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Size at maturity in the mud spiny lobster *Panulirus polyphagus* (Herbst, 1793)

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Abstract

The size at sexual maturity of the mud spiny lobster *Panulirus polyphagus* was estimated by assessing the sizes at which the animals become morphologically, physiologically and functionally mature, from samples collected from the wild along the Saurashtra coast. The size at physiological maturity was assessed from the condition of the gonad and its stage of development. The size at morphological maturity was assessed by following the development of external indices of maturity. Change in the length of the penile process in relation to the carapace length (CL) was also studied in males. Linear plots of the somatic lengths against the carapace lengths in size groups <50 mm CL and > 50 mm CL were used to assess changes in growth patterns from juvenile phase to sub-adult and adult phases. Comparisons were also made between growth patterns of males and females. The size at functional or physical maturity was assessed from the frequency distribution of males and females with respect to specialised structures which ensure the mating and propagative capabilities of the animals, namely, decalcified windows on the ventral side, well developed setal brush on the dactylii of the fifth pair of walking legs and ovigerous condition in females and penile process in males. Observations made in the study indicated that the size at onset of sexual maturity can be traced to 51–55 mm CL for males and 51–60 mm CL for females. The critical maturation phase extends between 56 and 65 mm CL for males and between 66 and 75 mm CL for females.

Keywords: *Panulirus polyphagus*, size at maturity, morphological maturity, mud spiny lobster

Introduction

Size at first maturity is an important indicator of the reproductive capacity of populations, and thus is an important tool in stock assessment as alterations in the size at maturity over space and time may be indicative of the effects of environmental and fishing impacts on the stock. Knowledge of size at maturity is also important in establishing management regulations such as fixing minimum legal size. The size at first maturity is defined as the size at which 50% of the population has entered into a state of advanced maturation and is usually estimated by plotting the percentage of mature animals in different body size classes in a sampled population against size and directly reading the size at which 50% are mature. In decapods, the size at first maturity is usually studied with reference to physiological maturation (the size at which the gonads attain maturity) and physical maturation (the size at which the animal is capable of mating and spawning). There is often a gap in time between the occurrence of physiological and physical maturity and hence the two phenomenon may not occur at the same size, and both must be known to determine the size at true sexual maturity (Stewart *et al*., 1997). Mac Diarmid and Sainte-Marie (2006) define three basic indicators of maturity that can each be assessed by one or more criteria: (i) morphological maturity, detected by development of external body parts representing secondary sexual characters; (ii) physiological maturity, reflected in the development of gonads and accessory glands; and (iii) functional maturity, revealed by internal or external features of behaviour indicating past or current breeding activity.

This paper seeks to identify the size at sexual maturity of male and female *P. polyphagus*, based on observations made on lobsters obtained from the wild.

Material and Methods

The size at sexual maturity of *P. polyphagus* was assessed from observations on 261 males and 289 females (35 – 110 mm CL) collected from trawl landings at Veraval and Mangrol in Gujarat's Saurashtra peninsula during October 2000 – September 2002. The trawlers operated in the depth range of 40 to 80 m about 15 to 20 km from the shore.

Following the definitions given by Mac Diarmid and Sainte-Marie (2006), the size at physiological maturity was assessed from the condition of the gonad and its stage of development, based on its colour and structure. All animals in an advanced state of gonadal maturation, those that had mature or ripe gonads and those that were in a state of rematuration were collectively grouped as "mature", while immature animals and those in which gonadal maturation had just begun were grouped as "immature". The frequency distribution of "immature" and "mature" lobsters in the sampled population was analysed, and the size at first (physiological) maturity was read as the size at which 50% of the lobsters were "mature".

The size at morphological maturity was assessed similarly by following the development of external indices of maturity such as the presence or absence of ovigerous setae in females and changes in the growth, relative to carapace length, of the last three pairs of pereiopods (walking legs), the ventral sternite length and the maximum width of the carapace in both sexes. Change in the length of the penile process in relation to the carapace length was also studied in males.

