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Revealing the natural diet of the phyllosoma larvae of spiny lobster

Andrew JEFFS *

Abstract An important bottleneck in the development of aquaculture of spiny lobsters is larval feeding and nutrition. Researchers have used a wide variety of natural foods and artificial food materials in attempts to improve the larval culture of these species. Unfortunately, very little is known about the natural feeding ecology and diet of spiny lobster larvae or phyllosomes. This paper reviews research undertaken in New Zealand over the past decade aimed at attempting to improve our understanding of the diet of spiny lobster phyllosomes.

Key words: spiny lobster, phyllosoma, diet, feeding behaviour, mouth-parts, food chain tracing

During the 1990's scientists at the National Institute of Water and Atmospheric Research undertook research aimed at developing methods for the larval rearing of two native species of spiny lobster in New Zealand, *Jasus edwardsii* and *Sagmariasus verreauxi* (Moss *et al*., 2001; 2004; Tong *et al*., 1997; 2000a; 2000b; 2000c; 2000d). Small numbers of pueruli were produced for both species after extensive culture periods in 1996 *J. edwardsii* in 416 days, and in 1999 *S. verreauxi* in 241 days. The key issues for culturing these larvae over such an extensive period were keeping them in suspension in culture, maintaining adequate water quality and feeding. The suspension of these naturally pelagic larvae was achieved through the use of an upweller tank (Illingworth *et al*., 1997), however, difficulties with maintaining water quality (Diggles *et al*., 2000) and feeding led to research on larval culture being paused whilst research on water conditioning bacteria (probiotics) and the natural diet of phyllosoma were progressed. Spiny lobster phyllosomes are extremely difficult to study in their natural pelagic environment due to their cryptic morphology, behaviour, and their relatively low abundance in the ocean. These are important reasons why there are no recorded observations of spiny lobster feeding in the wild (Cox and Johnston, 2003b). In the absence of opportunities for direct observation, indirect research approaches need to be used to elucidate the natural diet of phyllosomes. The research approaches used in New Zealand fell into five broad categories; feeding behaviour in captivity; feeding structures (appendages and mouthparts); digestive capacity (gut morphology and enzyme profiles); prey tracer studies (lipid biomarkers and genetic tools), and ecological associations. The results of the subsequent research on natural diet of phyllosoma have been outlined in this manuscript under these five research headings.

Feeding behaviour in captivity

Observations of the feeding behaviour of larvae in captivity is a useful technique for determining the methods for capturing and handling prey involved in feeding. This in turn can allow inferences to be made about the kind of natural prey items that might be captured in the wild, and also assist in the selection of cultured live prey, or for the design of artificial diet particles. Studies were undertaken of the feeding behaviour of the early larval development stages of *J. edwardsii* and *S. verreauxi* (Cox and Bruce, 2002; Nelson *et al*., 2002; Cox, 2004). Unfortunately, insufficient culturing resources were available to also examine behaviour in later developmental stages. The studies mostly involved analyzing video recordings of feeding events of cultured phyllosomes that were either

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*National Institute of Water and Atmospheric Research, P.O. Box 109-695, Auckland, New Zealand
E-mail: a.jeffs@niwa.co.nz

free-swimming or tethered.

These studies were useful in demonstrating that the early phyllosoma stages of both species are opportunistic feeders, capable of grabbing relatively large prey items using their pereiopods, usually after chance encounters with potential prey items. The captured prey was quickly and efficiently subdued and moved into position over the mouth ready for consumption. The feeding behaviour was consistent between the first three instars of both species suggesting that they do not specialize or change their diet over this period of development.

