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Changes in gut evacuation time of larval mud crab, *Scylla serrata* (Crustacea: Portunidae) fed artificial plankton or live food

Augusto E. Serrano Jr.

Institute of Aquaculture, College of Fisheries and Ocean Sciences, University of the Philippines Visayas, Miagao, Iloilo, Philippines. Corresponding author: A. E. Serrano Jr., serrano.gus@gmail.com

Abstract. To understand the feeding and digestive strategies of *Scylla serrata* larva and juvenile at various stages, gut evacuation time (GET) at different developmental stage were determined in the present study. GET in larval *S. serrata* ranged from 80 min in early zoeal stages to about 120–135 min in megalopa and crab first instar stages. GET differed significantly between stages and between diet but the interaction of stage and diet was not significant. GET for the artificial food is significantly longer than that for the live food. Movement of both the artificial (AF) and live food (LF) along the gut were traced from the hepatopancreas (HP) to the 2nd, 3rd, 4th and 5th abdominal segments (A.S.), midgut (MG), hindgut (HG), near telson and during evacuation. There were very slight differences between the movement of both food at Z1 and Z2. Starting from Z3 to Z5, LF moved faster than the AF but at the megalopa stage, both foods moved from HP to the 5th A.S. at the same time; the AF group exhibited delayed movement from MG until evacuation. At the C1 stage, both foods were only visible at the MG and their separation in time became marked i.e. the AF moving markedly slower than did the LF exhibiting GET values of 135 and 120 min, respectively. Thus, it appeared that the feeding strategy of the *S. serrata* larvae and juvenile modulated GET and digestive enzyme activities in response to the apparent digestibility of food presented.
Key Words: *Scylla serrata*, larva, gut evacuation time, live food, artificial food.

Introduction. The mud crab *Scylla serrata* (Forskål, 1775) (larvae, along with the caridean and homarid larvae, do not have anterior midgut diverticulae (AMD) that penaeid shrimps possess. During the early larval stages in penaeid, digestive enzymes are released from the AMD rather than from the hepatopancreas (HP) to enhance digestive intensity. Having no alternative source of digestive enzymes, the digestive capabilities of *S. serrata* larvae are very limited, exacerbated by the fact that their hepatopancreas is underdeveloped at the first zoeal (i.e. larval) stage to the fifth Z1-Z5 (Deru 1990; Abubakr 1991). Thus, the only ways for them to enhance digestive capability are to increase the food retention time in the gut and to digest and assimilate a higher percentage of energy and nutrients from their prey (Jones et al 1993).

Gut or gastric evacuation is a parameter that affect feeding and digestion. In the literature, the terms gut or gastric evacuation, emptying, residence, retention, passage, transit, throughput, clearance and digestion rate are used interchangeably to denote the rate of processing and movement of ingested food through the stomach or gut (Loya-Javellana et al 1995). Gastric evacuation rate enables one to evaluate food consumption, estimate feeding rates (Bromley 1987) and also food conversion.

Most species of decapods are omnivorous (Barshaw & Bryantrich 1988; Hinz et al 2001; McConaugha 2002; Perez & Sulkin 2005), including most crabs (Hinz et al 2001) but their larvae do not necessarily have the capability to digest the various nutrients ingested with the same efficiency. The ability to assimilate food effectively depends on two factors: (1) gut evacuation time (GET, the interval between first consumption of an item and its first appearance in fecal material) and (2) activity of digestive enzymes. Previously, we documented the ontogeny of the activities of digestive enzymes such as

amylase, trypsin and leucine aminopeptidase (LAP) (Serrano & Traifalgar 2012). To get a more complete scenario of the ability of the *S. serrata* larvae to assimilate both live and artificial feeds, it is necessary to document changes in GET.

In studies with fish larvae and juveniles, several methods of estimating food consumption have been tested with either live food or artificial diets. The methodology includes the use of radio-isotopes (Sorokin & Panov 1966; Kolkovski et al 1993) and X-radiography with metallic markers (Talbot & Higgins 1983; Hossain et al 1998), direct counting of food particles in experimental tanks after feeding (Fushimi 1983; Keckeis & Schiemer 1992) or in the fish digestive tract (Pedersen 1984), gravimetric (Kamler et al 1986) and fluorescence techniques (Morris et al 1990; Kelly et al 2000), and the use of ink labeling (Planas & Cunha 1999) and double markers (Teshima et al 2000) in live food and microparticulate diets. In crustaceans, the use of visible markers that pass along the gut has been used to measure GET (Wilcox & Jeffries 1974; Bayer et al 1979). There are a number of factors that affect GET of juvenile or adult animals such as temperature (Wlodarczyk et al 1992), food concentration (Murtaugh 1985), animal size (Kurmaly et al 1990), pre- and postprandial starvation (Kurmaly et al 1990) and ingestion and egestion rates (Murtaugh 1984).

