



Spiny lobster development: do the final-stage phyllosoma larvae of *Jasus edwardsii* swim towards the coast?

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Abstract

Several papers from New Zealand have all suggested that late-stages, or at least the final-stage phyllosomas of *Jasus edwardsii* can swim horizontally from offshore to inshore towards the coast. This was largely based on the observation that the late-stage phyllosomas were distributed inshore of the mid-stage phyllosomas off the east coast of New Zealand. A review of these data, plus additional information on the diurnal vertical migration behaviour of the phyllosoma larvae of *J. edwardsii* not available at the time of publication of the earlier papers, suggests an alternative explanation. These new data clearly show different diurnal vertical migration behaviour of the mid and the late-stage phyllosoma. It is suggested that even small differences in the vertical movements of the phyllosoma larvae can result in dramatic changes in their horizontal distribution because these movements take them into different current layers and this, not horizontal swimming, is probably responsible for the different locations of the mid and late-stage phyllosomas of *J. edwardsii* off the east coast of New Zealand.

Keywords: Spiny lobster; final stage phyllosoma, puerulus, swimming, *Jasus edwardsii*, New Zealand

Introduction

The phyllosoma larvae of spiny lobsters undergo swimming movements that appear to be confined to diurnal vertical migration (DVM). Propulsion is achieved by rapid beating of thoracic appendages, viz. the pereopodal exopods which are fringed with natatory, plumose setae (Fig. 1a). These movements, upwards as dusk approaches and downwards near dawn, are critical in larval transport (see review by Booth and Phillips, 1994). However, several papers from New Zealand (Chiswell and Booth, 1999, 2005, 2008) have all suggested that late-stage or at least the final-stage phyllosomas of *J. edwardsii* can swim horizontally from offshore to inshore towards the coast.

In this review we examine the evidence both supportive of this phyllosomal swimming hypothesis and also examine other interpretations which might

be made of the data used to develop this hypothesis. Knowledge of the differences in, both morphology and behaviour between the phyllosoma stages and the puerulus (postlarva, Fig. 1b) of spiny lobsters is critical in the development of models to explain larval recruitment in this family.

Inadequate knowledge of this behaviour is probably the reason for the limited success of models such as that of Griffin *et al.* (2001) developed for *Panulirus cygnus* and that of Bruce *et al.* (2007) developed for *Jasus edwardsii*.

Terminology

Staging: Mid-Stage phyllosoma larvae of *J. edwardsii* are defined as V-VIII and late-Stage as X-XI, Stage XI being the final-Stage (Chiswell and Booth, 1999), slightly different in Bradford *et al.* (2005) late-Stage being VIIIA–XI using the staging of Booth (1994).

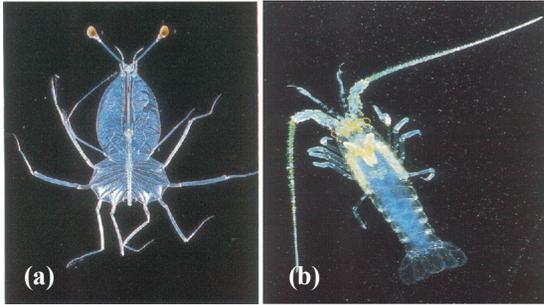


Fig. 1. Stages in early development of *Panulirus cygnus*: (a) late-stage phyllosoma, (b) puerulus. (Photographs not to scale). Note: photo (a) is of a preserved specimen and shows sampling damage - ruptured cephalic disc and missing pereopodal endopods, the exopods are present. From McWilliam and Phillips (2007)

Cincinnuli: These are a cluster of hooks near the end of the medial margin of the fully-developed appendix interna which articulates with the endopod of each pleopod in the puerulus. They function by attaching to the cincinnuli of the appendix interna of the opposite pleopodal endopod, thus providing synchronised sweeping movements of the paired pleopods and facilitating the strong, horizontal swimming of the puerulus. Although appendices internae buds usually appear in the penultimate and final-stage phyllosomas (Kittaka *et al.*, 2005, their Fig. 6, Part 17), it appears (from often inadequately detailed descriptions and figures) that cincinnuli do not develop until, and only in the puerulus stage of early development in any palinurid species described to date. The appendices internae are a characteristic morphological feature of the puerulus and are resorbed in the juvenile.

