VOLUME 10 ISSUE 2 2024

ISSN 2454 – 3055

INTERNATIONAL JOURNAL OF ZOOLOGICAL INVESTIGATIONS

Forum for Biological and Environmental Sciences

Published by Saran Publications, India

International Journal of Zoological Investigations Vol. 10, No. 2, 641-651 (2024)

International Journal of Zoological Investigations

Contents available at Journals Home Page: www.ijzi.net

Editor-in-Chief: Prof. Ajai Kumar Srivastav

Published by: Saran Publications, Gorakhpur, India

ISSN: 2454-3055

Functional Efficacy of Foregut Morphology of a Potentially Culturable Brakishwater Decapod *Metapenaeus monoceros* (Fabricius, 1798)

Jha Aniruddha and Homechaudhuri Sumit*

Aquatic Bio-Resource Research Laboratory, Department of Zoology, University of Calcutta, 35 Ballygunge Circular Road, Kolkatta 700 019, India

**Corresponding Author*

Received: 16th February, 2024; **Accepted:** 12th June, 2024; **Published online:** 7th September, 2024

https://doi.org/10.33745/ijzi.2024.v10i02.060

Abstract: The present scanning electron microscopic study analyzes the functional morphology of foregut structure from the digestive tract of *Metapenaeus monoceros* (Fabricius, 1798), a potential species of crustacean aquaculture. Like other decapods, the foregut is divided into a short esophagus opening into a large anterior cardiac chamber and a small posterior pyloric chamber. Various regions of the cardiac chamber, viz. cardiac setal screen, gastric mill, lateral accessory teeth, and the cardio pyloric valve, have been described in their ultrastructural details, relating to their functions in mastication and digestive processes. Essential structures in the pyloric chamber, i.e., gland filter and the compaction zone of the pyloric chamber, have been analyzed concerning the processing of residual food materials and filtrate. Separate groups of setae covering the cardiac chamber floor play a significant role in determining the particle sizes for their entry to ventrolateral filtration channels. Gastric mill armature suggests adapting the species to triturate a large as well as small pieces of food, which corroborates with their feeding habit. The presence of lateral accessory teeth is oriented to deliver solid materials into the gastric mill. The cardio pyloric valve ensures that the filtrate of the cardiac setal screen can pass into the gland filter of the pyloric, in which dense setal arrangement helps in the passageway of fine food particles to hepatopancreas. The fine cardiac setal mesh is structural evidence of their adaptation to small food items. The median and large lateral teeth with curved denticles also indicate their feeding habits. Considering the digestive mechanism, compounded feed particles of small sizes seem advantageous, which would increase the functional efficiency of *Metapenaeus monoceros*.

Keywords: Scanning electron microscopy, *Metapenaeus monoceros*, Shrimp, Digestive tract, Ultrastructure, Fisheries, Gastric mill, Denticles

Citation: Jha Aniruddha and Homechaudhuri Sumit: Functional efficacy of foregut morphology of a potentially culturable brakishwater decapod *Metapenaeus monoceros* (Fabricius, 1798). Intern. J. Zool. Invest. 10(2): 641-651, 2024.

https://doi.org/10.33745/ijzi.2024.v10i02.060

Introduction

The development of Crustacean aquaculture has led to the need for a better understanding of the relationship between the anatomy and function of the digestive tract of Decapod Crustaceans,

particularly shrimps. The process of ingestion, transportation of nutrients, mechanical digestion, chemical and biochemical hydrolysis, cellular absorption, and storage, as well as the transfer of excreta, detoxification of xenobiotics, synthesis of immune defense molecules, and osmoregulation, are all functions of the digestive tract of Crustaceans (Strus *et al.*, 2019). In brackish water shrimp ponds, only some organic matter and nutrients in pelleted feeds that enter the system are converted to shrimp flesh (Boyd, 1999). In addition to metabolic wastes, unused remains of the feed increase sediment lipid and organic matter content by 20% and 30%, respectively (Funge-Smith and Briggs, 1998). These facts underline the need for a better understanding of the digestive capabilities of the animals in their natural habitat and to develop cultural technologies that minimize ecological degradation. Among several alternatives, an approach based on the animal's functional anatomy and physiology of digestion has been developed. The present study was aimed to test this approach for a tropical estuarine penaeid species, *Metapenaeus monoceros* (Fabricius, 1798), which has excellent potential to be cultured under a semi-intensive system (Sudarsan and Joseph, 1975; Chakrabarty, 1981; Devanand *et al.*, 2018) and be a mainstay in coastal economics.

Restricting our knowledge towards Decapod foregut anatomy, histological observations of the digestive tract of penaeids are found in the works of Dall (1967). Meiss and Norman (1977) (on *Penaeus duodenum* and *Farfantepenaeus aztecus*) and Suthers (1984) (on *Penaeus plebejus*) described the gastric mill structure from the foregut. Felgenhauer and Abele (1989) were the first to describe scanning electron microscopic details of the digestive tract of *Litopenaeus setiferus*. However, as a generalized comparative work, detailed surface topography or functional anatomy in the group is still lacking. King and Alexander (1994) described the process of fluid extraction and circulation in the foregut of *Fenneropenaeus* (=*Penaeus*) *merguiensis*. Gland filters of *Marsupenaeus* (=*Penaeus*) *japonicas* have been described by Lin (1996). Lin (2000) also described the gland filter structure of *Penaeus monodon* and *Metapenaeus ensis*. Storch *et al.* (2001) described the ultrastructure of the digestive system of three Caridean Antarctic shrimps. Morphology and histology of the *Penaeus argentinus* digestive tract have been described by Sousa and Petriella (2006). Lima *et al.* (2016) described the foregut morphology of a Palaemonid shrimp *Macrobrachium carcinus*. Pattarayingsakul *et al.* (2019) described the gastric sieve of two Penaeid shrimp species (*Penaeus monodon* and *Penaeus vannamei*). Besides, the digestive structure of Decapod Crustaceans has been published in several reviews during the past years (Dall and Moriarty, 1983; Dall *et al.*, 1990; Dall, 1992; Felgenhauer, 1992; Icely and Nott, 1992; Brunet *et al.*, 1994; Ceccaldi, 1997, 2006; Walting, 2013; Strus *et al.*, 2019). Each review has contributed significantly toward the understanding of gut anatomy. In the present study, we describe the functional anatomy of the foregut structure of *Metapenaeus monoceros* (Fabricius, 1798) by using scanning electron microscopy and make inferences regarding the feeding and digestive strategies of the species.

