Sensory, feeding, and digestive systems in the phyllosoma and puerulus of palinurid lobsters

SHUHEI NISHIDA

Ocean Research Institute, The University of Tokyo, 1-15-1 Minamidai, Nakano, Tokyo 164-8639, Japan
(nishida@ori.u-tokyo.ac.jp)

SUMMARY: Palinurid lobsters spend their early life as a planktonic phyllosoma larva and swim back and settle to the coast as puerulus. Both of these stages have sensory, feeding, and digestive organs characteristic to the stages and closely related to their behavior and life history strategies. The known sensory organs include the numerous mechano- and chemosensory receptors in the phyllosoma, and the well-developed antennal mechanoreceptors in the puerulus. The morphological changes of feeding- and digestive systems through these stages suggest non-feeding and use of stored energy in the puerulus, physiological- and biochemical evidence for which has accumulated through recent studies. The natural food of phyllosoma, the role of the 'dorsal organ', and the sensory mechanism for puerulus' coast-directed approach are still unsolved interesting topics.

KEYWORDS: early-life stages, palinurids, functional morphology, non-feeding

INTRODUCTION

The palinurid lobsters drift in offshore waters as a planktonic phyllosoma larva and settle in the form of a puerulus, a natant stage performing a long-distance swim to the coast.¹⁾ Owing to recent investigations the ecology of palinurids during these larval- and post-larval stages has now been better understood. Particularly the non-feeding and use of stored energy during the puerulus,^{2,3)} a major strategy for settlement, now appears to be largely confirmed,⁴⁾ wherein functional morphology played a vital role in presenting the hypotheses which later were tested by ecological-, physiological-, and biochemical researches. Meanwhile, still much remains to be solved on the early-life ecology as a whole, wherein interesting hypotheses and cues to further research might be presented from morphological information. This paper reviews recent advances in the morphological research on the sensory, feeding, and digestive systems during the early life stages of the palinurid lobsters, discusses functional/ecological significance of the systems, and attempts to give some prospects for future research.

SENSORY SYSTEM

While the eyes are among the most distinct receptors in the palinurid lobsters throughout their life-stages, little is known on their structure and function particularly during the larval stages, and it is only suggested that vision must be important in the behavior in the phyllosoma, as indicated by their well-developed eyes and a large number of

innervating neurons.⁵⁾

Among other receptors, integumental sensilla have been studied in some details. The final-stage phyllosoma of *Jasus edwardsii* possesses seven types of organs on the integument of body trunk, antennules and antennae; these are plumose setae, simple setae, porous setae, aesthetasc setae, simple pores, dorsal cuticular organs and dome-shaped structures.⁶⁾ The functions presumed for these organs are: near-field water movement detection for the plumose setae, mechanoreception (but relevant stimulants unspecified) for the simple setae, and distant chemoreception for the aesthetasc setae. The dorsal cuticular organ resembles so-called 'dorsal organs' widely known in decapod larvae,⁵⁾ the function of which is only speculated as chemoreception or baroreception. The plumose setae and simple pores are abundant on the dorsal surface of body trunk, while the dorsal cuticular organs are restricted to the dorsal surface of the cephalosome and the aesthetasc setae to the antennule, suggesting that the dorsal surface of the body trunk is one of the major sites of receptors of near-field water movement.⁶⁾

In the puerulus and post-puerulus, the receptors on the antenna and the antennule, major sites for ambient-stimulus perception, have been examined.^{7,8)} Phillips and Macmillan⁷⁾ described, among others, an array of 'pinnate setae' extending through the length of the antenna in *Panulirus cygnus* with different arrangement between the puerulus and postpuerulus, and hypothesized that the whole antenna of the puerulus may serve as a vibration receptor, with the pinnate setae detecting minute movements of the

segments relative to each other.⁷⁾ They further suggested that the complex receptor system in the antenna plays a role in navigation during the puerulus' approach to the coast by orienting the animals to vibrational clues of coastal origin.⁷⁾ Jeffs *et al.*,⁸⁾ however, noted much similarity of the arrangement of the pinnate-setal system between the puerulus and postpuerulus of *Jasus edwardsii*, as well as their generality in the antenna among decapods, and stressed need for further behavioral/physiological evidence.

