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Starvation and recovery ability of phyllosoma of the tropical spiny lobsters *Panulirus ornatus* and *P. homarus* in captivity

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Abstract

The ability of planktonic crustacean larvae to survive initial periods of starvation is highly dependant on maternally provisioned endogenous reserves. For many lobster species lecithotrophic development is not common and feeding is required at some stage soon after hatching and during the first intermoult period. While the impact of providing or withholding feed on larval development has been examined in a number of temperate and sub-tropical spiny lobsters, such as *Jasus edwardsii*, *J. verreauxi* and *Panulirus japonicus*, less is known about tropical lobster species. This study examined the influence of starvation and feeding on the dry weight (dw), intermoult duration, point of no return of 50% (PNR_{50}) and point of reserve saturation of 50% (PRS_{50}) in the tropical spiny lobster spp. *Panulirus ornatus* and *P. homarus*. In both species, continuous feeding or starvation from hatch resulted in a doubling in initial dw or a reduction of 20%, respectively. Starvation of larvae resulted in a PNR_{50} for both species of 5.9 days, with no significant reduction in the ability to moult when starved for between 4-5 days. Moulting commenced after 5-6 days of feeding in both species. A delay in moulting was equivalent to the initial duration of starvation of up to a total of 4 days. The PRS_{50} was 3.8 and 4.4 days for *P. ornatus* and *P. homarus* respectively. Moulting was severely curtailed if phyllosomas were fed for < 3 days. The ability to maintain survival and growth after bouts of starvation indicates that phyllosomas in the wild can have significant temporal plasticity with a consequential variation in the total length of their larval period. The implications for commencing or withholding first feeds with respect to PNS_{50}, PRS_{50}, larval duration and development are discussed, with emphasis on the development of appropriate aquaculture hatchery technology.

Keywords: Phyllosoma, *Panulirus ornatus, P. homarus*, starvation, PNR_{50}, PRS_{50}

Introduction

The marine environment has historically been an important source of protein in many regions of the world. Approximately 30% of global animal protein supply is of aquatic origin, both freshwater and marine. In recent decades the continued intense harvesting of wild populations, and increased fishing effort, has seen exploitation exceed natural replenishment rates with a consequential plateauing, and decline, in world fishery harvests (FAO, 2006). Globally the most valuable fisheries sector, in terms of the landed price of live fresh product, is achieved for palinurid (spiny) lobsters (FAO, 2008). Lobster populations are vulnerable to overexploitation through sheer demand and lack of regulation or insufficient fisheries data that would allow effective management (FAO, 2006). For example, the fishery for *Panulirus argus* exceeds 42,000 t per annum, however many regions in the Caribbean are now considered overexploited and in need of managerial control to sustain future stocks (Chavez, 2009). One possible mechanism to address issues of overexploitation of wild populations is to develop

a closed life cycle farming sector, which will require the commercial hatchery rearing of spiny lobsters. Of all candidates for aquaculture some of the most promising in terms of favourable culture attributes, wide geographical distribution and existing market acceptance are the tropical spiny lobsters (Holthuis, 1991; Smith *et al.*, 2009).

The tropical spiny lobsters *Panulirus ornatus* and *P. homarus* are distributed from the Indo-West Pacific from the Red Sea and East Africa to southern Japan, Solomon Islands, Papua New Guinea, Northern and Western Australia, with *P. homarus's* Australian distribution limited to the North Eastern coastline (Holthuis, 1991). There is a highly regulated but sustainable commercial fishery for *P. ornatus* in Northern Australian waters (Ye *et al.,* 2008), in contrast to the *P. homarus* fishery in India, which is in significant decline (Radhakrishnan *et al.,* 2005; Al-Marzouqi *et al.,* 2007). The hatchery rearing of tropical spiny lobsters for commercial aquaculture has been investigated since 1999 for *P. ornatus* (Benzie and Yoshimura, 1999) and the mid-1980's for *P. homarus* (Vijayakumaran and Radhakrishnan, 1986). Whereas the larval cycle of *P. ornatus* has been completed by researchers on numerous occasions, albeit in small numbers (Smith *et al.*, 2009), this goal has not yet been achieved with *P. homarus* (Radhakrishnan pers. comm.).