Materials and Methods

Tropical estuarine penaeid species *Metapenaeus monoceros* (Fabricius,1798) were collected from high saline (30-32 ppt), embanked shallow water bodies, connected with estuarine Matla river system at Port Canning of South 24 Parganas (Latitude 21°32′ N to 22° 20′ N; Longitude 88° 05′ E to 89° 00′ E), West Bengal, India.

For scanning electron microscopic investigations, foregut region of the digestive tract from immediately sacrificed animals was fixed in 4% glutaraldehyde solution (pH 7.2) for 4 h at 4°C. Longitudinal incision in the region was made to view the inner surface area. It was followed by exposing the inner layer with microneedles and clearing the surface with a fine brush. Double distilled water-washed tissues were post-fixed in 2% OsO_4 solution at room temperature for 2 h. Later, fixed tissues were dehydrated through

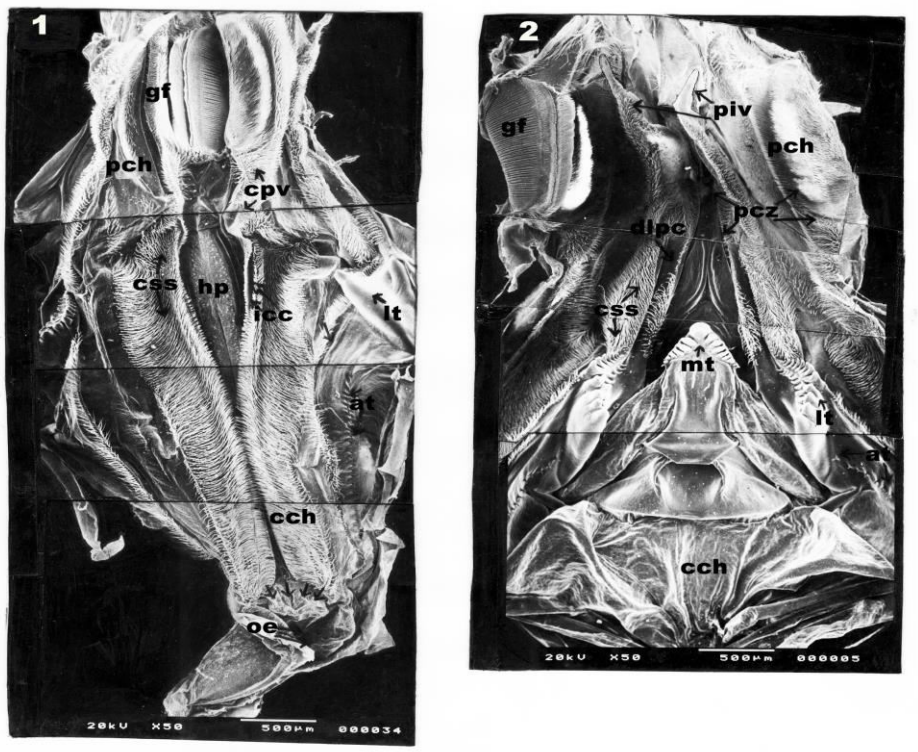

Fig. 1: Internal foregut feature of *Metapenaeus monoceros* showing the floor surface with functional morphology of various regions indicated.
Fig. 2: Internal foregut feature of *Metapenaeus monoceros* showing the roof surface with gastric mill indicated.
at, accessory teeth; **ccfs**, coarse cardiac filter setae; **cch**, cardiac chamber; **cfls**, cardiac floor setae; **cpv**, cardiopyloric valve; **css,** cardiac setal screen; **dlpc**, dorsolateral pyloric channel; **fcfs**, fine cardiac filter setae; **gf**, gland filter; **hp**, hastate plate; **icc**, inferior cardiac channel; **lt**, lateral teeth; **mt**, median tooth; **oe**, oesophagus; **pch**, pyloric chamber; **pcz**, pyloric compaction zone; **piv**, pylorointestinal valve; **s**, setae; **scc**, superior cardiac channel; **st**, setule. **(These abbreviations are common for all figures)**

graded amyl acetate.

Critical point drying was done in the Polaron machine (model no. 3000). The specimens were coated with 10-20 nm of gold-palladium in the S150 sputter coater machine. Scanning electron micrographs were taken in JEOL JSM-5200 microscope at USIC, Jadavpur University, and CDRI, Lucknow, at accelerating voltages of 15-20kV. The terminology for different digestive tract regions follows Felgenhauer (1992).

Results

Like other Decapods, the digestive tract of *Metapenaeus monoceros* is divided into fore, mid, and hindgut regions. Both the foregut and hindgut are derived from ectoderm and thus lined by cuticle, which sheds and is replaced during growth by molting. The foregut consists of a simple esophagus that opens into a large anterior cardiac chamber, followed by a small posterior pyloric chamber partly surrounded by the digestive gland or hepatopancreas.

