CSIRO PUBLISHING

Marine & Freshwater Research

Volume 48, 1997

A journal for the publication of original contributions
in physical oceanography, marine chemistry,
marine and estuarine biology and limnology

www.publish.csiro.au/journals/mfr

All enquiries and manuscripts should be directed to
Marine and Freshwater Research
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood Telephone: 61 3 9662 7618
Vic. 3066 Facsimile: 61 3 9662 7611
Australia Email: ann.grant@publish.csiro.au

Published by **CSIRO** PUBLISHING
for CSIRO Australia and
the Australian Academy of Science

© CSIRO Australia 1997 *Mar. Freshwater Res.*, 1997, **48**, 777–782

Influence of light regimes on phyllosomal growth and timing of moulting in *Thenus orientalis* (Lund) (Decapoda: Scyllaridae)

Satoshi Mikami[A] and Jack G. Greenwood[B]

[A]*Australian Fresh Corporation, 65 Berwick St., Fortitude Valley, Qld 4006, Australia; present address: QDPI Bribie Island Aquaculture Research Centre, PO Box 2066, Bribie Island, Qld 4507, Australia*
[B]*Zoology Department, The University of Queensland, St Lucia, Qld 4072, Australia*

Abstract. Newly hatched phyllosomas of *Thenus orientalis* (Lund) were successfully reared under conditions of natural light (D/L), continuous dark (24D) or continuous light (24L). Survival, duration of intermoult periods, moult increment in total body length, and timing of moulting through larval stages were monitored. Survival and growth under 24L was lower than that under D/L and 24D; this may be a result of decreased phyllosomal feeding activity under 24L, caused by a photopositive reaction drawing the phyllosomas away from food at the bottom. There were no differences in phyllosomal development under D/L and 24D. When phyllosomas were reared under D/L, moulting was synchronized and occurred around dawn. Moulting of those reared under 24D or 24L was not synchronized and occurred irregularly. These results indicate that, in phyllosomas, light regime influences the endogenous rhythmic function responsible for the regulation of moulting time. When phyllosomas reared under D/L metamorphosed to the nisto stage, synchronized moulting switched from dawn to after dusk. Furthermore, nistos and juveniles moulted only nocturnally, with apparent synchronicity. This suggests that the switch from planktonic to benthic lifestyle, with consequent different predation pressures, necessitates a change in the timing of moulting.

Introduction

Several ecological studies have examined behavioural responses of scyllarid and palinurid phyllosomas to environmental factors, particularly in relation to vertical migration (Rimmer and Phillips 1979; Phillips *et al.* 1979, 1981). However, the influence of environmental variables on behaviour remains unclear.

A number of studies have attempted to rear phyllosomas to the nisto/puerulus stage (see Kittaka 1994). However, in all previous studies except that of Kittaka *et al.* (unpublished, cited in Kittaka 1994), survival through to the nisto/puerulus stage has been very low (at best, just a few nistos/pueruli survived from newly hatched phyllosomas), and these studies have been mainly concerned with description of larval morphology. As a result, there is limited information on relationships between environmental factors and behavioural responses and growth of phyllosomas.

Thenus species have a wide tropical and subtropical distribution in the Indo-West Pacific region and inhabit relatively soft muddy or sandy substrata (George and Griffin 1972; Barnett *et al.* 1984; Kailola *et al.* 1993). In Australia, the two species of *Thenus*—*T. orientalis* and an undescribed *Thenus* species—are found along the northern coasts from Shark Bay in Western Australia to Coffs Harbour in New South Wales (Kailola *et al.* 1993). Until recently, there have been no published reports of the successful rearing of the phyllosomas of *Thenus* to the nisto stage, even though Ito (1988) reported culturing *T. orientalis* phyllosomas to the 4th (final) instar. Recently, Mikami (1995) reported an 80% survival success in culturing newly hatched phyllosomas of *T. orientalis* to the juvenile stage through four phyllosomal stages, taking approximately 30 days; that study detailed larval morphology and provided information on relationships between environmental factors and behavioural responses of phyllosomas.

The present paper describes the influence of light regimes (natural light, continuous dark and continuous light) on phyllosomal survival and growth, and the diel timing of moulting and metamorphosis in *T. orientalis*. The results provide comparative data for evaluating possible ecological relationships.

