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Growth and moulting in the mud spiny lobster, *Panulirus polyphagus* (Herbst, 1793)

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ABSTRACT

Growth rates in the mud spiny lobster, *Panulirus polyphagus* held in captivity were assessed and compared with growth estimates derived from length composition of these lobsters in trawl landings at Veraval, north-west coast of India. The von Bertalanffy's growth parameters 'L_∞' and 'K' derived for male *P. polyphagus* were 135 mm (carapace length, CL) and 0.46 y^{-1} in the wild and 144.8 mm (CL) and 0.51 y^{-1} in captivity. The values derived for female *P. polyphagus* were 124.7 mm (CL) and 0.38 y^{-1} in the wild and 119 mm (CL) and 0.43 y^{-1} in captivity. There was a clear difference in the growth curves of males and females in captivity and in the natural habitat. The VBGF curves indicated that males had a better growth output than females, both in the wild and in captivity. Juvenile lobsters exhibited higher moulting frequency, with the intermoult period increasing steadily as CL increased. Increments in CL at each moult showed significant correlation with increasing CL in both males and females. The rate of growth was found to decrease with age in both sexes. In males there was renewed burst of growth after the attainment of sexual maturity (65-75 mm CL) but beyond 80 mm CL, the growth was steady. In females however, there was drastic reduction in growth rates in the 63-68 mm CL range, and it steadied at 70-80 mm CL when the breeding and rematuration processes are more prominent in its life cycle.

Keywords: Growth, Moulting, Mud spiny lobster, *Panulirus polyphagus*

Introduction

Growth patterns in crustaceans have been described in detail by Hartnoll (1982, 2001) as highly variable ranging from indeterminate growth and reproduction at every instar after maturity in some groups to the occurrence of a terminal or maturation moult in groups that reproduce only once. Lobsters are at one end of the continuum, exhibiting indeterminate growth and capable of reproducing at every instar after the onset of maturity (Wahle and Fogarty, 2006). Even though growth in size in lobsters occurs during the intermoult periods, the very concept of growth permits its definition as a continuous process and the change in length and weight of an individual can be represented as a continuous function over time.

The rate of growth is determined by the frequency of moulting within a specific period of time; usually tmoulting frequency is higher in the juvenile stages. Berry (1971) found that the growth rates of male and female spiny lobsters are similar until sexual maturity is attained. Spiny lobsters are known to have faster growth rates, particularly under tropical conditions (Mohammed and George, 1968). The moulting frequency in tropical species is reported to be higher, with relatively shorter intermoult duration usually varying from 36-107 days, depending upon the age of the animal (Berry, 1971).

While animals maintained in captivity over a period are ideal for growth studies, there is always the risk of growth in such animals being influenced by controlled environmental factors and feed. Hence assessment of the animal's growth is never complete without comparison with the growth observed in animals sampled from the wild stock. While there is some information on the growth and stock dynamics of *P. polyphagus* from the north-west coast of India (Kagwade, 1987, 1993, 1994) and a preliminary assessment of the growth of *P. polyphagus* in captivity (Kathirvel, 1973; Radhakrishnan and Devarajan, 1986), no comprehensive study has been conducted so far to compare their growth performance in captivity with that in the wild. In the present study, growth rates in *P. polyphagus* held in captivity were assessed and compared with growth estimates derived from length composition of these lobsters in trawl landings at Veraval on the north-west coast of India. Observations on moulting in captivity were also recorded.

Materials and methods

For estimates of growth parameters in the wild, length frequency data of 1302 males and 954 females of

P. polyphagus in the length range of 35-133 mm CL and weight range of 30-1690 g, collected from commercial trawl landings at Veraval during October 1997 to March 2003 were pooled and analysed using the FiSAT package (Gayanilo *et al.*, 1996). The VBGF growth parameters were estimated from the restructured data generated using ELEFAN I programme of the FiSAT package. Reverse estimation of t_0 was done from the VBGF.

Growth increments at moult measured over a period of 24 months were used as the base data to derive growth curves for *P. polyphagus* held in captivity. Estimates of L_∞ were made by plotting the increase in carapace length every 3 months against the CL at the start of the 3-month period. For this purpose, the growth increments for the entire size range of reared lobsters (46 males and 43 females) was used to generate a more or less continuous series of growth measures that could be considered to represent the growth of an individual lobster over various phases of its life history, following the method described by Berry (1971) for *P. homarus*. Estimates of L_∞ and K were obtained as the intercept and slope of the regression line of carapace lengths at 3 months intervals, following the method of Manzer and Taylor (1947). This method was chosen over the more common Ford-Walford plot, as the precise age of the lobsters was not known.

