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Mouthpart morphology of phyllosoma of the tropical spiny lobster *Panulirus homarus* (Linnaeus, 1758)

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ABSTRACT

Mouthpart morphology of *Panulirus homarus* phyllosoma larva was studied under scanning electron microscope in order to analyse the developmental changes during growth. Phyllosoma larvae have six pairs of mouthparts (mandibles, maxillule, maxilla, maxillipeds I, II, and III), labrum, and paired paragnaths. Increased length of second and third maxillipeds in late stage phyllosoma resulted in the increase of oral field, thus increasing its ability to catch prey. Labrum and paired paragnaths form a semienclosed oral chamber where mastication by the mandibles occurs. The improved threshing and tearing efficiency in late instars (stage VI-VIII) is facilitated by morphological changes in the mouthparts *viz*., increase in oral field, increased robustness and number of spinose setations of maxillule, and lengthy maxillipeds, indicating that the late instar larvae can process fleshier prey as compared to the early instar counterparts.

Keywords: Mouthpart morphology, *Panulirus homarus*, Phyllosoma larva, Scanning electron microscopy, Spiny lobster

Introduction

In recent times, the pressure to increase lobster production from the exploited fisheries has stimulated interest in their aquaculture potential. One prominent candidate species is *Panulirus homarus* (Family: Palinuridae), an ecologically significant tropical spiny lobster, which plays an important role in shaping tropical reef systems along the south-west and south-east coast of India. Since most of the lobster fisheries are either fully exploited or in the verge of extinction, cultured phyllosoma are considered the most sustainable option for aquaculture as this does not involve the removal of juveniles from already depleted wild stocks (Schaap, 1997). There is a global interest for the culture of spiny lobsters to boost its production and to ensure sustainability of spiny lobster fishery. The greatest challenge to establish a lobster aquaculture industry is the development of commercial scale larval rearing system for the phyllosoma larvae. Depending on the family and the species, the phyllosomal larval phase may range from 4 months to 2 years, consisting of 6-15 morphological stages, with a final planktonic larval peurulus stage (Abrunhosa and Kittaka, 1997). The larval phase of *P. homarus* was predicted to be 9-11 months with 10-12 stages (Berry, 1974). Though the life cycle has been completed in a number of species like *Jasus verreauxi* and *Jasus edwardsii* (Nishida *et al*., 1990; Nelson *et al*., 2002; Cox and Johnston, 2003a; b) commercial scale rearing of *P. homarus* has been unsuccessful to date, with high mortalities often occurring in early to mid larval stage. Attempts have been made to culture this particular species available in tropical waters since 1980s but without any significant success. Till today, no effort has been given to perfect the technology, perhaps either due to its long larval phase or presumably due to the limited knowledge of developmental changes occurring in mouthpart morphology and preference in their food and feeding habits. Earlier attempts to culture phyllosoma larvae of *P. homarus* under laboratory conditions in India were only partially successful, and attained a maximum of stage VI within a span of 52-54 days (Radhakrishnan and Vijayakumaran, 1994; Vijayakumaran and Radhakrishnan, 1986). An in-depth knowledge of the chronological changes occuring in mouthparts during the course of larval development of phyllosoma larvae could provide an understanding about the nature of feed required with every change in stage. Mouthpart morphology of various adult palinurid lobsters was studied in detail by various workers (Patwardhan, 1935; Paterson, 1968; Maynard and Dando, 1974; Mikami and Takashima, 2000), but very few studies were reported on mouthparts of phyllosoma larvae. Mouthparts have been comprehensively studied in larval nephropid lobster (Hinton and Corey, 1979; Factor, 1977; 1981) and scyllarid lobsters (Mikami and Takashima, 1993). There is little information on the developmental changes in mouthpart morphology of *P. homarus.*

In the present context, we have made an attempt to study the developmental changes in the mouthpart morphology that occur chronologically in early

(stage I-III), mid (stage IV-V) and advanced stages (stages VI onwards) of cultured *P. homarus* phyllosoma larvae, using scanning electron microscopic (SEM) analysis.

Materials and methods

Maintenance of Panulirus homarus broodstock

Experimental work was carried out at Marine Hatchery Complex, Central Marine Fisheries Research Institute, Kochi, Kerala, India. Berried female of *P. homarus* having total length (TL) 310 mm; carapace length (CL) 100 mm; and weighing 750 g were collected from south-west coast of India (N 8.09^0, E 77.35^0) at a depth of 5-7 m, by skin divers in December 2005. The captive broodstock were maintained in outdoor circular holding tanks (4 m diameter) of 10^4 l capacity. The environmental parameters *viz.*, temperature, salinity, and pH were maintained in the order of 26–30 ^oC, 33–35 ppt, and 7.5-8.5, respectively. The lobsters were fed with fresh mussel (*Perna indica* and *P. viridis*), clam, or shrimp meat. Seawater was filtered through 1 µm and sterilised by ultraviolet radiation before using in the experimental tanks.