Materials and methods

Rearing conditions and larval growth

Ovigerous females of *T. orientalis* were caught by an otter trawler off Hervey Bay, south-eastern Queensland, in October 1993. The females were then transported to the Bribie Island Aquaculture Research Centre of the Queensland Department of Primary Industries in a 100-L plastic vessel containing approximately 40 L of lightly aerated sea water. Ovigerous females were maintained in a 14-m^3 holding tank equipped with a sand bottom filter. Temperature and salinity were maintained at 24–28°C and 34–35 respectively. These females were fed twice daily with frozen flesh of the mussel *Perna canaliculus*. When embryos became visibly amber-brown in colour, ovigerous females were removed to individual 200-L hatching tanks until the eggs hatched. Sea water flowed through the hatching tanks at approximately 40 L h^{-1}. A 500-μm mesh covered the outflow port to prevent the escape of hatched larvae.

Newly hatched phyllosomas (hatched on 26 November and 1 December 1993 from two females) were transferred from the hatching tanks to a temperature-controlled laboratory for rearing. They were reared in 1·2-L glass culture bowls containing approximately 1 L of sea water filtered

10.1071/MF97083 1323-1650/97/080777$05.00

through 1·0- and 0·5-μm cartridge filters. Each bowl was placed in a water bath equipped with a temperature-controlled immersion circulator to maintain constant water temperature. Larvae were transferred twice daily to new culture bowls containing clean new sea water. Finely chopped fresh flesh of the bivalve *Donax brazieri* was provided for food during the experiments, with 20–30 pieces (1–2 mm in size) being added to each culture bowl immediately after the transfer of larvae. Nistos were not fed.

Phyllosomas were reared under three different light conditions: natural light (D/L), continuous dark (24D) and continuous light (24L). Under D/L, 100 newly hatched phyllosomas (20 per bowl) were reared to the juvenile stage in an experimental room with a south-facing window under a natural photoperiod of approximately 14 h light and 10 h dark. Maximum light intensity was approximately 600 μmol m^{-2} s^{-1} at the water surface. Temperature was maintained at 26·5 ± 0·1°C. Under 24D and under 24L, 40 newly hatched phyllosomas (20 per bowl) were reared to the juvenile stage. The 24D group was maintained in a dark room equipped with a revolving door. Red illumination (Kodak OA Safelight filter) was used when water was changed in the bowls (approximately 15 min each time). The 24L group was illuminated at approximately 200 μmol m^{-2} s^{-1} at the water surface by an incandescent lamp mounted above the rearing bowls. Water was maintained at 26·5 ± 0·1°C (24D) or 26·4 ± 0·1°C (24L). All experiments were repeated twice with different batches of phyllosomas. Phyllosoma density in each rearing bowl was progressively decreased by the introduction of additional bowls, from the original 20 (1st instar) down to 10–15 (2nd instar), then to 5–8 (3rd instar), and finally to 1–2 (4th instar).

Survival to the juvenile stage, and the duration and total body length of each instar, were monitored. Total body length was measured from the anterior tip of the cephalic shield between the eye-stalks to the posterior end of the abdomen (or telson when this was differentiated). Data were pooled for all phyllosomas in each bowl and subjected to analysis of variance (ANOVA) between the three light conditions. Although parametric analyses (general one-way ANOVAs) were appropriate for duration and moult increment data, a non-parametric test (Kruskal–Wallis one-way ANOVA) was required for survival data. Multiple comparisons of means were made with the aid of Duncan's Multiple Range test.

Diel timing of moulting

The diel timing of ecdysis of phyllosomas reared under D/L, 24D or 24L was observed over a 47-day period from 2 December 1993 (sunrise, 0444–0503 hours; sunset, 1828–1844 hours). Observations in the D/L case were made every 10 min from 0300 to 0800 hours and once again at 1500 and at 2000 hours throughout the experimental period. This schedule was designed to indicate whether moulting of phyllosomas occurred at night or during the day, with particular detail around dawn. In all, 500 phyllosomal ecdyses, including 116 metamorphoses to the nisto stage, were observed. Three stages in the moulting process under D/L were recorded: premoult, when the normally transparent phyllosomal carapace changed to pale red; initiation, when the next phyllosomal instar began to emerge dorsally between the thorax and abdomen of the old cuticle; and completion, when the old exuviae were completely removed from phyllosomal legs. Metamorphic stages under D/L were recorded as: initiation, when the eye-stalks began to shrink; and completion, when the nisto swam out from the phyllosomal exuviae. The timing of ecdysis of phyllosomas and nistos reared under 24D or 24L was observed four times daily (0300, 0900, 1500 and 2100 hours).