While the above findings clearly indicate a considerable change in the receptor system from phyllosoma to puerulus along with the drastic change of body form as a whole, they tell little about the targeted stimuli, or the exact functions of the receptors *in situ*. To fill this gap it would be interesting, from a viewpoint of functional morphology, to compare the types and arrangements of different receptors among pelagic larvae and post-larvae of different crustaceans, either closely- or distantly related, or with similar or different behaviors, while concurrent behavioral/physiological approach is undoubtedly important. It should be also noted, in the comparison of puerulus and postpuerulus, that the former encompasses not only a natant life but also a benthic life after settlement, hence an array of receptors for a benthic life would be a prerequisite, presumably including receptors with dual function for both natant and benthic life.

FEEDING SYSTEM

The developmental sequence in the morphology of feeding appendages and/or foreguts has been studied in *Jasus edwardsii*,^{9,10)} *Panulirus argus*,¹¹⁾ *P. japonicus*,¹²⁾ and *P. cygnus*.¹³⁾ and proved to be highly similar both between genera and between species. In general, the feeding appendages in the phyllosoma and postpuerulus are characterized by well-developed specialized setae/spines on the surfaces of food-manipulating appendages such as the maxillule and maxillipeds. In addition, the mandible of the phyllosoma has a well-toothed blade and a granular molar process, while it is heavily calcified in the postpuerulus. In contrast, the puerulus has maxillipeds and maxillae with only small numbers of setae, uncalcified mandibles with a rudimentary incisor. The foregut shows a similar trend of development: with well-developed grooves and brushes but no gastric teeth in the phyllosoma, well-developed ossicles, grooves, brushes, and strong gastric teeth in the postpuerulus, but only a small numbers of ossicles and setae, and rudimentary

lateral teeth in the puerulus.⁹⁾

These findings, incorporating other fragmental ecological/behavioral observations, led to the hypotheses that the natural diet of the phyllosoma may be relatively large and soft material existing *in situ*, and that the puerulus does not feed during some or all of its existence. The first hypothesis still remains to be tested, since we still have only poor information on the foregut contents of phyllosomas collected *in situ*; only nematocysts have been identified from feces of scyllarid phyllosomas, but not in palinurids.¹⁾ This observation, coupled with those on scyllarids mounting on jellyfishes and absence of recognizable material in the guts, suggests jellyfishes and other gelatinous plankton as possible foods. Possible approach will include immunochemical analysis of gut contents, and evaluation of phyllosoma's trophic position from stable-isotope ratios and lipid composition of body tissues.¹⁴⁾ The second hypothesis on the possible non-feeding status of the pueruli has been elaborated to include a possible use by the puerulus of stored energy accumulated during the phyllosoma,¹⁵⁾ and further stimulated histological, biochemical, and physiological researches that have been providing supportive evidences as described in the next section.

INTERNAL DIGESTIVE SYSTEM

The non-feeding hypothesis on the puerulus necessitated an array of researches into details of the physiological adaptation, including those on the histology of hepatopancreas and energy-reserve sites and biochemical analyses on elemental composition of tissues and energy requirements.

The structure of the hepatopancreas in the phyllosoma has been studied in the first-stage *Panulirus japonicus*¹²⁾ wherein the epithelium consists of four types of cells (E-, B-, F-, and R-cells) as reported in other decapods, and it was concluded that the hepatopancreas is the major site of extra- and intracellular digestion, as in the adult lobsters, and that the final phase of absorption occurs mainly within the R-cells, which are the most abundant cell type in the hepatopancreas. However, Macmillan *et al.*¹⁰⁾, who examined the first-stage phyllosoma of *Jasus edwardsii*, found only one cell-type resembling the E-cells. One of the possible causes for this difference may be insufficient coverage of the whole digestive cycle in the latter study while it appears to be sufficiently covered in the former; the fine structure and composition of hepatopancreatic cells in decapods are known to change according to phases in a digestive cycle,¹⁶⁾ which is an essential property

of digestive systems.

During their study on the hepatopancreas in *Jasus edwardsii*, Takahashi *et al.*¹⁵⁾ found 'fat bodies' associated with the hepatopancreas of settled pueruli and the first-molt postpueruli. The fat bodies got smaller as the lobsters developed from transparent (newly-settled) to pigmented pueruli, suggesting that the fat bodies are storage sites of energy for the puerulus' long-distance swim and for subsequent developmental changes after settlement. Along with this finding, Nishida *et al.*¹⁷⁾ examined structural changes in the hepatopancreas in these stages, wherein the newly settled puerulus only had 'young R-cells' which showed pinocytosis at the basal region, while R-cells with large lipid drops dominated the pigmented puerulus, and suggested transfer of stored lipid into the hepatopancreatic cells after settlement as a preparatory stage for the molt to the post-puerulus.

