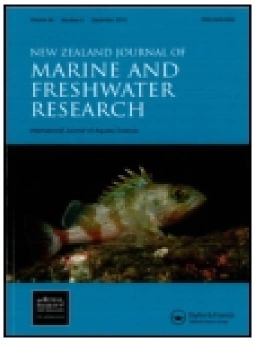

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Growth and moulting of captive *Panulirus homarus homarus* in Kenya, western Indian Ocean

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Abstract *Panulirus homarus homarus* is the most widely distributed of the three *P. homarus* subspecies and is the second most important spiny lobster in the Kenyan lobster fishery after *Panulirus ornatus*. Growth and moulting of lobsters held in concrete tanks with a flow-through sea-water system and at ambient temperatures, were monitored for 18 months (October 2001 – March 2003). Both moult increment and moulting frequency were inversely correlated with size. Mean moult increment ranged from 4 mm in the 36–45 mm carapace length (CL) size class to 0.6 mm in the 86–95 mm CL size class. Mean intermoult period increased from 49 days in the 46–55 mm CL size class to 66 days in the 76–85 mm CL size class. Growth rates were 19% and 46% higher for males and females, respectively during the south-east monsoon (low temperature) season than during the north-east monsoon (high temperature) season. A shift in energy use from growth to reproduction rather than the influence of temperature was responsible for the variation in the growth rates between the two seasons. Marking-induced injury caused a significant 65% growth reduction in the affected individuals. Mean moult increments calculated for most size classes of uninjured lobsters were comparable to those observed in the subtropical *P. homarus rubellus* reared in the laboratory in South Africa but smaller than those reported in the Indian *P. homarus* under similar conditions.

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Keywords *Panulirus homarus*; growth; moulting; injury; seasonality; Kenya

INTRODUCTION

The scalloped spiny lobster *Panulirus homarus homarus* (Linnaeus 1758) is the most widely distributed of the three subspecies of *P. homarus* and is found throughout the Indo-Pacific region with pockets of high concentrations in East Africa and Indonesia (Berry 1974; Pollock 1993). The other two subspecies, *P. homarus megasculptus* and *P. homarus rubellus*, are restricted to the Arabian Sea and the south-east coasts of Madagascar and Southern Africa, respectively. All three subspecies inhabit shallow waters mostly between 1 and 5 m depth among rocks, often in the surf zone and sometimes in highly turbid estuarine areas (Holthuis 1991). However, they respond to different environmental conditions that prevail in their respective areas (George 1997).

Populations of *P. homarus homarus* on the East African coastline occur between those of *P. homarus megasculptus* (to the north) and *P. homarus rubellus* (to the south) with respective populations overlapping at the flanks. Hybrids are common in areas where the subspecies overlap (Pollock 1993). Successful interbreeding suggests that these subspecific separations are fairly recent (George 1997). *P. homarus homarus* is the second most important spiny lobster in the Kenyan lobster fishery after *P. ornatus* and accounts for c. 32% of the total landings (Kulmiye 2004). The Kenyan lobster fishery is artisanal in nature and represents one of the few activities from which local fishers derive a good return since spiny lobsters fetch far higher prices per unit weight than finfish and other crustaceans.

Despite its wide distribution and local importance, an in-depth study on many fundamental aspects of the biology, ecology, and fishery of *P. homarus homarus* is lacking in the western Indian Ocean. Previous studies on *P. homarus* have either exclusively dealt with the other two subspecies