In order to understand the feeding and digestive strategies of *S. serrata* larva and juvenile at various stages, GET at different developmental stage were determined in the present study.

Material and Method

Broodstock and live feeds. The broodstock females, whose progeny were used in these experiments, were identified as *S. serrata* according to the description of Keenan et al (1998). Mature females were purchased from Roxas City, Capiz which were collected from the wild. Preparation and daily feeding of the broodstocks, collection of Z1 larvae and the method of transferring to incubation and hatching tanks were as described by Serrano & Traifalgar (2012).

Rotifers were maintained and propagated in fiberglass tanks and fed green algae *Tetraselmis chuii* or marine *Chlorella sp.*. Rotifers were harvested by filtration using 30 µm mesh plankton nets. Commercially available *Artemia salina* cysts were hatched in the laboratory following the manufacturer's instruction.

Estimation of GET. GET was determined by microcoscopic observation through time of the movement of fluorescent dye labeled rotifers in the larval and juvenile gut. Rotifers were collected from the rearing tank, concentrated using 30 µm mesh plankton net and stained with 0.1 mg ml^{-1} of phloxine dye in phosphate buffered saline (pH 8.0). Unbound and excess stain was removed by flowing seawater through the plankton net with the rotifers until the out-flowing water turned colorless. A similar procedure was employed in the staining of microencapsulated artificial feed (100 µm, Argent, USA) used in the assessment of acceptability of artificial feed by the crab larvae.

Based on preliminary experiments conducted in the laboratory, the ingested food was visible only after it reached the hepatopancreas or the abdominal segment which took about 60 min. Following clearance of gut contents, a batch of larvae were held in 20 L tanks and allowed to prey on tagged rotifers. To minimize the effect of search time and to maximize feeding rate, the crab larvae were exposed to high prey density of 10 individuals/ml^{-1} for about 60 min in a homogeneous prey distribution. About 10 larvae were kept in a 90 x 15 mm size Petri dish with 25-30 ml of seawater and the movement of feed in the gut was observed under microscope. Larvae that were suspected not to have ingested food item were not sampled. The position of the food was examined every 5 min until it has completely evacuated at ambient temperature of about 26^{o}C. Presence and location of the tagged prey in larval gut was detected using epifluorescence microscope (Hund Wetzlar, Germany). Seawater used in the Petri dish was just enough to submerge the larvae or juvenile and they were always lying on the bottom of the Petri dish laterally. Illumination was provided from the bottom of the Petri dish to make the larvae transparent.

Median minimum GET for individual shrimp was estimated as time between introduction of fluorescent meals and first detection of fluorescent fecal matter after ejection to the nearest 5 min. Artificial feed acceptability study was performed by incorporating phloxine dye to microbound diet. Feeding protocol was the same as described above. Acceptability was determined by the presence of optically detectable artificial diet in larval digestive tract.

Statistical analysis. Statistical analysis of the data was performed using a graph-statistical software package (Statistica, Stat Soft., Inc., USA and Sigma plot 11, Systat, USA). Homogeneity of variances and normality were tested (using Levene's test and Shapiro–Wilk's test, respectively) before analyzing the data with an ANOVA. Differences between GET at various stages fed either live food (LF) or artificial food (AF) were determined by one way ANOVA. Those between diet and developmental stages and their interaction were determined by a factorial ANOVA. Post hoc analysis among groups after finding significant differences were performed by Tukey tests with the level of significance preset at $p<0.05$. Data were reported as mean ± standard error (or residual error in the case of multivariate or two-way ANOVA) except those in Figure 3 where only one series of observation was done and was meant to be descriptive.