Length measurements were done using a vernier caliper. Details of length measurements taken for studying different aspects of growth and maturity are as follows: (i) carapace length (CL, mm), as the distance along the dorsal midline from the transverse ridge between the supraorbital horns to the posterior extremity of the cephalothorax. The carapace length, as described by Berry (1971), was used as a standard for all definitions of growth and maturity. (ii) Maximum width of carapace (MWC, mm), the dorsal distance along the posterior edge of the carapace, from one side to the other. (iii) Ventral sternite length (VSL, mm), the distance along the ventral midline from the tip of the fused sternum to the posterior margin of the sternum. (iv) Lengths of the third, fourth and fifth pairs of pereiopods or walking legs (III LL, IV LL and V LL, mm), the distance along the ventral surface from the tip of the dactylii to the proximal margin of the coxa. Although only the second and third pairs of walking legs are known to show secondary sexual characteristics in male spiny lobsters, the third, fourth and fifth pairs of walking legs were used for this study, since the third and fourth legs in females and the fifth in males bear the gonopore, and thus must undergo structural transformation. (v) Length of penile process (PPL, mm), the maximum length on the longitudinal plane from the inner side of the penile process (at the point of attachment to the coxa of the fifth pereiopod) to its tip.

Linear plots of the lengths of the various body parts mentioned above relative to the carapace lengths in size groups <50 mm CL and > 50 mm CL were used to assess changes in growth patterns from juvenile phase to sub-adult and adult phases based on the method of George and Morgan (1979). Comparisons were also made between growth patterns of males and females. The sizes at which deflections (if any) in regression lines between juveniles and sub-adults, or between males and females, were studied for indications of the onset of sexual maturity, as suggested by George and Morgan (1979).

The size at functional or physical maturity was assessed from the frequency distribution of males and females with respect to specialised structures which ensure the mating and propagative capabilities of the animals: (i) the formation of decalcified windows on the ventral side and the formation of well developed setal brush on the dactylii of the fifth pair of walking legs in females; (ii) the development and pigmentation of the penile process in males: and (iii) the distribution of ovigerous condition in females.

Results

Males

Penile process: The male gonopore was visible in juveniles as small as 25 mm CL, but only in the form of a tiny inconspicuous spot on the coxa of the fifth pair of pereiopods, ventrally. In older males, the gonopore had developed into a penile process with a hairy tip. The formation of the penile process was first noticed in male lobsters of 36 – 40 mm CL. The smallest size at which a penile process was observed was 36.6 mm. Development of the penile process, however, appears to be slow. About 28% of the animals in the size range of 51 – 55 mm CL, 53% of the animals in the size range of 56 – 60 mm CL and 100% of the animals above 62 mm CL had well developed penile processes (Fig. 1).

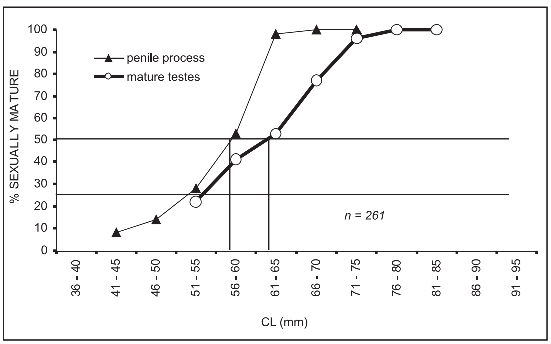


Fig. 1. Size at sexual maturity in male *P. polyphagus* (wild) derived from physiological and functional maturity indices

Maturing/mature testes: Males in the size range of 36 – 40 mm CL had immature testes. Signs of gonadal development were observed in some males in the size range of 41 – 45 mm CL. In males of 51 – 55 mm CL, the gonads were fully developed structurally though the vas deferens remains thin without any swollen ends. In all, 53% of the males in the size range of 56 - 60 mm CL had structurally complete and mature gonads with thickened vas deferens, swollen at the distal end. In the size range of 61-65 mm CL, 98% of the males were functionally mature.

Relationship between carapace length and somatic lengths as indices of sexual maturity: (Table 1)

***(i) Carapace length (CL) – Maximum width of carapace (MWC)*:**

The lines of regression between CL and MWC (at the posterior end of the carapace) for male lobster <50 mm CL and >50 mm CL did not show any significant variation in slope or elevation (p=0.05).