The evidence

Three papers by Chiswell and Booth (1999, 2005, 2008) present different evidence and comments in support of their phyllosoma swimming hypothesis.

Chiswell and Booth (1999) examined the distribution of the phyllosomas and pueruli of *J. edwardsii* off the east coast of New Zealand and observed, to their surprise, that the late-stage phyllosomas were distributed inshore of the mid-stage phyllosomas (their Fig. 3a and b). They then stated that “If there is no physical mechanism for producing such a distribution, then presumably a

biological mechanism exists, suggesting the possibility that the late-stage phyllosomas have a better horizontal swimming ability than previously thought, and are starting to migrate inshore prior to metamorphosis.”

Chiswell and Booth (1999) used modelling techniques to simulate the larval concentrations. They reported that the simulation suggested that passive drift alone would explain the distribution of the mid-stage phyllosomas but does not explain the distributions of the late-stage phyllosomas and pueruli. They concluded that if the late-stage phyllosomas were not actively swimming shoreward, “there must be some mechanism that differentially advects late-stage phyllosomas inshore compared to the mid-stages.” Chiswell and Booth (1999) pointed out that the numbers of late-stage larvae and pueruli outnumbered the numbers of mid-stage larvae. They suggested this was because of sampling error, but perhaps the mid-stage phyllosomas had already moulted to late-stage larvae and some of the latter to pueruli.

Chiswell and Booth (2005) examined relative distributions of mid- and late-stage phyllosomas, as well as pueruli, of *J. edwardsii* from five research cruises off the east coast of the North Island of New Zealand. On average, late-stage phyllosomas were found 49 km further inshore than mid-stage phyllosomas, but not over the shelf. However, two cruises showed a non-significant result and one station during one cruise and one transect during another cruise showed such high abundances of late-stage phyllosomas, which affected the analyses. When these outlier data were excluded, the differences in mid and late-stage distributions became significant with 99% confidence. Again these authors suggested that “One explanation for observed distribution differences is that the late-stage phyllosomas swim shoreward”.

Chiswell and Booth (2008) looked for sources and sinks of larval settlement in *Jasus edwardsii* around New Zealand. They used a modelling approach and phyllosomas were treated as passive drifters in the surface currents. Their only reference to phyllosoma swimming was a referral to their previous papers “Chiswell and Booth (1999, 2005)

suggested that late stage phyllosomas of *J. edwardsii* may exhibit directed swimming towards the coast during the last few weeks of their development, but there is not enough specific information on this behaviour to warrant incorporation in the present study.”

Diurnal vertical migration behaviour

As pointed out by Chiswell and Booth (1999), data on the vertical distributions of mid and late-stage phyllosoma of *J. edwardsii* were not available when they wrote their paper and therefore they could not examine whether this mechanism was involved in the phyllosoma larvae achieving these distributions. Chiswell *et al.* (2008) discussed the results of Bradford *et al.* (2005) on the vertical distribution and DVM of *J. edwardsii* off the east coast of the North Island of New Zealand. They pointed out that currents at 100 m depth will be slightly different to those at the surface, but they stated that they could not model the differences accurately, nor did they know the details of larval diel migration well enough to warrant including this process in their model.

The vertical distribution of phyllosomas of *J. edwardsii* and comparative data on the vertical movements of some other species was reported by Bradford *et al.* (2005) in their Table 1. The Table by Bradford *et al.* (2005) clearly shows different diurnal vertical behaviour of the phyllosoma larvae of the two developmental groups of *J. edwardsii*, but it did not include the data on *P. cygnus* from the study by Phillips and Pearce (1997) which has been included in Table 1 in this present paper.

This new data clearly shows that the later stages of the phyllosoma larvae, and the puerulus, are capable of making considerable vertical movements in the water column. It is likely that the vertical movements of *J. edwardsii* are more extensive than the studies have revealed to date.

Evidence from aquaculture

Chiswell and Booth (1999) suggested that the data from the aquaculture of *J. edwardsii* showed mid- and late-stage phyllosomas swimming in spirals in the direction in which the larva is headed (Kittaka, 1994). However, such swimming behaviour is highly

dubious for interpretation of their behaviour in the wild as, under aquaculture conditions, the phyllosomas are subjected to water currents created by the design of the culture system to keep them suspended in tanks.