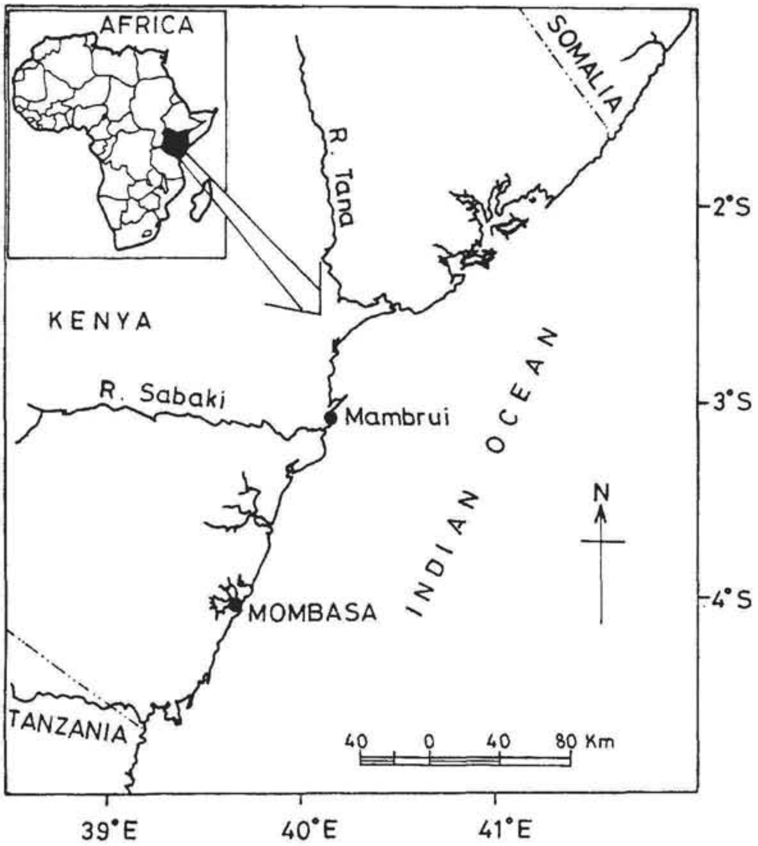


Fig. 1 Map of the Kenyan coast showing location of the live lobster collection site (Mambrui) and the rearing experimental station (Mombasa).

(Heydorn 1969; Berry 1970, 1971a,b; Smale 1978; Al-Abdulsalaam 1989; Johnson & Al-Abdulsalaam 1991; Liss et al. 1994; Fielding 1997; Mohan 1997; Fielding & Mann 1999) or addressed *P. homarus homarus* populations outside the region (De Bruin 1962, 1969; Jayawickrema 1991; Jayakody 1989, 1993; Thuy 2000). In this paper we present and discuss the growth and moulting of male and female *P. homarus homarus* monitored for 18 months in captivity.

MATERIALS AND METHODS

Specimen collection and laboratory conditions

This experiment was performed at the Mombasa Station of the Kenya Marine and Fisheries Research Institute. Lobsters were hand-collected at night by wading fishers from the reefs at Mambrui (Fig. 1) and were immediately put in large polythene bags with aerated sea water. They were brought to the laboratory and released into four outdoor, sheltered concrete tanks (193 × 103 × 106 cm) with a flow-through sea-water system and good aeration. After a 5-day acclimatisation period, each lobster was measured (carapace length (CL) ± 0.1 mm) and tagged by punching coded holes in the uropods and telson with a sterile leather punch for easy identification (Chittleborough 1976; Plaut & Fishelson 1991). Lobsters were provided with artificial shelters using flat coral rocks and asbestos tubes. All the size classes dealt with in the experiment were stocked in each tank at a density of 10 individuals per m^2. Mortalities were occasionally replaced with wild captures of similar sizes. The animals were fed daily *ad libitum* on a diet of deck mussel (*Septifer bilocularis*), clam (*Anadara antiquata*), and chopped fish (mostly reef fish). Food was supplied in the late afternoon and any uneaten food items were removed the following morning. Tanks were cleaned thoroughly once a week.

Although no complications were reported for captive *P. cygnus* and *P. penicillatus* tagged in the same manner (Chittleborough 1976; Plaut &

Fishelson 1991), *P. homarus homarus* developed deteriorating necrotic wounds, which resulted in the complete loss of both telson and uropods for some individuals. All lobsters were quarantined in a recirculating anti-bacterial solution (1 ml Sera Baktopur to 20 litre sea-water ratio) for 3 days while holding tanks were thoroughly cleansed with antiseptic solutions. Except for a few animals with advanced injuries, the majority of the affected lobsters were successfully treated. Subsequent markings of both wild replacements and newly moulted animals were made by tying a numbered Dymo Scotch tape to the base of an antenna with a nylon monofilament line. Growth measurements of newly moulted lobsters were made 3 days after ecdysis when the carapace was hard enough to ensure precise measurements. Carapace length (CL ± 0.1 mm) was measured mid-dorsally from the transverse ridge between the frontal spines to the posterior margin of the cephalothorax using a vernier caliper.