Feeding structures: appendages and mouthparts

Video recordings of the feeding of phyllosomes in captivity followed by subsequent microscopy of feeding appendages and mouthparts in a wide range of larval stages of *J. edwardsii* and *S. verreauxi* were useful in determining how the morphology of these structures related to feeding on potential prey items (Cox and Bruce, 2002; Nelson *et al*., 2002; Cox and Johnston, 2003a; 2003b; 2004). Again, from these studies it was possible to make inferences about the types of natural prey items that could be utilized by phyllosomes in their natural environment. The examination of the pereiopods of phyllosomes indicated that they had hydrodynamic and chemosensory setae which were involved in tactile and chemically induced prey capture behaviour. The mouthparts of the early larval stages were better suited to soft or fleshy prey items. However, there were marked changes in the structure of the mouthparts of *S. verreauxi* observed through the developmental stages indicating that their ability to handle and devour larger and more robust prey items increased dramatically in later larval stages.

Digestive capacity: gut morphology and enzyme profile

Video recordings of the feeding of larvae in captivity also allowed for observations of movement of food material into and through the gut. In addition, histological examination of the gut, and the identification and measurement of gut enzyme activities allowed for inferences to be made about possible natural diets (Nelson *et al*., 2002; Cox, 2004; Cox and Johnston, 2004; Johnston *et al*., 2004). Video observations of feeding showed that food was sucked into the foregut through peristalsis of the oesophagus and contractions of lobes of the digestive gland. The processing of food by the gut was found to become increasingly complex with larval development and this was mirrored in the greater complexity and robustness of the digestive system. For example, the foregut in the early phyllosomes of *S. verreauxi* consists of a simple chamber with two dorsal and ventral grooves and a few very small setae on the ventral floor. In mid-stage larvae the setae are more numerous and well developed, as are the dorsal and ventral grooves of the anterior foregut, which has also become more cuticularised. The ventral chamber has also become folded in order to form a filter press. In late-stage larvae this filter press has become even more complex and efficient. Changes in the gut morphology suggest that phyllosomes probably undergo marked dietary shifts at around instars 3 and 4 and again at instars 8 and 9. The gut of early instar phyllosomes appears well suited to processing soft prey such as fish larvae or gelatinous zooplankton, while later instars should be able to process much larger, fleshier prey, such as small crustaceans. Analyses of gut enzymes of phyllosomes of *J. edwardsii* tended to support this same conclusion with analyses of both cultured and wild larvae indicating they were all capable of readily digesting dietary protein, lipid, and carbohydrate, including chitin at all stages of development. Gut enzyme activities increased significantly with larval development, reflecting an increase in digestive capacity of later larval stages. There was a marked increase in protease, trypsin and amylase enzyme activity at stages VI and VII consistent with a marked change in diet. Overall, the results indicated that the larvae are capable of digesting a wide range of prey, but they will make best use of prey that are rich in protein and lipid.

