.7 ± 134.4	160.0 ± 226.3	230.0 ± 42.4	302.3 ± 173.0	165.0 ± 21.2	16.7 ± 23.6	26.7 ± 9.4	66.7 ± 94.3	0.79	2.45
Nov.	1467.2 ± 113.8	280.0 ± 56.6	293.3 ± 75.4	1060.7 ± 354.5	106.7 ± 37.7	40.0 ± 56.6	66.7 ± 18.9	40.0 ± 56.6	0.74	2.28
Dec.	1481.7 ± 346.5	268.3 ± 16.5	210.0 ± 33.3	894.7 ± 43.4	105.0 ± 16.5	23.3 ± 33.0	93.3 ± 33.0	0.0 ± 0.0	0.79	2.30
Jan.	858.3 ± 58.9	191.7 ± 82.5	0.0 ± 0.0	350.7 ± 23.6	66.7 ± 23.6	0.0 ± 0.0	16.7 ± 23.6	66.7 ± 47.1	0.77	2.20
Mean	1192.8	196.3	178.2	710.8	96.4	23.1	35.7	61.7		
%	47.8	7.9	7.1	28.5	3.9	0.9	1.4	2.5		

Larapan (Station 2)

	Copepods (COP)	Gastropod Veliger (GAV)	Bivalve Veliger (BIV)	Decapod Crustacea (DCR)	Chaetognaths (CHA)	Echinoderm Larvae (ECH)	Ostracods (OST)	Tintinnids (TIN)	*J'*	*H'*
Feb.	1341.7 ± 148.5	280.0 ± 66.0	23.3 ± 33.0	181.3 ± 49.5	128.3 ± 16.5	0.0 ± 0.0	81.7 ± 16.5	0.0 ± 0.0	0.76	2.10
Mar.	787.5 ± 277.0	33.3 ± 37.1	41.7 ± 58.9	105.0 ± 78.3	41.7 ± 35.4	4.2 ± 5.9	16.7 ± 23.6	4.2 ± 5.9	0.69	2.04
Apr.	487.5 ± 135.5	112.5 ± 17.7	54.2 ± 41.2	57.2 ± 5.9	0.0 ± 0.0	0.0 ± 0.0	41.7 ± 1.6	0.0 ± 0.0	0.71	1.82
May	2073.3 ± 1348.2	286.7 ± 9.4	0.0 ± 0.0	614.0 ± 656.2	170.0 ± 70.7	18.3 ± 25.9	50.0 ± 70.7	0.0 ± 0.0	0.68	2.01
June	2006.7 ± 377.1	165.0 ± 233.3	36.7 ± 51.9	1426.3 ± 325.7	241.7 ± 82.5	0.0 ± 0.0	111.7 ± 54.2	0.0 ± 0.0	0.75	2.13
July	806.7 ± 122.6	113.3 ± 84.9	60.0 ± 84.9	1784.7 ± 47.1	53.3 ± 18.9	0.0 ± 0.0	33.3 ± 9.4	0.0 ± 0.0	0.63	1.61
Aug.	1603.3 ± 617.5	225.0 ± 21.2	0.0 ± 0.0	973.2 ± 266.1	145.0 ± 7.1	30.0 ± 42.4	38.3 ± 11.8	0.0 ± 0.0	0.76	2.06
Sept.	2043.3 ± 853.2	120.0 ± 28.3	113.3 ± 103.7	675.0 ± 219.2	76.7 ± 23.6	0.0 ± 0.0	111.7 ± 73.1	0.0 ± 0.0	0.79	2.11
Oct.	877.8 ± 557.4	115.6 ± 45.4	105.6 ± 82.2	291.9 ± 128.2	128.9 ± 34.2	5.6 ± 9.6	10.0 ± 17.3	63.3 ± 55.1	0.73	2.33
Nov.	1733.3 ± 254.5	133.3 ± 70.6	106.7 ± 46.2	210.7 ± 101.8	71.1 ± 61.6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.68	1.84
Dec.	1140.0 ± 396.0	120.0 ± 56.6	140.0 ± 56.6	215.0 ± 104.7	150.0 ± 127.3	0.0 ± 0.0	20.0 ± 1.1	30.0 ± 14.1	0.76	2.62
Jan.	1038.3 ± 305.4	146.7 ± 167.7	82.2 ± 73.1	409.9 ± 270.9	42.8 ± 24.3	22.2 ± 20.4	33.3 ± 41.6	23.9 ± 22.6	0.74	2.32
Mean	1345.0	154.3	63.6	578.7	104.1	6.7	45.7	10.1		
%	58.3	6.7	2.8	25.1	4.5	0.3	2.0	0.4		