The diel timing of metamorphosis from the nisto stage to the juvenile stage and of moulting during the juvenile stage in the D/L case was recorded from the emergence of the first nisto on 20 December 1993 through to 23 January 1994. In all, 96 ecdyses of nistos and 56 ecdyses of juveniles were observed. Nistos were transferred into a 200-L flow-through tank with a sandy bottom. Temperature was maintained at 26·5 ± 0·1°C. Juveniles were fed fresh chopped *D. brazieri* flesh. The rearing tank was checked four times daily (0300, 0900, 1500 and 2100 hours) for individuals undergoing ecdysis. Cast nisto and juvenile exuviae were collected at each observation time.

Results

Larval survival and growth

Phyllosomas reared under each of the three light conditions successfully metamorphosed to the nisto stage through four phyllosomal instars. Although highest survival to the juvenile stage was obtained when phyllosomas were reared under D/L, survival was not statistically different ($P > 0·05$) among phyllosomas reared under D/L or 24D (Table 1). Durations of the 1st, 2nd, 3rd and 4th phyllosomal instars under 24L were approximately 3, 2, 1 and 1·5 days longer, respectively, than those under either D/L or 24D (Table 2). As a result, total development time to the nisto stage was approximately 7 days longer for phyllosomas reared under 24L than for those reared under D/L or 24D. After phyllosomas metamorphosed to the nisto stage,

Table 1. Average survival (%) of phyllosomal instars and nistos of *Thenus orientalis* reared under three light conditions (numbers of surviving larvae in parentheses)

D/L, natural light; 24D, continuous dark; 24L, continuous light

Light regime	Phyllosomal instar 1	2	3	4	Nisto
D/L	100 (200)	85 (170)	60 (120)	58 (116)	48 (96)
24D	100 (40)	75 (30)	55 (22)	55 (22)	40 (16)
24L	100 (40)	65 (26)	50 (20)	50 (20)	20 (8)

Table 2. Average duration of larval stages (days, av. ± s.d.) and accumulated duration after hatching (days, in parentheses) of phyllosomal instars and nistos of *Thenus orientalis* reared under three light conditions

D/L, natural light; 24D, continuous dark; 24L, continuous light. Within columns, values with different superscripts are significantly different ($P < 0·01$)

Light regime	Phyllosomal instar 1	2	3	4	Nisto
D/L	6·83 ± 0·76[a]	6·68 ± 0·66[a]	7·12 ± 0·70[a]	8·62 ± 0·72[a]	7·39 ± 0·06
	(—)	(12·55)	(18·12)	(26·27)	(32·66)
24D	6·80 ± 0·14[a]	6·56 ± 0·20[a]	7·19 ± 1·16[a]	8·45 ± 0·40[a]	7·00 ± 0·00
	(—)	(12·36)	(18·55)	(26·00)	(32·00)
24L	9·65 ± 0·25[b]	8·43 ± 0·75[b]	8·00 ± 0·00[b]	10·00 ± 0·00[b]	7·00 ± 0·00
	(—)	(17·07)	(24·00)	(33·00)	(39·00)

Table 3. Average total body length (mm, av. ± s.d.) of phyllosomal instars and nistos of *Thenus orientalis* reared under three light conditions (numbers of measured individuals in parentheses)

D/L, natural light; 24D, continuous dark; 24L, continuous light. Within columns, values with different superscripts are significantly different ($P < 0{\cdot}01$)

Light regime	Phyllosomal instar 1	2	3	4	Nisto
D/L	3·97 ± 0·17 (20)	6·68 ± 0·66[a] (20)	11·38 ± 0·12[a] (20)	19·41 ± 0·26[a] (20)	17·77 ± 0·10[a] (20)
24D	3·94 ± 0·03 (20)	6·63 ± 0·07[a] (20)	11·36 ± 0·17[a] (20)	19·35 ± 0·16[a] (20)	18·46 ± 0·14[a] (16)
24L	3·94 ± 0·03 (20)	5·78 ± 0·07[b] (20)	9·61 ± 0·30[b] (20)	13·13 ± 0·24[b] (8)	14·70 ± 0·31[b] (8)

duration of the nisto stage was similar under all light conditions ($P > 0{\cdot}05$). Total body length of phyllosomas differed significantly between the three groups. Total body lengths of 2nd, 3rd and 4th phyllosomal instars reared under 24L were approximately 13%, 15% and 32% smaller, respectively ($P < 0{\cdot}01$), than those of phyllosomas reared under D/L or 24D (Table 3).