Data on metabolic activities in the larval- to juvenile stages have recently been accumulated including those on offshore-collected puerulus. Lemmens¹⁸⁾ examined *in situ* changes in C:N ratio of *Panulirus cygnus* as an indicator of energy reserves and found that the values increased towards the last phyllosoma and decreased considerably during the puerulus stage. The RNA/DNA ratio, an indicator for cellular activity, of the field-collected animals was also high in the final phyllosoma and decreased during the puerulus and the first-molt juvenile, and only slightly increased after second molt.¹⁹⁾ Laboratory experiments on the same species showed that oxygen consumption in pigmented pueruli and intermolt juveniles was substantially higher than in newly settled puerulus and that temperature increase had no significant effect on newly settled puerulus, unlike on the other stages.²⁰⁾ A recent, more direct observation on the biochemical composition of the *Jasus edwardsii* indicated a significant difference of lipid content between the offshore- and onshore-collected pueruli, and confirmed the lipid storage to suffice the energy demand for the puerulus' settlement.⁴⁾

CONCLUSION

The 'non-feeding' and 'energy reserve' hypotheses appears to be substantiated by the above findings, and the life-history strategy in the puerulus is now referred to as 'secondary lecithotrophy', a concept originally applied to hermit crabs.^{14,21)} While these progresses in our understanding of the early life history of palinurid lobsters appears to be a result of morphology-based hypothesis presentation followed

by appropriate testing through multidisciplinary approach, still many challenging mysteries remain, as summarized below.

(1) The natural diet of phyllosoma is still unknown, while 'soft' material is only suggested from mouthpart morphology. Novel approach¹⁴⁾ would be fruitful as mentioned above. (2) The mechanism for puerulus' direction detection in their approach to the coast is not known. Evidence from the antennal-receptor morphology in the puerulus and postpuerulus for the use of acoustic signal of coastal origin appears inconsistent between species and/or genera. Behavioral and physiological studies, as well as more extensive comparative morphology, are necessary. (3) The sensory biology of the larval- and postlarval stages should be intensively investigated, particularly on photobiology. In addition, The function of the 'dorsal cuticular organ' is essentially unknown. This organ is similar in appearance to those widespread in the integument of larval crustaceans and may be significant in larval migration and settlement in general. (4) The energy reserve sites and the structural changes of hepatopancreas during the late phyllosoma and newly-molted, offshore puerulus still remain to be investigated.

Finally, it should be noted that significant differences have been suggested in the behavior and morphology between palinurids and scyllarids, and between palinurid genera as well. Hence the functions and ecological role of the sensory, feeding, and digestive systems would be more clear by incorporating an evolutionary viewpoint. For a better understanding of the early life history of lobsters, it would be essential to synthesize our knowledge with their evolutionary history, based on phylogeny and biogeography.

ACKNOWLEDGMENTS

I thank Drs Jiro Kittaka and John D. Booth for their arrangement of and cooperation during the research project on which this review is based, and for their valuable discussion on the topics in question.

REFERENCES

1. Phillips BF, Sastry AN. Larval ecology. In Cobb JS, Phillips BF (eds) *The Biology and Management of Lobsters*. vol. 2, Academic press, New York, 1980, pp. 11-57.
2. Booth JD, Phillips BF. Early life history of spiny lobster. *Crustaceana* 1994; **66**: 271-294.
3. Butler MJ, Herrnkind WF. Puerulus and juvenile ecology.