Morphological evidence

Chiswell and Booth (1999) stated that in the final stage the pleopods are ‘almost’ as well developed as they are in the pueruli; but ‘almost’ is not identical. According to the descriptions of Kittaka *et al.* (2005) cincinnuli have not yet developed in the final-stage phyllosoma (Kittaka *et al.*, 2005 for Fig. 2a), and so the appendices internae are still not functional in swimming. While it is

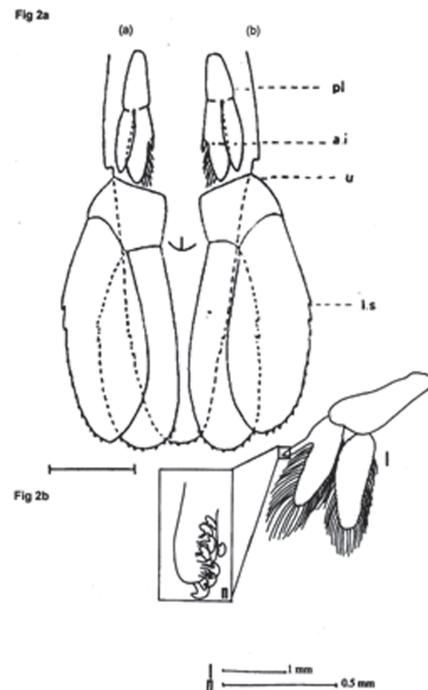


Fig. 2. (a) Uropods and pleopods of final phyllosomal instar of *Jasus edwardsii*. Labels are: pl: pleopod; u: pleopod; ai: appendix externa; ls: lateral spine. The scale on the Figure for 1 mm (from Kittaka *et al.*, 2005). (b) Right first pleopod of the puerulus of *Panulirus longipes bispinosus* with fully-developed appendix interna, labelled I; and enlargement of cincinnuli on its distal end, labelled n (from Inoue *et al.*, 2002).

possible that increased propulsion due to further (but still incomplete) development of the pleopods, in conjunction with beating of the natatory exopodal setae of the pereopods, may enhance the rate and extent of vertical swimming in the diurnal migrations of these phyllosomas (which remain much lower in the water column by day than do mid-stages), the question remains still: Are these larvae also capable of directional, horizontal swimming?

This question is also applicable to the final-stage phyllosomas of other species of *Panulirus* viz. *P. argus* described by Goldstein *et al.* (2008) and *P. ornatus* described by Smith *et al.* (2009). In both cases, the appendices internae are not yet functional. In the final phyllosoma of *P. argus*, the authors note that there are no cincinnuli present; they only appear in the puerulus. In the final phyllosoma of *P. ornatus*, cincinnuli are absent by default as the authors neither mention nor illustrate them, thus the appendices internae are not fully developed.

Discussion

The phyllosomal larvae and puerulus stages, which together make up the oceanic phase of the life cycle of spiny lobsters, have evolved with their current specialisations (in morphology and behaviour), which enable some unknown numbers of each cohort of each species to recruit successfully back to the coast and to the benthic stage. Each species, through natural selection, has probably developed slightly different behavioural traits which assist the larval recruitment of the species in the particular ecosystems in which they occur.

There are other physical mechanisms which transport numbers of late-stage phyllosomas back to near the continental (or insular) shelf region from which they originally hatched. The transport mechanisms which achieve this are ocean currents operating together with the vertical migration movements of the larvae.

Metamorphosis to the puerulus occurs near to but beyond the shelf (Phillips and McWilliam, 2009). If the phyllosoma do not metamorphose, they may continue to be transported coastward by the same mechanisms which brought them back to the area from offshore. They do not need to swim horizontally or navigate to do this. The final stages may have

improved vertical swimming ability, through further development of natatory setae not only on pereiododal exopods, but also on the endopods of the pleopods (Inoue *et al.*, 2002 for Fig. 2b).

These larger vertical movements may cause them to be transported horizontally but they do not need to swim horizontally to be transported shoreward.

It was Sir Alister Hardy in the 1950s who first proposed that the degree of DVM movements of zooplankton, coupled with surface currents and other water movements, could return animals from offshore areas to inshore areas (Hardy, 1969). We have to remember that it is a whole dynamic system involved and very hard to elucidate even modelling-known larval DVM ranges, and surface water movements of the particular region in which a final phyllosoma metamorphoses.