Current research at the Australian Institute of Marine Science (AIMS) is focused on aspects of system design, health and nutrition of captive phyllosoma with insights gained from assessing the health and nutritional status of wild phyllosoma. Access to wild phyllosoma and their prey has proven invaluable in confirming the scarcity of larger planktonic prey organisms (Omori and Hamner, 1984), the ability of phyllosoma to optimise the use of feed items when available, their ability to remain in stasis in the absence of feed and the possible role that microbes may play in optimising nutritional uptake (Forward, 1988; Jeffs *et al.,* 2004; Bradford *et al.,* 2005). The aims of this study were to assess the ability of tropical spiny lobster phyllosoma to withstand periods of starvation; as they may well experience in the wild, and assess how energy depletion, time to the commencement of moult, moult duration and mortality associated with food withdrawal, may provide insights into progressing the hatchery culture of these species. Larval starvation and refeeding experiments have previously been conducted on clawed, spiny and slipper lobsters (Mikami and Thakashima, 1993; Mikami *et al.*, 1995; Abrunhosa and Kittaka, 1997) and numerous other crustacean species (Anger and Dawirs, 1981; Anger *et al.*, 1981; Dawirs 1986; Staton and Sulkin, 1991; Figueiredo *et al.,* 2008) and the effects are assessed through Point of no return 50 (PNR_{50}) and Point of reserve saturation 50 (PRS_{50}) experiments. A PNR_{50} is defined as the critical point (day) in larval development where feeding is commenced and ³50% of larvae fail to progress to a later developmental stage (Anger, 1987). A PRS_{50} is a test of accumulated reserves and is the critical point (day) where food intake is no longer required for ³50% of larvae to progress to a subsequent developmental stage. This is also known as the 'D_0 threshold' in a moult cycle, it is the transitional stage between intermoult and early premoult (Anger, 1987).

Material and Methods

Newly hatched *P. ornatus* and *P. homarus* phyllosoma were sourced from broodstock, originally obtained from the wild in the Coral Sea, that had been held in the Tropical Aquaculture Facilities of AIMS, Townsville, Australia (16∨ 17.728'S lat., 145∨ 27.121'E long.) for at least 1 year in captivity. Prior to and during the spawning season, broodstock were maintained on a diet of squid (*Loligo opalescens*), mussel (*Perna canaliculus*), pilchards (*Sardinops neopilchardus*) and a fresh moist pellet manufactured on site. Broodstock were fed daily at 16:00 to satiation with remnant food removed at 8:00 the next day. Phyllosoma were sourced from broodstock maintained under phase shifted conditions of light and temperature to produce spawning, egg and phyllosoma during spring; three months prior to the natural spawning season. Previous studies demonstrated no significant differences between natural or phase shifted phyllosoma, evident by the production of puerulus from all broodstock groups (Smith *et al.,* 2009). Prior to hatch broodstock were isolated into a spawning tank. On the morning after the hatch, larvae were selected by harvesting active phyllosoma that expressed strong positive phototaxis.

Newly hatched phyllosoma were reared in 6 x 50 L cylindrical mass culture vessels comprised of two treatments; fed (x3) and starved (x3), replicates were stocked at 200 phyllosoma L^{-1}. Sub-samples were taken daily for dry weight (dw), and for stocking the PNR_{50} and PRS_{50} experimental systems which comprised of 42 x 250 ml mini kriesels stocked at 80 phyllosoma L^{-1}.

Mass rearing and experimental tanks were supplied with flow-through water equivalent to 3 exchanges per hour. Seawater was supplied from a shoreline pumphouse with water being settled for 1- 4 days in a 1.2 megaliter polyethylene lined storage dam followed by sequential passage through bag filters (100, 50 and 10 µm), foam fractionation, ozonation (700-750 mV), UV (254 nm) and particulate/carbon filtration to 1µm. Seawater within this system was delivered to the point of usage within 20 minutes of processing. Salinity was 34 ± 0.2, temperature was maintained at 28 °C for the duration of the experiment and oxygen was introduced to the mass rearing system to maintain saturation at >80%.

Phyllosomas removed from the starved and fed mass culture vessels were stocked daily into the respective PNR_{50} and PRS_{50} mini-kriesel tanks. For example, in the PNR_{50} study phyllosoma starved for 1 day in the mass cultures tanks were placed into the mini-kriesels and fed until moulting or death occurred, the next day phyllosoma starved for 2 days were removed from the mass culture vessels and fed until moulting or death occurred, and so on daily until phyllosoma that had been starved for a total of 7 days had been examined. By contrast, for the PRS_{50} examination, the opposite starting procedure was carried out, with phyllosoma sourced daily from fed mass cultures and then subject to starvation until moulting or death occurred. Each experiment was conducted using triplicate treatments with 20 phyllosoma per replicate.