Test animals (18-110 mm CL) collected live from trap gillnets operated along Sutrapada coast (south of Veraval), were stocked in FRP tanks of 1 t capacity, filled with 800 l seawater run on a closed recirculatory system. The tanks were provided with shelters (PVC pipes and tiles). The animals were fed *ad libitum* twice a day with fresh meat of the gastropod, *Turbo* sp. Faecal pellets were removed every morning. Water exchange was carried out @ 10% every day, when the sides of the tanks were also cleaned. Water temperature ranged between 27 and 30 ^oC in all the tanks; salinity and pH were maintained at 36 to 37 ppt and 7.8 to 8.0, respectively. Nitrite and ammonia levels were monitored daily, so as to avoid any adverse effects on growth caused by an increase in these limiting factors. Necessary buffers were added to regulate the pH and maintain uniform water chemistry throughout the period of study. Light exposure was not controlled and the animals were uniformly exposed to the photoperiod conditions prevalent in the station.

A minimum of four animals were maintained in each tank in order to avoid any depression in growth rate likely to be caused by isolation, as reported by Chittleborough (1975). Individual lobsters were tagged with coloured wires wound around the base of the antennae. The colour of the wires and the number of windings were used as identification keys. Growth was recorded in terms of carapace length (CL, mm) and total wet weight (W, g) (excluding weight of eggs in berried females). The occurrence of moulting, duration of intermoult period for each individual lobster and frequency of moulting in relation to lunar periodicity were recorded systematically. Growth increments were recorded after every moult.

Results and discussion

Growth

The von Bertalanffy growth equation derived for wild and captive *P. polyphagus* are as below:

Male (wild)	$L_t = 135\ [1\text{-}e^{-0.46(t+ 0.269)}]$
Male (captive)	$L_t = 144.8\ [1\text{-}e^{-0.51(t- 0.39)}]$
Female (wild)	$L_t = 124.7\ [1\text{-}e^{-0.38(t+ 0.003)}]$
Female (captive)	$L_t = 119\ [1\text{-}e^{-0.43(t- 0.09)}]$

The results show that, there is clear difference between the growth curves of male (Fig. 1) and female (Fig. 2) in captivity and in the natural habitat, and also between wild