The data on the phyllosoma larvae of *P. cygnus* in Western Australia do not indicate any information on a distribution of different mid and final-Stage larvae such as that found for *J. edwardsii* by Chiswell and Booth (1999). The data shown in Phillips and Pearce (1997) indicate all late-Stage phyllosoma larvae of *P. cygnus* (Stages VI-IX) in the same area. However, final Stage (IX) phyllosomas of this species do make large DVM movements (Table 1).

Even small differences in the vertical movements of phyllosomal larvae can result in dramatic changes in their distribution. Studies of the phyllosomal larvae of the Scyllaridae in Western Australia, from the same samples used to catch the phyllosomas of *P. cygnus*, showed that the phyllosomas of *Scyllarus bicuspidatus* made similar diurnal movements to *P. cygnus*. The early-stage phyllosomas of *S. bicuspidatus* were at the surface at night and at 40 to 80 m during the day. Mid-stage and late-stage phyllosomas were at or near the surface at night and at 80 to 100 m during the day (Phillips *et al.*, 1981). These slight differences in diurnal vertical movements probably allowed these larvae to achieve a different geographic distribution to those of *P. cygnus*. The larvae of *S. bicuspidatus* were not transported offshore with the phyllosomas of *P. cygnus* but were able to remain on the continental shelf where they moulted into the nisto stage and recruited to the benthic population.

Table 1. Diurnal vertical distribution of phyllosomas of *J. edwardsii* in New Zealand from Bradford *et al.* (2005) and phyllosomas and pueruli of *P. cygnus* from Phillips and Pearce (1997).

Species	Phyllosoma stage	Day	Night
<i>Jasus edwardsii</i>	Mid-stage	20 m	20 m
	Late-stage	20-100 m or below	20 m
<i>Panulirus cygnus</i>	Mid and Final-stages	60-140 m	0-60 m
	Pueruli	100-340 m	0-40 m

Absence of identified water current or currents which carry the final- stage phyllosomas coastward is irrelevant. The oceanographers did not know of currents which might carry the early stage phyllosomas of *P. cygnus* offshore until this transport process was hypothesised by Chittellborough and Thomas (1969). The likely existence of such water movements capable of transporting the phyllosomas off Western Australia was then described by Creswell (1972) and then physically demonstrated by the biologists (Phillips *et al.*, 1979; Rimmer, 1980).

Examination of the morphology of integumental organs of the antennules, antennae and dorsal and ventral body surfaces of the final - stage phyllosoma of *J. edwardsii* examined by Nishida and Kittaka (1992) and compared with the morphology of sense organs of known function in other decapods, suggested that the dorsal surface of the body is one of the major sites of reception of near-field water movement. Their results also suggested that the antennae may have some auxiliary function in near-field, mechano- and chemo-reception, “but have little ability for such direction detection as required for long-distance navigation, assuming such an ability is dependent on the pinnate setal system unique to the antennae of the puerulus of *P. cygnus*” (Phillips and Macmillan, 1987).

The question of how the horizontally-swimming pueruli can navigate toward the coast is still not answered. Jeffs *et al.* (2005) listed and reviewed a number of possible navigational cues, but concluded that it is still no answer to how the pueruli orient towards the shore line. Thus, looking for “similar navigational systems” in final stage phyllosomas is not possible.

