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Reproductive biology and size at onset of sexual maturity of the spiny lobster *Panulirus homarus homarus* (Linnaeus, 1758) in Khadiyapatnam, southwest coast of India

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Original Article

Abstract

The size at first sexual maturity is described for females of the Scalloped spiny lobster *Panulirus homarus homarus* (Palinuridae) sampled from landings at Khadiyapatnam in Kanyakumari district of Tamilnadu, on the southwest coast of India, based on physiological and functional maturity indices. The size at 50% physiological maturity was estimated at 55.0 mm carapace length (CL), based on regression of percent of females with mature, maturing and spent - recovery ovary against carapace length. The smallest female with a mature ovary was 45.5 mm CL compared to the smallest female (46.5 mm CL) with external eggs. Logistic relationships between CL and percentage of females with external eggs (berried) and with ovigerous setae on endopod of pleopods indicated that 50% maturity was attained at 61.0 mm CL (berry method) and 54.0 mm CL (setal method), respectively. Size at maturity based upon appearance of well - developed pairs of 'windows' on the last pair of sternal plates at the base of fifth pereiopods was estimated at 55.0 mm CL. The analyses show that the external secondary sexual characters may be useful as morphological measures of functional sexual maturity in the spiny lobster *Panulirus homarus homarus* from Indian waters, as these values are very close to the size at physiological maturity (55.0 mm CL) obtained based on the ovarian maturation. On the basis of this study, a minimum legal size (MLS) of 65.0 mm CL for fishing *P. homarus homarus* from Indian waters is recommended.

Keywords: *size at maturity, secondary sexual characters, Panulirus homarus homarus, reproductive biology, spiny lobster.*

Introduction

Panulirus homarus homarus is a commercially important spiny lobster occurring off both the east and west coast of India, but form fisheries of magnitude only along the southwest and southeast coasts (Radhakrishnan *et al*., 2005). The palinurid lobster is predominantly a shallow - dwelling species and are caught both by artisanal and mechanized boats. On the southwest coast of India, *P. homarus homarus* is mainly caught by gillnets, traps and trammel nets and in some areas the diver fishermen catch them by hand from rocky crevices when the water clarity is good.

The spiny lobster *P. homarus* is widely distributed in the Indo - West Pacific region. *P. homarus homarus* and *P. homarus rubellus* are the two confirmed subspecies, though earlier *P. homarus megasculpta* distributed along the Somalia coast and Arabian Gulf was considered to be a subspecies. Since the widely distributed *P. homarus homarus* has not genetically diverged at all from the described *P. homarus megasculpta*, this subspecies has been synonymized with *P. homarus homarus* (Lavery *et al.*, 2014). *P. homarus homarus* has the widest distribution extending from East Africa to India and in South - East Asia to Indonesia and Australia (Holthuis, 1991). In the West Pacific, it is distributed as far eastwards as Japan and New Caledonia (Kulmiye *et al.*, 2006). *P. homarus rubellus* is distributed along the east coast of South Africa, Mozambique and Madagascar (Berry, 1974).

Studies on biology, ecology, fishery and stock assessment of *P. homarus homarus* inhabiting the inshore fishing grounds off Kanyakumari district on the southwest coast of India have been well documented (George, 1965; Radhakrishnan *et al.*, 2005; Vijayanand *et al.*, 2007; Thangaraja, 2011; Thangaraja and Radhakrishnan, 2012; Radhakrishnan *et al.*, 2015; Thangaraja *et al.*, 2015). Although the species is the dominant component of the lobster fishery from this part of the coast, published information on the reproductive biology is limited (George, 1965).Though a minimum legal size limit for export has been introduced by the Government of India, lobsters of all sizes and reproductive condition are caught, in the absence of a minimum legal size for fishing (Radhakrishnan *et al.*, 2005). The species has been overexploited due to the unregulated fishing and efforts are underway to conserve the resource from further collapse through a participatory fishery management programme.