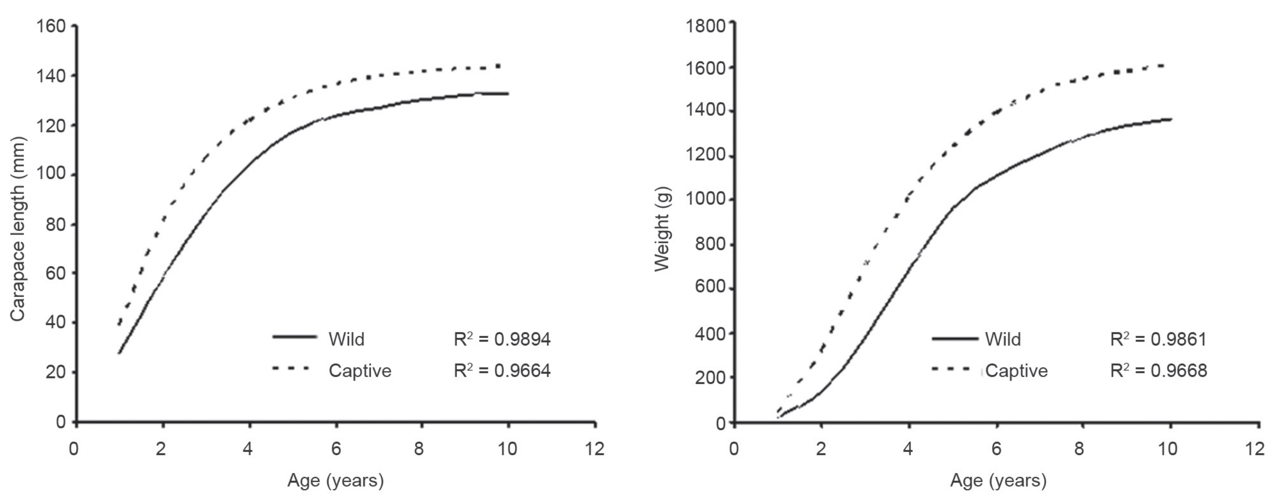

Fig. 1. von Bertalanffy growth curves for wild and captive male *P. polyphagus*

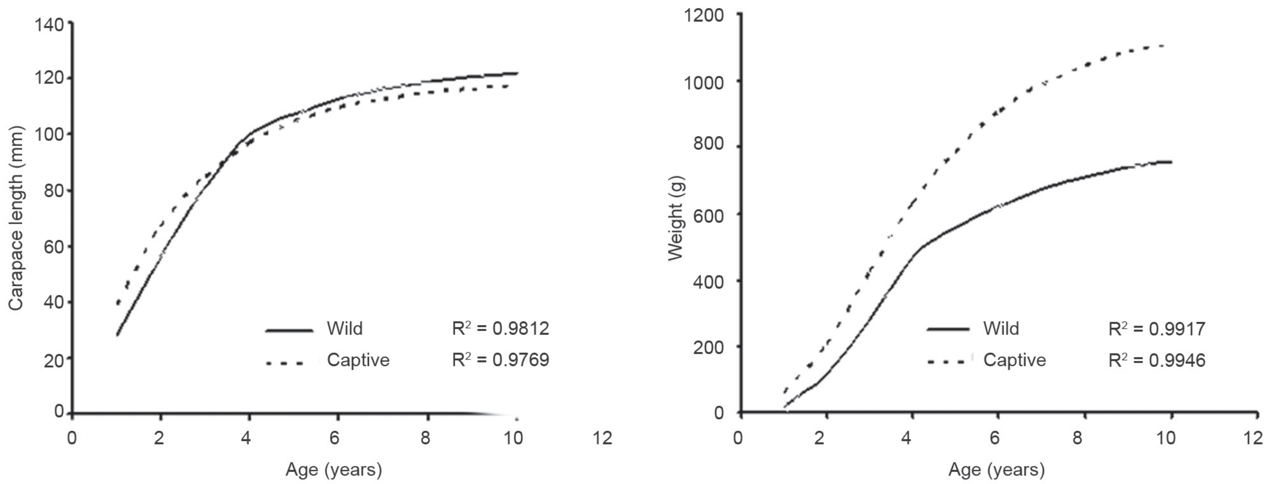

Fig. 2. von Bertalanffy growth curves for wild and captive female *P. polyphagus*

and captive lobsters of the same sex. The growth potential, as judged from the VBGF growth equation parameters, can be improved in captivity. The VBGF curves indicate that male *P. polyphagus* has better growth output than the female, both in wild and in captivity (Fig. 3 and 4)

The von Bertalanffy growth model, which essentially defines growth as continuous over a time scale, has been widely applied to several lobster species, particularly on account of its analytical convenience and use in other size-based stock and mortality estimator models (Cobb and Caddy, 1989). Growth rates tend to vary strongly between species, with warm-water forms growing faster when compared with cooler-water forms (Booth and Kittaka, 1994). Among the spiny lobsters of the genus *Panulirus*, the growth coefficient 'K' has been reported to vary from as less as 0.00026 in *P. cygnus* off W. Australia (Phillips *et al*., 1992) to as high as 0.58 in *P. penicillatus* in the Marshall Islands (Ebert and Ford, 1986). Kagwade (1987) obtained very high L_∞ values of 537 mm and 443 mm TL for male and female *P. polyphagus* off Maharashtra coast, with annual 'K' = 0.2 and 0.2231 respectively.

The analysis of size frequency distributions remains the most common indirect method for assessing growth in lobsters, but this method has been found most useful when the representation of particular age classes is clearly reflected in the frequency distribution of the samples. In the case of lobsters, however, there is always the highest chance of overlap between two or more age classes. The trawl sector in Gujarat mostly exploits adult and breeding spiny lobsters which tend to prevail along the sandy and clayey bottom off the coast, more susceptible to trawling activity. Moreover, with dwindling fishery, the availability of sufficient numbers of sample is always a hurdle, as was experienced in the course of the present study.

