Temporal Patterns in the Abundance and Diet of *Acetes erythraeus* Nobili 1905 (Crustacea, Decapoda, Sergestidae) in the Nearshore Waters of Iligan Bay, Northern Mindanao, Philippines

Ephrime B. Metillo
Department of Biological Sciences
Mindanao State University - Iligan Institute of Technology
Andres Bonifacio Ave., Iligan City, Philippines 9200
Tel/Fax: (063) 221-4056; (063) 221-4068
E-mail: ovcre-ebm@sulat.msuiit.edu.ph

ABSTRACT

Two adjacent nearshore estuaries in Iligan Bay (8°N, 124°E), Northern Mindanao were sampled to investigate annual temporal patterns in the abundance and stomach contents of *Acetes erythraeus*, and selected hydrometeorological factors. Principal Components Analysis (PCA) reveals temporal variations in *A. erythraeus* abundance and diet composition that appear to conform not only to the typical northeast and southwest monsoons, but also to three-month seasons (March-April-May [dry hot], June-July-August [wet hot], September-October-November [wet cold], December-January-February [dry cold]). Rainfall and tide largely explain variations of abundance and stomach contents. Peaks in *A. erythraeus* abundance are similar to those found in other tropical *Acetes* species whose bimodal temporal distribution patterns coincide with the start of the southwest monsoon and the end of the northeast monsoon. *A. erythraeus* is a zooplanktivorous omnivore with copepods, ostracods, other crustaceans, and molluscan veligers as the predominant food. A total of twelve (12) diet categories were recorded, including, for the first time, dinoflagellates and tintinnids. A comparison of stomach contents of shrimps, caught before and after midnight, showed higher ingestion after midnight. Diet composition of juvenile and adult shrimps, generally, is independent of sex and sampling location. Although there is overlap in the diet between adults and juveniles, the latter ingest more small-sized food categories.

Key words: *Acetes erythraeus*, abundance, diet analysis, temporal patterns

INTRODUCTION

Hutchinson (1953) defined pattern in ecological communities as the structure that results from the distributions of organisms in, or from, their interactions with their physical and biological environments. Understanding the processes that generate these patterns is very important in ecology, and is the key to the development of principles for management (Levin, 1992). The quest for pattern in tropical community ecology is as disputed as in temperate and sub-tropical ecological realms (Krebs, 1985; Deshmukh, 1986; Pulman, 1994). There is disagreement on whether or not species components of a community do reveal any pattern at all. Nevertheless, communities do show properties, such as species richness and diversity, food web and food chains, and stability and resilience, and that these change with time and space (Steele, 1974). For instance, the maintenance of the structure and function in marine pelagic communities is often viewed within the context of biological (predation and competition) and/or physical control (McGowan & Walker, 1985; Longhurst, 1985).

The role of physical or biological factors on the spatio-temporal dynamics of tropical plankton remains less understood. Although the effect of monsoons has been identified as a strong predictor of these dynamics (Edra, 1975; Longhurst & Pauly, 1987; Schalk, 1987), much still have to be studied particularly on the role of a micronekton that directly feeds upon phytoplankton and zooplankton. For example, the micronektonic sergestid shrimps of the genus *Acetes* are quite common in many coastal areas of the tropics and sub-tropics, and they are known to be selective omnivores upon phytoplankton and zooplankton (Xiao & Greenwood, 1993; McLeay & Alexander, 1998).

Acetes is caught from 0.5 cm to 150 m depth range, depending on geographic location. Adult size ranges from 1.5 to 2.5 cm long. Almost all species are naturally gregarious and exhibit spatio-temporal migration patterns. *Acetes* is an extremely euryhaline micronekton which could tolerate freshwater to full strength seawater. It is eurythermal, based on its warm-temperate to tropical distribution. Periodicity in feeding is evident in their intensive feeding at night. In the sub-tropical neritic waters of the South China Sea, *Acetes* shows positive selection for certain species of diatoms during summer. However, data from other biotopes and from laboratory experiments proved strong preference for animal-based food, mainly zooplankton. *Acetes* is somehow the Antarctic krill in their habitats because of its importance to many predators, such as squids, 151 species of fish (including whale shark), prawns, young crocodiles, and the many peoples of Asia (Xiao & Greenwood, 1993; Omori 1974, 1975, 1977). During certain times of the year, they become extremely abundant. The average annual catch of *Acetes* from Indo-Asia during the period 1979 to 1989 exceeded 228,850 tons, 25% of the world's annual total shrimp catch. In the Philippines, an *Acetes* fishery production of 17,260 tons was registered in 1989.

Artisanal fishers catch *Acetes* spp. from Iligan Bay for bait and shrimp paste industry. *Acetes'* potential in the aquaculture industry (as fish food) remains to be explored. Xiao & Greenwood (1993) emphasize a huge information gap in the tropical waters where most *Acetes* species are found. Except for very little data on its fishery, no published data on the ecology of *Acetes* in the Philippine waters is available.

The abundance and feeding patterns of the tropical micronektonic sergestid shrimp *Acetes erythraeus* were investigated in an attempt to relate these patterns with temporal changes of selected physical and chemical factors in Iligan Bay. The abundance of *A. erythraeus* in two sampling sites for one year, and the relative importance of the different prey items in the diet of *A. erythraeus* from the two study sites between February 1999 to January 2000 were estimated.

Hydrometeorological factors (salinity, temperature, total suspended solids, rainfall, and tide) in the nearshore waters of Iligan Bay were studied in order to explain temporal changes in the abundance and the stomach contents of *A. erythraeus*.

MATERIALS AND METHODS

Sampling of *A. erythraeus* and seawater

Monthly sampling of *A. erythraeus* and various physical and chemical parameters was made monthly from October 1998 to January 2000 in two coastal sites (Fig.1) of Iligan Bay. One of the sampling sites is located off Tambacan, Iligan City (8° 12' 50" N; 124° 11' 7" E), adjacent to the Iligan City port. Close to a reef flat, the second sampling site is off Larapan, Kauswagan (8° 11' 58" N; 124° 6' 20"E), and is located at about 20 km from the other site. Both sampling sites are estuarine, with characteristic muddy-sand substratum and freshwater (riverine) input. Fifteen-minute sub-surface collection of *A. erythraeus* was done once a month from 2000H to 0400H at depths of 20 to 45 m using a General Oceanics (GO) conical plankton net with 275 μm mesh and 0.3 m mouth diameter. Sampling was done at nighttime, following results that zooplankton and micronektonic shrimps normally peak at night (Mauchline, 1980; Longhurst & Pauly, 1987; Flock & Hopkins, 1992; Takahashi & Kawaguchi, 1998). From February 1999 to January 2000, a different conical net with a bigger mesh (1000 μm) and 1 m mouth diameter was used to prevent *A. erythraeus* net feeding. Preliminary diet analysis of shrimps caught using the