Table 3. Average total length ± standard deviation (S.D.; mm), number of individuals with stomach contents (*N*), and average percent gut fullness (%GF ± S.D.) of adult (from Feb. 1999 to Jan. 2000) and juvenile (from May to Oct. 1999) *Acetes intermedius*

	Tambacan (station 1)			Larapan (station 2)		
	Total length	*N*	%GF	Total length	*N*	%GF
Adults						
Feb. 1999	21.59 ± 2.52	24	27.08 ± 17.81	21.34 ± 2.93	32	32.19 ± 20.44
Mar.	21.11 ± 3.48	35	70.29 ± 25.95	20.74 ± 3.43	35	64.55 ± 17.69
Apr.	15.02 ± 1.27	30	92.33 ± 15.91	15.47 ± 4.95	35	74.29 ± 25.47
May	20.11 ± 4.30	33	63.33 ± 21.75	20.79 ± 2.70	35	64.14 ± 27.72
June	19.38 ± 1.99	31	51.29 ± 26.80	21.55 ± 4.72	30	43.83 ± 28.76
July	17.97 ± 2.37	34	70.00 ± 27.08	18.60 ± 3.15	35	69.43 ± 20.43
Aug.	20.48 ± 2.16	35	56.57 ± 20.71	23.58 ± 2.40	17	44.12 ± 25.51
Sept.	21.34 ± 2.60	33	62.42 ± 22.08	19.56 ± 3.61	26	68.85 ± 25.51
Oct.	18.58 ± 1.85	30	65.33 ± 30.60	17.34 ± 2.11	30	48.33 ± 21.67
Nov.	21.22 ± 2.69	26	45.00 ± 30.23	22.23 ± 1.40	34	69.12 ± 21.93
Dec. 1999	21.76 ± 1.68	27	37.96 ± 25.58	21.20 ± 1.77	17	38.24 ± 22.70
Jan. 2000	20.88 ± 2.27	33	56.06 ± 25.36	19.01 ± 1.76	34	62.94 ± 27.91
Juveniles						
May 1999	9.50 ± 1.37	35	58.57 ± 24.96	9.78 ± 1.35	35	75.00 ± 19.17
June	8.30 ± 1.22	35	60.00 ± 23.64	9.90 ± 1.74	28	41.96 ± 19.31
July	9.27 ± 1.72	29	58.62 ± 25.25	8.40 ± 1.20	31	54.03 ± 20.51
Aug.	7.94 ± 0.98	34	66.18 ± 20.30	8.24 ± 1.06	28	50.00 ± 22.70
Sept.	7.33 ± 0.85	23	51.09 ± 20.61	7.94 ± 1.30	32	56.25 ± 19.05
Oct. 1999	9.42 ± 1.25	30	67.00 ± 29.38	8.33 ± 1.85	27	49.81 ± 22.47

Table 4. Summary of food categories found in the foreguts of *A. intermedius* from Iligan Bay, the Philippines

Bacillariophycea (DF)	Fragments of diatoms, primarily *Coscinodiscus* spp.
Protoctista	
Tintinida (TI)	Entire cells and thecae of *Favella* spp. and *Tintinnopsis* spp.
Dinoflagellida (DI)	Entire cells and thecae of *Peridinium* spp. and *Dinophysis* spp.
Crustacea	
Copepoda (CF)	Entire individuals, but predominantly fragments of calanoid copepods including antennules, pleopods, mouthparts, and prosome; occasional entire individuals and fragments of harpacticoid and cyclopoid copepods
Ostracoda (OF)	Carapace, appendages, and other fragments of ostracods
Crustacean remains (CR)	Spines and appendages of other crustaceans, mainly decapod crustaceans
Mollusca	
Gastropoda (GF)	Intact and crushed individuals and fragments of gastropod veligers including spires, operculum, and soft mantle tissue
Lamellibranchia (BF)	Intact and crushed individuals and fragments of bivalve veligers including the umbo, shells, and mantle tissues
Pteropoda (PF)	Fragments of pteropod bodies and shells
Chaetognatha (CS)	Fragments of body tissues and oral spines
Echinodermata (EL)	Entire bipinnaria and auricularia larvae
Amorphous materials (AM)	Brownish or greenish mushy materials
Others (OT)	Small animals comprising foramineferans (*Globigerina* spp.), sponge spicules, and macrophyte fragments that were mixed with silt or fine particles