Phyllosoma larval rearing

First instar phyllosomata gathered at the surface of the tanks under light, were scooped up with a beaker. About 200-300 healthy, active and free-swimming larvae were used for conducting the experiment. Cylindroconical non-transparent FRP tank having a water holding capacity of 150-200 l was provided with mild aeration. About 10-15 l algal culture of *Nannochloropsis salina* (20-30 million cells l^{-1}) was added to the phyllosoma rearing system to maintain the algal count. Environmental parameters were monitored and maintained at optimum. Bacteriological quality indicating total plate count (TPC) and water quality parameters *viz.*, dissolved ozxygen, ammonia, nitrite and nitrate were analysed once in a week. Probiotic bacteria (Cycle, Biological Aquarium Supplement, USA) were added once in a week (10 ml per tank). Instar-II *Artemia* nauplii (0.45-0.48 mm) were fed to phyllosoma for the initial 10 days till it reached stage III. Subadult *Artemia* metanauplii (1.14-1.31 mm, 5 days old) were fed for the next 12-14 days (stages IV and V) or juvenile *Artemia* for further 16-20 days of the culture period (stage VI onwards). Phyllosoma were fed with enriched *Artemia* at a rate of 3-5 numbers per ml every day, following daily total water exchange, and flushing away uneaten *Artemia*. Progressive stages of phyllosoma larvae were collected after each moult; the developmental stage was identified and confirmed under light microscope (model SZ-PT, Olympus, Japan) following larval classification as per Radhakrishnan and Vijayakumaran (1994) at a magnification of 40X. Larval measurements were recorded using ocular micrometer within the microscope. Phyllosoma larvae were grouped into early (stage I–III), mid (IV–V), and late (VI–VIII) larval stages based on the development.

Scanning electron microscopy

Live phyllosoma larvae of each stage were collected during May-June 2005, and the larval stages were fixed in chilled (4 ^0C) buffered glutraldehyde (3%, v/v) for 4 h. The fixed larvae were thoroughly washed with a buffer made of sodium cacodylate (0.2 M), NaCl (0.2 M), and sucrose (15% w/v) mixed in the ratio 6:1:1 (v/v/v), and post-fixed with 1% osmimum tetroxide (OsO_4) for 2 h. The pereiopods were trimmed, and the larvae were dehydrated in ascending grade of acetone (30%, 50%, 70%, 80%, 85%, 90%, and 95% v/v), with two changes of 20 min each, and absolute acetone with two changes of 30 min each. The dehydrated larvae were subjected to critical point drying, and were sputter-coated with gold (Robinson *et al*., 1987). The larvae were observed under a Hitachi H-600 Electron Microscope with H-6010A scanning attachment operated at 50 KV accelerating voltage and photographs were taken. The differentiation of various stages (stage I-VIII) was carried out primarily based on the morphological parameters *viz.,* development of pereiopods, number of setae on exopods, and endopods.

Statistical analyses

The mouthpart dimensions as measured at different stages of phyllosoma were subjected to one-way analysis of variance (ANOVA). Correlations between mouthpart dimensions were investigated using SPSS (ver. 13.0) software. Pairwise comparisons after ANOVA were made using Tukey's multiple range test. A significance level of 95% (p=0.05) was used throughout. All measurements were performed in triplicate and values were expressed as mean $\pm$ standard deviation (S.D.).

Results

Morphology of phyllosoma larvae

The general morphology of phyllosoma larvae of *P. homarus* is illustrated in Fig. 1. The body of larvae, which is dorsoventrally flattened, is composed of two parts, cephalic and thoracic parts. The lobes of the digestive gland can be observed through the transparent cuticle of the cephalic shield. The thorax of the larvae bears three pairs of pereiopods (Fig. 1) and six pairs of mouthparts comprising mandibles, maxillule, maxilla, maxillipeds, labrum, and paragnaths (Fig. 2a, 2b and 2c). The size, compactness, shape, and number of setae changed as development proceeds. The relative spatial location of mouthparts was consistent during the developmental stages, but the distance between maxillule and maxilla, as well as second and third maxillipeds increased during development. The oral field was measured as the distance between