Diel timing of moulting and metamorphosis

Summary details of moulting times in the D/L case are shown in Table 4, and the frequency distribution of diurnal timing of moulting through the phyllosomal instars is shown in Fig. 1. Ecdyses of the phyllosomal instars reared under D/L were strongly synchronized, with maximum moulting activity occurring around dawn (0320–0700 hours). No moulting was observed at any other time during the observation period. Although phyllosomal ecdyses principally occurred around dawn, the process began (as indicated by the premoult stage) in the dark period before dawn (Table 4). Metamorphosis to the nisto stage was also highly synchronized, but the peak of such activity was after sunset (1900 and 2220 hours; Fig. 1). The metamorphic process was completed very rapidly (average was 35 min; Table 4). Moulting from the nisto to the 1st juvenile instar, and to subsequent juvenile instars, was observed only at night between 1800 and 0300 hours. Approximately 80% of

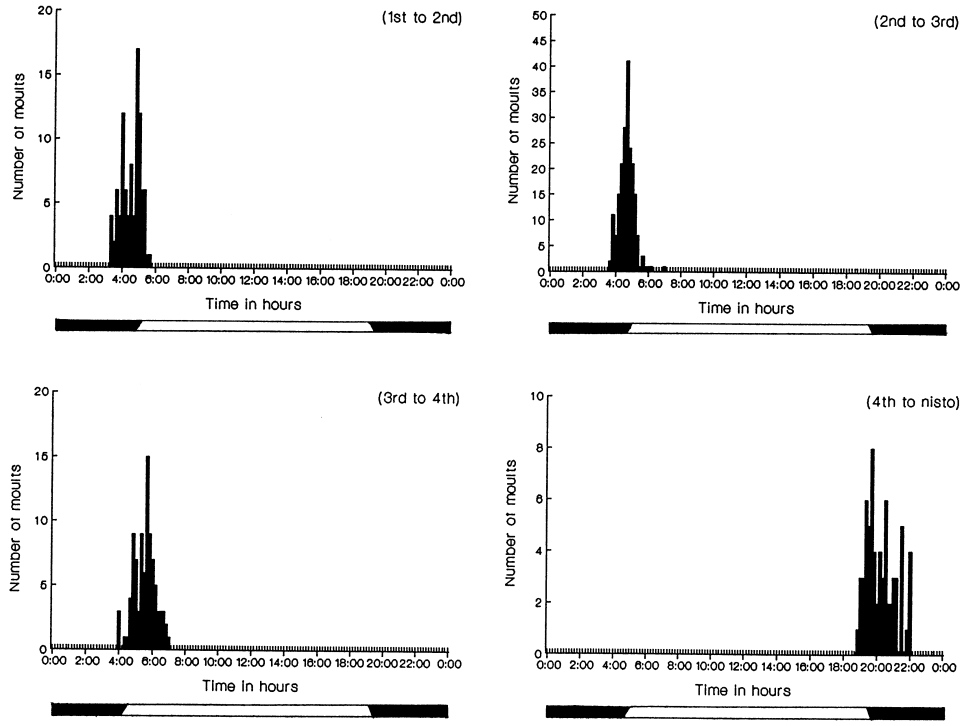

Fig. 1. Diel timing of phyllosomal moulting and metamorphosis to the nisto stage in *Thenus orientalis* reared under natural light.