Phyllosoma in the mass cultures and PNR_{50} experiment were fed newly-hatched *Artemia* at a rate of 5 ml^{-1} day^{-1}. *Artemia* cysts (INVE, Great Salt Lake) were hatched in 50 L white fibreglass cones using aerated, 1µm filtered ozonated seawater, maintained at 34 ± 1‰ and 28 ± 1°C. At hatch (24 h) *Artemia* nauplii were harvested, rinsed, and disinfected for 30 min with formalin (400 µg L^{-1}) before again rinsing and storage in clean filtered seawater at 4 °C. Prior to the introduction of a new batch of *Artemia* those from the previous day were passively removed by flushing out through larger screens in the mass culture vessels. *Artemia* in the PNR_{50} experiment were removed during the daily monitoring of phyllosoma mortality or moulting to Stage II.

Samples for total length (20 phyllosoma) were taken on days 0 and 7 from the mass culture vessels. Total length was defined as the distance from the anterior margin of the cephalic shield; between the eyestalks, to the posterior edge of the pleon. A total of 100 phyllosoma were collected daily from each of the fed (x3) and starved (x3) mass culture vessels to obtain a measure of sample dw. Samples were screened to remove excess seawater, rinsed three times with 0.5 M ammonium bicarbonate to remove salt crystals, resuspended in freshwater and filtered on a pre-dried (24 hr at 60 °C) and pre-weighed (Sartorius AG, Germany) GF/C filter (Wattman Ltd. UK), then oven dried (60 °C) and reweighed after 24 hr to obtain the total weight of samples + filters. Filter dw was subtracted from the total dw to give a phyllosoma sample dw, this was divided by 100 to obtain individual phyllosoma weights.

Statistical analyses were conducted using regression analysis, one-way analysis of variance with Tukey-Kramer HSD tests used for post-hoc comparison. ArcsinÖ transforms were performed on percentage data. $P < 0.05$ was considered significantly different (Sokal and Rohlf, 1995). Data are presented as mean ± SEM. Statistics were executed using JMP version 7.1 (SAS Institute Inc.).

Results

The dw of fed and starved *P. ornatus* and *P. homarus* Stage I phyllosoma exhibited similar trends across species; dw increased with feeding and decreased with starvation (Fig. 1). During the 7 days from hatch to the initiation of moulting, fed phyllosoma approximately doubled in weight, while the weight of starved phyllosoma was reduced by approximately 20%. The total length of Stage I and II *P. ornatus* was 1.72 ± .05 and 2.05 ± .10 mm,

respectively, compared to 1.41 ± .03 and 1.83 ± .05 mm for Stage I and II *P. homarus* phyllosoma, respectively. The dw follows a similar trend to the

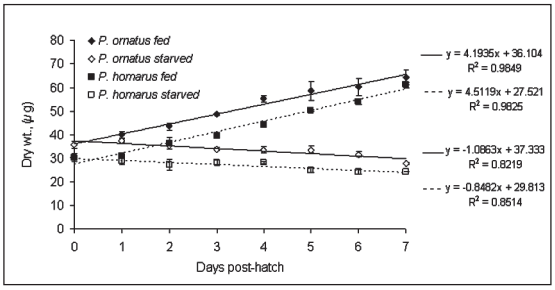

Fig. 1. Dry weight of *P. ornatus* (—) and *P. homarus* (- - -) phyllosoma fed or starved during Stage I of development

total length differential, with fed Stage I and II *P. ornatus* weighing 35.8 ± 1.6 and 64.3 ± 3.1 µg, respectively, compared to 30.0 ± 1.7 and 61.0 ± 1.3 µg for Stage I and II fed *P. homarus* phyllosoma.