***(ii) Carapace length (CL) – Ventral sternite length (VSL)*:**

Analysis of covariance showed that the regression lines of VSL on CL in male *P. polyphagus* <50 mm CL and >50 mm CL did not show any marked difference in slope or elevation (p=0.05).

Table 1. Relationship between carapace length and somatic lengths in male *P. polyphagus*

Somatic length studied	Size group	Linear regression equation of CL *vs* Somatic length	R^2
Maximum width of carapace (MWC, mm)	<50 mm CL	MWC = 0.8172CL + 1.6887	0.993
	>50 mm CL	MWC = 0.9964CL - 7.7588	0.99
Ventral sternite length (VSL, mm)	<50 mm CL	VSL = 0.5575CL - 0.8548	0.984
	>50 mm CL	VSL = 0.4595CL + 3.004	0.996
Length of penile process (PPL, mm)	<50 mm CL	PPL = 0.2848CL - 8.0593	0.935
	>50 mm CL	PPL = 0.2109CL - 2.3287	0.962
Length of III walking leg (III LL, mm)	<50 mm CL	III LL = 1.1413CL - 1.913	0.995
	>50 mm CL	III LL = 1.1076CL + 1.6567	0.992
Length of IV walking leg (IV LL, mm)	<50 mm CL	IV LL = 1.0218CL + 0.638	0.978
	>50 mm CL	IV LL = 1.1593CL - 4.5821	0.992
Length of V walking leg (V LL, mm)	<50 mm CL	V LL = 0.735CL + 4.2995	0.998
	>50 mm CL	V LL = 0.8583CL + 4.2855	0.992