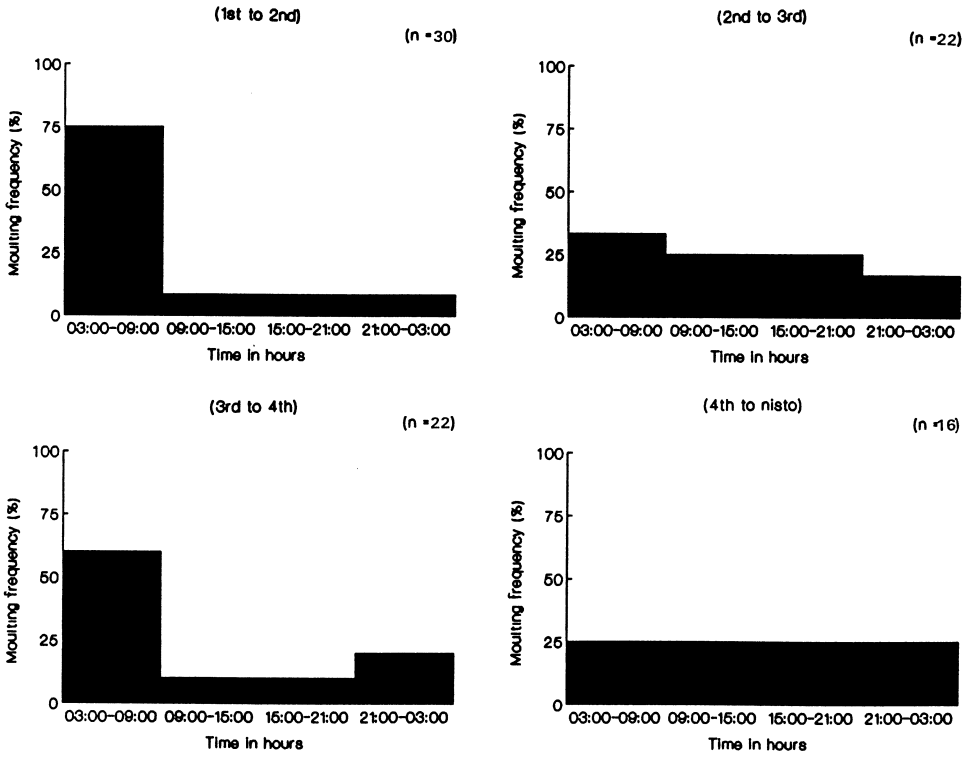

Fig. 2. Diel timing of phyllosomal moulting and metamorphosis to the nisto stage in *Thenus orientalis* reared under continuous dark.

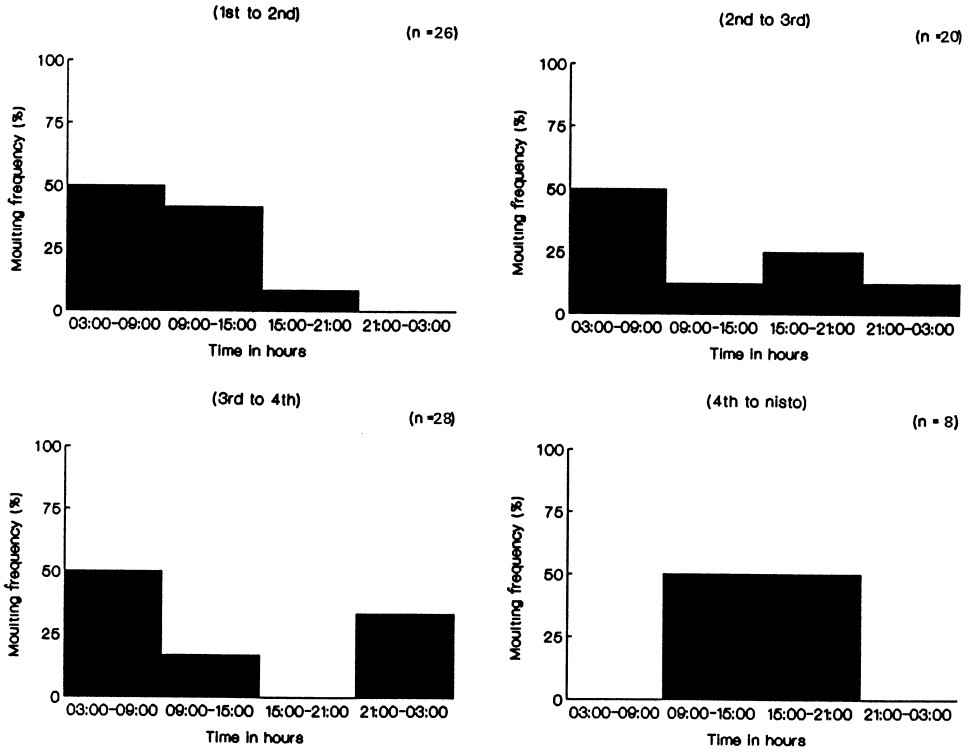

Fig. 3. Diel timing of phyllosomal moulting and metamorphosis to the nisto stage in *Thenus orientalis* reared under continuous light.

Table 4. Daily timing of moulting or metamorphosis of *Thenus orientalis* phyllosomal instars (24-hour clock, av. ± s.d.) and average duration of moulting or metamorphosis (minutes, completion minus initiation) under the natural light condition

Sunrise occurred at 0444–0503 hours and sunset at 1828–1844 hours during the experimental period

Larval transition	Premoult	Initiation	Completion	Duration
1st to 2nd	0332 ± 22	0402 ± 29	0430 ± 35	28
2nd to 3rd	0331 ± 32	0403 ± 26	0439 ± 28	36
3rd to 4th	0345 ± 43	0444 ± 36	0532 ± 39	48
4th to nisto	—	2014 ± 35	2049 ± 36	35

nisto moults and 90% of juvenile moults were observed between 2100 and 0300 hours.