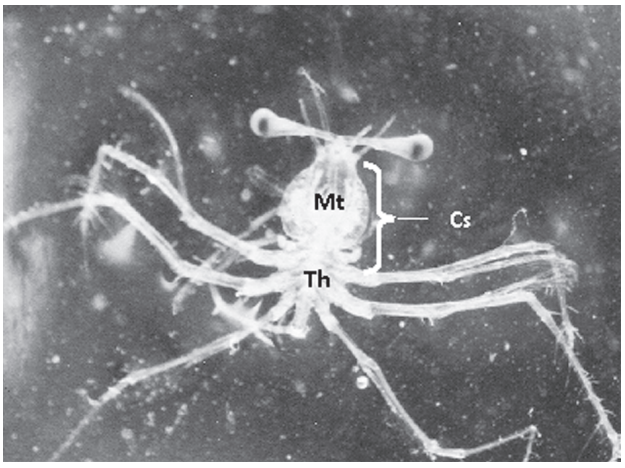

Fig. 1. Light microscopy picture of *P. homarus* phyllosoma larva, showing external morphology: cephalic shield, mouth, and thoracic region with appendages. Stage I, Magnification 40X. Cs, Cephalic shield; Mt, mouth; Th, thorax

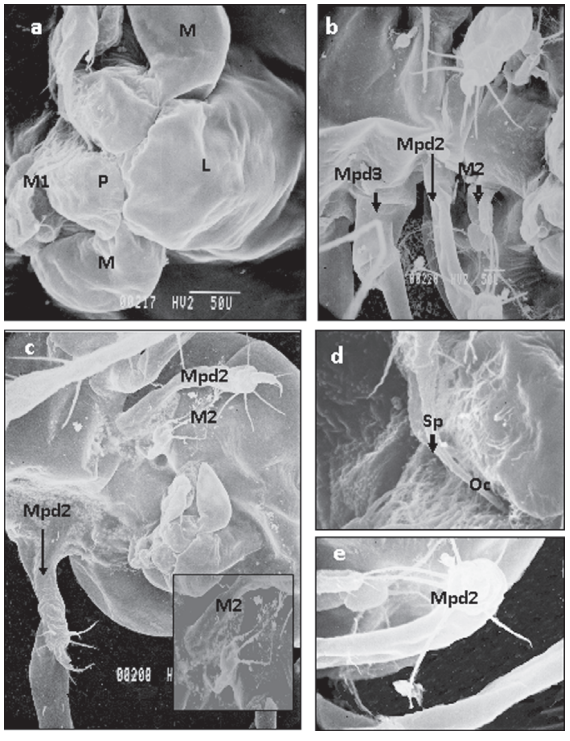

Fig. 2. Scanning electron micrographs of the mouthparts of *P. homarus* phyllosoma larvae. (a) Frontal view of the inner mouthparts, maxillule, labrum, paragnaths and mandibles. Stage I, Scale 50 µm. (b) Oral region showing spatial relationship between mouthparts. Stage I, Scale 50 µm. (c) spatial location of mouthpart in the cephalic shield. Scale 50 µm. (d) Posteroventral view of maxillule, paragnaths. Stage I, Scale, 50 µm. (e) Second maxillipeds. Stage I, Scale, 50 µm. L, labrum; M, mandibles; M1, maxillule; M2, maxilla; P, paragnaths; Mpd2, second maxilliped; Mpd3, third maxilliped; Sp, spine; Oc, oral cavity

mandible and the base of third maxilliped, and it appeared to be significantly larger in advanced stage (mid and late stage) larvae, exhibiting an increase from 492 µm (IV stage) to >700 µm (stage VII) (Fig. 3a, 3b; Table 1). The maximum width between the mandibles is termed as mouth-field which revealed an increase from 361 to 579 µm, and the mouth aperture from 14 to 68 µm in stage I and stage VII, respectively. Increase in the mouth aperture width was not in proportion with the increase in total length of phyllosoma larvae (1.06% in stage II to 1.5% in stage VII of total length) (Table 1).