References

- Booth, J. 1994. *Jasus edwardsii* larval recruitment off the east coast of New Zealand. *Crustaceana*, 66(3): 295-317.
- Booth, J. D. and B. F. Phillips. 1994. Early life history of spiny lobster. *Crustaceana*, 66: 271-294.
- Bradford, R. W., B. D. Bruce and S. M. Chiswell. 2005. Vertical distribution and diurnal migration patterns of *Jasus edwardsii* phyllosomas off the east coast of the North Island. *N. Z. J. Mar. Freshwat. Res.*, 39: 593-604.
- Bruce, B., D. Griffin and R. Bradford. 2007. Larval transport and recruitment processes of southern rock lobster, FRDC 2002/007 Final Report, October 2007. IV : 105 pp).
- Chiswell, S. M. and J. D. Booth. 1999. Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. *Mar. Ecol. Prog. Ser.*, 183: 227-240.
- Chiswell, S. M. and J. D. Booth. 2005. Distribution of mid-and late-stage *Jasus edwardsii* phyllosomas: implications for larval recruitment processes. *N. Z. J. Mar. Freshwat. Res.*, 39: 1157-1170.
- Chiswell, S. M. and J. D. Booth. 2008. Sources and sinks of larval settlement in *Jasus edwardsii* around New Zealand: Where do larvae come from and where do they go? *Mar. Ecol. Prog. Ser.*, 354: 201-217.
- Chittellborough, R. G. and L. Thomas. 1969. Larval ecology of the Western Australian marine crayfish, with notes on other Palinurid larvae from the Eastern Indian Ocean. *Aust. J. Mar. Fresh. Res.*, 20: 199-223.
- Cresswell, G. R. 1972. Wind-driven ocean surface transport around Australia. *CSIRO Division of Fisheries and Oceanography Report*, 52: 1-5.
- Goldstein, J. S., H. Matsuda, T. Takenouchi and M. J. Butler. 2008. The complete development of larval Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) in culture. *J. Crustacean Biol.*, 28: 306-327.
- Griffin, D. A., J. L. Wilkin, C. F. Chubb, A. F. Pearce and N. Caputi. 2001. Ocean currents and the larval phase of Australian western rock lobster, *Panulirus cygnus*. *Mar. Freshwat. Res.*, 52: 1187-1199.
- Hardy, Sir. A. 1969. The open sea. Its natural history Part 1, *The World of Plankton*. Collins, London. (XV : 335 pp.)
- Inoue, N., H. Seckiguchi and H. Misaki. 2002. Pueruli of *Panulirus longipes bispinosus* (Crustacea, Decapoda, Palinuridae) stranded on the beach of Kuroshima Island, Ryukyu Archipelago, southern Japan. *Fisheries Sci.*, 68: 332-340.
- Jeffs, A., J. Montgomery and C. T. Tindle. 2005. How do spiny lobster post-larvae find the coast?. *N. Z. J. Mar. Freshwat. Res.*, 39: 605-617.
- Kittaka, J. 1994. Culture of phyllosomas of spiny lobster and the application to studies of larval recruitment and aquaculture. *Crustaceana*, 66: 238-270.
- Kittaka, J., K. Ono, J. D. Booth and R. Webber. 2005. Development of the red rock lobster, *Jasus edwardsii*; from egg to juvenile. *N. Z. J. Mar. Freshwat. Res.*, 39: 263-277.

- McWilliam, P. S. and B. F. Phillips. 2007. Spiny lobster development: mechanisms inducing metamorphosis to the puerulus: a review. *Rev. Fish. Biol. Fisheries*, 17: 615-632.
- Nishida, S. and J. Kittaka. 1992. Integumental organs of the phyllosoma larva of the rock lobster *Jasus edwardsii* (Hutton). *J. Plankton Res.*, 14: 562-573.
- Phillips, B. F. and D. L. Macmillan. 1987. Antennal receptors in puerulus and postpuerulus stages of the rock lobster *Panulirus cygnus* (Decapoda: Palinuridae) and their potential role in puerulus navigation. *J. Crustacean Biol.*, 7: 122-135.
- Phillips, B. F. and A. F. Pearce. 1997. Spiny lobster recruitment off Western Australia. *Bull. Mar. Sci.*, 61: 21-41.
- Phillips, B. F. and P. S. McWilliam. 2009. Spiny lobster development: where does successful metamorphosis to the puerulus occur?: a review. *Rev. Fish. Biol. Fisheries*, 19(2):193-215.
- Phillips, B. F., P. A. Brown and D. W. Rimmer. 1979. Distribution and dispersal of the phyllosoma larvae of the western rock lobster, *Panulirus cygnus*, in the south-eastern Indian Ocean. *Aust. J. Mar. Fresh. Res.*, 30:773-783.
- Phillips, B. F., P. A. Brown, D. W. Rimmer and S. J. Braine. 1981. Descriptions, distribution and abundance of the late larval stages of the Scyllaridae (slipper lobsters) in the south eastern Indian Ocean. *Aust. J. Mar. Fresh. Res.*, 32: 417-437.
- Rimmer, D. W. 1980. Spatial and temporal distribution of early-stage phyllosoma of western rock lobster, *Panulirus cygnus*. *Aust. J. Mar. Fresh. Res.*, 31: 485-497.
- Smith, G., M. Salmon, M. Kenway and M. Hall. 2009. Description of the larval morphology of captive reared *Panulirus ornatus* spiny lobsters, benchmarked against wild caught specimens. *Aquaculture*, 295: 76-88.

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