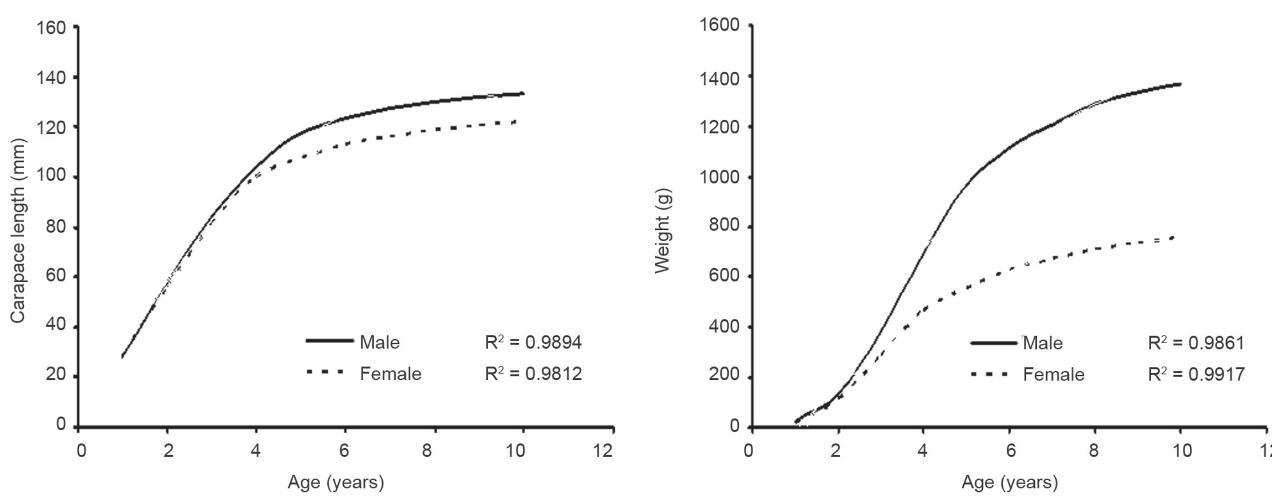

Fig. 3. von Bertalanffy growth curves for wild male and female *P. polyphagus*

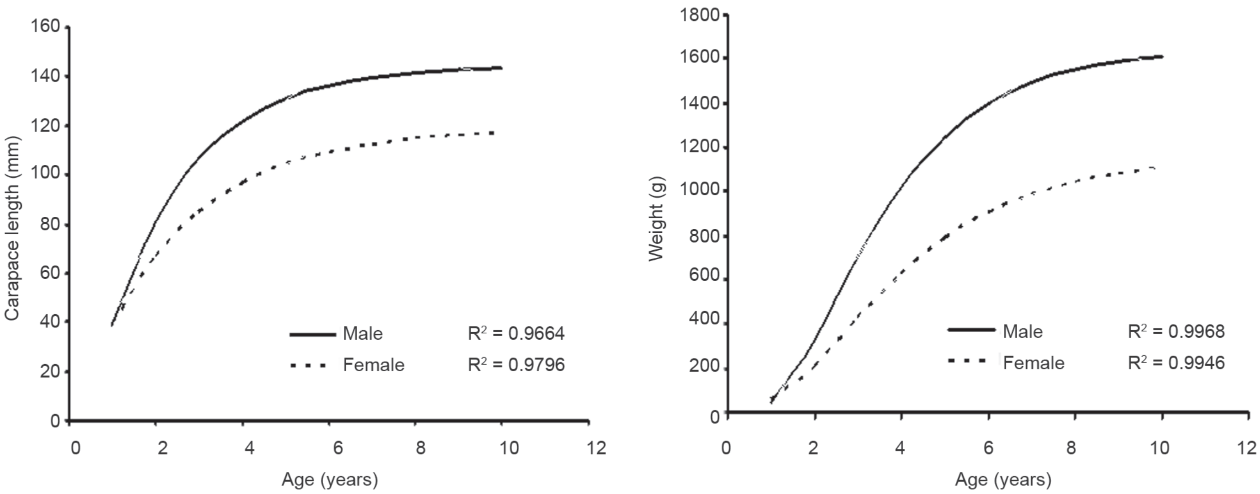

Fig. 4. von Bertalanffy growth curves for male and female *P. polyphagus* held in captivity

Moulting

As the lobsters exhibited strong tendency to consume moult exuviae, whole moult recovery from the rearing tanks was difficult. Moulting takes place by rupture along the branchiostegal line and the animal pushes itself out from the old shell. The freshly moulted animal is soft and remains so, for a few days before the new shell begins to harden. During this period, cannibalism occurs as the freshly moulted animal is very soft-bodied and inactive, thereby becoming easy prey to the stronger and more active lobsters in the tank. This was overcome to some extent by providing shelters and hiding places within the tanks.

Males

Juvenile lobsters exhibited higher moulting frequency, with the intermoult period significantly increasing with increase in CL (R^2 = 0.979) (Fig. 5a). The duration of each intermoult increased over the preceding one except in the length groups of 65-70 mm CL and 85-90 mm CL.

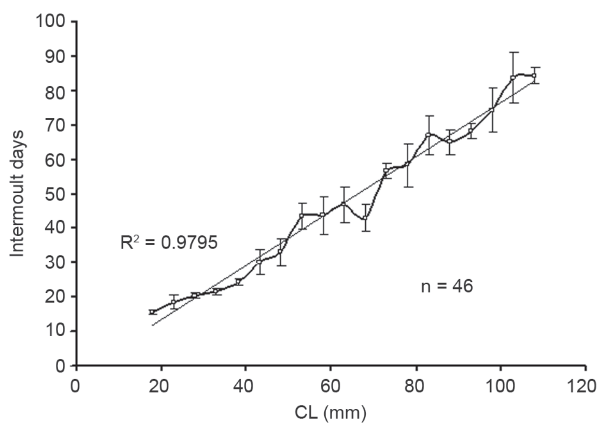

Fig. 5a. Average intermoult days (±S.D.) in male *P. polyphagus* held in captivity