The esophagus (oe) (Fig. 1) is a simple tube extending vertically from the mouth to the stomach, the internal lining of which shows the presence of a setal structure (Fig. 3) covering through it in a posterior direction, possibly to aid in the movement of food bolus into the stomach. At the junction between the esophagus and the stomach (Fig. 1), the walls are seen to be modified to form a sphincter that may prevent the reflux of ingested material from the stomach. The stomach

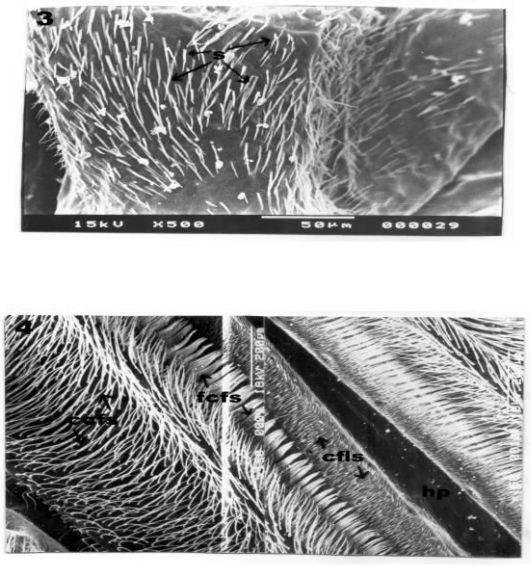

Fig. 3: Internal surface of esophagus showing posteriorly directed setae(s).
Fig. 4: Dorsal view of the floor of the cardiac chamber showing various setal groups.

is separated into anterior spacious cardiac (cch) and posterior reduced pyloric (pch) chambers (Figs. 1, 2). Various regions of the cardiac chamber have been observed and demarcated in the present study.

The floor of the cardiac chamber is covered with the cardiac setal screen (css) (Figs. 1, 4).There are longitudinal ridges (see arrow) in the ventrolateral walls and on the floor of the chamber, which produce ventrolateral channels (e.g., dorsolateral pyloric channel (dlpc); superior cardiac channel (scc); inferior cardiac channel (icc). These cardiac channels are screened by five (actually three) layers of setae which provide a sieve of increasingly fine mesh size. The upper margin of the lateral folds is covered by (i) simple coarse setae (ccfs) and (ii) identical to the first form projects medially from beneath the lateral fold (ccfs). The other two layers of fine, more elaborate setae include (a) the lower layer (fcfs) that projects medially into the cardiac stomach, and (b) the upper layer (fcfs) that originates further laterally to the lower layer and projects it medially. These four layers lie immediately above a dense mat of cardiac floor setae (cfls) that covers the lower margins of each ventrolateral filtration channel (Fig. 4). There is also a ridge or hastate plate (hp) along the floor of the chamber, which is covered with fine setae. The superior cardiac channels extend into the pre-ampullary chamber of the pyloric gland filter, while the inferior cardiac channels and the central section of the cardiac floor terminate at the cardiopyloric valve (cpv).

Dorsal to the cardiac setal screens, an area supported by a complex of ossicles, has been observed. The roof of the cardiac chamber internally produces the median tooth (mt) (Figs. 2, 5). In addition, the lateral walls are supported by ossicles that protrude into the lumen along the anteroposterior axis as a pair of opposing lateral teeth (lt). Together they form the gastric mill structure. Close observation at the level of the triangular median tooth shows that the margins of this tooth extend outward from its anterior tip. Each lateral side of the tooth bears closely packed denticles, which are increased in size towards the apex, and the extreme lateral denticles are seen to be sharply curved inwards. The surface topography of the median tooth does not show any grinding area (Fig. 5). While surveying the