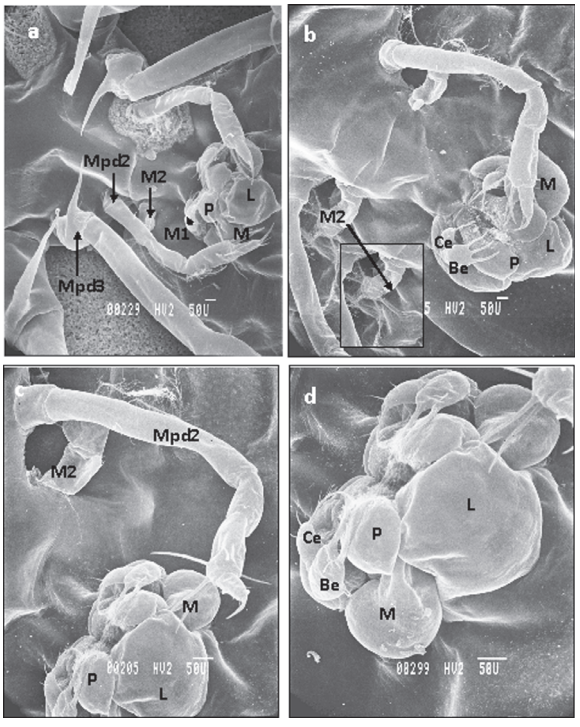

Fig. 3. Scanning electron micrographs of the mouthparts of *P. homarus* phyllosoma larvae. (a) Oral region showing the spatial relationship between mouthparts. Stage IV, Scale, 50 µm. (b) Oral region showing the spatial relationship between mouthparts. Stage VII, Scale, 50 µm. (c) Oral region showing the spatial relationship between mouthparts. Stage VI, Scale, 50 µm. (d) Frontal view of the inner mouthparts with basial endites, coxal endites, labrum, mandibles, paragnaths. Stage VII, Scale, 50 µm. L, labrum; M, mandibles; P, paragnaths; M1, maxillule; M2, maxilla; Be, basial endites; Ce, coxal endites; Mpd2, second maxilliped; Mpd3, third maxilliped.

Labrum and paragnaths

Labrum is a large fleshy structure lying in the anterior-most region, just above the mandible while a pair of paragnaths are located lateral side. Labral and paragnath width increased from 153 to 232 µm and 93 to 118 µm (Table 1) from stage I to stage VII, respectively. The space between the lower lip of labrum and paired paragnaths

forms an oral cavity where mastication occurs consisting of scale-like teeth directed towards the cavity from the labrum and paragnaths. The density of setae increased from stage V onwards in the oral cavity (Fig. 4b and Fig. 5a). Labrum and paragnaths are almost triangular and round shaped in stage I. In addition, 2-3 cuticular pores (1.56 µm diameter) were apparent from stage IV onwards, which found to increase in number with development. No gap was observed between labrum and paragnaths in stage I, but from stage IV onwards the gap increased considerably (Fig. 3a and 4f).

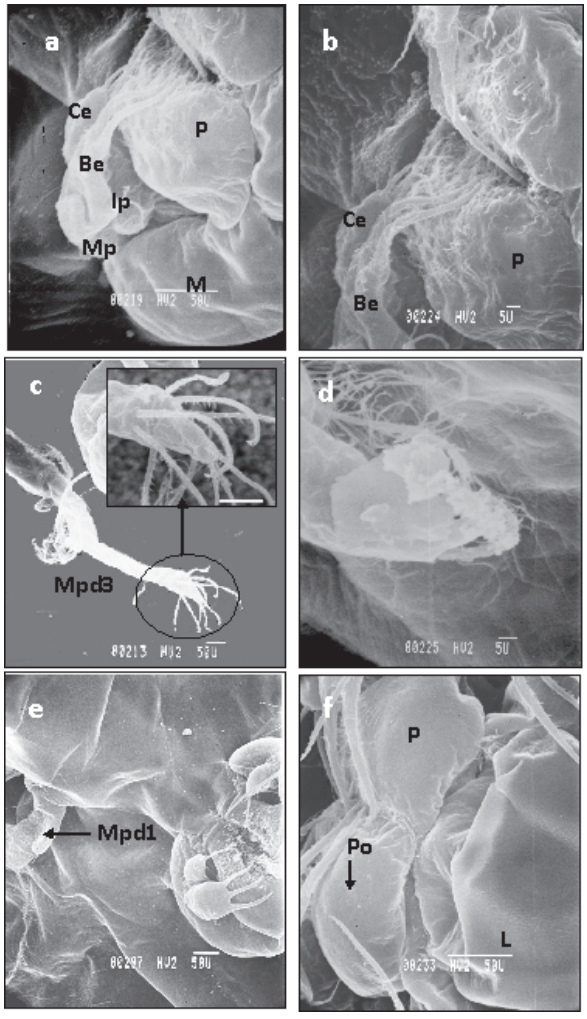

Fig. 4. Scanning electron micrographs of the mouthparts of *P. homarus* phyllosoma larvae. (a) Ventrolateral view of mandibles with molar process, incisor process, paragnaths and maxillulewith basial endite and coxal endites. Stage I. Scale, 50 µm. (b) Zoomed picture of paragnaths, first maxillae, spines of basial endites projecting into the oral cavity. Stage I. Scale, 5 µm. (c) Third maxilliped. Stage I, Scale, 50 µm. (d) Maxilla. Stage I. Scale, 5 µm (e) Oral cavity showing mouthpart, basial endites, coxal endites, maxilla, first maxilliped. Stage VII. Scale, 50 µm. (f) Pore on the surface of paragnaths, fleshy mass between labrum and paragnaths. Stage IV. Scale, 50 µm. Mpd1, first maxilliped; Mpd2, second maxilliped; Mpd3, third maxilliped; Be, basial endites; Ce, coxal endites; L, labrum; M, mandibles; P, paragnaths; Ip, incisor process; Mp, molar process; Po, Pore