Results. Crab larvae typically consumed live food and tagged artificial feed throughout the course of the GET assay and fluorescent-labelled food were detectable under the microscope after 60 min when it reached the hepatopancreas or the abdominal segment (Figure 1). Individual food item could be identified and fluorescence within the organs could be easily distinguished from background 60 min and longer following ingestion. Live food appeared undigested when evacuated at the zoeal stages but at megalopa and crab stages, they seemed to be more digested.

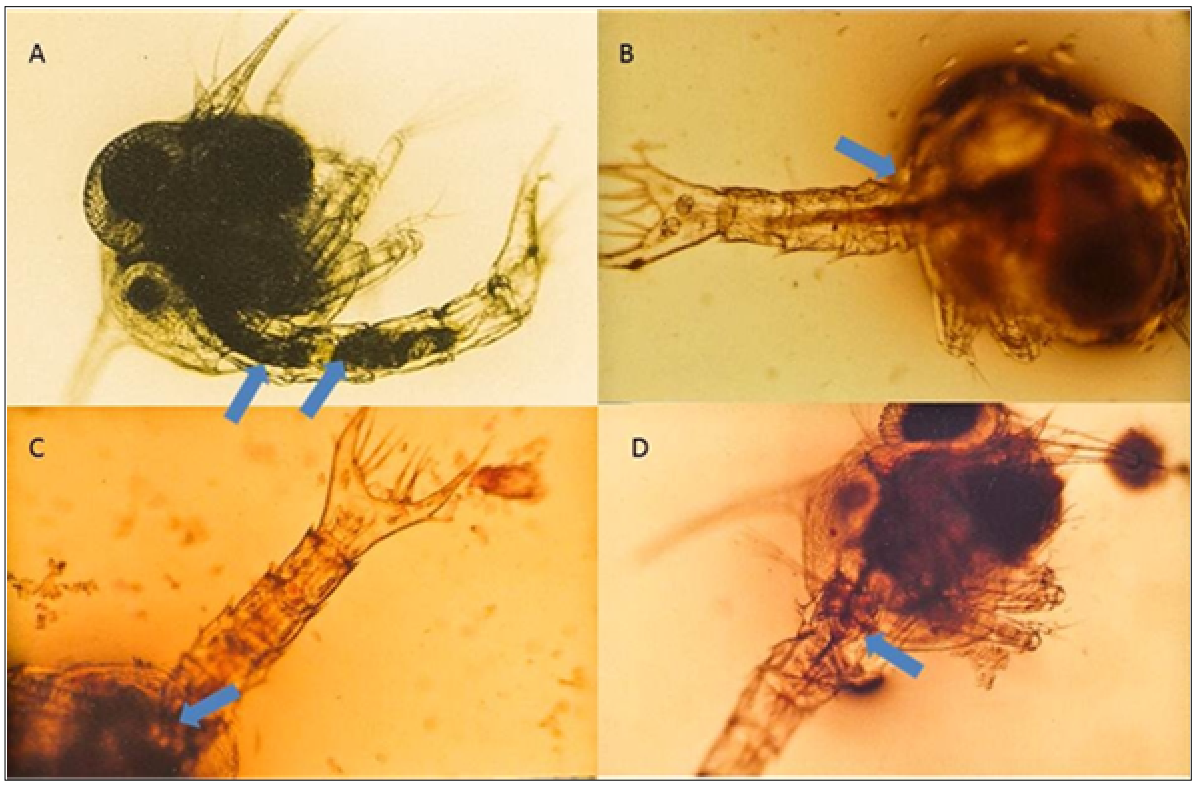

Figure 1. Photos of *S. serrata* (A) Z1 larvae with the ingested artificial plankton, (B) Z3 larvae fed *Artemia* nauplii, (C) Z3 larvae fed artificial plankton, and (D) Z4 larvae with ingested artificial plankton. Arrows indicate ingested feed in the gut.

GET differed significantly between stages and between diet but the interaction of stage and diet was not significant (Table 1). Figure 2 shows the GET of larval of different stages

and diet. A two-tailed Student t-test showed that the GET for the artificial food is significantly longer than that for the live food ($p<0.05$).

Table 1

Factorial ANOVA of gut retention time of mud crab larvae and juveniles fed live food or artificial feed at seven developmental stages

SV	*d.f.*	*SS*	*MS*	*F ratio*	*p*
Stage	6	14220.2	2370.0	20.846*	0.0000
Diet	1	1314.9	1314.9	11.565*	0.0000
Stage x Diet	6	806.0	134.3	1.182	0.345
Error	28	3183.3	113.7		
Total	41	19524.4			

SV is source of variation; d.f. is degrees of freedom; SS is the sum of squares; MS is mean square; The F-ratio is the variation in the dependent variable (i.e. gut evacuation time) explained by the independent variable (i.e. development stage, diet as live or artificial food, or their interaction) other than due to random variation;

*Significant variation ($p<0.05$).