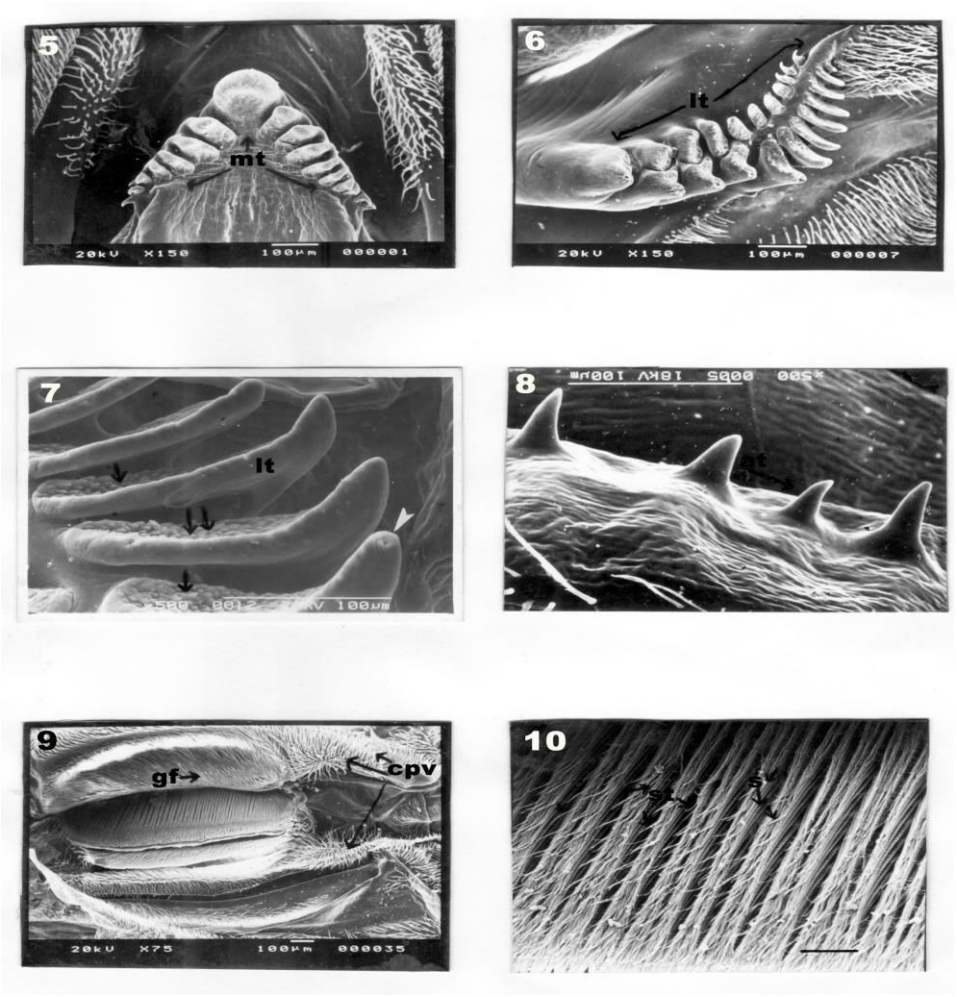

Fig. 5: Median tooth (mt) of gastric mill.
Fig. 6: Lateral teeth (lt) of gastric mill.
Fig. 7: Surface topography of denticles of lateral teeth showing grinding surface (black arrows) and broken area (white arrowhead).
Fig. 8: Magnified view of lateral accessory teeth (at).
Fig. 9: Pyloric chamber showing the gland filter (gf) and cardiopyloric valve (cpv).
Fig. 10: Magnified view of the gland filter showing setae (s) and setules (st). Scale bar 50µm

level of paired lateral teeth, and it is found that these are dorsally curved and heavily calcified. Paired lateral denticles gradually reduce in size towards their apex (Fig. 6) and become slightly curved outwards (Fig. 6). In the present study, 10-12 pairs of denticles are seen in fully mature adult ones. The denticle topography clearly shows grinding surfaces (Fig.7) in which denticle tips are found to break in certain areas, probably during crushing with hard particles (Fig. 7). A pair of lateral accessory teeth (Figs. 1, 2, 8) extend along the walls of the cardiac chamber, ventral to the gastric mill. The sharp, pointed, curved accessory teeth (at) probably help in holding the food material within the cardiac chamber. The cardio pyloric valve (cpv) (Fig. 9) separates the ventral region of the cardiac chamber from the pyloric one. It is produced by a fold across the floor of the cardiac chamber at the posterior end of the hastate plate and inferior cardiac channel. A pair of ventral lateral folds extending over the superior cardiac channels toward the central fold is also observed here. The pyloric chamber is ventral in position compared to the cardiac chamber and has

the following regions:

(a) The gland filter occupies the ventral half of the pyloric chamber, separated from the dorsal region by lateral folds along the sides of the foregut. The gland filter (gf) (Figs. 1, 2, 9, 10) is separated into two halves by the intrusion of the interampullary ridge. An ampullary setal screen separates two upper ampullary chambers from the lower ampullary chambers. The latter opens directly to the chamber leading to the hepatopancreas of the midgut. The ampullary setal screen is supported by parallel rows of ridges along the pyloric stomachs inter ampullary ridge and floor. Each ridge with rows of setae overlies the setae of the adjacent ridge. The setal mesh structure is evident in this region (Fig. 9). Rows of setae (s) support the ampullary setal screen, and each seta has rows of setules (st) (Fig. 10).

(b) The entrance to the dorsal region of the pyloric stomach has a smaller volume than the cardiac chamber, which is progressively reduced toward the posterior end at the foregut-midgut junction. The setal covering is dense at the entrance to the compaction zone. The crest of the cardio pyloric valve, along with dorsal margins of the filter press and inter-ampullary ridge, forms the floor of the pyloric compaction zone (pcz) (Fig. 2). The lateral walls of the compaction zone have a pair of pyloric channels, which anteriorly extends into the cardiac chamber on either side of the median tooth. Posteriorly, these dorsolateral channels become more lateral and terminate adjacent to the pylorohepatopancreatic valve. The pyloro-intestinal valve occurs at the foregut-midgut junction. As observed in the SEM analysis, the pylorointestinal valve (piv) (Fig. 2) comprises protrusions of the dorsal and lateral walls at the posterior end of the pyloric chamber and terminates within the intestine's lumen.

Discussion

The main features of the foregut of *Metapenaeus monoceros* conform with the general body plan of Decapods—the tubular esophagus transfers ingested material from the ventral mouth to the cardiac chamber of the foregut. Longitudinal folds in the wall accommodate the expansion of the lumen when food passes. Besides, posteriorly directed setae lining probably helps them transfer food bolus upwards into the cardiac chamber. The wall at the junction between the esophagus and cardiac chamber being modified to form a sphincter is also described in other Decapods (Barker and Gibson, 1978; Felgenhauer and Able, 1989; Factor, 1995). The sphincter probably prevents the reflux of ingested material from the cardiac chamber (Powell, 1974). In addition, the sphincter contributes to the posterior movements of solids within the chamber (De Jong and Casanova, 1997).