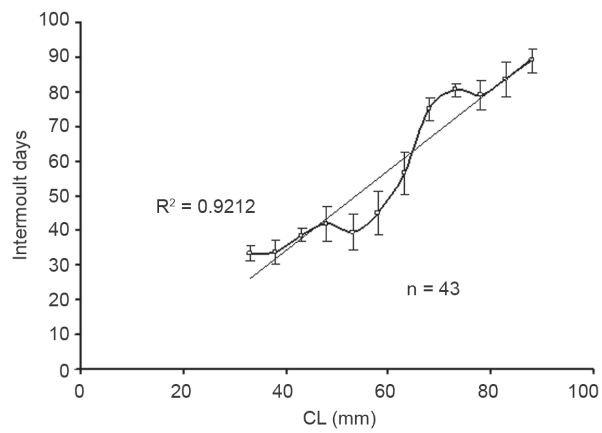

Fig. 5b. Average intermoult days (±S.D.) in female *P. polyphagus* held in captivity

Increments in CL at each moult showed significant positive correlation (R^2 = 0.861) with increasing CL; the parabolic trend line for increment at moult tended to peak at 50-70 mm CL (Fig. 6a). This peak incidentally coincides

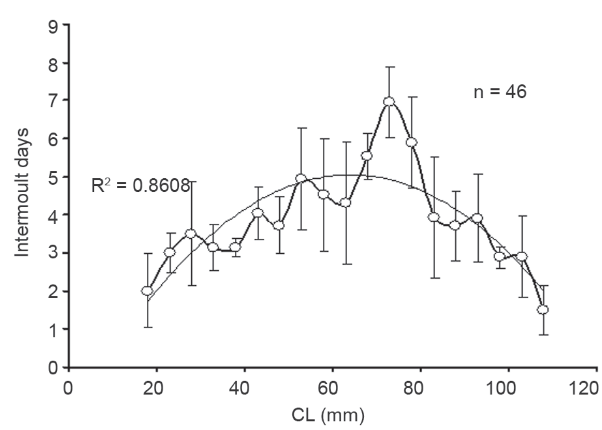

Fig. 6a. Average moult increment in CL (mm) (±S.D.) in male *P. polyphagus* held in captivity

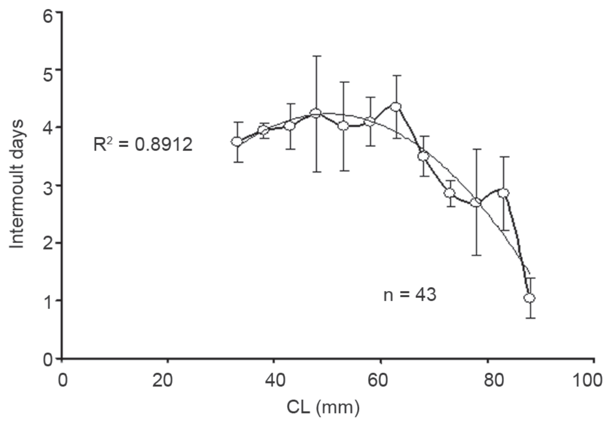

Fig. 6b. Average moult increment in CL (mm) (±S.D.) in female *P. polyphagus* held in captivity

with the onset of sexual maturity and development of secondary sexual traits at 51-55 mm CL as reported by Kizhakudan and Patel (2010) for male *P. polyphagus*, culminating in the formation of a functionally sexual male with developed gonads at 61-65 mm CL. The average increment in CL per moult was found to increase from about 2 mm in the size range of 16-20 mm CL, to about 5-7 mm in the size range of 51-80 mm CL, and decrease to about 1.5 mm in the size range of 106-110 mm CL. The estimated average daily increment in CL showed a decreasing trend with increasing CL (R^2 = 0.876) (Fig. 7a). While the average moult increments in CL were @ 0.7% of the initial CL in the size groups 16-25 mm CL, there was a steady rate of decline in this proportion, and it was @ only about 0.02% of the initial CL in the larger size groups of 105-110 mm CL.