Phyllosoma in the PNR_{50} experiment were starved for an initial period then fed until moulting or mortality occurred. For both species, moulting in the mass rearing tanks commenced after 6 days feeding. The PNR_{50} for both Stage I *P. ornatus* and *P. homarus* was 5.9 days (Fig. 2). Whereas there were no significant reductions in the ability to moult to Stage II with an initial non-feeding period of 4-5 days in *P. ornatus* and 5 days in *P. homarus*, both species were significantly compromised with any further delay in feeding. Moulting from Stage I to II in *P. ornatus* commenced after 6 days in fed phyllosoma and thereafter was delayed by a time period equivalent to the initial starvation duration up to and including the first 4 days of starvation (Fig. 3). The exception was those starved for 1 day only requiring 5 days to moult, while 5 and 6 days starved phyllosoma were delayed for 7 days, while 7 day starved phyllosoma required a 8 days of feeding to facilitate moulting. The duration of the moult period was 3-4 days in all treatments with the exception of Day 1 and 7 starved phyllosoma with 2 day moult durations and 100% and 3% attainment of moult to Stage II, respectively. Moulting from Stage I - II in the *P. homarus* PNR_{50} trial was starvation dependant, it took an additional 5 days of feeding for those starved for an initial 1, 2, or

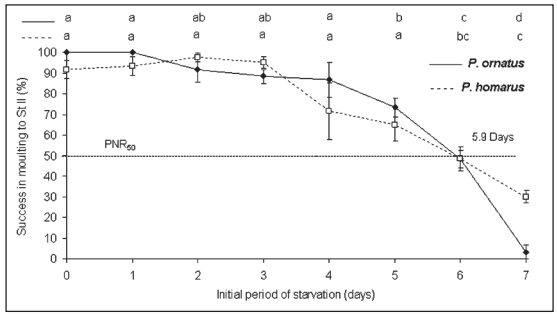

Fig. 2. Point of no return 50% (PNR_{50}) for Stage I *P. ornatus* and *P. homarus* phyllosoma. Phyllosoma were first starve for an initial period and then fed until moulting or mortality occurred. Different letters denote significant differences between the attainment of Stage II in both *P. ornatus* (—) and *P. homarus* (- - -) phyllosoma groups

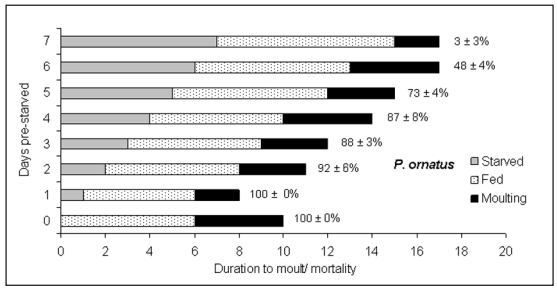

Fig. 3. Moult pattern of Stage I *P. ornatus* phyllosoma subjected to an initial period of starvation before being fed. Phyllosomas were examined until they had either moulted or died. The percentage notation indicates the proportion of phyllosoma successfully moulting to Stage II in each treatment group

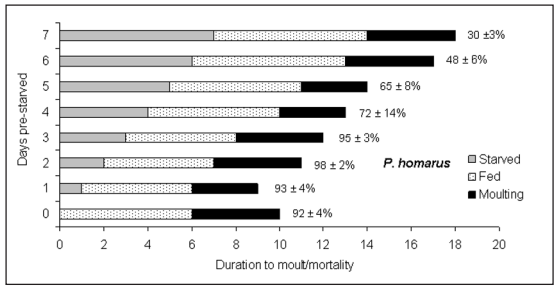

Fig. 4. Moult pattern of Stage I *P. homarus* phyllosoma subjected to an initial period of starvation before being fed. Conditions as per details in Fig. 3 legend

3 days, 6 days for those starved for 4 or 5 days, while 6 and 7 days starvation required 7 days feeding prior to a moult event (Fig. 4). The moult duration in all treatments was 3-4 days.

Phyllosoma in the PRS_{50} experiment were fed for a specified period then subjected to starvation until moulting or mortality occurred. The PRS_{50} was 3.8 days for *P. ornatus* and 4.4 days for *P. homarus* (Fig. 5). The ability of phyllosoma of both species to successfully moult was severely compromised when fed for an initial period of up to 3 days and starved thereafter. Feeding for 5-7 days followed by starvation provided for the greatest moulting success in both species but was not significantly different between the two groups. An initial feeding period of between 0-2 days followed by starvation did not result in successful moulting to Stage II in *P. ornatus* phyllosoma (Fig. 6). Moulting commenced on Day 6 in all treatments fed ³ 3 days. However, the duration was highly variable in all treatments with the exception of those fed 6 or 7 days with 100% success in moulting over a 4 day period. *P. homarus* demonstrated similar moulting patterns to *P. ornatus* (Fig. 7). There were no moults in *P. homarus* with 0-2 days feeding followed by starvation, moulting commenced after 5-6 days in phyllosoma fed for 3 days and optimal moulting success was obtained after 5 days feeding, albeit with a prolonged moulting duration in those fed for 5 days.