The cardiac chamber of *Metapenaeus monoceros* is an elongated sac with calcified structures in the interior identical to other Decapods (Icely and Nott, 1992; Ullrich and Storch, 1993; Abrunhosa and Melo, 2008). A cardiac setal screen with five separate groups of setae covering the cardiac chamber floor plays a significant role in determining particle sizes permitted to enter the ventrolateral filtration channels. The dense mat of cardiac floor setae near the hastate plate, as observed in the *Metapenaeus monoceros,* indicates the sizes of the food particles that can move through this area. In *Fenneropenaeus merguiensis,* King and Alexander (1994) measured those particles and opined that those greater than 900 nm would be excluded from the primary filter. The structure equivalent to mesh in the cardiac setal screen was also below 1 μm in the present study. In other related studies from Crustacean foregut, the mesh size of the cardiac setal screen was measured (Powell, 1974; Kunze and Anderson, 1979; Ngoc-Ho, 1984). All estimates show that the screen retains particles greater than 1 μm. The filtrate that enters the superior cardiac channels has direct access to the pre-ampullary chamber of the gland filter in the pyloric stomach. It is estimated that the primary function of the setal screen is to filter the squeezed fluid of a particular size (>900 nm) from food mass. Thus, any triturated food is filtered first time on the floor of the cardiac setal screen

(Storch *et al.*, 2001). The filtrate is then transported via cardiac channels to the pyloric filters, and the solids are transferred into the dorsal portion of the pyloric stomach. Each of the two ventral pyloric chambers consists of numerous longitudinal channels covered with dense mats of setae that retain particles larger than 100 nm (Vogt, 2002). These filters serve for further filtration of the first filtrate. The secondary filtrate is then transported into the hepatopancreas tubules, where the nutrients are absorbed, and larger food particles that are too coarse to pass through the setal screen enter the midgut (Strus *et al.*, 2019).

Metapenaeus monoceros can ingest and process a wide variety of macro and microscopic food (Rao, 1988; Nandakumar and Damodaran, 1998; Devanand *et al.*, 2018), which has been confirmed by our observation during the present study. The gastric armature of the foregut suggests that the shrimp is adapted for the trituration of large food items since the median tooth is cusp shaped and equipped with curved lateral spines. The denticles of each lateral tooth are almost pointed and curved for a firm grip. The grinding surface area of lateral tooth denticles is suggestive of crushing ability. In addition to other soft prey, these shrimps are reported and found to feed on other Crustaceans, bivalves with calcareous shells, and mud and sand particles. Aspects of gastric mill function have been under study for many years. Suthers (1984) suggested that shrimps used their cardiac chamber as gizzards, where the gastric mill was used to mix digestible food with shell fragments and sand particles. Heinzel (1987) filmed two types of movement in the spiny lobster *Panulirus,* and it was found that the simultaneous movement of three teeth occurred to crush the food between their cusps. The lateral teeth were found to move medially at the base of the median tooth. The serrated edges of the lateral tooth were pushed against each other to fragment the food trapped by the cusps; subsequently, the lateral and median teeth moved towards each other to grind the food segments on the ridged surface of the median tooth. King and Alexander (1994) described a similar chewing and compression movement at the gastric mill level in *Fenneropenaeus merguiensis*. Therefore, it is understandable that the cardiac ossicles are pulled anteriorly while the pyloric ossicle is pulled posteriorly during chewing. This is responsible for causing the median tooth to swing anteriorly. Simultaneously the anterior cusps of the lateral teeth come together due to the anterior movement of their supporting cardiac ossicles. As a result of these movements, the anterior part of the cardiac chamber bulges anteriorly. This sequence of movements has probably several consequences: (1) food material may be crushed between the median tooth and the lateral teeth, although they do not appear to come into direct contact with one another; (2) the anterior part of lateral teeth may act as shears and slice food coming between them; (3) the anterior movement of the median tooth moves fluid from the digestive gland back into the cardiac chamber. During compression, cardiac ossicles are depressed towards the floor of the cardiac chamber, with the median tooth being forced further back. This motion may be repeated five times before a chewing sequence. Compression has probably two principal functions: (1) to hold the food within the cusps of the anterior part of lateral teeth, maximizing trituration, and (2) to squeeze fluid from the food mass so that it is forced into the ventrolateral filtration channels. The alternate action of both these movements allows only the finest particles, in a colloidal state or less, to enter the midgut gland or hepatopancreas. The sharp pointed accessory teeth, as evident from our observation, helps hold the food material within the cardiac chamber. Polychaetes, insect larvae, and other crustaceans identified from the foregut study probably are captured in a 'live' state by the shrimps. Therefore, it is evident that small living prey must be retained in the cardiac chamber for some time after feeding. Sharply curved denticles probably help hold the live prey during this time. King and Alexander (1994) reported that accessory teeth could further lacerate pulled triturated food matter during the anterior bulging

of a cardiac chamber. It is also suggested that the lateral accessory teeth and setation on the lateral walls are oriented to deliver solid material into the gastric mill.