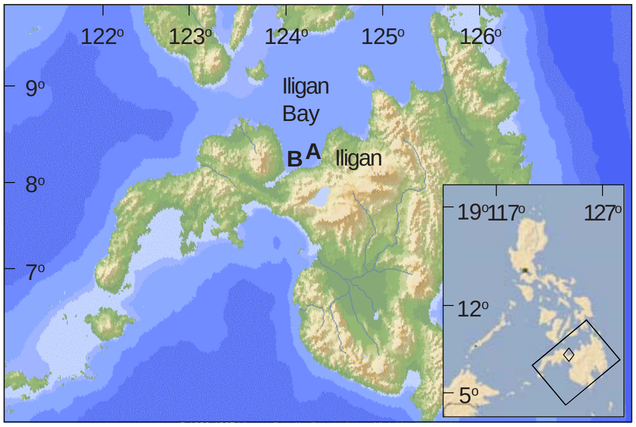

Fig. 1. Map of Iligan Bay showing sampling sites A (Tambacan) and B (Larapan). Inset is the map of the Republic of the Philippines with Iligan Bay enclosed in a square.

GO net from October 1998 to January 1999 showed strong net feeding with *A. erythraeus* stomachs stuffed with calanoid copepod prey. The diet data reported in this study came from shrimps caught from February 1999 to January 2000. The use of the GO net was continued, though, up to September 1999 mainly for the abundance estimate of *A. erythraeus*. Horizontal tows using both nets were made parallel to the shore at a speed of 0.5 m/s. Both nets were mounted in such a manner that no briddles obstructed the mouth in order to maximize capture efficiency.

Immediately after hauling of catch, *A. erythraeus* were fixed in 5% formaldehyde in Millipore (pore size = 1 µm)-filtered seawater. A total of four samples were collected; two for shrimp abundance and another two for shrimp diet analysis.

Soon after shrimp sampling, replicate sub-surface water samples were collected for the determination of water temperature, salinity, and total suspended solids. Sub-surface water temperature was measured using a mercury thermometer, salinity using a titration-calibrated refractometer, and total suspended solids by gravimetric methods. Total monthly rainfall data was obtained from a National Power Corporation (NPC) weather station closest to the two sampling sites. Tidal height values were obtained from published tidal predictions.

Sorting of shrimps was done after samples were processed in a laboratory equipped with an exhaust fan in order to remove formaldehyde. After analysis, samples were stored in glass jars still using 5% formaldehyde as preservative.

Analysis of diet composition

Prior to the dissection of *A. erythraeus*, total body lengths of 35 sexed individuals were measured using a Vernier caliper with an accuracy of 0.01 mm. Sexing was based on the descriptions of Xiao & Greenwood (1993). The stomach of the shrimp was removed under a Stemi 2000 Zeiss stereomicroscope using a microdissecting needle (Dumont, Switzerland), slit-opened dorsally, and spread apart. An opened gut was placed on a glass slide with a drop of glycerol and covered with a glass cover slip. Gut contents were examined under the Zeiss stereomicroscope and an Olympus compound microscope at low and high magnifications, counting and identifying meticulously all ingested prey to the lowest taxonomic level possible. Scoring of gut contents was on per individual shrimp basis.

Since micronektonic shrimps, like most crustaceans, macerate captured food prior to ingestion, the individual prey item of *A. erythraeus* was enumerated by weighted points method (Williams, 1981; Takahashi & Kawaguchi, 1998), following the equation:

Percentage weighted points for the *i*th prey is equal to:

$$\frac{\sum_{j=1}^{n} w_j a_{ij} \text{ x } 100}{\mathbf{A}}$$

where:

$$\mathbf{A} = \sum_{j=1}^{n} \cdot \sum_{j=1}^{s} w_j a_{ij}$$

a_{ij} = number of points of prey item in the foregut of the j^{th} shrimp

w_j = weighting with the value dependent on the class (1,2,3,4,5) of stomach fullness of the j^{th} shrimp

n = number of shrimps examined for diet analysis

s = number of prey categories

Chi square test was used to test the independence of gut contents from sex and sampling location.

Analysis of diet overlap between juveniles and adults

The diet overlap between juveniles and adults within site was compared using the formula of Schoener (1970):

$$R_o = 100 (1 - \Sigma | p_{xi} – p_{yi} | / 2)$$

where R_o is the overlap index expressed as percentage, and p_{xi} and p_{yi} are the relative importance (ratio of the points) of each food item *i* in the stomachs of predator species *x* and *y*.

Principal components analysis of stomach contents data

The Principal Component Analysis (PCA) (Ludwig & Reynolds, 1988; Grossman et al., 1991) was used to determine if sampling months could be grouped on the basis of the composition of *A. erythraeus* diet. PCA was also used to explore possible groupings of the different categories of stomach contents of *A. erythraeus*. Multiple partial regression was employed on the eigenvalues of the first principal component of each analysis and the different monthly hydrometeorological data to find out the degree to which these physico-chemical factors contribute to the variations in *A. erythraeus* stomach contents.

RESULTS

Temporal variation in abundance

A. erythraeus was present all throughout the year in both sites, but in some months numbers per haul were too few (Fig. 2). Very similar temporal patterns of abundance are seen in both sites that show major peaks occurring in October, February, and June. These peaks