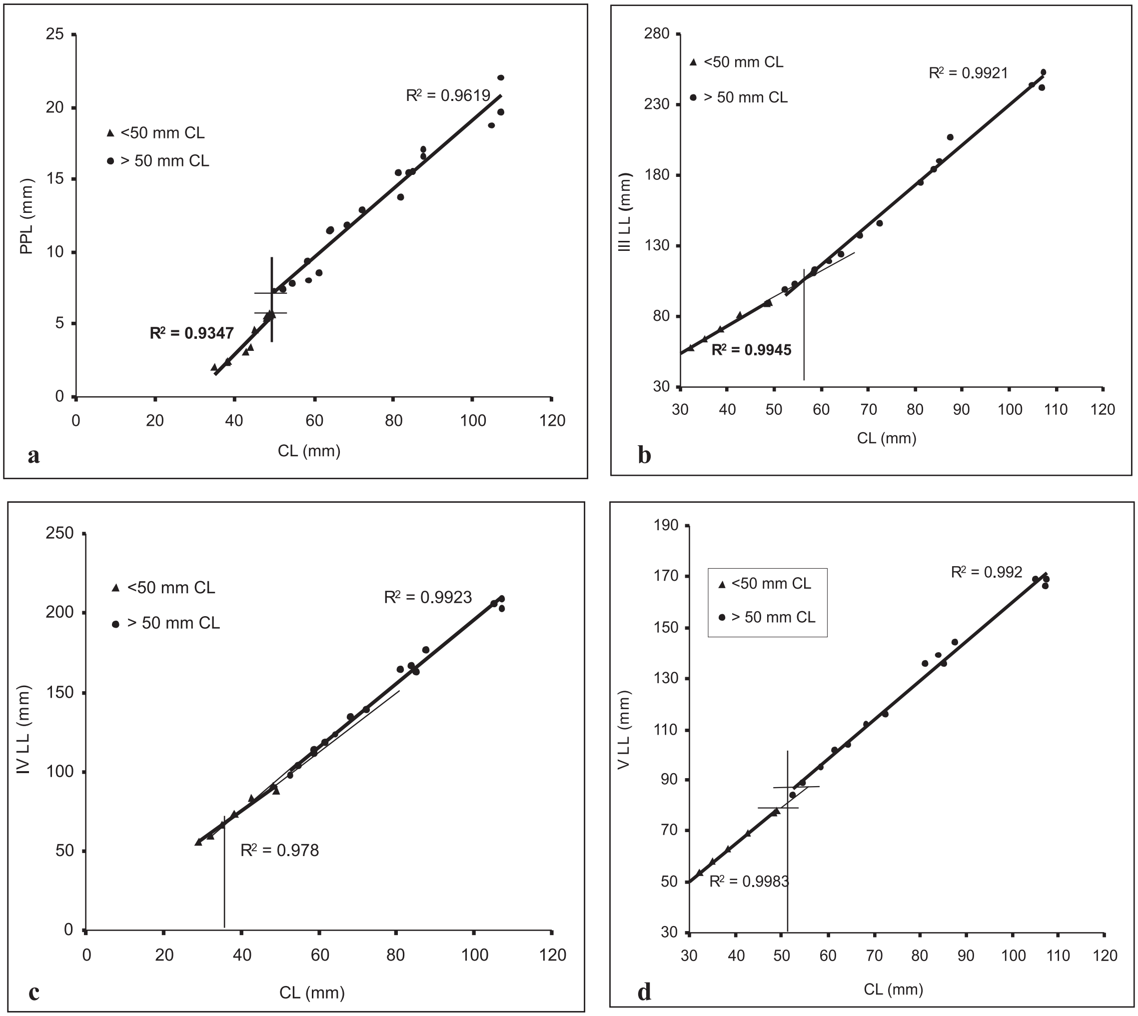


Fig. 2. Relationship between carapace length and somatic lengths as indices of sexual maturity in male *P. polyphagus*. a. carapace length (CL) vs length of penile process (PPL); b. carapace length (CL) vs length of III walking leg (III LL); c. carapace length (CL) vs length of IV walking leg (IV LL); d. carapace length (CL vs length of V walking leg (V LL)

(iii) Carapace length (CL) – Length of penile process (PPL)**:** (Fig. 2a)

The regression lines of PPL on CL in juvenile and sub-adult/adult male *P. polyphagus* had two different elevations and the deflection from one line of growth to the other was at 50 mm CL. This is the most important external index of the onset of sexual maturity in the males as the development of the penile process signifies the functional status of the male's capacity to impregnate a female.

(iv) Carapace length (CL) – Leg lengths (III LL, IV LL and V LL)**:**

The regression lines between CL and length of the third pair of pereiopods in male *P. polyphagus* of <50 mm CL and > 50 mm CL had different slopes and the point of intersection was estimated to be 55.4 mm CL (Fig. 2b). In the case of the fourth (Fig. 2c) and fifth (Fig. 2d) pairs of pereiopods in male *P. polyphagus*, the regression lines differed significantly in their elevations (p=0.05), indicating sharp deflections in growth patterns of the legs during the transition from juvenile to sub-adult phase.

Females

Ovigerous setae: More than 50% of the females of 51 – 55 mm CL had well developed pleopods. Development of ovigerous setae also began at this size. The minimum size at which development of ovigerous setae was noticed was 51.7 mm CL. About 50% of the females in the CL range of 61 – 65 mm have fully developed ovigerous setae (Fig. 3).

Maturing/mature ovary: Maturation of ovary was studied in females collected from the fishery. Females in the size range of 36 – 45 mm CL had immature ovaries. Signs of ovarian development were observed in some females in the size range of 46 – 50 mm CL. Ovarian development was evident in females of 51 – 55 mm CL, with the development of orange colour of the ovary, visible through the dorsal musculature. More than 50% of the females in the size range of 66- 70 mm CL had ripe ovaries (Fig. 3).

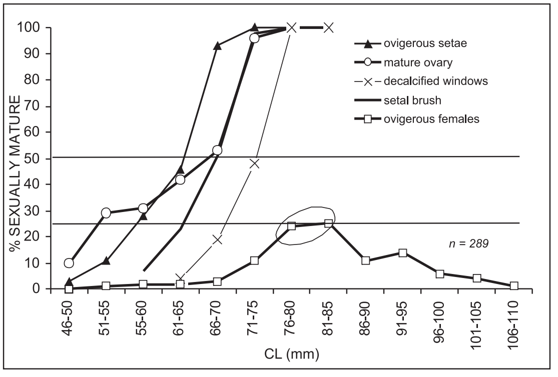


Fig. 3. Size at sexual maturity in female *P. polyphagus* (wild) derived from physiological and functional maturity indices

Setal brush: The development of the setal brush at the tips of the pereiopods coincides with the development of ovigerous setae and maturation of the ovary. Setal brush formation was found in 7% of the sampled females in the size range of 56 – 60 mm CL. 50% of the females in the size class of 66 - 70 mm CL and 98% of the females in the size class of 71 - 75 mm CL had well developed setal brushes (Fig. 3).