Introduction of a minimum legal size limit, normally set above the size at maturity, probably helps protection of the spawning population and a chance to breed at least once before being caught (Bowen, 1971). The visible indicator of female maturity in lobsters is the presence of eggs on the pleopods. However, female lobsters can also be considered sexually mature when they have attained physiological (gonadal) maturity or when they are physically capable of mating, oviposition and brooding eggs (functional maturity), for which they develop certain specialized morphological features such as well - developed pleopodal (ovigerous) setae, cement glands and decalcified zones ('window') on the sternal plates. Many earlier studies have successfully applied various methods based on gonadosomatic index (GSI) to improve accuracy in determining maturity stages (McQuinn, 1989; Flores *et al.,* 2014). However, Minagawa and Sano (1997) are of the view that GSI may provide only limited information on actual ovarian changes. Flores *et al.* (2014) suggested to explore alternative approaches for the purpose of maturity staging to avoid errors in macroscopic staging of gonads and to reduce expenditure and time involved in histological examination.

The terms size at maturity or size at breeding in palinurid lobsters usually refer to functional maturity (Chubb, 1994). The usual practice of estimating size at maturity is to regress percent mature against a certain body part such as carapace length and to fit a logistic model to predict the size class in which 50% of the population is mature (DeMartini *et al.*, 2005). The size at physiological maturity is estimated from the percentage of females with maturing, mature and spent - recovery ovary, based on macroscopic examination of structure, weight and colour of the ovary and histological examination of gonads and accessory glands (Juinio, 1987; Gomez *et al.*, 1994; Minagawa, 1997; Goni *et al.*, 2003; MacDiarmid and Sainte - Marie, 2006; Chang *et al.*, 2007). Macroscopic examination of the ovary is the quickest method to assess ovarian maturity in lobsters. The functional maturity has been estimated by several methods, including the presence of fresh or remains of spermatophore on female sternum and eggs on pleopods (Berry, 1971; Chittleborough, 1974, 1976; Kanciruk and Herrnkind, 1976; Aiken, 1977; Warner *et al.*, 1977; Juinio, 1987, Lipcius and Herrnkind, 1987; Jayakody, 1989, Chubb, 1991; Briones and Lozano, 1992; Groenweld and Melville - Smith, 1994; Mohan, 1997; DeMartini *et al.*, 2005; Kulmiye *et al.*, 2006; Chang *et al.*, 2007; Perez - Gonzalez *et al.*, 2009), pleopodal ovigerous setae (Nakamura, 1990; George, 1958; Kensler, 1967; Street, 1969; Newman and Pollock, 1971; Beyers, 1979; Roscoe, 1979; Annala *et al.,* 1980; Gregory and Labisky, 1981; Booth, 1984; MacDiarmid, 1989; Montgomery, 1989, 1992; Pollock, 1991; Groenveld and Melville - Smith, 1994 (Chubb, 2000; Kulmiye *et al.*, 2006), changes in the relative width of abdominal and thoracic segments (Jayakody, 1989; Aiken and Waddy, 1980; Kizhakudan and Patel, 2010; Radhakrishnan *et al.*, 2015), the length of plepodal exopodites, (Juinio, 1987; Plaut, 1993; Gomez *et al.,* 1994; Minagawa and Higuchi, 1997; DeMartini *et al.*, 2005; Kulmiye *et al.,* 2006), or the telson length (Hossain, 1978; Jones, 1988). The development of decalcified 'windows' on the female sternum (George, 2005) has also been used to estimate the size at sexual maturity in the lobster genus *Panulirus* (Lindberg, 1955; Vega - Velazquez, 2003). Ovarian maturity is used as a means of validating estimates of size at functional maturity (Ennis, 1984).

The objectives of this study were to estimate the size at sexual maturity in female *P. homarus homarus* based on (i) macroscopic examination of changes in structure and colour of ovary to determine physiological maturity, (ii) presence of external eggs and (iii) presence of ovigerous setae and appearance of 'window' on the sternal plates. Based on these results, a minimum legal size limit for the fishery for the spiny lobster *P. homarus homarus* from Indian waters has been recommended.