Prey tracer studies: lipid biomarkers and genetic tools

Research on the distribution and abundance of phyllosomes and pueruli of *J. edwardsii* in the offshore waters off New Zealand and *P. cygnus* off Western Australia has led to opportunities to investigate their biochemical composition and that of by-catch species which could include potential prey species (Jeffs *et al*., 1999; 2001a; 2001b; 2002; 2004; 2005; Phleger, *et al*., 2001; Wells *et al*., 2001; Bradford *et al*., 2005; Phillips *et al*., 2006). These studies indicate that lipid plays an important role in the energetics and development of phyllosomes. Late-stage phyllosomes accumulate large amounts of lipid (up to 34.4% of dry mass in late-stage *J. edwardsii*) material mostly in a phospholipid format which is a relatively unusual storage lipid among marine organisms. These energy stores appear to be important for fueling the subsequent non-feeding puerulus stage. The phyllosomes have well developed lipid metabolic capabilities, such as being able to convert a variety of sterols to cholesterol, alter lipid chemical structures, and to selectively utilise different fatty acids while retaining others. Therefore, attempts to use fatty acid and sterol food chain tracing methods to identify the prey of phyllosomes were not particularly insightful (Jeffs *et al*., 2004). However, the results indicated that phyllosomes are likely to be opportunistic predators that feed on a variety of prey. Differences in the fatty acid profile between mid- and late-stage larvae were thought to be consistent with a possible dietary shift to some crustacean prey, such as shrimps, copepods and amphipods. The fatty acid food chain tracing techniques were useful in revealing the nature of the food web operating in oligotrophic conditions commonly found in the offshore waters east of New Zealand and Western Australia (Jeffs *et al*., 2004; Phillips *et al*., 2006). These food webs are typified by low productivity and high abundance of gelatinous zooplankton. This in itself would tend to suggest that gelatinous zooplankton would be an obvious food source for phyllosomes as they are large slow moving prey, with soft and fleshy bodies, and offering a relatively rich nutrient source. The difficulties with using fatty acid food chain tracing techniques with phyllosomes resulted in the recommendation to attempt to use emerging molecular genetic tools to identify prey species (Jeffs *et al*., 2004). Extractions of genetic material from the hepatopancreas of mid- to late-stage phyllosoma of the Japanese spiny lobster *Panulirus japonicus* have been recently used to identify the presence of DNA from Cnidaria and Urochordata (Suzuki *et al*., 2006). These results provide further support to the suggestion that gelatinous zooplankton play a key role in the nutrition of spiny lobster phyllosomes

Ecological associations

Studies of the distribution and abundance of phyllosomes of *J. edwardsii* in relation to potential prey species in the offshore waters of New Zealand are also helping to provide some insight into the predatory habits of these larvae (Bradford *et al*., 2005; Jeffs *et al*., 2006). Analyses of the catch of phyllosoma and by-catch species from trawls with a MIDOC net indicated that the vertical and horizontal distribution of by-catch of some taxonomic groups was strongly correlated with phyllosomes which may indicate an association of phyllosoma with their prey. The abundance of phyllosomes from all developmental stages (5-11) were found to be strongly correlated with total zooplankton biomass and the biomass of gelatinous zooplankton captured in the samples. The abundance of mid-stage (5-8) phyllosomes were also strongly associated with shrimp biomass, while the abundance of late-stage (9-11) phyllosomes was strongly associated with amphipod biomass. These developmental differences were also reflected in the vertical distribution of phyllosomes with the mid-stages tending to remain in surface waters both day and night (＜20 m) while the late-stages moved into deeper water during the day (20-50 m) along with the dominant potential prey category, gelatinous zooplankton. A gradual upwards shift in the vertical distribution of phyllosomes in the water column from stage 8 onwards was identified, which may also reflect a possible shift in diet of the phyllosoma. Overall, the results of this study when taken in the context of previous studies on phyllosoma feeding abilities and behaviour, strongly suggest that phyllosomes are preying on gelatinous zooplankton, as well as some small crustacean prey, and that there are marked changes in the prey between the mid- and late-stages of development.

Conclusions

Overall, the results of the various indirect studies of the natural diet of phyllosoma strongly suggest that phyllosomes are opportunistic predators that prey on a variety of species, but probably rely on gelatinous zooplankton when living in oligotrophic waters, as well as some small crustacean prey. There are marked changes in the prey between the mid- and late-stages of larval development that are evidenced through several indirect research methods. These dietary changes are likely to be associated with the late-stage larvae taking on a more active predatory role, pursuing more active prey with higher nutritive returns, such as larger crustaceans (*e.g.*, shrimps and amphipods). The application of emerging genetic "fingerprinting" techniques has the promise to further pinpoint the prey species of spiny lobster phyllosoma. The results of the studies to date would tend to suggest that artificial feeds should be soft to fleshy in texture and rich in protein and lipid. Given the size of some gelatinous zooplankton, and the body form of phyllosomes, it is possible that phyllosomes attach to living gelatinous zooplankton and feed on them for some time. This being the case, it may be possible to use static feed stations in phyllosoma culture systems.

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