Table 5. Temporal change in the percent (%) niche overlap between adult and juvenile individuals of *A. intermedius* from the 2 sampling sites from May to Oct. 1999

Developmental stage	May	June	July	Aug.	Sept.	Oct.
Adult vs. juvenile	53	60	60	39	24	62

amorphous materials, plant cells, and fine particles were ingested by juveniles than adults.

Ordination analysis of environmental variables and diet composition of adults

The multivariate DCA of monthly diet composition data revealed a short gradient of 1.22 along the 1st axis, suggesting the use of the linear ordination RDA. The percent variances of diet data explained by axes 1 and 2 were 31.4% and 24.8%, respectively. Monte Carlo test results showed a non-significant (F = 1.981, p > 0.05) relation between stomach prey items and the entire set of environmental variables for the 1st canonical axis, but showed significance for all canonical axes (F = 1.542, p < 0.04), suggesting that more than 1 dominant gradient was driving relations between prey items and physicochemical variables. Forward-selection ranking of these variables showed that rainfall (F = 2.35, p < 0.02) and water temperature (F = 2.10, p < 0.04) significantly contributed to variability in prey. Relationships among diet, sampling months, and environmental variables (Fig. 3A) indicated that the most common prey item, copepod fragments, became the most abundant diet category in Mar., Apr., and May, months in which high rainfall and higher sea temperatures were recorded, while the other stomach items occurred in months of low rainfall (June to Feb.). For instance, ostracods became abundant prey items in the months of July, Dec., and Feb.; gastropod and bivalve veligers in Oct. and Feb.; decapod crustaceans and chaetognath fragments in June, Aug., and Jan.; and tintinnids in Sept. and Dec. Notably, amorphous material coincided with high TSS and low salinity which were linked to high rainfall.

Monte Carlo permutations of the diet data and zooplankton abundances failed to show significant correlations in either the 1st or all canonical axes (p > 0.28), indicating a weak concordance of the 2 datasets. However, percent variations explained by axes 1 and 2 were high at 33.3% and 26.8%, respectively. These values indicate that the 1st 2 canonical axes accounted for 60% which would allow us to infer possible associations of diet and prey by looking at tri-plots of the 1st 2 axes (Fig. 3B). For instance, peak variances of both copepod dietary items and copepods were grouped together in the warmer sampling months of Mar. to May. Also, food items of ostracod fragments and potential ostracod prey were grouped in the months of July, Sept., and Oct., while bivalve veligers and plankton in the stomachs were grouped in Aug., Nov., and Dec.