Influence of light on diel timing of moulting

When phyllosomas were reared under 24D (28 ecdyses) or 24L (38 ecdyses), moulting was not synchronized except for 1st instar phyllosomas under 24D (Figs 2 and 3). No relationship was evident between moulting frequency and diurnal timing of moulting.

Discussion

The effects of changes in photoperiod on crustacean larval development differ depending on species. Lin (1991) reported for *Macrobrachium rosenbergii* larvae that survival was higher under 8L, 12L and 24L conditions than under a 4L condition and that larval duration was shorter and growth improved progressively with increasing daylight. Negative effects of continuous light on zoeal growth and development of *Ranina ranina* have recently been found by Minagawa (1994). He concluded that negative growth under continuous light may be due to an imbalance in energy uptake and consumption and that more energy was consumed under continuous light than under continuous darkness. Knowlton (1974) reported that larvae of *Palaemontes vulgaris* passed through an extra instar when reared under short photoperiods. In the present study, continuous light had negative effects on the survival and growth of *Thenus orientalis* phyllosomas, but continuous dark or natural light did not. One possible explanation for this is that since *T. orientalis* phyllosomas show a strong photopositive reaction throughout all phyllosomal stages (Mikami 1995), as has been found for phyllosomas of other species (Saisho 1966; Ritz 1972; Inoue 1981), those reared under continuous light tended to remain near the surface of rearing containers and hence may have had fewer opportunities to obtain food from the bottom of the containers, resulting in an energy imbalance.

DeCoursey (1983) summarized the timing of biological activities in crustaceans and defined five environment-related behavioural periodicities: tidal, diurnal, semilunar, lunar and annual. Endogenous rhythms associated with these environmental factors appear in behaviour such as emergence, movement, locomotor rhythms and swimming activity (reviews: DeCoursey 1983; Naylor 1985; Dall *et al.* 1990). In nature, light is probably the most important single factor influencing endogenous activities and affecting diurnal rhythmic activities such as feeding and vertical migration of scyllarid and palinurid phyllosomas (e.g. Rimmer and Phillips 1979; Phillips *et al.* 1981). The present study showed that varied light conditions affected the diurnal timing of ecdysis of *T. orientalis* phyllosomas. This result may be an indication that light is a factor influencing those endogenous functions of phyllosomas that in turn influence the timing of rhythmic moulting.

When planktonic phyllosomas metamorphose to the nisto stage, synchronized ecdysis switches from dawn to after dusk, and subsequent juvenile moults become nocturnal. Metamorphosis after dusk has been observed in aquarium-reared phyllosomas of *Ibacus ciliatus* (Dotsu *et al.* 1966*a*, 1966*b*), *Jasus edwardsii* (described as a hybrid species between *J. novaehollandiae* and *J. edwardsii*; Kittaka *et al.* 1988), *Panulirus japonicus* (Yamakawa *et al.* 1989), and *I. peronii* (Marinovic *et al.* 1994). Nocturnal metamorphosis has also been reported in *Scyllarus americanus* (Robertson 1968), *S. martensii* and *T. orientalis* (Barnett *et al.* 1986), and *J. lalandii* (Kittaka 1988). Nocturnal ecdysis of juvenile and adult lobsters has been observed in all investigated species, including *J. lalandii* (Fielder 1964), *J. edwardsii* (= *J. novaehollandiae*) (MacDiarmid 1989), *Panulirus cygnus* (Thomas 1966), and *P. argus* (Lipcius and Herrnkind 1982).

One possible explanation for the observed switching of moult timing between phyllosomas and nistos is a readjustment of biological clocks induced by the photoperiod. Since the diel frequency of ecdysis under constant light or dark conditions did not show any rhythmicity, it appears that the moulting cycle is largely regulated by a circadian light–dark cycle. When phyllosomas metamorphose to the benthic nisto stage, genetically based rhythmic activities relating to the moulting cycle may change (reverse) in relation to the light–dark cycle.