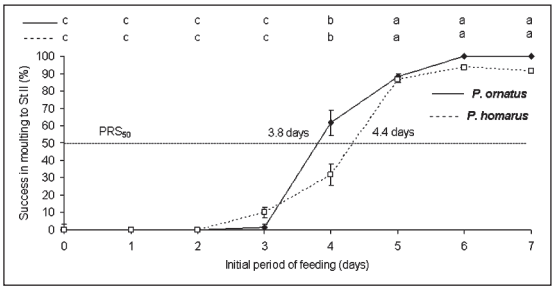

Fig. 5. Point of reserve saturation 50% (PRS_{50}) for *P. ornatus* and *P. homarus* Stage I phyllosoma. Phyllosoma were fed for an initial period then subjected to starvation until moulting or mortality occurred. Different letters denote significant differences between the attainment of Stage II in both *P. ornatus* (—) and *P. homarus* (- - -) phyllosoma groups

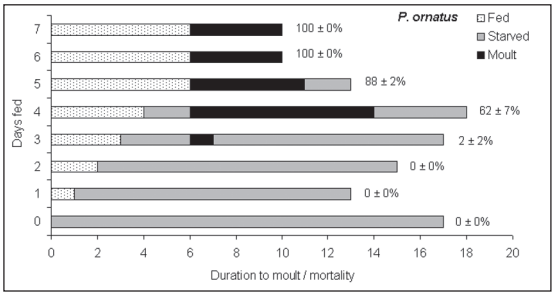

Fig. 6. Moult pattern of Stage I *P. ornatus* phyllosoma subjected to an initial period of feeding. Phyllosomas were examined until they had either moulted or died. The percentage notation indicates the proportion of phyllosoma successfully moulting to Stage II in each treatment group

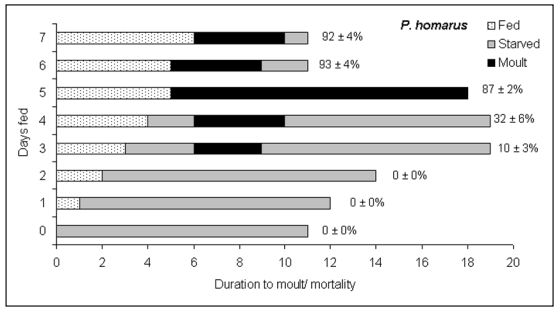

Fig. 7. Moult pattern of Stage I *P. homarus* phyllosoma subjected to an initial period of feeding. Conditions are per details in Figure 6 legend

Discussion

Phyllosoma pass through progressive larval developmental stages between hatch and metamorphosis with the ability to do so in the shortest duration being controlled by intrinsic factors, such as hormone regulation. However, it is the extrinsic factors, including the provision and timing of suitable nutrition, which provides an overarching influence (Anger, 2001). During this study we noted the ability of *P. ornatus* and *P. homarus* phyllosoma to increase their body weight by 100% during 7 days feeding. By contrast, phyllosoma only sustained a 20% loss in body weight over a similar period of starvation. This suggests fast growth when food is available and a holding pattern in its absence; potentially a larval strategy to sustain phyllosoma through periods of variable temporal and geographical prey abundance, and mirrors similar responses noted in other larval crustaceans (Dawirs, 1986). It is a common adage that in oceanic systems 'plankton is patchy' (Omori and Hamner, 1984) therefore predators must have a strategy to circumvent this, which may include the accumulation of available nutritional reserves and their conservation in its absence (Anger, 2001; Figueiredo *et al.,* 2008).