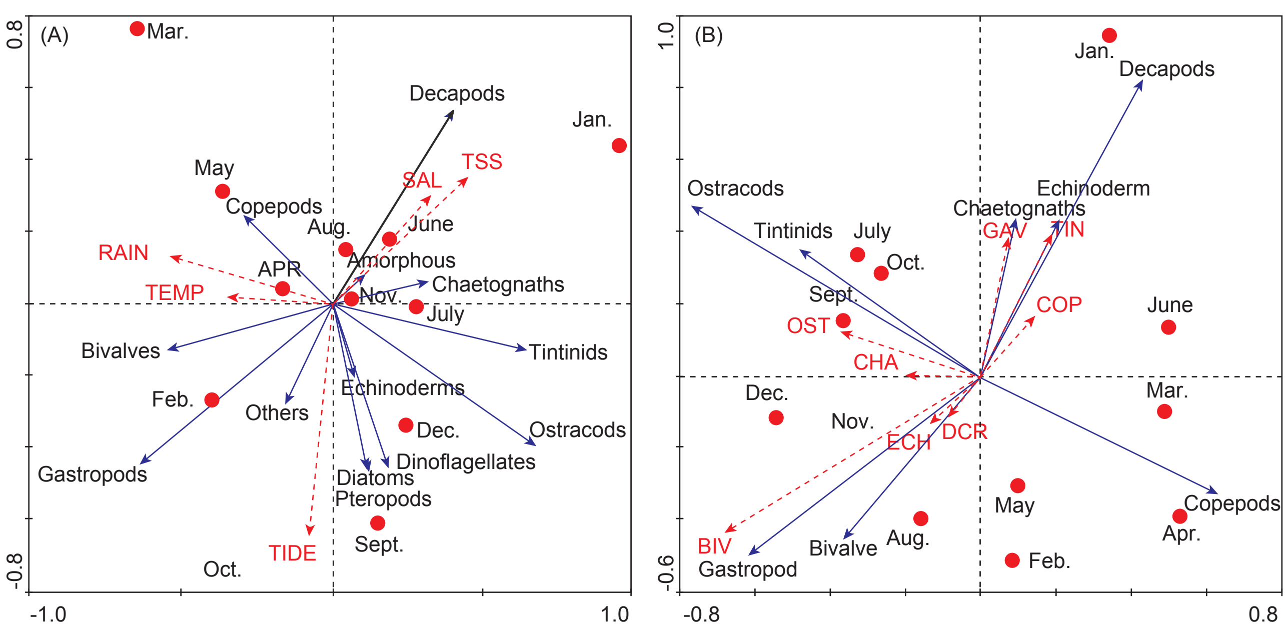

Fig. 3. Redundancy analysis tri-plots of monthly (dots) temporal variations in stomach contents (indicated by solid arrows) of adult *Acetes intermedius* and environmental variables (physicochemical conditions (A) and zooplankton abundances (B)) (indicated by broken arrows). Refer to table 1 for codes of physicochemical conditions and to table 2 for zooplankton category codes. Descriptions of stomach content categories are in table 4.

Ordination analysis of environmental conditions and diet composition of juveniles

A short gradient length of 1.18 was generated by the DCA; this justified the use of the RDA. Monte Carlo permutations showed no significant relationships between diet and abiotic conditions (p > 0.05 for all axes), suggesting difficulty in inferring a possible explanatory environmental variable for the diet of juvenile *Acetes*. However, percent variances of diet data explained by the 1st 2 axes were 54.5% and 24.4%, respectively, which explained > 75% of temporal variations in the diet. The 1st horizontal axis of the RDA tri-plot indicated that copepods and dinoflagellates were associated with the warmer months of May and June, and gastropod and bivalve veligers with the month of Oct. (Fig. 4A). Amorphous material was associated with the high-rainfall month of Oct. Ostracods, pteropods, tintinids, diatoms, and decapod crustacean fragments had strong affinities with the rainy months of July, Aug., and Sept.

Monte Carlo tests failed to find significant relationships between zooplankton abundances and the diet composition in juveniles (p > 0.89), but the percent variances of the data explained by the 1st 2 canonical axes were high, at 53.3% and 31.2%, respectively. The 1st 2 axes explained > 84%, indicating that these axes may help infer associations between dietary items and zooplankton abundances. The tri-plot showed strong associations between stomach contents and zooplankton categories including copepods and chaetognaths in the months of May and June, ostracods in Aug., and decapod crustaceans and tintinnids in Sept. (Fig. 4B). Brownish-green amorphous materials coincided with the presence of dinoflagellates.

DISCUSSION

Diet composition and variability

Over the course of 12 mo, the present study observed 13 prey categories in the diet of *A. intermedius*, indicating the trophic plasticity of this ecologically important species. For the first time, small quantities of dinoflagellates (*Peridinium* spp. and *Dinophysis* spp.) and tintinnids (*Favella* spp. and *Tintinnopsis* spp.) were observed in the diet of *Acetes*. According to Xiao and Greenwood (1993), *Acetes* ingests 11 food categories, namely diatoms, protozoans, chaetognaths, copepods, branchiopodan crustaceans, molluscan larvae, small fish scales, amorphous material, debris, sand