The cardio pyloric valve ensures that the filtrate of the cardiac setal screen can pass uncontaminated food into the gland filter of the pyloric chamber, which lies posterior to it. Thick setal covering in this area, as observed in the present study, indicates selective particle size movement. It was observed by Powell (1974) that from the ventrolateral filtration channels, fluids were moved directly to the gland filter through the pyloric ventral fluid passageway. The structural and morphological aspect of gland filter has been reported in various Decapod species (Lin, 1996, 2000; Diaz *et al.*, 2008; Muhammad *et al.*, 2012; Lima *et al.*, 2016). All these studies reported the gland filter, as an inverted V covered with numerous stacks of overlapping fine setae located in the ventromedial side of the pyloric stomach. The gland filter shows a dense setal arrangement between the opening of lateral channels of the lower ampullary chamber. The position of each seta with setules, as observed from the SEM study, also gives some idea of the narrow spaces between them that act as the passageway of fine food particles to enter first in longitudinal channels and then into the antechamber of hepatopancreas. Investigating the functions of the gland filter in Crustacea, Powell (1974) suggested that cardiac setal screens might prevent the passage of material as small as 1 μm, similar to the mesh size measured for the ampullary setal screen. King and Alexander (1994) observed the forced movement of fluid and particles between the upper and lower ampullary chambers. The setules of the lower ampullary chamber were found to exclude particles exceeding about 170 nm and forcing their opening into the gland through longitudinal channels. Tidal movements in the gland filter, which oscillate material across the setal screen between the upper and lower ampullary chamber, were also observed in *Litopenaeus setiferus* (Lovett and Felder, 1990). Simon *et al*. (2012) found that the pore size of a spiny lobster (*Sagmariasus verreauxi*) was smaller than 1 μm. Sub-adults of *Penaeus monodon* allowed particles below 400 nm to pass through the hepatopancreatic lobules (Wade *et al.*, 2018), and the gland filter excluded larger molecules (>3 μm). The sieve exclusion limit of the gland filter of *Penaeus monodon* and *Penaeus vannamei* was found to be less than 1 μm (Pattarayingsakul *et al.*, 2019). It is also suggested that the gland filter ensures vigorous mixing of the filtrate from the cardiac chamber with digestive enzymes from the hepatopancreas, thereby promoting rapid chemical digestion after the physical mastication of food in the cardiac chamber (Icely and Nott, 1992). The pyloric compaction zone receives residual solid material from the cardiac stomach, including finer material collected on the cardiac setal screens. The residual bolus is squeezed to remove fluid and fine particles within the dorsal part of the pyloric chamber. Observations of Lovett and Felder (1990) and King and Alexander (1994) indicated that fluids in the compaction zone might be transferred to the cardiac chamber and digestive enzymes from the hepatopancreas. Lovett and Felder (1989) reviewed the literature and found that most descriptions related to the junction of the foregut with the midgut region are incomplete. The pylorointestinal valve is considered to control the final extrusion of fecal material into the intestine without contamination from the gland filter filtrate (Icely and Nott, 1992). Although comparative analyses of digestive tracts in Penaeid shrimps are scanty, several studies are on a wide range of other Decapods. The internal chewing structures of the foregut are almost absent in Palaemonid prawns (Lima *et al.*, 2016), while it is relatively simple in Caridean shrimps (Storch *et al.*, 2001) but elaborate in Penaeid shrimps, crayfish, and crabs (Icely and Nott, 1992; Vogt, 2002). On the other hand, within a given higher taxon, they are modified according to different feeding and dietary strategies (Brosing and Turkay, 2011). For example, the robustness of the gastric mill and the cardio pyloric valve directly reflected the level of macrophagy in different species of anomuran hermit crabs

(Kunze and Anderson, 1979). Icely and Jones (1978) found different gastric mill structures in four brachyuran fiddler crabs inhabiting the same shore. The gastric mill structure of three species of *Eucopia* was found to differ, as observed by De Jong and Casanova (1997). Pinn *et al.* (1999) found differences in the gastric mill structure of seven species of mud shrimps. However, studies on 15 species of astacid freshwater crayfish (Caine, 1975; Growns and Richardson, 1990) showed that the gastric mill varies little with diet, apart from some reduction in the size of teeth. Felgenhauer and Abele (1989) showed many examples of closely related species with similar foregut anatomy and broad dietary diversity in lower Decapoda. The form of foregut structure is believed to depend primarily on the phylogenetic history of the species, as established by Felgenhauer and Abele (1989). The differences are probably minor and related to broad dietary diversity. The gastric mill of *Metapenaeus monoceros* is a typical structure enabling them to crush hard food materials. Although macrophagous in nature, they can consume microorganisms too. The fine cardiac setal mesh is structural evidence of their ingestion of small food particles. The relatively simple yet robust median tooth and proportionately large lateral teeth with curved denticles indicate their deposit-feeding habit similar to other Crustaceans (Nickell and Atkinson, 1995; Pinn *et al.*, 1999). Dense internal setal covering observed in the cardiac (cardiac setal screen etc.) to the pyloric chamber (within gland filter, in the pyloric compaction zone e*tc*.) indicates their adaptation and ability to handle fine food particles in the foregut. King and Alexander (1994) reported on the fluid extraction and circulation in *Fenneropenaeus merguiensis* foregut. They observed the backward movement of fluid from the hepatopancreas through the fully enclosed passageway to the cardiac chamber. Circulating the digestive fluid in the foregut may increase digestion efficiency in shrimps. About 75% of the foregut contents of *Penaeus esculentus* were found to be cleared in 60 min with soft natural food (Hill and Wassenberg, 1987). The size exclusion limit of the lateral channels of gland filters of most investigated Decapods is below 1 µm (Lin, 1996; Simon *et al.*, 2012; Wade *et al.*, 2018). Pattarayingsakul *et al.* (2019) opined that the findings have important implications for preparing shrimp feeds that contain microencapsulated nutritional additives such as vitamins. The size of feed particles should be under 1 µm for their full utilization.

Conclusion

From the analysis of the foregut structure of *Metapenaeus monoceros,* it can be concluded that compounded feed particles of small sizes may be advantageous for their culture. Any supplementary feed, if used in the process of culture, should be in small amounts at a time to ensure total utilization of food for sustainability.

Acknowledgements

The authors thank the technicians of USIC, Jadavpur University and CDRI, Lucknow for their assistance during Scanning Electron Micrography. The authors also extend their gratitude towards the Head of the Department of Zoology, University of Calcutta; Dr. Soumyadip Punja and Mr. Soumyodeep Guha for their kindness and help. This work was supported by a project under Labonya Prova Bose Trust, Calcutta, India.