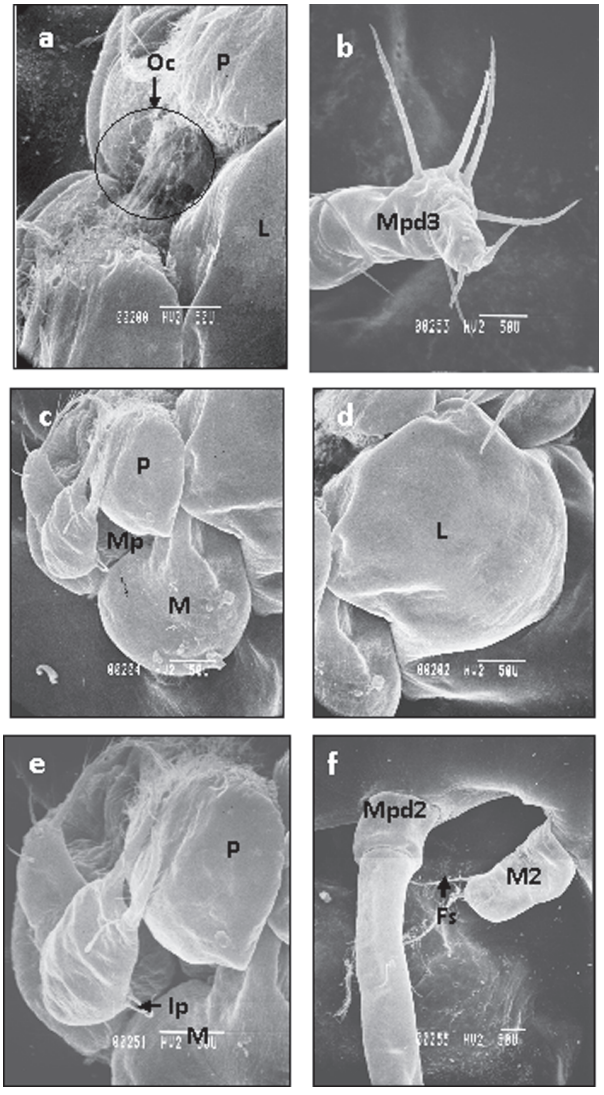

Fig. 5 Scanning electron micrographs of the mouthparts of *P. homarus* phyllosoma larvae. (a) Frontal view of the inner mouthparts, showing oral cavity enclosed by labrum, paragnaths. Stage VII. Scale, 50 µm. (b) Second maxilliped. Stage VII. Scale, 50 µm. (c) Lateral region of inner mouthparts showing labrum, paragnaths, molar process, mandibles, basal and coxal endites. Stage VI. Scale, 50 µm. (d) Zoomed picture of labrum. Stage VII. Scale, 50 µm. (e) Projected region between paragnaths, mandibles and first maxillae. Stage VII. Scale, 50 µm. (f) Zoomed view of maxilla with filamentous setae. Stage VII. Scale, 50 µm. L, labrum; M, mandibles; P, paragnaths; Po, pore; Ip, incisor process; Mp, molar process; M2, maxilla; Mpd2, second maxilliped; Mpd3, third maxilliped; Fs, filamentous setae.

Table 1. Mouthpart dimensions (μm) in different stages of *P. homarus* phyllosoma larvae [a]

Phyllosoma mouthparts	Larval stages			
	I	II	IV	VII
Mouth field [b]	361 ± 1.53c	468 ± 1.73b	492 ± 1.85b	579 ± 2.68a
Oral field [c]	338 ± 1.74c	500 ± 1.29b	492 ± 2.10b	700 ± 2.08a
Mouth aperture [d]	14 ± 2.00c	17 ± 1.96bc	22 ± 1.95b	68 ± 1.28a
% Mouth aperture in total length	1.06 ± 0.04a	1.19 ± 0.04a	0.8 ± 0.28b	1.5 ± 0.16a
Mandible width	101 ± 2.69b	112 ± 1.90b	107 ± 2.84b	171 ± 2.07a
Labrial width	153 ± 3.65b	175 ± 4.20b	207 ± 1.09a	232 ± 2.64a
Paragnath width	93 ± 1.77b	113 ± 2.08a	114 ± 3.11a	118 ± 1.69a
Distance between:				
1) M1 & M2	53 ± 2.07c	108 ± 1.55bc	214 ± 2.14b	350 ± 1.86a
2) Mpd1 & Mpd2	40 ± 3.60c	42 ± 1.58c	85 ± 2.97b	191 ± 2.68a
3) Mpd2 & Mpd3	21 ± 1.62c	58 ± 2.78b	66 ± 1.33bc	191 ± 1.88a