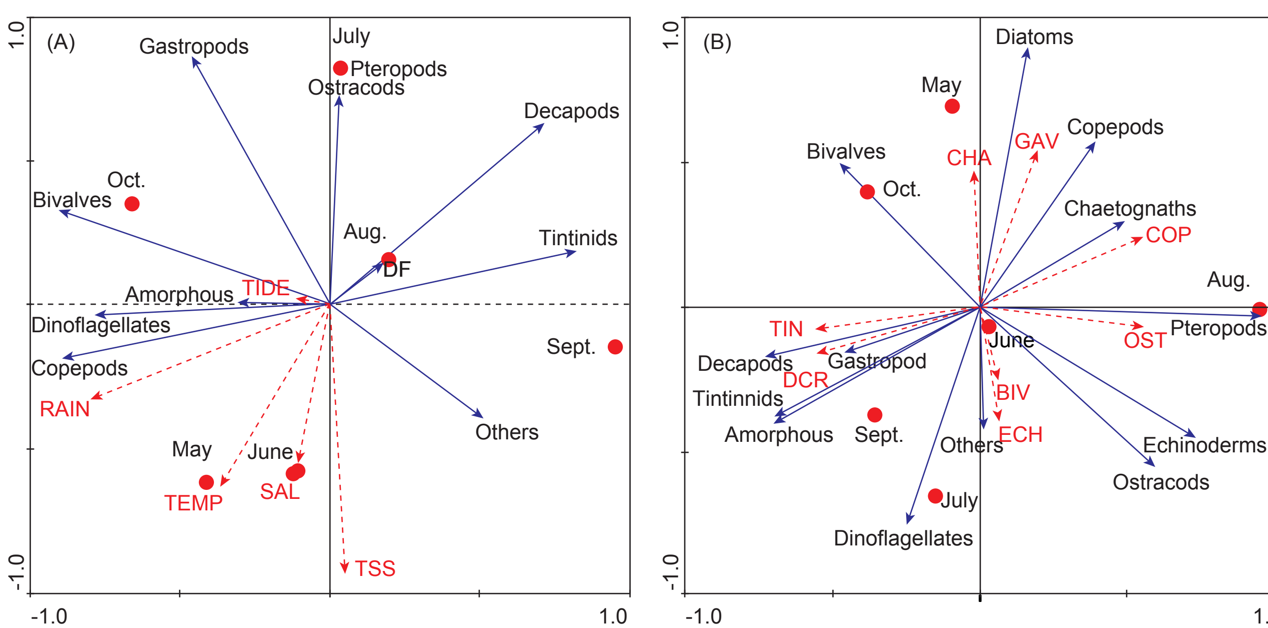

Fig. 4. Redundancy analysis tri-plots of monthly (dots) temporal variations in stomach contents (indicated by solid arrows) of juvenile *Acetes intermedius* and environmental variables (physicochemical conditions (A) and zooplankton abundances (B)) (indicated by broken arrows). Refer to table 1 for codes of physicochemical conditions, and to table 2 for zooplankton category codes. Descriptions of stomach content categories are in table 4.

grains, foraminiferans, and mud. Omnivory seems to be common in *Acetes*, but species- or habitat-specific feeding selectivity is widely observed. For instance, seasonal omnivorous feeding on phytoplankton was inferred for the subtropical *A. chinensis* (Xiao and Greenwood 1993). It is interesting to note that *A. intermedius* from neritic waters off Tungkang, southwestern Taiwan was shown to mainly feed on phytoplankton (Chiou et al. 2005). In the present study, the fact that more phytoplankton cells were found in juveniles than in adults and that greenish-brown amorphous material was common and abundant in the stomachs suggest the ingestion of more plant than animal materials among juveniles. However, this study demonstrates that *A. intermedius* collected at nighttime in Iligan Bay is a selective omnivore, with adults showing a strong preference for animal prey as noted in *A. erythraeus*, *A. indicus*, *A. japonicus*, *A. sibogae australis* (Le Reste 1970, Xiao and Greenwood 1993, McLeay and Alexander 1998, Coman et al. 2006a), and other sergestid species (Flock and Hopkins 1992). Such a strong preference for animal prey may be associated with the presence of elaborate antennal sensilla in *Acetes* which allows them to feed intensively at night (Ball and Cowan 1977) and even possibly track amino acids from animal prey in highly turbid coastal waters (Hamner and Hamner 1977). This study further demonstrated that locality-specific and opportunistic feeding proclivities are typical of *A. intermedius*, which could be responsible for its relatively wide biogeographic distribution (Omori 1975, Xiao and Greenwood 1993, Chiou et al. 2000).