Temperature and salinity

The rearing experiment was run for 18 months (October 2001 – March 2003) under ambient conditions of sea-water quality and temperature. Measurements of temperature and salinity of holding tanks and the adjacent Tudor Creek (pumping station) were simultaneously made once daily with a portable probe (Aanderaa S/T/D Sensor 3230/ Aanderaa Dupley Unit 3315). Since no marked differences were observed between temperature and salinity readings recorded from the tanks and those from the creek, the daily data were combined and mean monthly readings calculated for both temperature and salinity.

Analytical methods

For statistical purposes, data sets for injured and uninjured lobsters were treated separately and compared for differences using Students' *t*-test and ANOVA. Data for uninjured lobsters were further used to estimate growth parameters as well as to assess the effect of temperature on growth and the intermoult period. For interpretation of moult increment and intermoult period, size class averages were taken. The von Bertalanffy growth function (von Bertalanffy 1938) was used to estimate growth rates:

$$L_t = L_\infty\,(1 - e^{(-K\,(t - t_0))}) \qquad (1)$$

where L_t is the predicted carapace length at age t, L_∞, the asymptotic CL (mm), K, the growth constant (year^{-1}), t, the age (year), and t_0, the age at zero length. Growth parameters were estimated using Fabens' method (Fabens' 1965) by fitting a rearranged function of Equation 1 to the data on moult increment and intermoult period using FISAT software (Gayanilo et al. 1996):

$$L_2 = L_1 + (L_\infty - L_1) * (1 - e^{(-K\,(t_2 - t_1))}) \qquad (2)$$

where L_1 is the CL at the marking (initial moult), L_2 is the CL at the remarking (following moult), and t_1 and t_2 are the corresponding dates.

RESULTS

Growth in captivity

The mean moult increments of males and females separated into injured and uninjured lobsters are presented in Fig. 2A,B. In the smallest (36–45 mm CL) size class, uninjured males and females attained almost similar moult increments (4 mm CL). Moult increment of uninjured males steadily decreased to 0.6 mm CL in the 86–95 mm CL size class. Female moult increment also decreased to 1.1 mm CL in the 46–55 mm CL size class before recovering and stabilising at 1.6 mm CL in the 66–75 and 76–85 mm CL size classes. There were no significant differences in the mean moult increments among size classes and within sexes of uninjured lobsters except in the 46–55 and 56–65 mm CL female size classes ($P < 0.05$, multiple comparisons among pairs of means, Tukey Honest Significant Difference (HDS) test). Variability in moult increment was high between individual lobsters and between moults of the same individual.

Moult increments of injured male and female lobsters ranged between 0.6 and 1.8 mm CL with no significant differences observed among size classes and within sexes ($F = 1.2695$, $P > 0.05$, one-way ANOVA). The effect of injury on growth was examined by comparing the moult increments of injured and uninjured lobsters (Table 1). Injury significantly affected the moult increment of lobsters, regardless of size, depressing it by an average of 1.06 mm CL (range 0.77–1.16 mm CL) amounting to 65% reduction.

Growth parameters

By directly fitting Fabens' method (Equation 2) to the data on moult increment and intermoult period for the uninjured male and female lobsters, growth parameters, L_∞ and K, were estimated (Table 2). However, the theoretical L_∞ values estimated for the

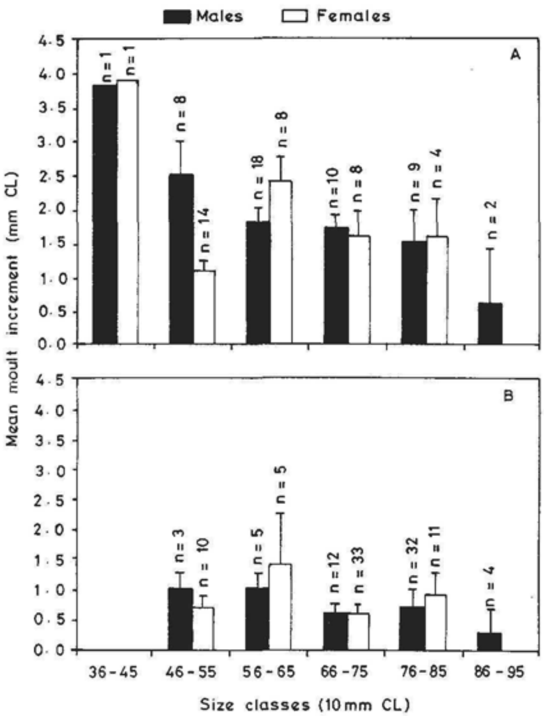


Fig. 2 Mean moult increment of **A**, uninjured and **B**, injured male and female *Panulirus homarus homarus* in captivity. Bars indicate standard error (+ SE).