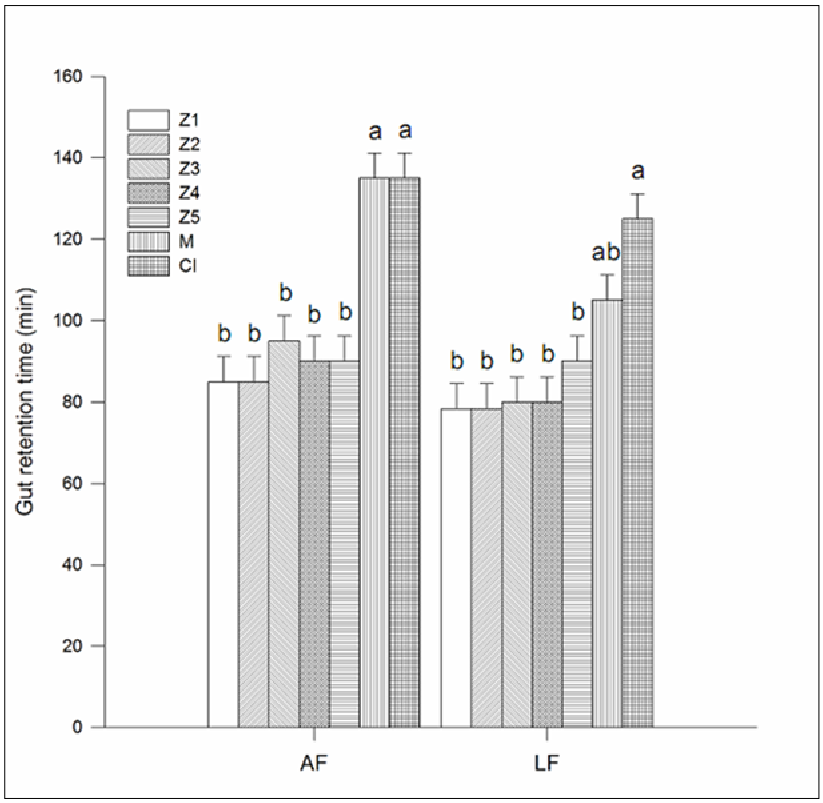

Figure 2. Gut evacuation time (mean ± error) at 7 developmental stages determined in two diets (LF=live food, AF= artificial feed). Different letters indicate significant differences ($P<0.05$).

Figure 3 shows the movement of both the artificial (AF) and live food (LF) along the gut of the crab larvae from the HP where the food started to become visible, to the 2nd, 3rd, 4th and 5th abdominal segment, to the midgut (MG), hindgut (HG), near telson and finally when the food was evacuated. There were very slight differences between the movement of both food at Z1 and Z2. Starting from Z3 to Z5, LF moved faster than the AF but at the megalopa stage, both food moved from the hepatopancreas (HP) to the 5th abdominal segment and the AF exhibited delayed movement from MG until evacuation. At the C1 stage, both food were only visible at the MG and their separation in terms of time became very apparent with the AF moving quite slower than did the LF with the final GET value of 135 min and 120 min, respectively.