Crustacean mandibles usually macerate prey items, rendering their identification very difficult or cause an underestimation of the importance of large prey items and an overestimation of smaller ones (Williams 1981, Flock and Hopkins 1992, McLeay and Alexander 1998). In the present study; however, the high frequency of full stomachs with diverse identifiable prey items may have reduced the inherent bias of the stomach content analysis. Furthermore, by using a combination of methods (Williams 1981, Takahashi and Kawaguchi 1998) to estimate the relative contributions of dietary items, the present study mitigated the problem of overestimating the importance of a small quantity of 1 form that appears in many stomachs compared to other items with large amounts, but observed in fewer stomachs. The possibilities that some individuals regurgitated food upon being captured in the net, and non-feeding due to molting and even senescence cannot be ruled out.

Influence of environmental conditions on the diet

A multivariate analysis indicated seasonal peaks in abundances of certain dietary items, highlighting the importance of wet (monsoon) and dry months. Monte Carlo simulations significantly identified high rainfall and warmer water temperature as the strongest explanatory variables. Rainfall was reported to be a cue for large swarms of pre-spawning *A. intermedius* off southwestern Taiwan during monsoon months of May to Oct. (Chiou et al. 2003). Acting independently or simultaneously, rainfall, water temperature, and perhaps other environmental conditions probably strongly influence the availability of prey of *A. intermedius* as also reported by Chiou et al. (2000). In neritic tropical waters, higher zooplankton biomass levels are commonly observed during months with low salinity, heavy monsoonal rains, high tides, and strong wind-driven onshore currents (Brinton 1979 as cited by Schalk 1987, Dalal and Goswami 2001, Krume and Liang 2004, Champalbert et al. 2007). Heavy rainfall produces runoff that elevates levels of estuarine dissolved phosphates and nitrates, which promote localized algal blooms and in turn allow increased zooplankton production (Schalk 1987, Madhu et al. 2007). High tides and the predominant shoreward current from July to Oct. in Iligan Bay may also restrict a narrow band of inshore water resulting in an aggregation of zooplankton (Metillo and Dapanas 2007); *A. intermedius* may exploit this aggregated and abundant supply of animal prey.

Although Monte Carlo simulations failed to show a significant relationship, dietary abundances varied with patterns of relative abundances of different zooplankton categories, as seen in the > 60% of variation explained by the 1st and 2 canonical axes. This indicated that temporal peaks of certain prey items are tightly coupled with seasonal abundance patterns of potential prey as exemplified by the matching of variability peaks among the major dietary items of *A. intermedius* (copepod fragments, crustacean fragments, gastropod and bivalve veligers, and ostracods) and the dominance of the same zooplankton categories. It is likely that the optimal foraging strategy of *A. intermedius* is to feed on the most frequently encountered and nutritious prey. Despite emphasizing the importance of zooplankton prey in the diet, Coman et al. (2006a b) did not find a correlation between zooplankton abundance and stomach contents of *A. siboga australis* in prawn ponds.

There were similarity and overlap in the diet compositions between adults and juveniles, but a higher percentage of small-sized food categories in the stomachs of juveniles indicate diet differences due most probably to size and size-selective feeding behaviors as seen among different life history stages of micronektonic mysids and euphausiids (Mauchline 1980, Metillo and Ritz 1993). Lower values of the index of niche overlap in certain months further support differences in ingested prey sizes.

Coman et al. (2006a) examined *A. sibogae* from artificial shrimp ponds and suggested that there might be a greater dependence on macroalgae by *A. sibogae* within those systems, and that zooplankton are not the only food source. Although many prey items cannot be ruled out, attached macroalgae appears highly unlikely to contribute to the diet of *A. intermedius* in our study area. One aspect of this may be a greater ability of adults to exhibit a diel vertical migration which allows the animals to better take advantage of epipelagic food sources. It is very likely that *A. intermedius* is omnivorous, with adult stages feeding mainly on crustacean zooplankton and younger stages possibly utilizing other prey lower in the food web.

The diet composition of *A. intermedius* showed temporal fluctuations that appear to conform to monsoonal climate patterns in the region. This study demonstrates the omnivorous trophic niche of this species, with adult stages being primarily zooplanktivorous, that is closely aligned with abundances of available prey. As an intermediate zooplanktivore, *A. intermedius* forms an important link between its fish predators and zooplankton, and may potentially compete for similar prey with other micronekton, e.g., fish larvae and post-larval penaeid shrimps that also intensely feed on plankton. This species is believed to occupy an important niche in the structuring of pelagic communities in Iligan Bay.

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