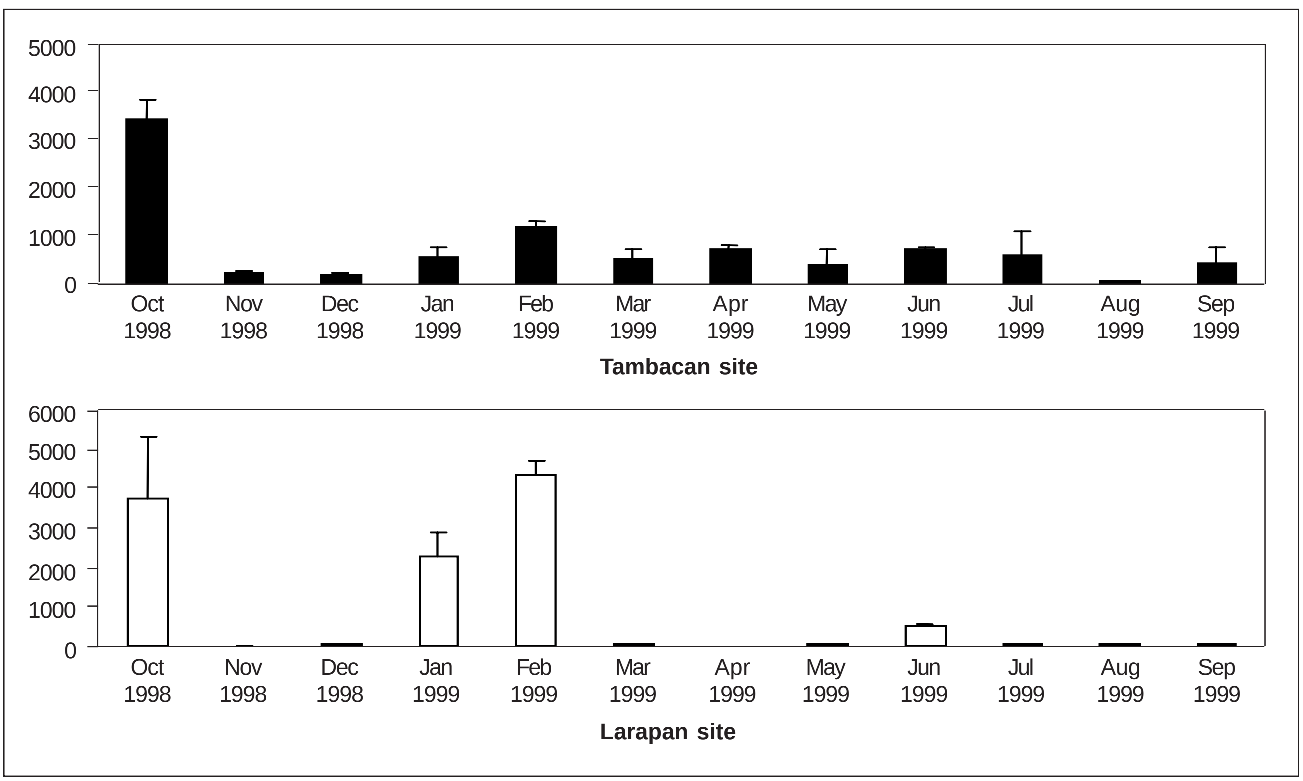

Fig. 2. Mean abundance (number of individuals per haul) of *Acetes erythraeus* in two coastal areas of Iligan Bay. Error bars = standard error.

Table 1. Summary of food categories found in the foreguts of *Acetes erythraeus* in Iligan Bay, Northern Mindanao, Philippines. (Codes used in the diet analysis and in PCA graphs are in parenthesis).

Bacillariophycea (DF)	Fragments of diatoms, primarily *Coscinodiscus* spp.
Protoctista	
Tintinnida (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 (CPF)	Entire individuals, but predominantly fragments of calanoid copepods including antennae, peraepods, mouth parts, 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, e.g., decapods
Mollusca	
Gastropoda (GF)	Intact and crushed individuals and fragments of gastropods 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 shells
Chaetognatha (CS)	Fragments of oral spines and body tissues
Echinodermata (EL)	Entire bipinnaria and auricularia larvae
Others (OT)	Amorphous materials and fine particles; foraminiferans (*Globigerina* spp.), sponge spicules, and macrophyte fragments that are mixed with silt or fine particles

are attributed to the dominance of juvenile individuals in the sample. Larapan showed relatively higher abundance during peak months than those in the Tambacan site.

Temporal variability in the diet composition of adult *A. erythraeus*

A total of 12 food categories were identified from the foregut contents of *A. erythraeus* (Table 1).

Tambacan site

Except for the months of July, September, and January, intact and fragmented copepods form the bulk of the foregut contents of adult shrimps throughout the sampling period (Table 2). It contributed 15% (September) to 55% (May). Bivalve veliger fragments ranged from 0% to 36% and showed three peaks that occurred in March, May, and November. Gastropod veligers also have three peaks (February, October, and December), with values ranging from 0% to 20%. Ostracods peaked in August and January. Other materials were highest in February and lowest in April. Crustacean remains showed a range of 0% to 17%, with a peak occurring in January. Chaetognath spines showed a range of 0% to 2.4% with the peak observed in November. Pteropods and tintinnids peaked in September. Although diatoms were ingested in September, relatively more dinoflagellates were ingested in July and October. Echinoderm larvae were only observed in August.

Larapan site

As in the other site, copepod fragments dominated the diet (Table 3), with two major peaks occurring in June and January, and a contribution with a range of 17% to

Table 2. Proportion of stomachs containing food and the stomach contents of adult *A. erythraeus* from the Tambacan site. The ratio under each sampling date represents the number of stomachs examined against the number of stomachs with food.

Date	Stomach contents (% contribution)											
	CPF	BF	GF	OF	CR	CS	PF	DI	DF	TI	EL	OT
08 February 1999 (35:24)	34.1	12.0	21.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	30.0
26 March 1999 (35:33)	29.9	25.0	16.0	0.2	4.7	0.0	0.0	0.0	0.0	0.0	0.0	23.0
27 April 1999 (35:30)	54.9	18.0	20.0	1.0	3.5	0.9	0.0	0.0	0.0	0.0	0.0	1.7
30 May 1999 (35:33)	43.0	36.1	13.6	1.3	0.0	0.0	0.1	0.0	0.0	0.0	0.0	5.8
29 June 1999 (35:31)	38.6	34.0	0.8	1.2	3.1	0.2	0.1	1.5	0.0	0.0	0.0	20.7
30 July 1999 (35:34)	21.0	27.0	7.8	29.0	1.9	0.4	0.0	0.0	0.0	1.6	0.0	8.8
28 August 1999 (35:35)	35.0	21.0	4.4	32.0	0.0	0.5	0.0	0.0	0.0	0.0	1.4	5.8
29 September 1999 (35:33)	15.0	14.0	14.0	31.0	0.0	2.4	2.1	0.0	0.8	1.6	0.0	16.0
29 October 1999 (35:35)	40.0	19.4	20.4	12.0	1.1	0.0	0.0	1.3	0.0	0.2	0.0	5.1
29 November 1999 (35:25)	33.2	20.8	16.3	21.0	0.0	6.0	0.0	0.0	0.0	0.2	0.0	2.2
29 December 1999 (35:27)	26.0	14.7	23.0	19.4	0.0	4.9	0.0	0.0	0.0	0.2	0.0	11.3
10 January 2000 (35:35)	31.2	0.0	0.0	32.0	17.0	3.0	0.0	0.0	0.0	0.0	0.0	15.0

80%. Bivalve veliger fragments peaked in June and October, with nothing in August and January. Gastropod veligers peaked in May and November. Ostracods have one peak in August. Other materials and/or fine particles range from 0% to 22%. Although crustacean remains peaked in March and while chaetognaths have one peak in October, both prey types were not ingested in other months. Tintinnids peaked in September, while pteropod fragments, in January, but both prey types were also not ingested in other months. As in the other site, dinoflagellates contributed higher to the diet than diatoms.