Whereas some palaemonid shrimp and brachyuran crabs are capable of lecithotrophic development through at least one developmental stage (Anger, 2001; Calado *et al.,* 2008), most crustaceans have minimal endogenous reserves at hatch and require food within the first development period to successfully moult (Dawirs, 1986; Anger, 2001). Temperature is a major extrinsic factor that regulates moulting (Anger, 2001). In the temperate spiny lobsters *J. edwardsii* and *Sagmariasus verreauxi* a PNR_{50} of 4.2 and 6.5 days, respectively, was obtained (Abrunhosa and Kittaka, 1997) using elevated and suppressed temperatures of 19-22°C and 16-17°C, respectively. The standard culture temperature for *J. edwardsii* is 18°C (Smith *et al.,* 2003) while *S. verreauxi* has a culture optimal between 20 (Kittaka, 1997) and 24°C (Moss *et al.,* 2001). It is reasonable to expect that at 'standard' culture temperatures the PNR_{50} would be lengthened for *J. edwardsii* and shortened for *S. verreauxi*; with both species possibly in the range of 5-5.5 days, and likely to be less than the 5.9 days noted using the standard culture temperature for *P. ornatus* and *P. homarus*. This indicates an elevated PNR_{50} for the tropical species and suggests an enhanced ability to sequester and store reserves; despite the fact that elevated experimental temperatures increase the consumption of endogenous reserves (Alekseeva and Zotin, 2001). PNR_{50} experiments have also been conducted on sub-tropical spiny (*Panulirus japonicus*) and slipper (*Thenus* spp.) lobsters incubated at 28°C (Mikami *et al.,* 1995). Mikami *et al.* (1995) found a differential between the PNR_{50} durations of *P. japonicus* and *Thenus* spp. of 3.4 and 1.7 days respectively and suggested that this was associated with differences in metabolic and/or growth rates (Mikami *et al.,* 1995). The optimal culture temperature for *P. japonicus* is 26°C (Matsuda and Yamakawa 1997; Matsuda *et al.,* 2003), with a 2°C reduction to the incubation temperature it is likely the PNR_{50} would be greater than 3.4 days but unlikely to approach that achieved for *P. ornatus* and *P. homarus* of 5.9 days. This further suggests an enhanced ability of *P. ornatus* and *P. homarus* to sustain prolonged periods of starvation compared to other spiny lobster spp. When *P. ornatus* and *P. homarus* were subject to a PNR_{50} the delay in commencing moulting was equivalent to the corresponding starvation duration and similar to that experienced in other crustaceans (Anger *et al.,* 1981; Mikami *et al*., 1995; Abrunhosa and Kittaka, 1997). During a starvation period growth is arrested, and where a PNR_{50} is not reached minimal consequences are evident in later stages (Mikami *et al*., 1995). Longer periods of starvation in excess of the PNR_{50} are known to impact the ability of the R cells within the hepatopancreas to process and store lipids, which is often accompanied by irreversible swelling and degradation of the mitochondria (Storch and Anger, 1983).

The PRS_{50} is the point at which larval reserves have been stored to enable them to complete the next scheduled moulting event independent of additional feeding (Anger, 2001). Both *P. ornatus* and *P. homarus* phyllosoma demonstrated relatively extended PRS_{50} durations of 3.8 and 4.4 days, respectively, occupying ³50% of the normal intermoult duration of 6-7 days. This is in contrast to most species where the PRS_{50} is attained within 20-50% of the intermoult duration (Anger, 2001). An extended PNR_{50} (50% of intermoult duration) suggests that the nutritional reserves at hatch are of high quality and quantity, *i.e.* a degree of lecithotrophic development. Although it may be counterintuitive to also have a long PRS_{50} it is potentially more a measure of the quality of the larval food source, or perhaps the phyllosomas ability to assimilate it. In this study newly hatched *P. ornatus* and *P. homarus* phyllosoma were fed on *Artemia* nauplii. Although *Artemia* are a convenient, readily hatched, off-the-shelf product, they are nevertheless an extremely poor source of highly unsaturated fatty acids. As such, phyllosoma may require additional time to accumulate the necessary reserves to undertake a moult event on an *Artemia* only diet. The ability to suspend growth in the absence of food, and recommence within a defined period, is a phenomenon suggested to explain the considerable temporal distribution of wild larval stages in the Coral Sea gyres, despite a strictly defined breeding season for *P. ornatus* in this region (Smith *et al*., 2009). The uncoupling of moult synchrony due to variable prey access is not quarantined to wild phyllosoma but also occurs within culture conditions.