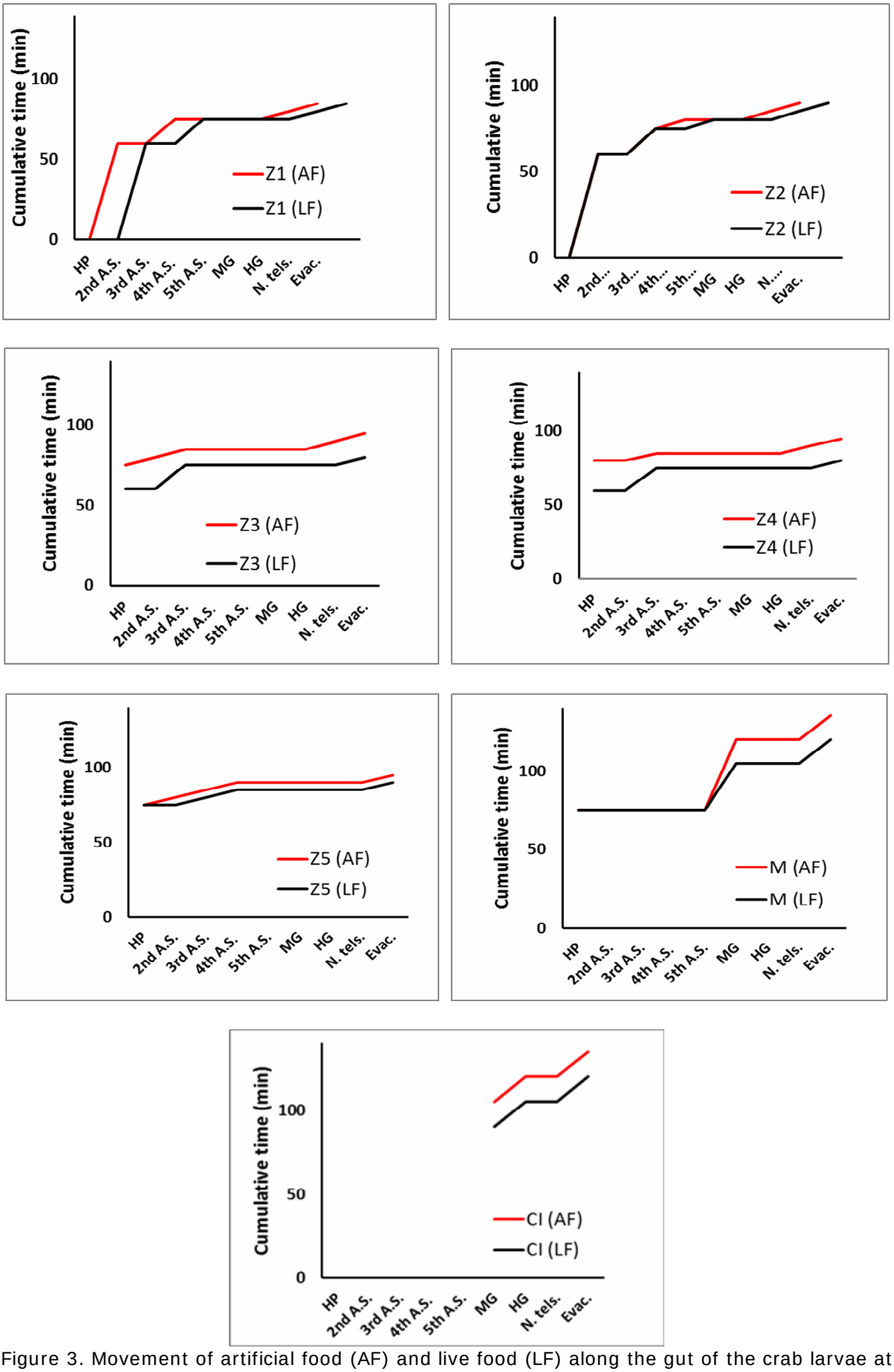

Figure 3. Movement of artificial food (AF) and live food (LF) along the gut of the crab larvae at various developmental stages (A - Z1; B - Z2; C - Z3; D - Z4; E - Z5; F - megalopa; G - C1) from hepatopancreas (HP), to 2nd, 3rd, 4th and 5th abdominal segment (A.S.), midgut (MG), hindgut (HG), near telson until the food is evacuated.

Discussion. GET has been measured in *Penaeus monodon* (Fabricius, 1798) to be 12 min for the protozoea, 20 min for the mysis, and 30 min for the postlarva (Jones et al 1993). In *Artemia sp.*, it is 10 and 3 min for nauplii and adult *Artemia*, respectively (Dobbeleir et al 1980). The retention time of the mud crab larvae in the present study was much longer than either of its prey, allowing for 80-135 min before it was egested. Smith et al (2002) considers first feeding larvae of caridean shrimp such as *Macrobrachium rosenbergii* (De Man, 1879) to have longer comparative GET as a consequence of their being carnivorous and active raptorial feeders. We assume that this is also the case of the larvae of the mud crab being carnivorous (Genodepa et al 2004) and a raptorial feeder (Holme et al 2009). In reviews of Le Vay et al (2001) they observe a general pattern of longer GET for carnivorous crustaceans, feeding on less abundant but digestible and energy-rich prey, as part of the overall feeding strategy of possessing low enzyme content and exhibiting much higher assimilation efficiency. Jones et al (1997) extend this observation to all late stage larval crustaceans.