Temporal change in the diet composition of juvenile *A. erythraeus*

Tambacan site

Brownish green amorphous materials (fine particles) were the main item in the gut of juveniles. Two peaks occurred in June and September (Table 4). Copepod fragments that peaked in June were also common in juvenile foreguts. Its contribution ranges from 6% to 33%. Bivalve veligers peaked in October, with nothing in September. Gastropod veligers were also highest in

Table 3. Proportion of stomachs containing food and the stomach contents of adult *A. erythraeus* from the Larapan site. The ratio under each sampling date represents the number of stomachs examined against the number of stomachs with food.

Date	Stomach contents (% contribution)											
	CPF	BF	GF	OF	CR	CS	PF	DI	DF	TI	EL	OT
08 February 1999 (35:33)	24.6	12.0	23.0	5.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0	22.0
26 March 1999 (35:35)	57.1	1.9	9.5	3.0	8.2	0.1	0.0	1.1	0.0	0.1	0.0	19.0
27 April 1999 (35:35)	39.0	22.0	18.0	8.0	3.0	0.8	0.1	3.0	0.5	1.5	0.0	11.0
30 May 1999 (35:35)	36.4	24.3	23..2	3.2	5.5	0.0	0.0	0.3	0.0	0.4	0.0	4.2
29 June 1999 (35:29)	69.8	11.3	0.0	0.9	0.0	0.0	1.4	0.0	0.0	0.0	0.0	17.9
30 July 1999 (35:35)	17.0	9.9	10.0	37.0	2.1	0.9	0.0	0.1	0.0	0.9	4.2	16.0
28 August 1999 (35:27)	19.0	0.0	2.4	79.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
29 September 1999 (35:26)	43.0	16.0	12.0	6.8	0.0	0.0	0.0	0.0	0.0	14.0	0.0	8..2
29 October 1999 (35:32)	18.0	29.0	3.9	29.4	6.7	8.7	0.0	0.4	0.0	0.0	0.0	4.0
29 November 1999 (35:34)	18.0	27.0	28.0	20.2	1.0	0.0	0.0	0.0	0.0	0.2	0.0	1.1
29 December 1999 (35:25)	23.0	24.0	26.0	26.4	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
10 January 2000 (35:34)	79.9	0.0	0.5	5.0	0.1	0.0	1.9	0.0	0.0	0.0	0.0	14.0

October, and nothing for the months of May and September. The highest ostracod contribution to the diet was in July, with the only other record in August. Crustacean fragments peaked in September and lowest in October. Tintinnids peaked in August, but were only present from July to September. Pteropod fragments were only seen in July. Dinoflagellates were found from June to August and peaked in October while diatoms were only found in August. Ingested phytoplankton is higher in juvenile shrimps than in adults caught in the same site.

Larapan site

As in the other site, fine particles were the major ingested food item (Table 5). It peaked in September, and became lowest in October. Copepod fragments had its highest contribution in June and lowest was in July. Peak values for bivalve veliger fragments were in May and October. Gastropod veliger fragments were only found in May and July, ostracods in July, while crustacean fragments peaked in October. Tintinnids peaked in May while pteropods were only observed in June. Dinoflagellates were surprisingly very high in May,

Table 4. Proportion of stomachs containing food and the stomach contents of juvenile *A. erythraeus* from the Tambacan site. The ratio under each sampling date represents the number of stomachs examined against the number of stomachs with food.

Date	Stomach contents (% contribution)											
	CPF	BF	GF	OF	CR	CS	PF	DI	DF	TI	EL	OT
30 May 1999 (35:35)	31.7	13.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0
29 June 1999 (35:35)	32.6	3.7	0.6	0.0	0.0	0.0	0.0	0.2	0.0	0.3	0.0	57.0
30 July 1999 (35:29)	18.0	13.0	6.0	8.4	7.6	0.0	0.2	0.4	0.0	1.3	0.0	40.0
28 August 1999 (35:34)	25.0	5.8	1.3	1.0	2.1	0.0	0.0	1.2	2.4	16.0	0.0	45.7
29 September 1999 (35:24)	6.3	0.0	0.0	0.0	15.0	0.0	0.0	0.0	0.0	11.0	0.0	69.0
29 October 1999 (35:30)	29.0	18.0	7.1	0.0	1.8	0.0	0.0	7.9	0.0	0.0	0.0	35.0

Table 5. Proportion of stomachs containing food and the stomach contents of juvenile *A. erythraeus* from the Larapan site. The ratio under each sampling date represents the number of stomachs examined against the number of stomachs with food.

Date	Stomach contents (% contribution)											
	CPF	BF	GF	OF	CR	CS	PF	DI	DF	TI	EL	OT
30 May 1999 (35:35)	16.0	19.4	0.8	0.0	1.2	0.0	0.0	21.7	0.2	2.6	0.0	34.9
29 June 1999 (35:29)	46.2	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.7	0.0	52.9
30 July 1999 (35:31)	6.1	5.4	2.5	6.7	0.0	0.0	0.0	0.1	9.1	2.3	0.0	62.0
29 September 1999 (35:32)	7.2	2.3	0.0	0.0	5.4	0.0	0.0	0.0	1.1	0.0	0.0	83.0
29 October 1999 (35:27)	18.0	17.0	0.0	0.0	33.0	0.0	0.0	4.7	0.0	2.0	0.0	21.0

and present again in October. Diatoms peaked in July, but became rare in May and September. Dinoflagellates and diatoms are more abundant in the guts of juveniles than those in adults from the same site. August samples from this site were lost.

Differences in diet composition between location and sex

Adult shrimps taken in March, June, August, September, October, and January had stomach contents that are

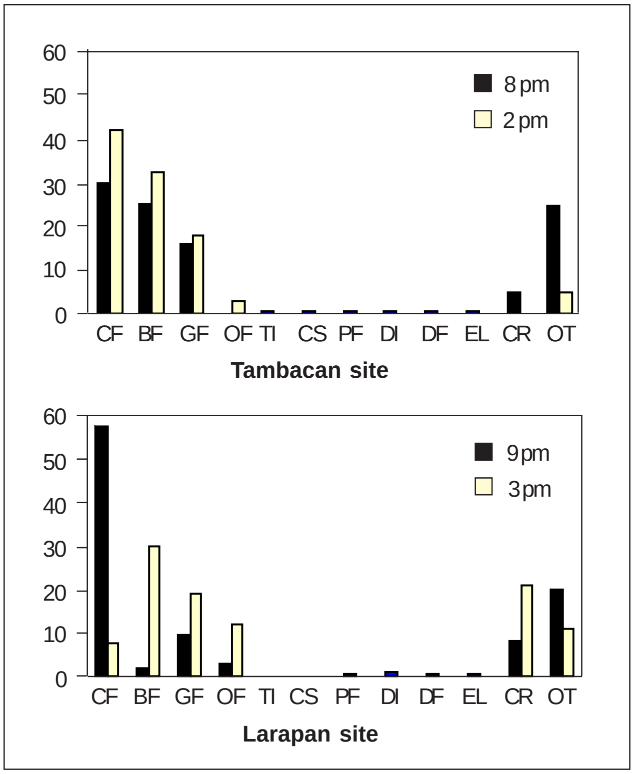

Fig. 3. Percentage contribution of stomach contents of adult *A. erythraeus* caught before and after midnight in the Tambacan and Larapan sites.

not independent of sampling site (chi-square test, $p < 0.05$ for all). This is also true among juvenile shrimps collected in May, July, and September (chi-square test, $p < 0.05$ for all). Adult shrimps from the Tambacan site in August had stomach contents that are not independent of sex (chi-square test, $p < 0.001$). This is also shown in the Larapan shrimps caught in November and December (chi-square test, $p < 0.025$). Stomach contents are independent of sex among juvenile shrimps taken from the two sites.