captive lobsters were smaller than the maximum sizes observed in the commercial catch for both males and females (115 and 105 mm CL, respectively; Kulmiye 2004). This indicates that L_∞ was underestimated and K was overestimated because the two growth parameters are inversely related (Pauly 1979). Misleading values of L_∞ can be obtained when high variability in moult increment is observed among individual captive lobsters, as was the case in this study.

In an attempt to obtain more realistic growth parameters, the data were recalculated by running the growth routine again with fixed L_∞ values (i.e., 115 and 105 mm CL, for males and females, respectively) employing Munro's Method (Munro 1982) and the resulting parameters are given in Table 2. The estimated parameters were in turn used to plot the growth curves (Fig. 3). The predicted growth patterns are very similar for both sexes until a CL of 72 mm is attained, after which females grow more slowly than males.

Moulting in captivity

Intermoult periods of injured and uninjured animals that moulted twice or more in captivity are summarised in Table 3. Intermoult period increased with increase in size in both injured and uninjured lobsters. This pattern was, however, more pronounced for the uninjured animals where there were significant differences among the size classes and within sexes ($F = 7.492$, $P < 0.05$; one-way

Table 1 Comparison of the moult increment between injured and uninjured lobsters within four size classes. (CL, carapace length.)

Size class (mm CL)	Status	No. of observations	Mean (± SE) moult increment (mm CL)	t (d.f.)	P level
46–55	Injured	13	0.76 ± 0.12	2.3676 (33)	0.0239*
	Uninjured	22	1.53 ± 0.23		
56–65	Injured	10	0.88 ± 0.27	4.5226(34)	0.0001*
	Uninjured	26	2.04 ± 0.18		
65–75	Injured	45	0.56 ± 0.12	4.0627 (61)	0.0014*
	Uninjured	18	1.57 ± 0.19		
76–85	Injured	43	0.67 ± 0.13	2.9798 (55)	0.0042*
	Uninjured	13	1.51 ± 0.32		
Overall mean:	Injured	111	0.66 ± 0.07	4.8560 (188)	0.0003*
	Uninjured	79	1.72 ± 0.11		

*Significant.

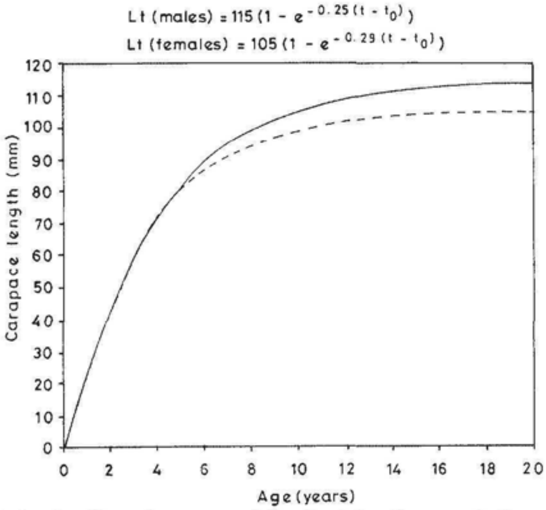


Fig. 3 Growth curves of the Bertalanffy growth function for uninjured male and female *Panulirus homarus homarus* in captivity. (*Lt*, predicted carapace length at age *t*; t_0, age at zero length.)

ANOVA). The intermoult period of smaller uninjured lobsters (46–55 mm CL) was c. 50 days, whereas that of the larger uninjured ones (76–85 mm CL) was 66 days. For the injured lobsters, the corresponding intermoult period of the smaller and the larger individuals was 57 and 67 days, respectively. On an annual basis, the smaller uninjured lobsters (46–55 mm CL) potentially undergo an average of 7.4 moults compared with 5.5 moults for the larger ones (76–85 mm CL). The effects of sex and injury on intermoult period were examined using two-way ANOVA (Table 4). Injury affected the intermoult period with injured animals moulting less frequently than uninjured lobsters. However, this effect progressively diminished as size increased. Overall, the intermoult period of injured lobsters was 8 days longer than that of uninjured individuals. The intermoult period was not affected by sex ($P > 0.05$), though females tended to have slightly longer intermoult periods than males, especially those below 66–75 mm CL size class.