Formation of decalcified windows: Formation of decalcified windows, i.e. decalcification of the ventral sternal plates at the base of the third, fourth and fifth pairs of pereiopods, begins in females in the size range of 66 – 70 mm CL, after ovarian maturation. Almost 50% of the females of 71 – 75 mm CL had well developed pairs of windows – two pairs each on the fifth and fourth pairs of pereiopods and one pair on the third (Fig. 3). Decalcification begins on the lower most sternal plate, i.e., at the base of the fifth pair of pereiopods. Window formation signifies that the female is completely (physiologically and functionally) ready for mating.

Occurrence of ovigerous females: The minimum size class in which ovigerous females were noticed in samples from the fishery was 51 – 55 mm CL and the smallest and largest ovigerous females recorded measured 54.3 mm CL and 108 mm CL respectively. The percentage frequency of ovigerous females could not be used as an index to estimate the size at first maturity as the percentage did not exceed 25% in any size class from 51 – 55 mm to 106 – 110 mm CL. There was a steady increase in the percentage of berried females upto 81 – 85 mm CL, followed by a decrease in the higher size classes and only 1% of the sampled females of 106 – 110 mm CL were berried (Fig. 3). The peak occurrence of berried females in the size range of 76 – 85 mm CL follows the completion of ovarian maturation, development of ovigerous setae, window formation and setal brush formation. The distribution of berried females thus served to corroborate the conclusions drawn from these indices.

Relationship between carapace length, maximum width of carapace, ventral sternite length and leg lengths as indices of sexual maturity: (Table 2)

(i) Carapace length (CL) – Maximum width of carapace (MWC): (Fig. 4a)

The lines of regression between CL and MWC (at the posterior end of the carapace) for female *P. polyphagus* <50 mm CL and >50 mm CL differed in their slopes and the intersection of the two lines was estimated to be at 45.7 mm CL, a size preceding the minimum size at which development of the ovary was observed in some females.

***(ii) Carapace length (CL) – Ventral sternite length (VSL)*: (Fig. 4b)**

The regression lines of VSL on CL in female *P. polyphagus* had different slopes and there was a clear difference in the relationship between the two parameters before 50 mm CL and after 50 mm CL. The intersection of the two lines was at 51.1 mm CL, signifying changes due to the animal's entry into sexual maturity from 51 – 55 mm CL onwards.

***(iii) Carapace length (CL) – Leg lengths (III LL, IV LL and V LL)*:** The regression lines between CL and different leg lengths showed variations in the two size groups with the intersection points lying at 65.2 mm CL for the third leg (Fig. 4c), 45.7 mm CL for the fourth leg (Fig. 4d) and 55.7 mm CL for the fifth leg (Fig. 4e). The fifth leg takes a different growth pattern just after 40 mm CL. The fourth leg is longer than the third initially but after 55 mm CL, the third leg overtakes the fourth. These legs play a role in copulation and later, in grooming of the eggs during incubation, for which the legs should be extended up to the brood chamber.