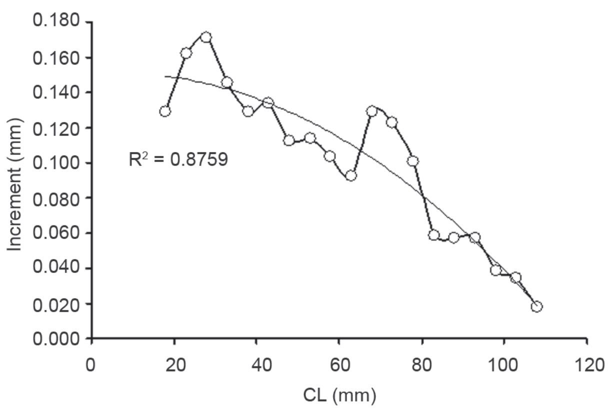

Fig. 7a. Average daily increment in CL (mm) in male *P. polyphagus* held in captivity

Females

Juvenile female lobsters also exhibited higher moulting frequency, with significant steady increase in intermoult period with increase in CL (R^2 = 0.921) (Fig. 5b). The duration of each intermoult increased over the preceding one except in the length groups of 51-55 mm CL and 76-80 mm CL. Maximum lag between successive intermoults was noticed in the size range of 61-70 mm CL, coinciding with the attainment of sexual maturity. Increments in CL at each moult showed significant positive correlation (R^2 = 0.891) with increasing CL; the parabolic trend line for increment at moult tended to peak at 45-60 mm CL (Fig. 6b). As in the case of males, this peak coincides with the onset of sexual maturity and development of secondary sexual traits at 51-60 mm CL and formation of a functionally sexual female with developed gonads (66-70 mm CL) (Kizhakudan and Patel, 2010). The average increment in CL per moult was found to increase from about 3.8 mm in the size range of 31-35 mm CL, to a peak of about 4 mm in the size range of 41-65 mm CL, and decrease to about 1 mm in the size range of 86-90 mm CL. The estimated average daily increment in CL followed a parabolic trend with increasing CL (R^2 = 0.891) (Fig. 7b). While the average moult increments in CL were @ 0.35% of the initial CL in the size groups of 31-35 mm CL, there was a steady rate of decline in this proportion, and it was @ only about 0.01% of the initial CL in the larger size range of 86-90 mm CL.

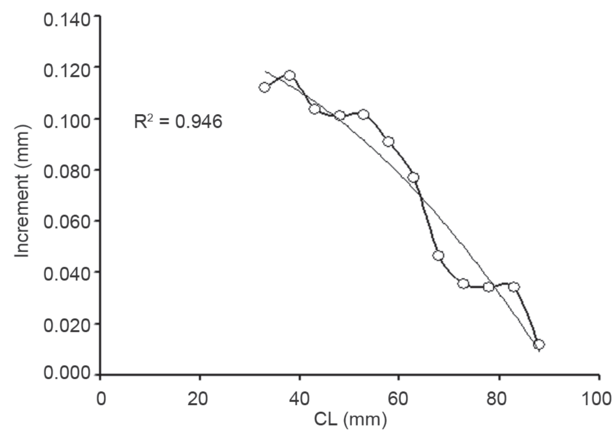

Fig. 7b. Average daily increment in CL (mm) in female *P. polyphagus* held in captivity

The moult and growth progression of two males and two females of *P. polyphagus* were followed over a period of one year. The initial carapace lengths were 29 mm and 28 mm for one pair of male and female and 63 mm and 56 mm respectively, for the second pair. Growth curves for male and female generated using the combined data of the two pairs so as to trace the growth from increments at moult of a single individual revealed that males at latter stages of life (>50 mm CL) had higher growth increments than females (Fig. 8).

The frequency of moulting in relation to lunar cycles assessed over a period of one year by directly fitting the moulting frequency against the dates of moulting in groups of captive lobsters showed that the number of moults within

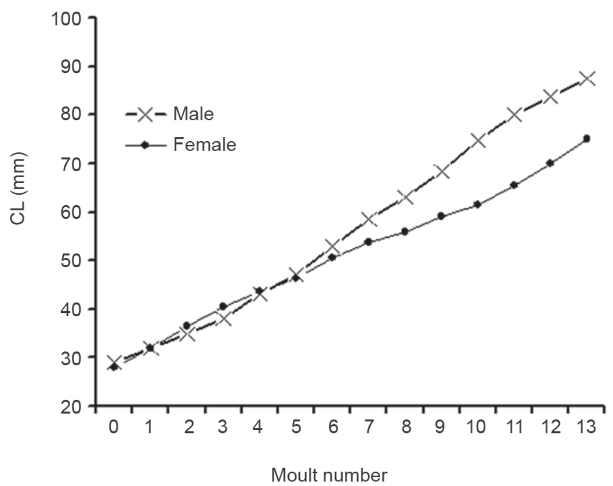

Fig. 8. Growth of male and female *P. polyphagus* held in captivity, from direct plot of moult increment data (Moult number is from the day of stocking; Moult increment data generated from two males and two females held in captivity)

a group was higher towards the new moon and full moon days, particularly two or three days before or immediately after the new moon day (Fig. 9), thus suggesting perhaps, a preference for darkness as a possible defense mechanism against predation.