Comparison of feeding intensity before and after midnight

Except for other materials (amorphous) and crustacean remains, all other diet categories observed in the stomachs of shrimps from the Tambacan site showed higher feeding intensity after midnight (Fig. 3). Shrimps caught in the Larapan site showed high feeding intensity after midnight, except those shown in copepod fragments and other (amorphous) dietary items (Fig. 3).

Diet niche overlap between adults and juveniles

The diet overlap between juvenile and adult individuals was computed from May to October 1999. In the Tambacan site <50% feeding niche overlap was shown in August (39%) and September (24%), while in the other site this was seen in May (44%), July (40%), September (17%), and October (48%). The rest of the months for both sites showed overlap values >50%.

Ordination analysis of the diet composition of *A. erythraeus* from the Tambacan site

In general, the PCI of the biplots (Figs. 4-5) for gut contents reveals the grouping of dietary items on the basis of similar peak months and stomach contents abundance trends, i.e., those with positive loadings reflect dietary items that have higher % contribution.

For adult shrimps in the Tambacan site (Fig. 4A.1), copepod fragments, bivalve veliger fragments, and dinoflagellates form Group I with common peaks in May, June, and October. Group II members (gastropod veliger and crustacean fragments, echinoderm larvae, and others) peaked in December, January, and February. Ostracod fragments and chaetognath spines form Group III with peaks in August and November. Group IV is composed of diatoms, pteropod fragments, and tintinnids that peak in September. The monthly biplot (Fig. 4B.1) shows three groups, namely: May-June-October; February-March-April; November-December, January-August, and July-September.

As in the diet of adults, PCA of juvenile shrimps diet reveals groupings based on peaks of dietary items. Dietary items were grouped into four (Fig. 4A.2). Having a common peak in October, Group I is composed of gastropod and bivalve veliger fragments, dinoflagellates, and copepod fragments. Group II comprises ostracod and pteropod fragments with common peaks in July. Group III is composed of diatom fragments, tintinnids, and others. Only crustacean remains with peak in September belong to Group IV. Monthly PCA generated four groups, namely, October, July, May-June-August, and September (Fig. 4B.2).

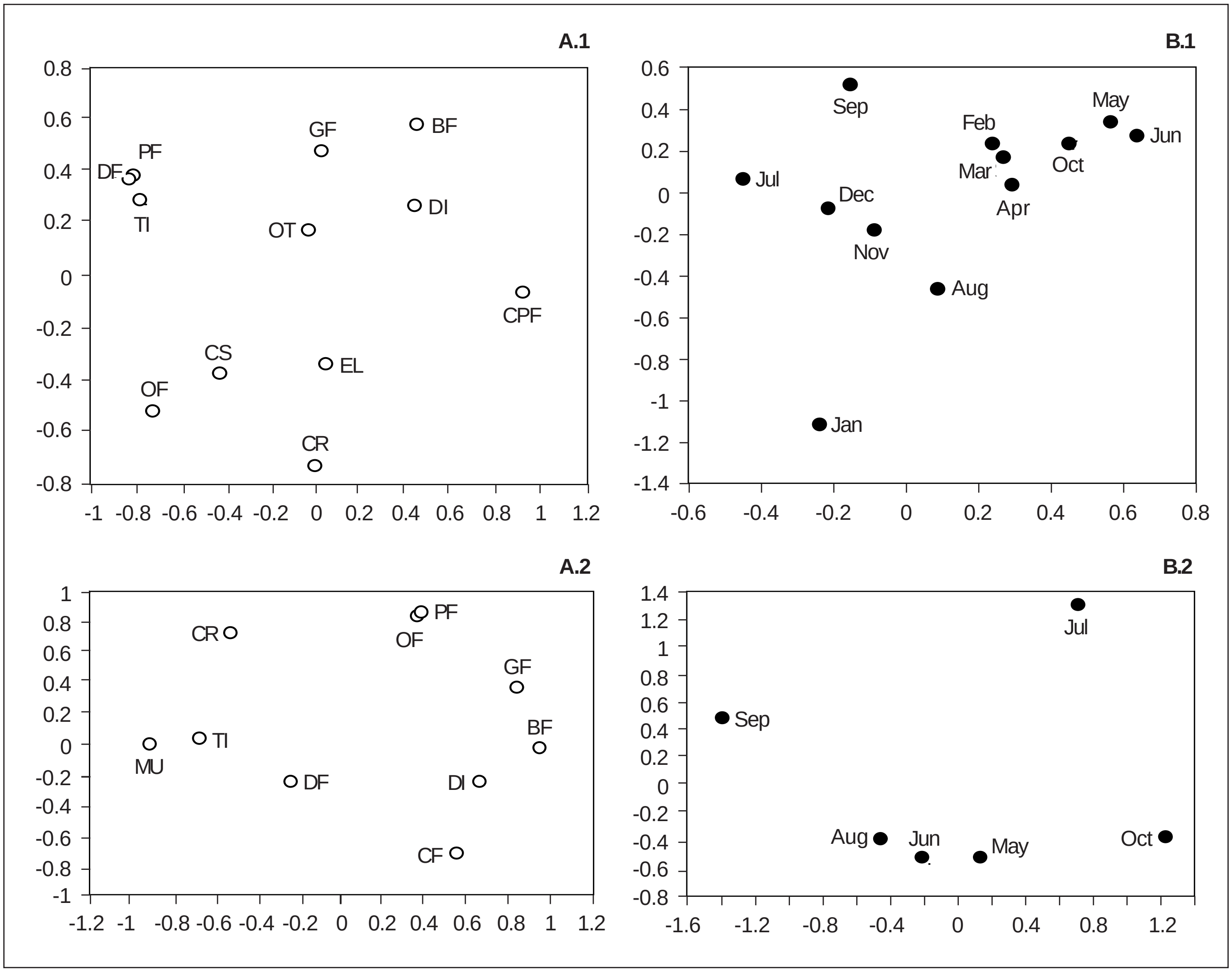

Fig. 4. Bivariate plots of Principal Components I (x-axis) and II (y-axis) for the variations in abundance of adult and juvenile *A. eryhthraeus* diet categories (A) and sampling months (B) in the Tambacan site.