To circumvent prolonged and asynchronous moulting in the hatchery that may be associated with nutritional deficits a number of strategies may be considered. They include better targeting phyllosoma dietary profiles to meet their requirements and boosting nutritional uptake through the application of a range of probiotics that assist in sequestering and digesting essential nutritional reserves. Why these two tropical species have greater PNR_{50} compared to other lobster species is unknown. It may well be due to differences associated with metabolism and growth but it may also be an adaptation to endure variable concentrations of primary and secondary productivity in tropical compared to that noted in temperate waters (Kirk, 1994).

In conclusion, phyllosoma of *P. ornatus* and *P. homarus* have long PNR_{50} indicating a high potential for enduring periods of starvation. A long PRS_{50} indicates a poor ability in the hatchery to sequester required nutritional reserves over a short duration, signalling a requirement for researchers to investigate a range of novel avenues to boost nutrition.

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References

Abrunhosa, F. A. and J. Kittaka. 1997. Effect of starvation on the first larvae of *Homarus americanus* (Decapods, Nephropidae) and phyllosomas of *Jasus verreauxi* and *J. edwardsii* (Decapoda, Palinuridae). *Bull. Mar. Sci.,* 6: 73-80.

Alekseeva, T. A. and A. I. Zotin. 2001. Standard metabolism and macrotaxonomy of crustaceans. *Biol. Bull.*, 28: 157-168.

Al-Marzouqi, A., A. Al-Nahdi, N. Jayabalan and J. C. Groeneveld. 2007. An assessment of the spiny lobster *Panulirus homarus* fishery in Oman – Another decline in the Western Indian Ocean? *J. Mar. Sci.,* 6: 159-174.

Anger, K. 1987. The D0 threshold: a critical point in the larval development of decapod crustaceans. *J. Exp. Mar. Biol. Ecol.,* 108: 15-30.

Anger, K. 2001. *The Biology of Decapod Crustacean Larvae*. A. A. Balkem Publishers, Lisse. 491 pp.

Anger, K. and R. R. Dawirs. 1981. Influence of starvation on the larval development of *Hyas araneus* (Decapoda, Majidae) Helgoländer Wiss. *Meeresuners.,* 34: 287-311.

Anger, K., R. R. Dawirs, V. Anger and J. D. Costlow. 1981. Effects of early starvation periods on zoeal development of brachyuran crabs. *Biol. Bull.,* 161: 199-212.

Bradford, R. W., B. D. Bruce, S. M. Chiswell, J. D. Booth and S. J. Wotherspoon. 2005. Vertical distribution and diurnal migration patterns of *Jasus edwardsii* phyllosomas off the east coast of the North Island, New Zealand. *N. Z. J. Mar. Freshwat. Res.,* 39: 593-604.

Benzie, J. A. H. and T. Yoshimura. 1999. Rock lobster aquaculture workshop. Australia-Japan Joint Science and Technology Consultative Committee, Perth 26-27 Jan. Australian Department of Industry, Science and Resources, Canberra. 16 pp.

Calado, R., G. Dionísio and M. T. Dinis. 2008. Starvation resistance of early zoeal stages of marine ornamental shrimps *Lysmata* spp. (Decapoda: Hippolytidae) from different habitats. *J. Exp. Mar. Biol. Ecol.,* 351: 226-233.

Chavez, E. A. 2009. Potential production of the Caribbean spiny lobster (Decapoda, Palinura) fisheries. *Crustaceana,* 82: 1393-1412.

Dawirs, R. R. 1986. Influence of limited food supply on growth and elemental composition (C, N, H) of *Carcinus maenas* (Decapoda) larvae, reared in the laboratory. *Mar. Ecol. Prog. Ser.,* 31: 301-308.

FAO. 2006. State of world aquaculture. *FAO Fisheries Technical Paper* 500, 147 pp.

FAO. 2008. Globefish European price report, April quarter. FAO, Fish Products and Fisheries Division, 14 pp.

Figueiredo, J., G. Penha-Popes, L. Narciso and J. Lin. 2008. Effect of starvation during late megalopa stage of *Mithraculus forceps* (Brachyura: Majidae) on larval duration, synchronism of metomorphosis, survival to juvenile, and newly metamorphosed juvenile size. *Aquaculture*, 274: 175-180.