[a] Total length (TL) of the phyllosoma larval stages I, II, IV, and VII are 1.33, 1.43, 2.72, and 4.40 mm, respectively, as measured from anterior tip of cephalothorax to posterior tip of abdomen; [b] Mouthfield (μm) was measured as the distance measured across widest lateral edges of the mandibles; [c] Oral field (μm) is the distance between mandible and maxilliped 3; [d] Mouth aperture (μm) is expressed as the lateral distance across mouth aperture at widest point. M1, M2, Mpd1, Mpd2, and Mpd3 are referred to as maxillule, maxilla, first maxillipeds, second maxillipeds, and third maxillipeds, respectively. The data represent the mean value of three replicates (mean ± S.D.). Different letters (a-c) within rows indicate significant differences between the mean values (ANOVA, p = 0.05).

Mandibles

A pair of asymmetrical mandibles is located on either side of labrum projecting from the thin space between labrum and paragnaths. Origin of mandibles is below the labral lower lip and top portion of paragnaths, with a length of 75 and 125 μm. The width of mandible increased from 101 to 171μm from stage I to stage VII (Fig. 2a and 3d). The mandible consists of three portions *viz.,* incisor process, molar process, and mandibular palp. The mandibular palp was absent in earlier stages (upto stage IV) but was found in the late stages (stage V onwards). The molar process is covered by small knob-like process, surrounded by slender sharp teeth that are larger towards the opening of the oral cavity (Fig. 4a and 5e). Width of the mandibles was more than its length in stage I-III (Fig. 2c), and it exhibited further increase in later stages of larval development (Fig. 5c).

Maxillule

Maxillule comprised of two parts *viz.*, basial and coxal endites located below the paragnaths. Both endites have spinose projections entering into the oral cavity (Fig. 2d). The spinose projections present on both endites of maxillule increased in number during the growth process. The basal and coxal endites of stage I have two medially directed projections bearing a number of sharp spines (Fig. 4b), while stage IV – VII have three projections on the basial endite (Fig. 4e). These projections were found to intermesh immediately ventral to the paragnaths in front of the oral cavity.

Maxilla

A pair of maxilla are located postereolateral to the maxillule, each consisting of a flattened basal protopodite, and a flattened distal exopodite, with four (stage I – III) (Fig. 2c and 4d) or five (stage IV –VII) (Fig. 3b) elongated pappose setae. The strength and the surface area of these setae increased with development forming the periphery of the oral region (Fig. 5f). Distance between first maxilla to second maxilla increased from 53 to 350 μm (Table 1) from stage I to stage VII developmental stage of phyllosoma.

First and second maxillipeds

In the early phyllosomal stages, first maxillipeds appear like small emerging bud located at the base of maxillule (stage I) (Fig. 2b). A small seta was evident on the distal tip in stage IV. Maxilliped I is extra robust and stretched out (Fig. 4e) in advanced stages (stages VI and VII). The second maxillipeds were located posterior to maxillule at a distance of 62 and 100 μm as in stage I and stage VII, respectively (Fig. 3a, 3c). They are elongated and each consists of five segments. The fourth segment consists of four simple setae, while the fifth has two robust, elongated spinose setae, and two simple setae at the distal tip (Fig. 5b). These setae grew stronger with change in stage, however, no change was apparent in their number as well as spatial arrangement throughout the developmental stages (Fig. 2e). The length of second maxillipeds was found to increase enormously extending from cephalic region to labium in stage I, and further extending to other mouthparts in stage VII.

Third maxillipeds

The third maxillipeds resemble more closely the second maxillipeds located posterior to the second maxillipeds. The structure revealed the presence of six

spinose setae on the fourth segment and three setae on the distal tip of fifth segment of stage I (Fig. 4c). These setae have two rows of pectinate denticles along the proximal shaft, which emerge into serrate scales on the distal shaft, to become densely arranged in stage VII. The increase in distance between maxilliped I to maxilliped II was found to be slightly lesser than between maxilliped II to maxilliped III (Table 1).