Ordination analysis of the diet composition *A. erythraeus* from the Larapan site

Group I comprises chaetognath spines, gastropod and bivalve veliger fragments, crustacean and diatom fragments, and dinoflagellates (Fig. 5A.1). These items share peaks in March-April and September-October. Group II is composed of ostracod fragments, tintinnids, and echinoderm larvae that show common peaks in July-August and September. Copepod and pteropod fragments, and other materials comprise Group III that show peaks in January-February. Three groupings (July-August; March-April-May and October-November-December; and January-February, June and September) are formed in the monthly biplots with each group comprising months reflective of those for the dietary items biplot (Fig. 5B.1).

For juvenile shrimps, three groups are depicted in Fig. 5A.2. Group I has a peak in July, and comprises gastropod veliger, diatom, and ostracod fragments. Group II (copepod and pteropod fragments and others) peaked in September, while Group III constitute the remaining dietary items (crustacean, dinoflagellate and bivalve veliger fragments, and tintinnids) that have common peaks in May and October. The monthly biplot shows the same monthly groupings as those in the dietary items (Fig. 5B.2).

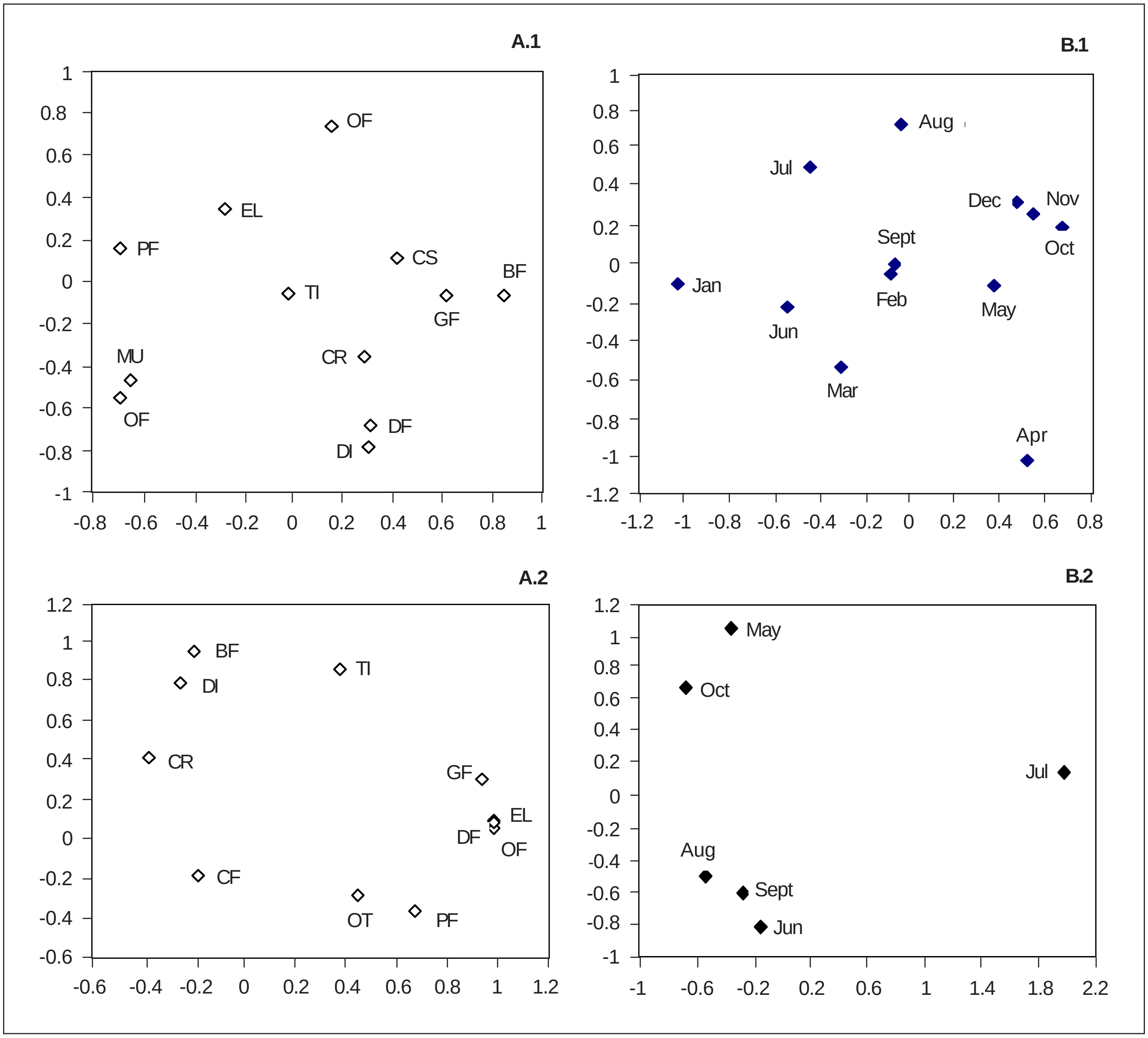

Fig. 5. Bivariate plots of Principal Components I (x-axis) and II (y-axis) for the variations in abundance of adult and juvenile *A. erythraeus* diet categories (A) and sampling months (B) in the Larapan site.

Variations in hydrometeorological parameters

Salinity from the Tambacan site ranged from 11% to 34‰ while that of the other site was 17% to 30‰ (Fig. 6A). Lowest records of salinity in the Tambacan site was in September and October 1999, but salinities below 25‰ were recorded in November and December 1998, and from March to November 1999. Below 25‰ in the Larapan site was observed in the months of February, August, and September 1999.

Sub-surface water temperature in the two sites also varied with the Tambacan site, showing a range of 26°C to 29°C, while that of the other site ranged from 27°C to 29°C (Fig. 6B). The lowest water temperature at the Tambacan site was recorded in the months of February and July 1999, while in the other site, it was in December 1999.

Average total suspended solids values ranged from 0.013 to 0.280 g in Tambacan site, while those in the other site was 0.01 - 0.21 g (Fig. 6C). Total suspended solids values in both sites remained below 0.05 g from October 1998 to February 1999, but showed a drastic increase in March 1999 and remained >0.05 g.

Tidal heights from the two sites showed a very similar pattern (Fig. 6D). High tides were observed in the months of September to December, average heights in February and from April to July, and low tides in January, March, and August. The highs and lows depict the dominant 24-h semi-diurnal pattern in Iligan Bay, with low tides observed from 0500H to 0700H and high tide at the approach of midnight to early dawn. The lowest low tides which occurred during the January and March 1999 sampling would explain the negative values.