Table 2 Growth parameters for captive uninjured male and female *Panulirus homarus homarus* estimated with "fixed" and "unfixed" L_∞ routines using two different methods. (CL, carapace length.) ([a] represents values used to fix male and female L_∞ which correspond to the largest animals encountered in the commercial catch.)

		Method	
Sex	Parameter	Fabens (unfixed L_∞)	Munro (fixed L_∞)
Males	L_∞ (mm CL)	95.90	115.00[a]
	K (year^{-1})	0.49	0.25
Females	L_∞ (mm CL)	93.10	105.00[a]
	K (year^{-1})	0.40	0.29

Table 3 Intermoult period of injured and uninjured male and female *Panulirus homarus homarus* in captivity. (CL, carapace length.)

Size class		No. of observations		Mean (± SE) intermoult periods (days)		Mean annual moulting frequency	
(mm CL)	Sex	Uninjured	Injured	Uninjured	Injured	Uninjured	Injured
46–55	males	7	2	49 (2.3)	55 (4.9)	7.4	6.6
	females	11	8	52 (2.7)	58 (2.5)	7.0	6.3
56–65	males	12	5	50 (2.3)	57 (2.7)	7.3	6.4
	females	7	2	57 (1.9)	60 (3.5)	6.4	6.1
66–75	males	7	4	61 (3.0)	59 (1.5)	6.0	6.2
	females	6	26	64 (2.5)	66 (2.0)	5.7	5.4
76–85	males	8	31	66 (2.5)	67 (3.6)	5.5	5.4
	females	3	10	66 (4.0)	67 (2.8)	5.5	5.4
86–95	males	1	3	81	71 (6.4)	–	5.1
Combined		93	61	57 (1.3)	65 (1.4)	5.6	6.4

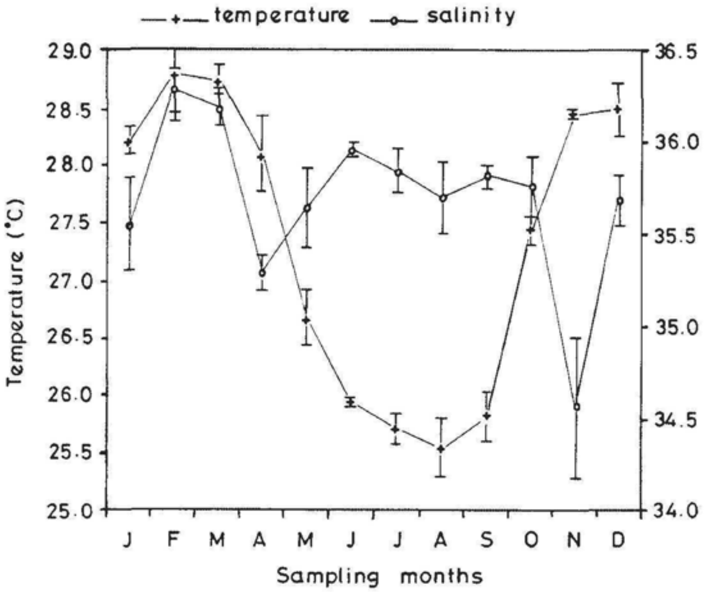


Fig. 4 Seasonal trends of water temperature and salinity measured as mean monthly temperature and mean monthly salinity (data for all holding tanks and adjacent Tudor Creek pooled). Bars indicate standard deviation (± SD).

Table 4 Results from two-way ANOVA of the effects of sex and injury on intermoult periods of *Panulirus homarus homarus* in captivity. (NS, not significant.)

Source of variation	d.f.	SS	MS	*F*	*P* level
Sex	1	6.848	6.848	0.430	0.836 NS
Injury	1	1963.123	1963.123	12.321	0.001*
Sex × Injury (interaction)	1	31.302	31.302	0.196	0.658 NS
Within groups (error)	146	23263.015	159.336		

*Significant.