Discussion

The detailed mouthpart morphology was studied in different lobster species (Patwardhan, 1935, Paterson, 1968, Maynard and Dando, 1974; Mikami and Takashima, 2000), however, very few studies have been attempted on its larvae (Mikami and Takashima, 1994). Mouthpart morphology exhibits little changes in its basic structure during larval development. However, increase in the size of mouthparts, oral chamber, robust setation, and spinose projections on the maxillule between early and late stage phyllosoma larvae suggest better capacity to manipulate larger prey, and effective mastication of food items with increase in size of the larvae. The presence of barbed setae on the maxilla, maxillipeds, incisor, molar processes, and scaled labral teeth imply that the mouthpart of stage I-III are well adapted for catching, tearing, and masticating soft, fleshy, and gelatinous food items like *Artemia*. In contrast, nephropid lobster larvae have heavily chitinised mandibles with a wide crushing surface and well developed maxilla and first maxillipeds that allow ingesting hard and calcified foods from early instar itself (Hinton and Corey, 1979; Factor, 1981). Paragnaths formed a semi enclosed chamber covering the lateral sides of the oral cavity lying over the mandibles in the larvae of *P. homarus*.

Phyllosoma larvae have a unique feeding behavior, as they employ the sharp spine at the tip of pereiopods to strike the prey. The feeding behavior of the phyllosoma larvae is indicative of their predatory nature (Kittaka, 1994; Doutsu *et al*., 1996). The larvae use their pereiopods for capturing prey, maxillipeds, maxillule, and maxilla for holding, and mandibles for mastication of food. The labrum provides a rigid abrasive surface for prey processing, and assists in external mastication. The paragnaths hold food pieces in place, while the mandibles cut them into smaller particles. Prey capture and manipulation between instar I–VIII *P. homarus* phyllosoma larvae was similar to that exhibited by early and late instar *J. edwardsii* and *J. verreauxi* (Nishida *et al*., 1990). The elongation of projections on the maxillule, and on the second and third maxillipeds resulted in the increase of oral field finally attributing to the ability of the larvae to catch prey located in wider area (Fig. 3). Mouthpart morphology revealed that although the distance between the maxillae and maxillipeds increased considerably, the spatial arrangement remained same between the mouthparts. This in turn resulted in the widening of oral field as apparent in mid (stage IV-V) to late instar larvae (stage VI onwards). The advanced larval stages (VI-VIII) by virtue of their increased robustness of mouthpart appendages facilitate an efficient manipulation of the food items into smaller pieces, which are more acceptable to the larvae. The larger pieces of prey items (like juvenile *Artemia* sized >1.50 mm as observed in this experiment) were readily fed by the advanced stage (VI-VIII) phyllosomata, owing to the well developed mandibles in this stage meant for effective grinding of the food items. While early and mid instar *P. homarus* phyllosoma larvae effectively capture the softer prey items like freshly hatched *Artemia*. The larger oral field facilitated with increased robustness of setae, and a greater number of spinose projections on the maxillule of late instar phyllosoma larvae suggests that the size of the prey manipulated and ingested becomes larger with the development of larvae. It was observed that growth in mouthfield was not in proportion with the body size of the larvae. This indicates mouthparts of the late stage larvae are well equipped with the ability to shred and tear larger food items efficiently. As the larvae grow, they find it difficult to capture young fast moving *Artemia* nauplii. It is evident that the larger sized *Artemia* move slowly than the smaller instar-II *Artemia* (0.45-0.48mm), and the mouthpart appendages of the late stage phyllosoma are well equipped to grasp them. Moreover the energy spent in catching food will be less and the energy gained due to the assimilation of bigger size *Artemia* will be high. But in the case of early instar phyllosoma larvae mouthpart appendages are not long and robust enough to efficiently grasp them. This result is consistent with the report of Cox and Johnston (2003a), which is attributed to the fact that the energy required for digestion of these big size *Artemia* was less than that spent on the intake of newly hatched *Artemia*. Similar observations were made by Abrunhosa and Kittaka (1997) in *J. edwardsii* phyllosomata (stage III and V), which are capable of feeding on 2-3 mm *Artemia,* while younger larvae (stage I) were able to feed on 1 mm *Artemia.*

This improved processing capacity implies that phyllosoma become more adapt at processing fleshier, muscular, and more fibrous prey items like juvenile *Artemia* from stage VI onwards. Therefore changes in feeding behavior were consistent with these morphological differences between instars. The finding of the present study pertaining to the developmental changes in the mouthpart morphology occurring during the chronological changes in cultured *P. homarus* phyllosoma larvae will enable to take up further studies on its dietary preference and digestive capabilities.

References

Abrunhosa, F. A. and Kittaka, J. 1997. Effect of starvation on the larvae of *Homarus americanus* (Decapoda, Nephropidae) and phyllosoma of *Jasus verreauxi* and *J. edwardsii* (Decapoda, Palinuridae). *Bull. Mar. Sci.,* 61: 73 –80.

Anonymous. 2004. *Statistics of Marine Product Exports*, 35: 195-202.