Normally, a unimodal annual pattern occurs with low rainfall in the months of March and April and heavy rainfall normally occurring from June to February. Old records show that from 1995 to 1997, low monthly rainfall would commence earlier on the last two weeks of February. An El Niño that occurred in 1997 resulted in very low rainfall starting in January 1998 and placed the low rainfall months (March to April 1998) to unusually very low rainfall levels. The 1998 El Niño was subsequently followed by a La Niña which started June 1998 that extended up to the usually low rainfall months of March and April 1999, resulting in an unusually high rainfall values in these months (Fig. 6E). No data were available for the months of October to December 1999.

Correlation between hydrometeorological parameters and the abundance of stomach contents of A. erythraeus

Multiple partial regression between the different hydrometeorological parameters and the First Principal Components (PCI) of the abundance of stomach contents reveal that rainfall and tide best explain variations of the abundance and feeding patterns of *A. erythraeus*. Rainfall explained 49.8% of the diet variations in the Tambacan site, while tide explained 40.6% of stomach contents variations in the Larapan site.

DISCUSSION

Temporal pattern in abundance

The pattern of abundance of *A. erythraeus* in Iligan Bay is similar to the other species of *Acetes* (Xiao & Greenwood, 1993), and penaeid shrimps (Vance et al., 1998) in having a marked seasonality. Despite large sample variations, the pattern of abundance in *A. erythraeus* is similar in both sites. Three peaks occurred in October, February, and July. Although abundance could range from 0.02 – 2.5 individuals m^{-2} for both sites, this is a very rough estimate considering the extremely patchy distribution of most *Acetes* (Omori, 1974; Xiao & Greenwood, 1993). In Bangladeshi waters, *A. erythraeus* has two peaks that coincide with the northeast and southwest monsoons, particularly in the months of February and August (Zafar & Alam, 1997). In this study, the peak in October 1998 is most probably an effect of the La Niña that started two months earlier in 1998. The major peak in abundance occurring in dry-cold month (February) and the minor peak during a wet-hot month (June) differ from those shown by subtropical species that generally has a single peak in warmer months and the lowest density occurring in colder months (Xiao & Greenwood, 1993). The temporal pattern of *A. erythraeus* abundance in Iligan Bay is similar to those species found in the Bay of Bengal in that the two peaks in abundance occur at the start of southwest monsoonal rains (June-July) and at the end of the northeast monsoon (February) (Deshmukh, 1993; Zafar & Alam, 1997).

Feeding ecology

Burkenroad (1945, as cited by Xiao & Greenwood, 1993) first reported that the diet of a single South American specimen of *Acetes* comprised small crustaceans and thin-shelled mollusks. Xiao & Greenwood (1993) noted 11 food categories have so far been identified in the diet of *Acetes*. These are diatoms, protozoans, chaetognaths or arrow worms, copepodan and branchiopodan crustaceans, molluscan larvae, small scales, amorphous materials, debris, sand grains, foraminiferans, and mud. An intensive and detailed study on diet composition of the sub-tropical *A. chinensis* revealed seasonality in feeding and food selection (Xiao & Greenwood, 1993). The diet of other

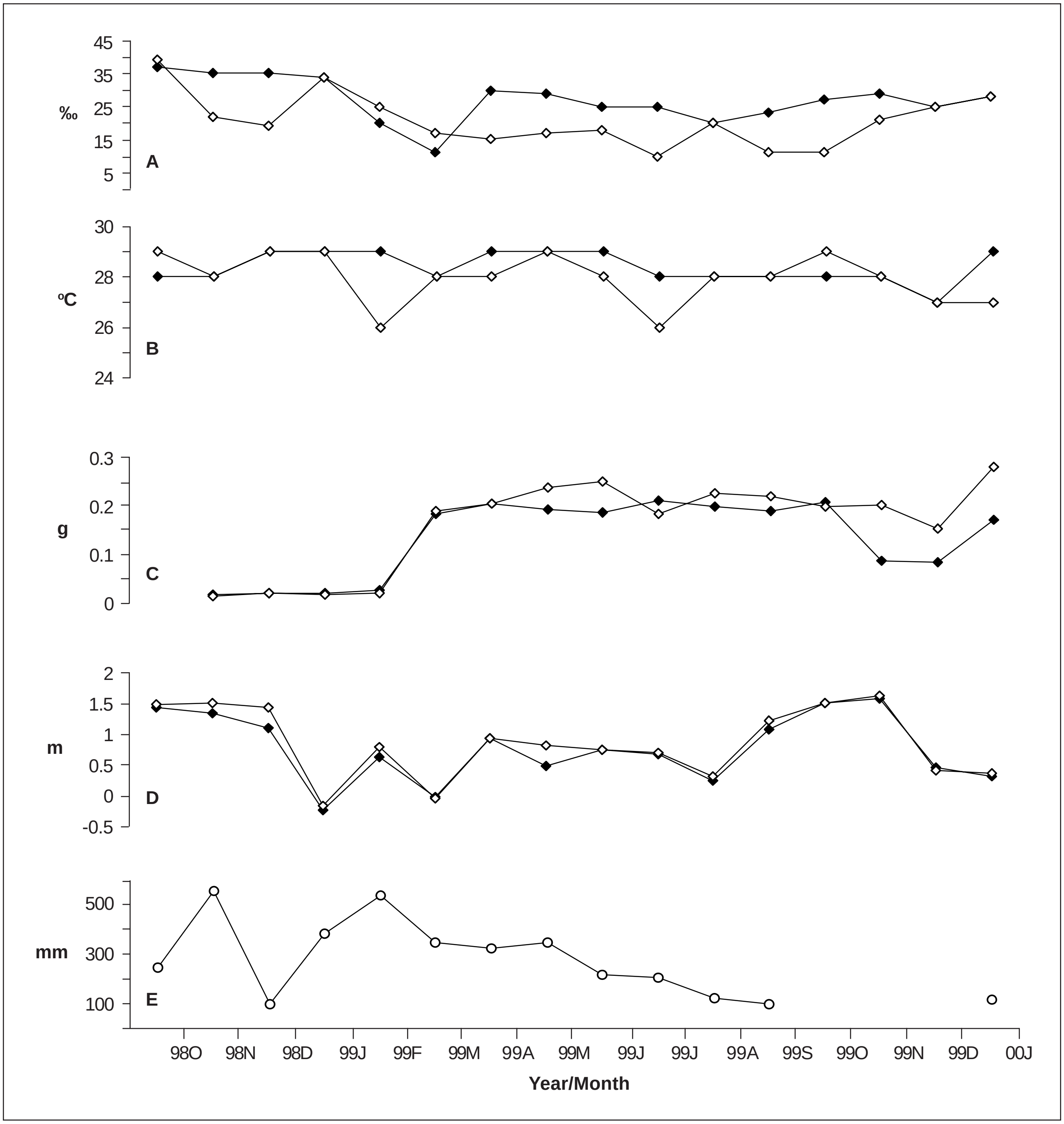

Fig. 6. Temporal variation in salinity (A), temperature (B), total suspended solids (C), and tidal height (D) in the Tambacan (open triangle) and Larapan (solid triangle) sampling sites. Both sampling sites share rainfall data (E).

species (*A. indicus* and *A. japonicus*) is also mainly composed of animal prey items. Le Reste (1970) reported a sole diet of copepods in *A. erythraeus*, but this was based on a very few specimens (n=10) collected in Ambaro Bay, Madagascar.