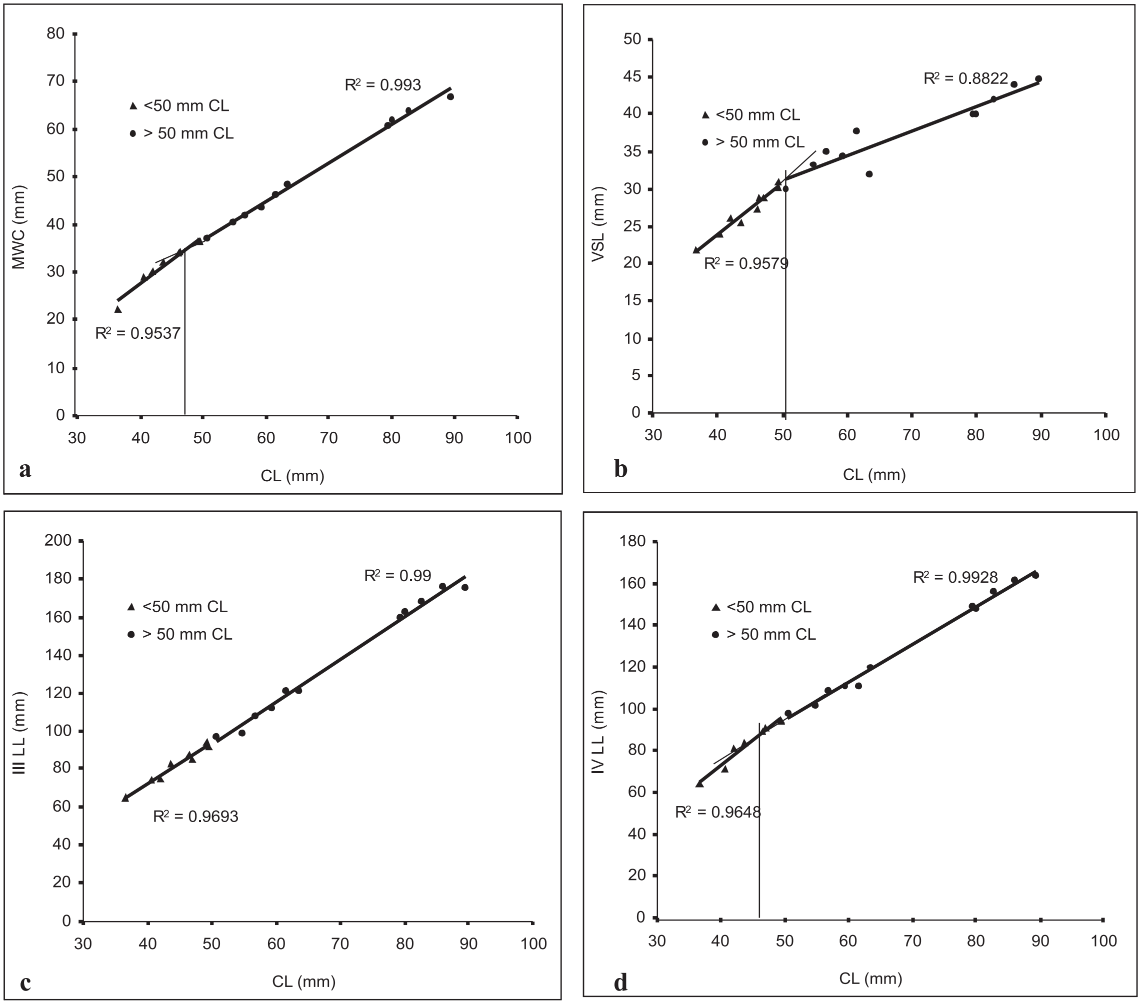
A comparison of regression lines of different somatic measurements mentioned above, relative to CL in male and female *P. polyphagus* indicate the following: (a) *CL vs MWC*: Initially, males have a higher ratio of MWC upon CL, but beyond 65 mm CL, females exceed the males in this ratio. (b) *CL vs VSL*: While females have a higher VSL to CL ratio initially, the males exceed them beyond 50 mm CL, indicating the changes required for the formation of decalcified windows. The ventral sternite in females becomes broader and increase in length is suppressed.

(c) CL vs Leg lengths: While the third and the fifth pairs of pereiopods are relatively longer in females in the juvenile phase, the lengths take an upper deflection in males at about 45.1 mm CL and 44 mm CL respectively. The fourth pair of pereiopods is almost similar in length in both the sexes initially, but the length in males takes an upward deflection at 36 mm CL. These are important indicators of the onset of sexual maturity in males as the pereiopods play a major role in the act of copulation and impregnation.

From the results obtained, it is evident that while the size at first physiological maturity is attained at 61 – 65 mm CL in male and at 66 – 70 mm CL in female, the size at morphological maturity is attained earlier, i.e., at 56 – 60 mm CL in males and at 61 – 65 mm CL in females. However, the size at functional maturity in the females sets at a larger size, i.e., 71 – 75 mm CL, in tandem with formation of the decalcified windows. From these inferences it may be concluded that the critical maturation phase extends between 56 and 65 mm CL for males and between 66 and 75 mm CL for females and the size at onset of sexual maturity can be traced back to 51 – 55 mm CL for males and 51 – 60 mm CL for females.