The probability of moulting in captive male and female lobsters of different size classes within specific time frames defining the intermoult period was estimated as a function of the number of animals of each size class that moulted during a given intermoult time frame, as described by Wahle and Fogarty (2006). For both, males and females, the moult probability for shorter intermoult periods was highest for smaller animals; as growth progressed, larger animals had longer intermoult periods (Fig. 10).

Wahle and Fogarty (2006) described lobster growth as highly variable, reflecting the effect of quantum changes associated with moulting and in the probability distribution of moult increments. The intermoult period is known to increase with size. Aiken (1980) gave the evidence for percent increment of growth per moult to typically diminish with body size. Growth rate has always been known to be variable even at the intraspecific level, being strongly influenced by the environment, geographic distribution and sex of the animal. Maturation has a retarding effect on growth, resulting in sex-specific allometric growth patterns, and the effect is usually greater in females than in males because of the greater energetic allocation to reproduction. The males of all taxa are known to mature physiologically at a smaller size than females (Wahle and Fogarty, 2006). When females mature, their intermoult period begins to increase, relative to males in the same instar. Sexual

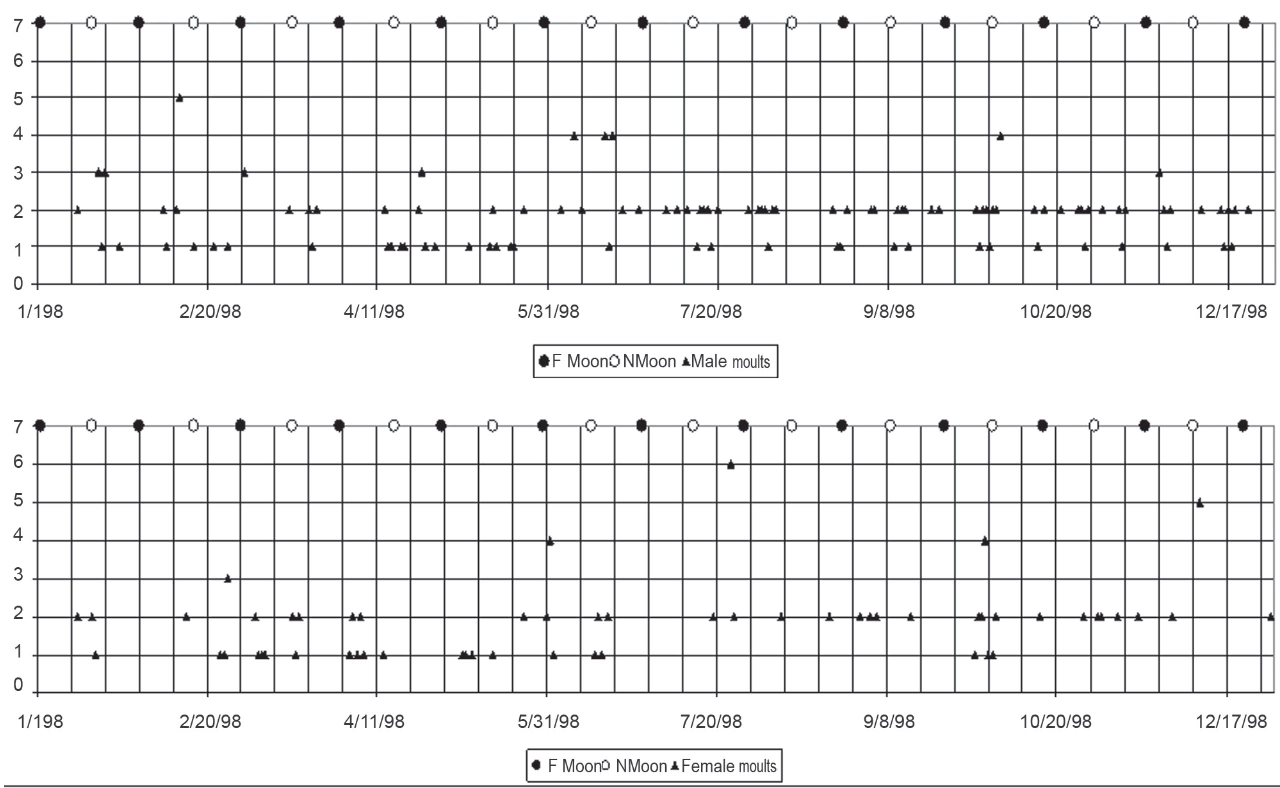

Fig. 9. Moulting frequency in relation to lunar cycle in male and female *P. polyphagus* held in captivity