References

Abrunhosa F and Melo M. (2008) Development and functional morphology of the foreguts of larvae and postlarvae of three crustacean decapods. Braz J Biol. 68: 221-228.

Barker PL and Gibson R. (1978) Observations on the structure of the mouthparts, histology of the alimentary tract, and digestive physiology of the mud crab *Scylla serrata* (Forskal) (Decapoda: Portunidae). J Exp Mar Biol Ecol. 32: 586-592.

Boyd CE. (1999) Codes of (ID 14) Practice for Responsible Shrimp farming, Global Aquaculture Alliance, St. Louis, MO, USA, pp. 1-48.

Brosing A and Turkay M. (2011) Gastric teeth of some thoracotreme crabs and their contribution to the brachyuran phylogeny. J Morphol. 272: 1109-1115.

Brunet M, Arnauld J and Mazza J. (1994) Gut structure and digestive cellular processes in marine Crustacea,

In: Oceanogr. Mar. Biol. Annu. Rev., (eds.) Ansell A.D., Gibson R.N. and Barnes M., UCL Press, London, Vol. 32, pp. 335-367.

Caine EA. (1975) Feeding and masticatory structures of six species of the craysifh genus *Procambarus* (Decapoda, Astacidae). Forma Functio. 8(1): 49-66.

Ceccaldi HJ. (1997) Anatomy and physiology of the digestive system. In: Crustacean Nutrition, Advances in World Aquaculture Society, (eds.) D'Abramo L.R., Conklin D.E. and Akiyama D.E., World Aquaculture Society, Baton Rouge, L. A., pp. 261-291.

Ceccaldi HJ. (2006) The digestive tract: anatomy, physiology and biochemistry. In: Treatise on Zoology - Anatomy, Taxonomy, Biology. The Crustacea, (eds.) Forest J. and von Vaupel Klein J. C., Brill, Leiden, pp. 85-203.

Chakrabarty NM. (1981) Fishery and culture possibilities of estuarine prawns in Sunderbans. Seafood Export J. 13(5): 17-21.

Dall W. (1967) The functional anatomy of the digestive tract of a shrimp *Metapenaeus bennettae*, Recek and Dall (Crustacea: Decapoda: Penaeidae). Aust J Zool. 15: 699-714.

Dall W. (1992) Feeding, digestion and assimilation in Penaeidae. In: Proc Aquacult Nutrition Workshop, NSW Fisheries, Salamander Bay, NSW (Australia), pp. 57-63.

Dall W and Moriarty DJW. (1983) Functional aspects of nutrition and digestion, In: The Biology of Crustacea, Internal Anatomy and Physiological Regulation, (ed.) Mantel L.H., Academic Press, N Y, pp. 215-261.

Dall W, Hill BJ, Rothlisberg PC and Staples DJ. (1990) The Biology of Penaeidae. In: Advances in Marine Biology, Academic Press, London, pp. 1-489.

De-jong L and Casanova B. (1997) Comparative morphology of the foregut of three *Eucopia* species (Crustacea: Mysidacea : Lophogastrida). J Nat Hist. 31(3): 389-402.

Devanand TN, Anjanayappa HN, Naik M, Somashekara SR, Lakshmipathi MT and Panda K. (2018) Food and feeding habits of *Metapenaeus monoceros* (Fabricius, 1798) from Mangaluru coast. India J Exp Zool. 21(2): 995-999.

Diaz AC, Fernandez Gimenez, AV, Velurtas SM and Fenucci JL. (2008) Ontogenesis changes in the digestive system of *Pleoticus muelleri* (Decapoda, Penaeoidea). Invertebr Reprod Dev. 52: 1-12.

Factor JR. (1995) The digestive system. In: Biology of the lobster *Homarus americanus*. Academic Press, New York, pp. 395-440.

Felgenhauer BE. (1992) Internal anatomy of the Decapoda: An Overview, In: Microscopic Anatomy of Invertebrates: Decapoda, Crustacea, (eds.) Harrison F.W. and Humes A.G., Wiley-Liss, Inc., NY, pp. 291-311.

Felgenhauer BE and Abele LG. (1989) Evolution of the foregut in the lower Decapoda, In: Functional morphology of feeding and grooming in Crustacea, (eds.) Felgenhauer B.E., Watling L. and Thistle A.B., Crustacean Issues 6: 205-219.

Funge-Smith SJ and Briggs MRP. (1998) Nutrient budgets in intensive shrimp ponds: implications for sustainability. Aquaculture 164(1-2): 117-133.

Growns IO and Richardson AMM. (1990) A comparison of the gastric mills of nine species of parastacid crayfish from a range of habitats, using multivariate morphometrics (Decapoda: Astacoidea). Crustaceana 58: 33-44.

Heinzel HG. (1987) Spontaneous and proctolin induced modes of operation of the isolated gastric osillator and of the gastric mill in the intact animal. In: The Crustacean Stomatogastric system, (eds.) Selverston A.I. and Moulin M., Springer-Verlag, NY, pp. 175-180.

Hill BJ and Wassenberg TJ. (1987) Feeding behaviour of adult tiger prawns, *Penaeus esculentus* under laboratory conditions. Aust J Mar Freshwat Res. 38: 183-190.

Icely JD and Jones DA. (1978) Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an East African shore. Est Coast Mar Sci. 6: 315-325.

Icely JD and Nott JA. (1992) Digestion and absorption: Digestive system and associated organs. In: Microscopic Anatomy of Invertebrates: Decapoda, Crustacea, (eds.) Harrison F.W. and Humes A.G., Wiley-Liss, Inc., N Y, pp.147-201.