Temperature and salinity

The mean monthly water temperature and salinity pooled from the rearing tanks and the adjacent Tudor Creek (from which sea water was pumped) are shown in Fig. 4. Temperature showed a seasonal trend with high values during the north-east monsoon season (November–March) and low values between May and October (south-east monsoon season). There was a 3.2°C difference between the month with the highest temperature (February, 28.7°C) and the one with the lowest temperature (August, 25.5°C). A clearly defined seasonal trend for salinity was absent except for the marked drop in values in both April and November, which correspond to the long and short rains, respectively.

Growth and temperature

The relationship between temperature and growth was investigated by plotting moult increments of uninjured males and females against sea-water temperature at which the animals moulted (Fig. 5). The moult increment is inversely correlated with temperature, with both males and females attaining higher moult increments at lower temperatures than at higher temperatures. However, the moult increment for females shows a stronger correlation with the sea-water temperature ($r^2 = 0.57$, Fig. 5). Analysis of covariance (ANCOVA, with season as the independent factor, moult increment as the dependent factor, and size as the covariate), also reveals that the difference in the mean moult increment between the south-east

Fig. 5 Relationship between sea-water temperature and moult increment of uninjured male and female *Panulirus homarus homarus* in captivity.

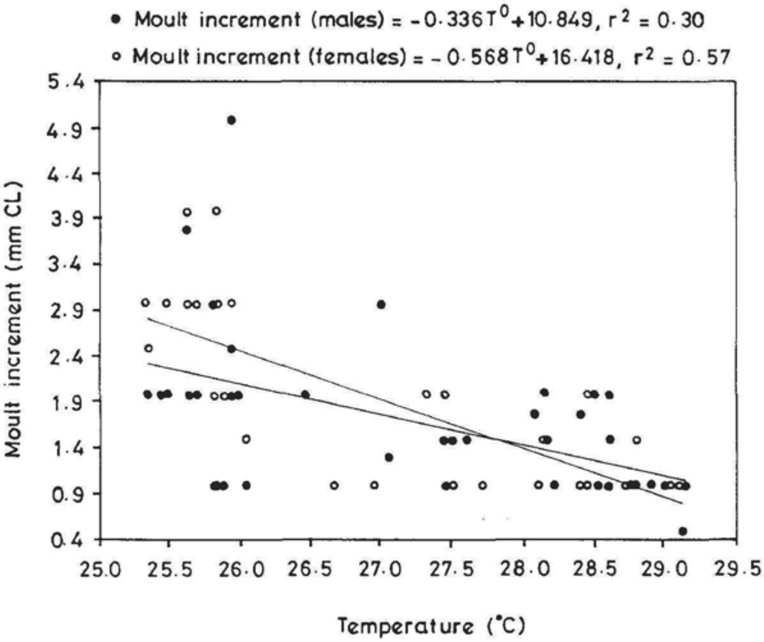
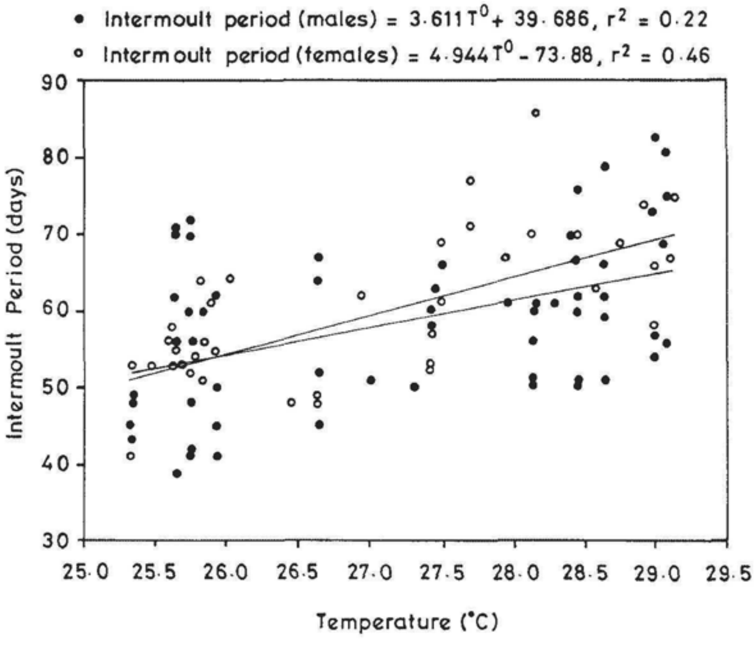


Fig. 6 Relationship between sea-water temperature and intermoult period of uninjured male and female *Panulirus homarus homarus* in captivity.



monsoon (low temperatures) season and the north-east monsoon (high temperatures) season is significant for females ($P = 0.001$) but not for males ($P = 0.321$). On average, males and females exhibited 19% and 46% larger CL increment per moult, respectively, during the south-east monsoon season in comparison with the values recorded during north-east monsoon season.