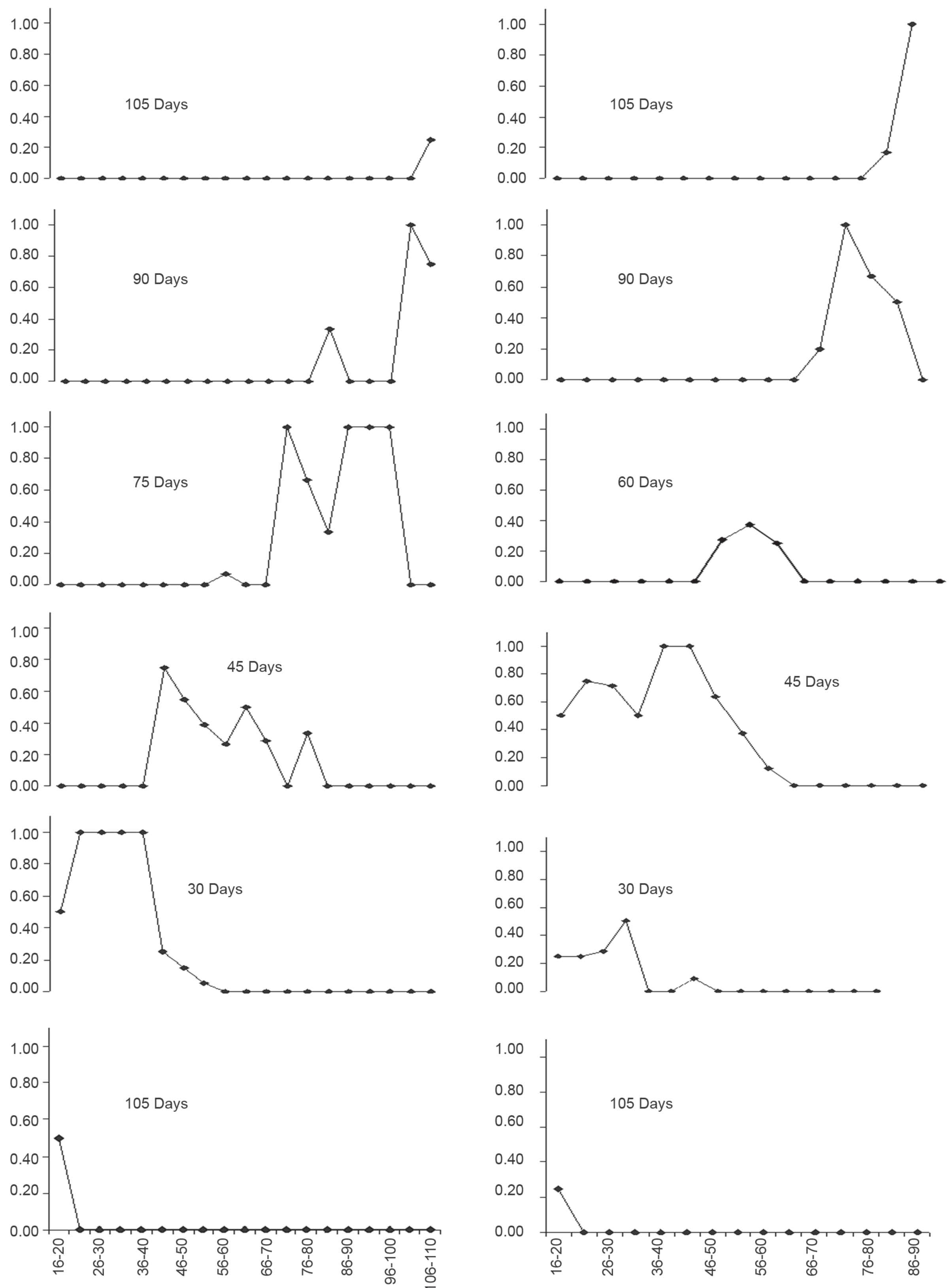

Fig. 10. Moult probability of size groups in relation to intermoult period in male and female *P. polyphagus* held in captivity

differences in allometry can be a useful indicator of size at onset of sexual maturity (Aiken and Waddy, 1989; Megumi and Satoru, 1997; Robertson and Butler, 2003; Wahle and Fogarty, 2006).

In the present study, it was observed that male *P. polyphagus* had a higher growth rate under different conditions. The rate of growth is superior in the males through all the size classes. In males and females, the rate decreases with age and only in males there is renewed burst of growth after the attainment of sexual maturity (65-75 mm CL). Beyond 80 mm CL, the growth is seen to be steady. In females however, there is drastic reduction in growth rates in the 63-68 mm size range, and it steadies at 70-80 mm CL when the breeding and rematuration processes are more prominent in its life cycle. From the trends in moult increments it is seen that the increments reach a peak which usually coincided with the attainment of sexual maturity. Beyond this, there is a slide, which is very prominent in the females, reflecting on the probable allocation of energy budget for breeding activities.

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