Table 2. Relationship between carapace length and somatic lengths in female *P. polyphagus*

Somatic length studied	Size group	Linear regression equation of CL *vs* Somatic length	R^2
Maximum width of carapace (MWC, mm)	<50 mm CL	MWC = 0.9964CL - 7.7588	0.954
	>50 mm CL	MWC = 0.93CL - 2.7361	0.993
Ventral sternite length (VSL, mm)	<50 mm CL	VSL = 0.9789CL + 7.8023	0.958
	>50 mm CL	VSL = 1.2359CL - 4.4365	0.882
Length of III walking leg (III LL, mm)	<50 mm CL	III LL = 1.2663CL - 5.9679	0.969
	>50 mm CL	III LL = 0.9105CL + 15.778	0.99
Length of IV walking leg (IV LL, mm)	<50 mm CL	IV LL = 0.8808CL + 8.8192	0.965
	>50 mm CL	IV LL = 0.9633CL + 8.5895	0.993
Length of V walking leg (V LL, mm)	<50 mm CL	V LL = 1.0752CL - 8.4495	0.92
	>50 mm CL	V LL = 0.8362CL + 3.0765	0.979



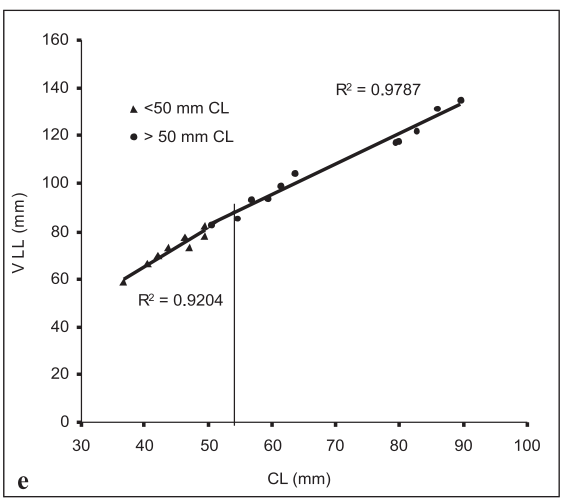


Fig. 4. Relationship between carapace length and somatic lengths as indices of sexual maturity in female *P. polyphagus*. a. carapace length (CL) *vs* maximum width of carapace (MWC); b. carapace length (CL) *vs* ventral sternite length (VSL); c. carapace length (CL) *vs* length of III walking leg (III LL); d. carapace length (CL) *vs* length of IV walking leg (IV LL); e. carapace length (CL *vs* length of V walking leg (V LL)

Discussion

Estimation of size at first maturity in lobsters is often limited by several factors. The probability of the sampled population representing only a small section of the size groups, or variability in the catchability of mature and immature lobsters (particularly if the lobsters tend to change habitats with the onset of maturation) are likely to make the estimates vulnerable to bias (Tully *et al*., 2001). The size at first maturity in female lobsters is usually estimated using functional criteria of egg-bearing (Aiken and Waddy, 1980), the presence of fresh or spent spermatophores and resorbing ova, physiological criteria of ovary colour and size, oocyte size and development of cement glands on the pleopods and morphological criteria of abdomen and pleopod development (Mac Diarmid and Sainte-Marie, 2006). Heydorn (1969) found that the percentage of ovigerous (berried) females in the sampled population gave a reliable estimate of the size at maturity in the spiny lobster *J. lalandii* (which breeds only once a year in the winter months) since he found that after a certain size there was sharp increase in the percentage of ovigerous condition and the same continued in higher lengths. However, Berry (1971) found that in *P. homarus,* the percentage of ovigerous females showed no marked increase at any particular size and the larger size classes did not show a very high incidence of ovigerous condition. He attributed this to repetitive breeding in this species, which breeds throughout the year with up to four broods within a moult cycle. Kagwade (1988) reported that the percentage frequency of ovigerous *P. polyphagus* in Bombay waters was erratic at various class intervals and at no length did the frequency reach beyond 20.7%. She too attributed this to repetitive breeding. Observations made in the present study on the distribution of ovigerous females in the trawl landings of *P. polyphagus* at Veraval and Mangrol trawl landing centres indicate a similar trend. The maximum occurrence (25%) of ovigerous females was observed in the size range of 81 – 85 mm CL. Ovigerous females were found to occur in the sampled population throughout the year. In captive breeding experiments, Kizhakudan (2007) observed that a single impregnation usually suffices for two and sometimes even three successive broods within the same moult cycle of a female.