Moulting and temperature

The relationship between temperature and moulting was investigated by plotting intermoult periods of uninjured males and females against the average sea-water temperatures that prevailed during the respective intermoult periods (Fig. 6). The intermoult period is positively correlated with sea-water temperature, with rising temperature resulting in prolonged intermoult periods for both males and females. This correlation is again more pronounced for females ($r^2 = 0.46$) than for males ($r^2 = 0.22$). Analysis of covariance (ANCOVA, with season as the independent factor, intermoult period as the dependent factor, and size as the covariate), also reveals that the difference in the mean intermoult period between the south-east monsoon (low temperatures) season and the north-east monsoon (high temperatures) season is significant for females ($F = 48.026$, $P = 0.000$) but not for males ($F = 0.6614$, $P = 0.4211$). The mean intermoult periods (days) of males and females were 5% and 21% shorter, respectively, during south-east monsoon season in comparison with the values recorded during north-east monsoon season.

DISCUSSION

Growth and moulting of uninjured lobsters

The mean moult increment of uninjured *P. homarus homarus* calculated for most size classes in the present study is comparable to that observed in captive *P. homarus rubellus* in South Africa (Berry 1971b) but is noticeably smaller than that reported by Nair et al. (1981) in the Indian *P. homarus* held under laboratory conditions (Table 5). The theoretical maximum sizes (L_∞) predicted for both sexes from growth increment data by the Fabens' method were also relatively smaller than the largest animals observed in the commercial catch (Table 2). Laboratory studies do not always reflect growth under natural conditions, and although all the factors that have been described to influence growth of palinurid lobsters (see Aiken 1980 for review) were either provided in excess (food, shelter, etc.) or taken care of by the tropical climate (temperature, photoperiod, etc.), there were several occasions when oxygen levels in the water gradually dropped from 90% down to 60% saturation as a result of power failure that interrupted both aeration and water inflow. Chittleborough (1975) working with *P. cygnus* reported that low oxygen availability not only lessened size increase at moulting but also increased risk of death if the saturation level dropped to between 47% and 50% during ecdysis. It is therefore possible that the growth rates observed in captive *P. homarus homarus* may have been lower than those in nature as a result of low oxygen availability during power interruptions. Another factor that cannot be ruled out, as a possible cause of low growth rates, is the effect of pathogens on uninjured lobsters in the early part of the study when serious bacterial infection overwhelmed the experiment. Lobsters may have shifted some energy to defensive purposes that would have otherwise been available for growth, resulting in low growth rates.

Despite the possible anomaly between laboratory and natural growth, both moult increment and intermoult period of *P. homarus homarus* followed the general growth pattern of palinurids where the moulting frequency and percentage size increase at moult tend to decrease gradually with increasing size. However, the absence of significant differences in the mean moult increments among the four size classes tested could be attributed to the narrow size range of the lobsters studied, the majority of which were mature and well past their rapid growth phase. The mean moult increments of mature specimens between the size range of 46 and 85 mm CL were more-or-less similar except for the notable decrease in the females of 46–55 mm CL size class. This is also discernible in the predicted growth curves which are very similar for both sexes until a CL of 72 mm is attained. The growth rate of another subspecies, *P. homarus rubellus*, was reported to remain constant throughout much of the sexually mature size range until the upper extremes were attained

Table 5 Comparison of mean moult increments between populations of *Panulirus homarus* subspecies from three different areas of the Indian Ocean. (CL, carapace length.)

Source	Location	Subspecies	Sex	Size class (mm CL) 40–49	50–59	60–69	70–79
Berry (1971b)	South Africa	*P. h. rubellus*	males	–	2.2	2.3*	2.3*
			females	–	2.1	2.0*	2.1*
Nair et al. (1981)	India	*P. homarus*	males	3.5	3.1	2.9	–
			females	2.5	3.0	2.3	–
Present study	Kenya	*P. h. homarus*	males	2.4	2.2	1.9	1.7
			females	1.6	1.7	2.5	1.3

*Slightly modified.