One benefit of these behaviours may be to minimize the risk of predation. Although predation is not necessarily the major cause of mortality in planktonic larvae (Dall *et al.* 1990), it is probably the major cause of natural mortality in juvenile and adult lobsters (MacDiarmid 1989). In parallel with the change in life habits from planktonic larvae to benthic nistos, juveniles and adults (Barnett *et al.* 1986), the suite of potential predators also changes. The major predators of phyllosomas, which have habitats similar to those of penaeid larvae, are likely to be planktotrophic fish and other macroplankton, including ctenophores, scyphozoan and hydrozoan medusae, chaetognaths and crustaceans (Dall *et al.* 1990). A benefit of initiating pre-dawn moulting during the phyllosomal stage is perhaps to minimize the impact of

these pelagic predators. The predators of benthic adult lobsters are mainly diurnal animals such as reef fish, sharks, rays, skates, octopus and marine mammals (Phillips and Sastry 1980; Lipcius and Herrnkind 1982; Russel 1983; MacDiarmid 1989). The nocturnal ecdysis observed in benthic nistos and juveniles of *T. orientalis* is therefore seen as a means of increasing the chance of individual survival by decreasing the potential for diurnal predation.

Acknowledgments

This study was financially supported by the Queensland Department of Primary Industries (QDPI) and a University of Queensland research grant. Laboratory facilities for this study were provided by the QDPI Bribie Island Aquaculture Research Centre (BIARC). We thank Drs David Mann and David Hewitt (BIARC) and Ms Sandy Petersen for their critical reading of the manuscript.

References

Barnett, B. M., Hartwick, R. F., and Milward, N. E. (1984). Phyllosoma and nisto stage of the Moreton Bay bug, *Thenus orientalis* (Lund) (Crustacea:Decapoda:Scyllaridae), from shelf waters of the Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* **35**, 143–52.

Barnett, B. M., Hartwick, R. F., and Milward, N. E. (1986). Descriptions of the nisto stage of *Scyllarus demani* Holthuis, two unidentified *Scyllarus* species, and the juvenile of *Scyllarus martensii* Pfeffer (Crustacea:Decapoda:Scyllaridae), reared in the laboratory, and behavioural observations of the nistos of *S. demani*, *S. martensii* and *Thenus orientalis* (Lund). *Australian Journal of Marine and Freshwater Research* **37**, 595–608.

Dall, W., Hill, B. J., Rothlisberg, P. C., and Staples, D. J. (1990). 'The Biology of the Penaeidae.' (Academic Press: London.)

DeCoursey, P. J. (1983). Biological timing. In 'The Biology of Crustacea. Vol. 7'. (Eds E. J. Vernberg and W. B. Vernberg.) pp. 107–62. (Academic Press: New York.)

Dotsu, Y., Seno, K., and Inoue, S. (1966*a*). [Rearing experiments on early phyllosomas of *Ibacus ciliatus* (von Siebold) and *I. novemdentatus* Gibbes (Crustacea:Reptantia).] *Bulletin of the Faculty of Fisheries, Nagasaki University* **22**, 181–94. [In Japanese]

Dotsu, Y., Tanaka, O., Shojima, Y., and Seno, K. (1966*b*). [Metamorphosis of the phyllosomas of *Ibacus ciliatus* (von Siebold) and *I. novemdentatus* Gibbes (Crustacea:Reptantia) to the reptant larvae.] *Bulletin of the Faculty of Fisheries, Nagasaki University* **21**, 195–221. [In Japanese]

Fielder, D. R. (1964). The spiny lobster *Jasus lalandii* (H. Milne-Edward) in South Australia. I. Growth of captive animals. *Australian Journal of Marine and Freshwater Research* **15**, 77–92.

George, R. W., and Griffin, D. J. G. (1972). The shovel nosed lobsters of Australia. *Australian Natural History* **17**, 227–31.

Inoue, M. (1981). [Studies on the cultured phyllosoma larvae of the Japanese spiny lobster, *Panulirus japonicus* (v. Siebold).] Special Report of the Kanagawa Prefectural Fisheries Experimental Station, No. 1. 91 pp. [In Japanese]

Ito, M. (1988). Mariculture-related laboratory studies on the early life histories of the scyllarid lobster (Crustacea:Decapoda:Scyllaridae): two forms of *Thenus* Leach, and *Scyllarus demani* Holthuis. M.Sc. Thesis, James Cook University of North Queensland, Townsville.

Kailola, P. J., William, M. J., Stewart, P. C., Reichelt, R. E., McNee, A., and Grieve, C. (1993). 'Australian Fisheries Resources.' (Bureau of Resource Sciences, Department of Primary Industries and Energy/Fisheries Research and Development Corporation: Canberra.)

Kittaka, J. (1988). Culture of the palinurid *Jasus lalandii* from egg stage to puerulus. *Nippon Suisan Gakkaishi* **54**, 87–93.