The analysis of feeding habits among crustaceans based on stomach contents needs to be taken with reservation due to biases associated with this method. For instance, crustaceans usually macerate their food using their powerful mandibles, making identification of prey items very difficult (Flock & Hopkins, 1992). Observations in the feeding mechanisms of *A. sibogae australis* indicated that the micro- and macrophagous opportunistic feeding of the species may underestimate the importance of large prey items and overestimate the contribution of smaller ones (McLeay & Alexander, 1998). However, this study has shown that the high frequency of full stomachs with diverse types of identifiable prey may reduce the inherent bias of stomach content analysis. Furthermore, the problem of overestimating the importance of a small quantity of one form that appear in many stomachs, as against other items with large amounts, but found only in fewer stomachs has been mitigated by using a combination of methods (Williams, 1981; Takahashi & Kawaguchi, 1998) in estimating the relative contribution of dietary items.

By far, this comprises the only report on the diet composition of *A. erythraeus* over several months in a tropical setting. Twelve (12) categories of foregut contents were identified. Like other species of *Acetes*, *A. erythraeus* is a selective omnivore that tend to include more animal prey than plant in their diet (Xiao & Greenwood, 1993; McLeay & Alexander, 1998). *Acetes*' high capture efficiency towards animal prey may be associated with its elaborate antennal sensilla which allow them to feed intensively at night (Ball & Cowan, 1977) and track amino acids from animal prey in highly turbid coastal waters (Hamner & Hamner, 1977). *A. erythraeus* ingested a fairly small amount of plant materials (diatoms and algal fragments), but this study reports for the first time relatively abundant dinoflagellates (*Peridinium* spp. and *Dinophysis* spp.) and tintinnids (*Favella* spp. and *Tintinnopsis* spp.) in the shrimp's diet. *A. erythraeus* appears to feed intensely after midnight as also observed by Takahashi & Kawaguchi (1998) for benthopelagic mysids and in other species of *Acetes* (Xiao & Greenwood, 1993).

There is overlap in the diet composition between adults and juveniles, but more small-sized food categories in the stomachs of juveniles indicate diet differences due to size. Size-selective feeding is also common among different life history stages of micronektonic mysids and euphausiids (Mauchline, 1980). Lower values in the index of niche overlap in certain months further support differences in prey size ingested. Diet composition of juvenile and adult shrimps, in general, is independent of sex and sampling location, which is similar to some species of micronektonic mysids (Metillo & Ritz, 1993; Takahashi & Kawaguchi, 1998). Instances where diet composition is not independent of sex and location may be explained by inherent variability of feeding state within a population. We cannot rule out possibilities of some individuals regurgitating food upon being captured in the net, non-feeding due to moulting and senescence. Small-scale variations in prey concentration and availability may also explain differences in ingested food by males and females.

Principal Components Analysis (PCA) indicates seasonality in the relative proportions of stomach contents, which appear to be similar to the seasonal peaks of certain planktonic prey items collected during the field sampling of this study (Metillo, unpublished data). McManus et al. (1992) first reported that the neritic zooplankton in the waters of Bolinao, Northwestern Philippines follow a three-month seasonal peaks which occur during March, April, May (dry-hot); June, July, August (wet-hot); September, October, November (wet-cold); and December, January, February (dry-cold). Peaks of certain dietary items seem to coincide with the three-month and monsoonal seasonal patterns. For example, combinations of the dry-cold (January-February), wet-cold (September), and the southwest (May-June) and northeast (October) monsoons are evident. Feeding in juvenile *A. erythraeus* appears to peak during wet-cold (September) and wet-hot (July) seasons. *A. erythraeus*, therefore, seems to show coupling of temporal peaks of certain stomach prey items with seasonal patterns of potential prey. Like other sergestids and micronektonic crustaceans (e.g., mysids, krill), *A. erythraeus* also closely align with what is relatively abundant available prey (Flock & Hopkins, 1992; Le Reste, 1970; Ball & Cowan, 1970; Atkinson et al., 1999; Rudstam et al., 1989; Takahashi & Kawaguchi, 1998).

Similar diet composition of shrimps from the two sampling sites may be due to shared hydro-meteorological dynamics and composition of potential prey. For instance, similar plankton assemblage may be transported by horizontal mixing of water masses in the two sites that may result in similar prey assemblages available to the shrimps. The differences in the relative proportion of prey items in the two sites may be attributed to site-specific physical processes. For example, multiple partial regression analysis indicates rainfall for the Tambacan site and tide for the other site. These are two dominant hydro-meteorological features explaining temporal variability in the shrimp diet. Acting singly or simultaneously, tide and rainfall probably have a strong influence on the availability of prey to *A. erythraeus*. For instance, in the neritic waters of the Gulf of Thailand, higher zooplankton biomass was observed during months with heavy monsoonal rain, high tides, and strong wind-driven onshore currents (Brinton, 1979, as cited by Schalk, 1987). Heavy rainfall produces runoff that elevates levels of dissolved phosphates and nitrates in the estuary. Elevated levels of nutrients promote localized algal bloom that in turn increases zooplanktonic production (Schalk, 1987). High tides and intense winds that drive surface currents towards the shore tend to restrict a narrow band of inshore water resulting in the aggregation of zooplankton (Vance et al., 1998). *A. erythraeus* may exploit this aggregated and abundant supply of prey.

CONCLUSIONS

To conclude, the temporal fluctuations in the population density and the diet composition of *A. erythraeus* appear to conform not only to typical monsoonal patterns but also to a three-month season in a year. During these periods certain hydrometeorological processes most probably influence the increased availability of planktonic prey to *A. erythraeus*. Adult and juvenile *A. erythraeus* occupy a trophic niche belonging to a primarily zooplanktivorous omnivore. As an intermediate micronektonic zooplanktivore, *A. erythraeus* may form 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 feed intensely upon plankton. *A. erythraeus* may assume an important role in the structuring of pelagic communities in Iligan Bay.

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