King RA and Alexander CG. (1994) Fluid extraction and circulation in the proventriculus of the banana prawn *Penaeus merguiensis* de Man. J Crust Biol. 14: 497-507.

Kunze JC and Anderson DT. (1979) Functional morphology of the mouthparts and gastric mill in the hermit crabs *Clibanarius taeniatus* (Milne Edwards), *Clibanarius virescens* (Krauss), *Paguristes squamosus* McCulloch and *Dardanus setifer* (Milne Edwards) (Anomura:Paguridae). Aust J Mar Freshw Res. 30: 683-722.

Lima JF, Garcia JS and Tavares M. (2016) Foregut morphology of *Macrobrachium carcinus* (Crustacea, Decapoda, Palaemonidae). Acta Amaz. 46(2): 209-218.

Lin FY. (1996) Structure of the gland filters in the pyloric stomach of *Penaeus japonicas* (Decapoda: Penaeidae). J Crust Biol. 16(3): 515-521.

Lin FY. (2000) Scanning electron microscopic observations on the gland filters of the pyloric stomach of *Penaeus monodon* and *Metapenaeus ensis* (Decapoda, Penaeidae). Crustaceana 73(2): 163-174.

Lovett DL and Felder DL. (1989) Ontogeny of gut morphology in the white shrimp *Penaeus setiferus* (Decapoda, Penaeidae). J Morphol. 201: 253-272.

Lovett DL and Felder DL. (1990) Ontogeny of kinematics in the gut of the white shrimp *Penaeus setiferus* (Decapoda, Penaeidae). J Crust Biol. 10: 53-68.

Meiss DE and Norman RS. (1977) Comparative study of the stomatogastric system of several decapod crustacea I: Skeleton. J Morphol. 152: 21-54.

Muhammad F, Zhang ZF, Shao MY, Dong YP and Muhammad S. (2012) Ontogenesis of digestive system in *Litopenaeus vannamei* (Boon, 1931) (Crustacea: Decapoda). Italian J Zool. 79: 77-85.

Nandakumar G and Damodaran R. (1998) Food and feeding habits of the speckled shrimp *Metapenaeus monoceros* (Fabricius). J Mar Biol Assoc India 40(1-2): 30-43.

Ngoc-Ho N. (1984) The functional anatomy of the foregut of *Porcellana platycheles* and a comparison with *Galathea squamifera* and *Upogebia deltaura* (Crustacea: Decapoda). J Zool Lond. 203: 511-535.

Nickell LA and Atkinson RJA. (1995) Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. Mar Ecol Prog Ser. 128: 181-197.

Pattarayingsakul W, Pudgerd A, Munkongwongsiri N, Vanichviriyakit R, Chaijarasphong T, Thitamadee S and Kruangkum T. (2019) The gastric sieve of penaeid shrimp species is a sub-micrometer nutrient filter. J Exp Biol. 222: 1-11.

Pinn EH, Nickell LA, Rogerson A and Atkinson RJA. (1999) Comparison of gut morphology and gut microflora of seven species of mud shrimp (Crustacea: Decapoda : Thalassinidae). Mar Biol. 133(1): 103-114.

Powell RR. (1974) The functional morphology of the foreguts of the thalassinid crustaceans, *Callianassa californiensis* and *Upogebia pugettensis.* Univ Calif Publ Zool. 102: 1-41.

Rao GS. (1988) Studies on the feeding biology of *Metapenaeus monoceros* (Fabricius) along the Kakinada coast. J Mar Boil Assoc India 30(1-2): 171-181.

Simon CJ, Carter CG and Battaglene SC. (2012) Development and function of the filter-press in spiny lobster, *Sagmariasus verreauxi*, phyllosoma. Aquaculture 370-371: 68-75.

Sousa L and Petriella M. (2006) Morphology and histology of *P. argentines* (Crustacea, Decapoda, Caridea) digestive tract. Biocell 30(2): 287-294.

Storch V, Bluhm BA and Arntz WE. (2001) Microscopic anatomy and ultrastructure of the digestive system of three Antarctic shrimps (Crustacea: Decapoda: Caridea). Polar Biol. 24: 604-614.

Strus J, Znidarsic N, Mark P, Bogataj U and Vogt G. (2019) Structure, function and development of the digestive system in malacostracan crustaceans and adaptation to different lifestyles. Cell Tissue Res. 377: 415-443.

Sudarsan D and Josheph PJ. (1975) On the location of a potential prawn fishing ground of the West Bengal coast. J Mar Biol Assoc India 17: 247-250.

Suthers IM. (1984) Functional morphology of the mouthparts and gastric mill in *Penaeus plebejus* Hess (Decapoda, Penaeidae). Aust J Mar Freshw Res. 35: 785-792.

Ullrich B and Storch V. (1993) Development of the stomach in *Euphausia superba* Dann (Euphausiacea). J Crust Biol. 13: 423-431.

Vogt G. (2002) Functional anatomy. In: Biology of freshwater crayfish, (ed.) Holdich D.M., Blackwell Science, Oxford, pp. 53-151.

Wade NM, Bourne N and Simon CJ. (2018) Influence of marker particle size on nutrient digestibility measurements and particle movement through the digestive system of shrimp. Aquaculture 491: 273-280.

Walting L. (2013) Feeding and digestive system. In: The natural history of the Crustacea. Vol. 1: Functional morphology and diversity. (eds.) Walting L. and Thiel M., Oxford University Press, New York, pp. 237-260.

Wolfe SH and Felgenhaure BE. (1991) Mouthparts and foregut ontogeny in larval, postlarval and juvenile spiny lobster *Panulirus argus* Latreille (Decapoda, Palinunidae). Zoologica Scr. 20: 57-75.