From the data of the present study, it appeared that as the development of the larva advanced, GET became longer. Radiotracer studies in *S. serrata* larvae have also shown that gut residence time was shortest in early zoea stages, but increased substantially with larval development (Genodepa 2003; Genodepa et al 2006). The same observation has been made in fish larvae such as the spotted seatrout (*Cynoscion nebulosus* (Cuvier in Cuvier and Valenciennes, 1830)) larvae (Wuenschell & Werner 2004) and the reason given was the increasing fish larval size. In *Clarias gariepinus* (Burchell, 1822) larvae (Garcia-Ortega et al 2008), food evacuation occurred faster during continuous feeding than when discontinuous feeding was applied. This could not be observed in the present study with the mud crab larvae since after an hour of feeding on either AF or LF the larvae were placed on Petri dish for observation under the microscope. Isolating them in a confined environment could have effected a discontinuous mode of feeding that affected the GET.

The pattern of longer GET of *S. serrata* larvae fed AF than in those fed LF in the present study disagreed with that observed in *M. rosenbergii* in which larvae fed artificial diet exhibit shorter gut retention times than do those larvae fed *Artemia* nauplii exclusively (Ohs et al 1998). In the present study, the longer GET in larvae fed AF compared to those fed LF coinciding with low endopeptidase (i.e. trypsin-like) and exopeptidase (i.e. LAP) activities in the previous study (Serrano & Traifalgar 2012) were adaptations to the poorly digested AF. Jones et al (1993) reported that a correlation exists between the level of enzymes present and gastro-evacuation rate in penaeid shrimp larvae, and that the highest enzyme activity coincided with the shortest GET. Moreover, omnivorous and carnivorous crustacean larvae lack the physiological capacity to raise enzyme levels in response to artificial diets (Jones et al 1997). Shorter GET for larvae and juveniles fed *Artemia* could be due to the highly digestible nature of this prey since it has been documented that it contains considerable amount of free amino acids ready for assimilation.

In the present study, the shorter GET at the megalopa and first crab instar stages were observed when LF was fed and that at these stages they exhibited higher endo- and exopeptidase activities than did those fed AF as was demonstrated previously (Serrano & Traifalgar 2012). Thus, it appeared that the feeding strategy of the *S. serrata* larvae and juvenile modulated GET and digestive enzyme activities in response to the apparent digestibility of food presented. It is hypothesized that GET was under stage-specific genetic control at stages Z1-Z5 since GET values were uniformly short regardless of diet in these stages. Diet modulation of GET might have begun at the megalopa and first crab stages. Mayzaud (1986) suggests that there may be a feedback mechanism between the activity of the digestive system and the energy demand of an organism, and that any change in energy requirement will induce an activation or repression of digestive enzymes. Another factor which could be subject to modulation is feeding frequency but was not included in the present study. It could be the case that increased feeding frequency, parallel to a continuous mode of feeding, could be a compensatory strategy to meet the energy requirement of the larvae especially so at stages when increases in GET and digestive ability are under genetic programme.

Conclusions. GET in larval *S. serrata* ranged from 80 min in early zoeal stages to about 120–135 min in megalopa and crab first instar. GET differed significantly between stages and between diet but the interaction of stage and diet was not significant. GET for the artificial food is significantly longer than that for the live food. There were very slight differences between the movement of both food at Z1 and Z2. Starting from Z3 to Z5, LF moved faster than the AF but at the megalopa stage, both food moved from HP to the 5th A.S. at the same time but the AF group exhibited delayed movement from MG until evacuation. At the C1 stage, both food were only visible at the MG and their separation in time became marked with the AF moving quite slower than did the LF with the final GET value of 135 min and 120 min, respectively. Thus, it appeared that the feeding strategy of the *S. serrata* larvae and juvenile modulated GET in response to the apparent digestibility of food presented**.**

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Author:
Augusto E. Serrano Jr., Institute of Aquaculture, College of Fisheries and Ocean Sciences, University of the Philippines Visayas, Miagao 5023 Iloilo, Philippines, e-mail: serrano.gus@gmail.com
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