Forward, R. B. Jr. 1988. Diel vertical migration: Zooplankton photobiology and behaviour. *Oceanogr. Mar. Biol.,* 26: 361-393.

Holthuis, L. B. 1991. Marine Lobsters of the World. FAO Species Catalogue, Synopsis 125, Vol. 13. Food and Agriculture Organization of the United Nations. 292 pp.

Jeffs, A. G., P. D. Nichols, B. D. Mooney, K. L. Phillips and C. F. Phleger. 2004. Identifying potential prey of the pelagic larvae of the spiny lobster *Jasus edwardsii* using signature lipids. *Comp. Biochem. Phys. B,* 137: 487-507.

Kirk, J. T. O. 1994. *Light and Photosynthesis in Aquatic Ecosystems*. 2nd Edn., Press Syndicate University of Cambridge, Cambridge. 509 pp.

Kittaka, J. 1997. Culture of larval spiny lobsters: a review of work done in northern Japan. *Mar. Freshwat. Res.,* 48: 923-930.

Matsuda, H. and T. Yamakawa. 1997. Effects of temperature on growth of the Japanese spiny lobster, *Panulirus japonicus* (V. Seibold) phyllosomas under laboratory conditions. *Mar. Freshwat. Res.,* 48: 791-796.

Matsuda, H., T. Takenouchi and T. Yamakawa. 2003. Diel timing of moulting and metamorphosis of *Panulirus japonicus* phyllosoma larvae under laboratory conditions. *Fish. Sci.,* 69: 124-130.

Mikami, S. and F. Takashima. 1993. Effects of starvation upon survival, growth and moulting interval of the larvae of the spiny lobster *Panulirus japonicus* (Decapoda, Palinuridea). *Crustaceana,* 64: 137-142.

Mikami, S., J. G. Greenwood and N. C. Gillespie. 1995. The effect of starvation and feeding regimes on survival, intermoult period and growth of cultured *Panulirus japonicus* and *Thenus* sp. phyllosomas (Decoapoda, Palinuridae and Scyllaridae). *Crustaceana,* 68: 160-169.

Moss, G. A., L. J. Tong and S. E. Allen. 2001. Effect of temperature and food ration on the growth and survival of early and mid-stage phyllosomas of the spiny lobster *Jasus verreauxi*. *Mar. Freshwat. Res.,* 52: 1459-1464.

Omori, M. and W. M. Hamner. 1984. Patchy distribution of zooplankton: Behavior, population assessment and sampling problems. *Mar. Biol.,* 72: 193-200.

Radhakrishnan, E. V., V. D. Deshmukh, M. K. Manisseri, M. Rajamani, J. K. Kizhakudan and R. Thangaraja. 2005. Status of the major lobster fisheries in India. *N. Z. J. Mar. Freshwat. Res.,* 39: 723-732.

Smith, G. G., A. J. Ritar and G. A. Dunstan. 2003. An activity test to evaluate larval competency in spiny lobsters (*Jasus edwardsii*) from wild and captive ovigerous broodstock held under different environmental conditions. *Aquaculture,* 218: 293-307.

Smith, G., M. Salmon, M. Kenway and M. Hall. 2009. Description of the larval morphology of captive reared *Panulirus ornatus* spiny lobster, benchmarked against wild-caught specimens. *Aquaculture,* 295: 76-88.

Staton, J. L. and S. D. Sulkin. 1991. Nutritional requirements and starvation resistance in larvae of the brachyuran crabs *Sesarma cinereum* (Bosc) and *S. reticulatum* (Say). *J. Exp. Mar. Biol. Ecol.,* 152: 271-284.

Storch, V. and K. Anger. 1983. Influence of starvation and feeding on the hepatopancreas of larval *Hyas araneus* (Decapoda, Majidae). *Helgoländer Meeresunters.,* 36: 67-75.

Vijayakumaran, M. and E. V. Radhakrishnan. 1986. Effects of food density on feeding and moulting of phyllosoma larvae of the spiny lobster *Panulirus homarus* (Linnaeus). *Proceedings of the 4th Symposium of Coastal Aquaculture.* Marine Biological Association of India, p. 1281-1285.

Ye, Y., D. Dennis and T. Skewes. 2008. Estimating the sustainable lobster (*Panulirus ornatus*) catch in Torres Strait, Australia, using an age-structured stock assessment model. *Cont. Shelf Res.,* 28: 2160-2167.

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