Kittaka, J. (1994). Larval rearing. In 'Spiny Lobster Management'. (Eds B. F. Phillips, J. S. Cobb and J. Kittaka.) pp. 402–23. (Blackwell Scientific: Oxford.)

Kittaka, J., Iwai, M., and Yoshimura, M. (1988). Culture of a hybrid of spiny lobster genus *Jasus* from egg stage to puerulus. *Nippon Suisan Gakkaishi* **54**, 413–17.

Knowlton, R. E. (1974). Larval development processes and controlling factors in decapod Crustacea, with emphasis on Caridae. *Thalassia Jugoslavica* **10**, 138–58.

Lin, X. (1991). Ecological study of larval feeding in *Macrobrachium rosenbergii*. Ph.D. Thesis, Tokyo University of Fisheries, Tokyo.

Lipcius, R. N., and Herrnkind, W. F. (1982). Moulting cycle alterations in behaviour, feeding and diel rhythms of a decapod crustacean, the spiny lobster *Panulirus argus*. *Marine Biology (Berlin)* **68**, 241–52.

MacDiarmid, A. B. (1989). Moulting and reproduction of the spiny lobster *Jasus edwardsii* (Decapoda:Palinuridae) in northern New Zealand. *Marine Biology (Berlin)* **103**, 303–10.

Marinovic, B., Lemmens, J. W. T. J., and Knott, B. (1994). Larval development of *Ibacus peronii* Leach (Decapoda:Scyllaridae) under laboratory conditions. *Journal of Crustacean Biology* **14**, 80–94.

Mikami, S. (1995). Larviculture of *Thenus* (Decapoda, Scyllaridae), the Moreton Bay bugs. Ph.D. Thesis, University of Queensland, Brisbane.

Minagawa, M. (1994). Effects of photoperiod on survival, feeding and development of larvae of the red frog crab, *Ranina ranina*. *Aquaculture* **120**, 105–14.

Naylor, E. (1985). Rhythmic behaviour of decapod crustaceans. *Symposia of the Zoological Society of London* **59**, 177–99.

Phillips, B. F., and Sastry, A. N. (1980). Larval ecology. In 'The Biology and Management of Lobsters. Vol. 2'. (Eds J. S. Cobb and B. F. Phillips.) pp. 11–57. (Academic Press: New York.)

Phillips, B. F., Brown, P. A., Rimmer, D. W., and Reid, D. D. (1979). Distribution and dispersal of the phyllosoma larvae of the western rock lobster, *Panulirus cygnus*, in the south-eastern Indian Ocean. *Australian Journal of Marine and Freshwater Research* **30**, 773–83.

Phillips, B. F., Brown, P. A., Rimmer, D. W., and Braine, S. J. (1981). Description, distribution and abundance of late larval stages of the Scyllaridae (slipper lobsters) in the south-eastern Indian Ocean. *Australian Journal of Marine and Freshwater Research* **32**, 417–37.

Rimmer, D. W., and Phillips, B. F. (1979). Diurnal migration and vertical distribution of phyllosoma larvae of the western rock lobster *Panulirus cygnus*. *Marine Biology (Berlin)* **54**, 104–24.

Ritz, D. A. (1972). Behavioural response to light of the newly hatched phyllosomal larvae of *Panulirus longipes* George (Crustacea:Decapoda:Palinuridae). *Journal of Experimental Marine Biology and Ecology* **10**, 105–14.

Robertson, P. B. (1968). The complete larval development of the sand lobster, *Scyllarus americanus* (Smith), (Decapoda, Scyllaridae) in the laboratory with notes on larvae from the plankton. *Bulletin of Marine Science* **18**, 294–342.

Russel, B. C. (1983). The food and feeding habits of rocky reef fish of north-eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* **17**, 121–45.

Saisho, T. (1966). [Studies on the phyllosoma larvae with reference to the oceanographical conditions.] *Memoirs of the Faculty of Fisheries, Kagoshima University* **15**, 177–239. [In Japanese]

Thomas, L. R. (1966). Moulting behaviour of the Western Australian crayfish *Panulirus cygnus* (George). *Crustaceana (Leiden)* **11**, 111–12.

Yamakawa, T., Nishimura, M., Matsuda, H., Tsujigado, A., and Kamiya, N. (1989). Complete larval under rearing of the Japanese spiny lobster *Panulirus japonicus*. *Bulletin of the Japanese Society of Scientific Fisheries* **55**, 745.