One of the most important external indicators of sexual maturity in females is the presence of fully developed ovigerous setae on the abdominal pleopods, to which spawned fertilized eggs remain attached till the larvae are hatched. Fielder (1964) and Pollock (1982) have recognised the identification of mature females through the presence of setae. Paterson (1969) reported that in some species like *J. lalandii* there is a regular cycle of appearance and disappearance of setae. Kagwade and Kabli (1996) did not find any significant relationship between ovigerous setae and maturity in female *T. orientalis*. In the present study it was observed that the appearance and development of the ovigerous setae for the first time coincides with the onset of sexual maturity in *P. polyphagus*. The number and size of the setae reach the maximum at the time of egg bearing. After the first batch of eggs is completely hatched/removed from the pleopods, there is a reduction in the density of the ovigerous setae, which later increases during the successive breeding cycle.

George (2005) mentions the role of decalcified windows on the female sternum in the spiny lobster genus *Panulirus*, which can be used to determine maturity (e.g. Lindberg, 1955; Velázquez, 2003). However, while George (2005) has described the presence of three pairs of decalcified windows in female *P. polyphagus*, the present study clearly shows the presence of four pairs of decalcified windows in this species – one pair each at the base of the third and fourth pairs of pereiopods and two pairs at the base of the fifth pair of pereiopods. The process of decalcification, beginning from the fifth pair of pereiopods and progressing up to the third, is found to be a good indicator of the functional maturity of the female, indicating that it is ready for impregnation.

In animals with highly complicated and specialised reproductive development and behaviour, it would always be advantageous to assess the sexual maturity on the basis of more than two external or internal indicators of maturity. The size at which physical maturity occurs in lobsters has been identified by examining discontinuities (changes in slope) in the linear relationships between body size and certain externally visible features. Female maturity has been associated with allometric changes in the length of pleopods, the length of the pleopodal setae, telson length or the width of the abdomen relative to carapace length, which all change in relation to preparation for first spawning (Hossain, 1978; Aiken and Waddy, 1989; Stewart *et al*., 1997;

Lizárraga-Cubedo *et al.*, 2003; DeMartini *et al.*, 2005). MacDiarmid and Sainte-Marie (2006) recommend that easily measured appendage length to body size relations should be routinely applied to provide estimates of female SOM (size at onset of maturity) in lobsters, but only after this approach has been validated by undertaking histological studies of gonadal maturation. In the present study, the size at maturity in females and males of *P. polyphagus* was estimated from different indices of maturity.

Assessment of size at maturity in males is much more difficult than in females. Male physiological maturity has been determined by the presence of mature spermatozoa in vasa deferentia of several spiny lobsters (Heydorn, 1969; Berry, 1970; MacDiarmid, 1989; Turner *et al*., 2002). However, physiological maturity need not necessarily indicate functional maturity. Male functional maturity has often been associated with a change in the dimensions of the first cheliped in clawed lobsters or of the second or third pereiopods in spiny lobsters, relative to CL (MacDiarmid and Sainte-Marie, 2006). Berry (1970), Lipcius *et al*. (1983) and Bertelsen and Horn (2000) have associated the extreme development of the second and third pereiopods of some male spiny lobster species, with their ability to extract females from their dens. The change in the size of the pereiopods normally occurs after physiological maturity has been attained. George and Morgan (1979) described a method of determining this by plotting the leg size against the CL, for immature and mature lobsters. The size at maturity is then indicated by the point of upward deflection or the point of intersection of the regression lines of immature and mature lobsters. In the present study comparative analyses were done from regression lines of different somatic length against the carapace length in two size groups within each sex and from regression lines generated for males and females without size differentiation. The results indicate that males mature earlier than the females.

Acknowledgements

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