- In Phillips BF, Kittaka J (eds) Spiny Lobsters: Fisheries and Culture, Blackwell Science, Oxford, 2000, pp. 276-301.
4. Jeffs AG, Willmott ME, Wells RMG. The use of energy stores in the puerulus of the spiny lobster *Jasus edwardsii* across the continental shelf of New Zealand. *Comp. Biochem. Physiol.* 1999; **A123**: 351-357.
 5. Laverack MS. Larval locomotion, sensors, growth and their implication for the nervous system. *Symp. zool. Soc. Lond.* 1988; No. 59: 103-122.
 6. Nishida S, Kittaka J. Integumental organs of the phyllosoma larva of the rock lobster *Jasus edwardsii* (Hutton). *J. Plankton Res.* 1992; **14**: 563-573.
 7. Phillips BF, Macmillan DL. Antennal receptors in puerulus and postpuerulus stages of the rock lobster *Panulirus cygnus* (Decapoda: Palinuridae) and their potential role in puerulus navigation. *J. Crust. Biol.* 1987; **7**: 122-135.
 8. Jeffs A, Diebel CE, Hooker SH. Arrangement and significance of pinnate sensory setae on antennae of the puerulus and post-puerulus of the spiny lobster, *Jasus edwardsii* (Palinuridae). *Mar. Freshwater Res.* 1997; **48**: 681-686.
 9. Nishida S, Quigley BD, Booth JD, Nemoto T, Kittaka J. Comparative morphology of the mouthparts and foregut of the final-stage phyllosoma, puerulus, and postpuerulus of the rock lobster *Jasus edwardsii* (Decapoda: Palinuridae). *J. Crust. Biol.* 1990; **10**: 293-305.
 10. Macmillan DL, Sandow SL, Wikeley DM, Frusher S. Feeding activity and the morphology of the digestive tract in stage-I phyllosoma larvae of the rock lobster *Jasus edwardsii*. *Mar. Freshwater Res.* 1997; **48**: 19-26.
 11. Wolfe SH, Felgenhauer BE. Mouthpart and foregut ontogeny in larval, postlarval, and juvenile spiny lobster, *Panulirus argus* Latreille (Decapoda, Palinuridae). *Zool. Scr.* 1991; **20**: 57-75.
 12. Mikami S, Greenwood JG. Functional morphology and cytology of the phyllosomal digestive system of *Ibacus ciliatus* and *Panulirus japonicus* (Decapoda, Scyllaridae and Palinuridae). *Crustaceana* 1994; **67**: 212-225.
 13. Lemmens JWTJ, Knott B. Morphological changes in external and internal feeding structures during the transition phyllosoma-puerulus-juvenile in the western rock lobster (*Panulirus cygnus*, Decapoda: Palinuridae). *J. Morph.* 1994; **220**: 271-280.
 14. McWilliam PS, Phillips BF. Metamorphosis of the final phyllosoma and secondary lecithotrophy in the puerulus of *Panulirus cygnus* George: a review. *Mar. Freshwater Res.* 1997; **48**: 783-790.
 15. Takahashi Y, Nishida S, Kittaka J. Histological characteristics of fat bodies in the puerulus of the rock lobster *Jasus edwardsii* (Hutton, 1875) (Decapoda, Palinuridae). *Crustaceana* 1994; **66**: 318-325.
 16. Al-Mohanna SY, Nott JA. R-cells and the digestive cycle in *Penaeus semisulcatus* (Cruatacea: Decapoda). *Mar. Biol.* 1987; **95**: 129-137.
 17. Nishida S, Takahashi Y, Kittaka J. Structural changes in the hepatopancreas of the rock lobster *Jasus edwardsii* (Cruatacea: Palinuridae) during development from the puerulus to postpuerulus. *Mar. Biol.* 1995; **123**: 837-844.
 18. Lemmens JWTJ. Biochemical evidence for absence of feeding in puerulus larvae of the Western rock lobster *Panulirus cygnus* (Decapoda: Palinuridae). *Mar. Biol.* 1994; **118**: 383-394.
 19. Lemmens JWTJ. Nucleic acid levels, cellular activity and growth during the puerulus stage of the Western Rock Lobster (*Panulirus cygnus* (George); Decapoda: Palinuridae). *J. Exp. Mar. Biol. Ecol.* 1995; **194**: 143-156.
 20. Lemmens JWTJ. The Western Rock Lobster *Panulirus cygnus* (George, 1962) (Decapoda: Palinuridae): the effect of temperature and developmental stage on energy requirements of pueruli. *J. Exp. Mar. Biol. Ecol.* 1994; **180**: 221-234.
 21. Anger K. Growth and exuvial loss during larval and early juvenile development of the hermit crab *Pagurus bernhardus* reared in the laboratory. *Mar. Biol.* 1989; **103**: 503-511.