(Berry 1971b). The marked drop in female moult increment in the 46–55 mm CL size class signifies the onset of sexual maturity and resource allocation to reproductive activity instead of growth. It is around this size class that females of the other two *P. homarus* subspecies also reach sexual maturity and start reproducing (Heydorn 1969; Berry 1971b; Fielding & Mann 1999).

Although the maximum variation in water temperatures between the south-east and north-east monsoon seasons is only 3.2°C, the growth rate of *P. homarus homarus* is distinctly seasonal and appears to be optimal at the lower limit of the prevailing temperatures in the East African coastal waters. Laboratory held lobsters grew faster at lower temperatures than at higher temperatures because of both increased moult increments and shortened intermoult periods. However, the stronger positive correlation observed to exist between the female intermoult period and temperature as well as the ovipositing of three captive females in February suggest that a shift in energy use from growth to reproduction rather than the influence of high temperature was responsible for the lower growth rates achieved during the north-east monsoon season. Similarly, the higher growth rates attained during the south-east monsoon period are undoubtedly a manifestation of increased energy apportioned to growth since little spawning activity was observed both in the field and in the laboratory. In field conditions, the main mating and egg-bearing season of this subspecies falls within the north-east monsoon period (Kulmiye 2004).

The alternating cycles of high growth rates and spawning activity in line with the changing monsoon seasons suggest a trade-off between reproduction and growth subject to the prevailing environmental factors. The incidence of high temperatures, relatively calm seas, and light winds as well as ocean-bound currents during the north-east monsoon season (McClanahan 1988) seem to be the ideal conditions for the dispersal and survival of larvae. It is therefore advantageous for the animals to invest energy in reproductive activity during this period rather than during the south-east monsoon season when the prevailing conditions are unfavourable.

Growth and moulting of injured lobsters

Mean moult increments were significantly smaller and mean intermoult periods were longer for injured lobsters than for uninjured individuals kept under the same holding conditions. The observed reduction in the mean moult increment of injured lobsters stemmed mainly from numerous moults with zero growth at moulting during and even after the infection period. It is not unusual for crustacean species to register zero or even negative growth at ecdysis owing to a variety of factors (Aiken 1980; Cockcroft & Goosen 1995). Moults with negative or zero growth seem to signify a shift in energy use from growth to other importunate needs such as reproductive activity, fighting disease, or simply maintenance of basic metabolic requirements in times of hardship. Affected individuals may sacrifice growth altogether at ecdysis but still compensate for the missed growth by markedly increasing in size at subsequent moultings when conditions improve (Travis 1954; Fielder 1964; Thomas 1972). In the present study, several large lobsters showed growth patterns similar to the above observations with zero increase in size at moulting during the infection period and high growth rates at successive moultings following treatment.

Several studies have shown the negative effects of injury on the growth rates of spiny lobsters. Smale (1978) reported lower growth rates for *P. homarus rubellus* similarly tagged and recaptured with necrotic wounds in a field study in comparison with laboratory-held individuals of the same subspecies on the east coast of South Africa (Berry 1971b). Davis (1981) reported that moult increment was 0.5 mm CL smaller and intermoult period 5 weeks longer for injured juvenile *P. argus* than for uninjured ones. Hunt & Lyons (1986) also observed that injury caused a 39% reduction in growth of small *P. argus* (≤60 mm CL) returned by fishers to the sea in Florida. Brown & Caputi (1985) noticed an inverse relationship between growth increment of injured *P. cygnus* and the number of missing limbs.

The implications of injury-induced lobster growth reductions on onset of sexual maturity and fecundity have been discussed (Davis 1981; Brown & Caputi 1985; Hunt & Lyons 1986). Injury-induced fishery yield losses are reported to be significant in both the Western Australian and Floridian lobster fisheries (Davis 1981; Brown & Caputi 1985). In the Kenyan lobster fishery, where divers catch lobsters with spears and other sharp objects, a large but as yet unquantified number of traumatised and injured lobsters are left behind holed up in narrow crevices after divers fail to flush them out during fishing expeditions owing to complexity of the coral reef habitat and/or the crude nature of the catching methods. However, the fate of the affected lobsters and the actual loss to the fishery as a direct result of injuries are not known.

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