Berry, P. F. 1974. Palinurid and scllarid lobster larvae of the Natal coast, South Africa. Oceanography Research Institute (Durban), *Invest. Rep.,* 34: 1-44.

Cox, S. L. and Johnston, D. J. 2003a. Feeding biology of spiny lobster larvae and implications for culture. *Rev. Fish. Sci.,* 11: 89 –106.

Cox, S. L. and Johnston, D. J. 2003b. Developmental changes in the structure and function of mouthparts of phyllosoma larvae of the packhorse lobster, *Jasus verreauxi* (Decapoda: Palinuridae). *J. Exp. Mar. Biol. Ecol.,* 296: 35-47.

Doutsu, Y., Seno, K. and Inoue, S. 1996. Rearing experiments on early phyllosomas of *Ibacus ciliatus* (Von Siebold and I. Novemdentatus Gibbies, Crustacea: Reptantia) *Bull. Fac. Fish.*, Nagasaki University, 21: 181-94.

Factor, J. R. 1977. Morphology of the mouthparts of larval lobsters *Homarus americanus. Am. Zool*., 17: 971.

Factor, J. R. 1981. Development and metamorphosis of the digestive system of larval lobsters, *Homarus americanus* (Decapoda: Nephrophidae). *J. Morph.,* 169: 225-242.

Hinton, D. J. and Corey, S. 1979. The mouthparts and digestive tract in the larval stages of *Homarus americanus*. *Can. J. Zool.,* 57: 1413– 1423.

Kittaka, J. 1994. Culture of phyllosomas of spiny lobster and its application to studies of larval recruitment and aquaculture. *Crustaceana,* 66: 258–270.

Maynard, D. M. and Dando, M. R. 1974. The structure of the stomatogastric neuromuscular system in *Callinectes sapidus*, *Homarus americanus* and *Panulirus argus* (Decapoda; Crustacea). *Philos. Trans. R. Soc. B.,* 268: 161–220.

Mikami, S. and Takashima, F. 1993. Development of the proventriculus in larvae of the slipper lobster, *Ibacus ciliatus* (Decapoda: Scyllaridae). *Aquaculture,* 116: 199-217.

Mikami, S. and Takashima, F. 1994. Functional morphology of the digestive system. In: Phillips, B. F., Cobb, J. S. and Kittaka, J. (Eds.), *Spiny Lobster Management*, Blackwell, Oxford, p. 473 –482.

Mikami, S. and Takashima, F. 2000. Functional morphology of the digestive system. In: Phillips, B. F., Cobb, J. S. and Kittaka, J. (Eds.), *Spiny Lobster Management,* 2nd edn, Fishing News Books, Oxford, p. 601– 611.

Nelson, M. M., Cox, S. L. and Ritz, D. 2002. Function of mouthparts in feeding behaviour of phyllosoma larvae of the packhorse lobster, *Jasus verreauxi* (Decapoda: Palinuridae*). J. Crust. Biol.,* 22(3): 595–600.

Nishida, S., Quigley, B. D. Booth, J. D., Nemoto, T. and Kittaka, J. 1990. Comparative morphology of the mouthparts and foregut of the final-stage phyllosoma, puerulus, and post-puerulus of the rock lobster *Jasus edwardsii* (Decapoda: Palinuridae). *J. Crust. Biol*., 10(2): 293– 305.

Paterson, N. F. 1968. The anatomy of the Cape rock lobster, *Jasus lalandii* (H. Milne Edwards). *Ann. S. Afr. Mus.,* 51: 1 –232.

Patwardhan, S. S. 1935. On the structure and mechanism of the gastric mill in Decapoda 4. The structure of the gastric mill in Reptantous Macrura. *Proc. Indian Acad. Sci. B*., 1: 414– 422.

Radhakrishnan, E. V. and Vijayakumaran, M. 1994. Early larval development of the spiny lobster *Panulirus homarus* (Linnaeus, 1758) reared in the laboratory. *Crustaceana,* 68: 151-159.

Robinson, D. G., Ehler, U. E. Herken, R. Hermann, B. Mayer, F. and Schurmann, F. W. 1987. *Methods of preparation for Electron Microscope: An introduction for the biomedical science.* Springer-Veragl, Berlin Heidelberg, p. 145-171.

Schaap, A. 1997. Tasmania looks to rock lobster culture. *Austasia Aquacult.,* 11: 40–45.

Vijayakumaran, M. and E. V. Radhakrishnan. 1986. Effect of food density on feeding and moulting of phyllosoma larvae of the spiny lobster *Panulirus homarus* (Linnaeus). *Proceedings of the Symposium on Costal Aquaculture,* 4: 1281-1285.

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