Material and methods

Monthly field visits were made during January 2006 to March

2007 to the Khadiyapatnam lobster gillnet landing centre in Kanyakumari district, on the southwest coast of India to collect data on morphometry and reproductive status of the spiny lobster *P. homarus homarus*. Though lobsters are landed throughout the year, the peak fishery is during November to January. The sexual parameters visually observed and recorded in female lobsters were: (i) presence of eggs, (ii) presence of fresh or remnants of spermatophore, (iii) presence of posterior 'window' on sternal plate and (iv) presence of ovigerous setae. The carapace length (CL) of each animal was measured (as the distance from the rostral sinus to the posterior edge of the carapace) to the nearest 0.1 mm using a Vernier caliper and weight to the nearest 0.1 g. Measurements of the length of setae on the endopod of the second left pleopod of each lobster to the nearest 0.01 mm were made. The presence or absence of the first 'window' on the sternal plate was also noted. Fifteen female lobsters representing the size range (30.0 - 90.0 mm CL) were purchased at each trip and brought to the laboratory for ovarian examination, classification and staging and for detailed studies on development of setae and cement glands. After measuring the CL and weight, each animal was dissected out. The texture, colour and weight of the ovary to the nearest 0.01 g were noted and the Gonado - somatic Index (GSI) of lobsters measuring 30.0 - 90.0 mm CL was calculated as:

$$GSI = Wg/W \times 100$$

where, Wg= gonad weight and W= total weight of the lobster

The size - wise mean GSI values with the standard error are presented after pooling the data collected in each month. Ovaries were classified into five macroscopically distinguishable stages (Rachel, 2002): stage V_1 (immature), stage V_2 (primary vitellogenic), stage V_3 (secondary vitellogenic), stage V_4 (mature), and stage V_5 (spent). There was no possibility of discrepancy in identifying a spent recovery ovary (stage V_5) from a developing ovary (stage V_3). The spent - recovery ovary is pale orange in colour and has a flaccid appearance. The size at which 50% of the females were physiologically mature was estimated by plotting the percentage of animals classified as 'secondary vitellogenic' (stage V_3), 'mature' (stage V_4) and spent - recovery stage (V_5) in each 5 mm CL size class against the CL. The proportions per 5 mm CL size class of females bearing eggs and those with fresh or remnants of spermatophore but without eggs during the peak breeding season (October to December) were plotted against the CL to estimate the size at breeding (functional maturity).In order to determine the length at which the seta becomes ovigerous, linear regression equations for length of setae against CL of lobsters measuring 24.0 - 110.0 mm CL were calculated. Lobsters with ovigerous setae (individuals with carapace length 50 mm and above derived from the regression graphs) were therefore grouped as mature lobsters in further analysis.

Microscopic examination of the morphological changes during the development of seta was also carried out. The size at which 50% of females are physically able to mate, spawn and carry eggs (functional maturity) was estimated by plotting CL against the proportion of females with ovigerous setae and those possessing the first pair of 'windows' on the fifth sternal plate. Logistic curves for each of the above four parameters were fitted based on the logistic equation of the form,

$$P = 1/(1+\exp[-r(L - L_m)])$$

Where P is the proportion of mature females, r, slope of the curve, Lm, mean length at maturity and L, the length class (King, 1995)

Results

A total of 392 females of *P. homarus homarus* in the size range of 24.0 mm to 110.0 mm CL were measured during the study. Ovigerous females were present throughout the year, constituting 5.2% (July) to 50.0% (November) of the total number of females measured in each month, but the percentage of egg bearing lobsters were higher from October to December. During these months, 42 - 50% of the females were egg bearing. July and August months are relatively low in reproductive activity and in September breeding activity is initiated with 21% of the lobsters carrying eggs.

A lobster with a freshly deposited spermatophore (Fig. 1a) or the remnants of a used spermatophore (tar spot) (Fig.1b) with or without spawned eggs is considered to be sexually mature. Females with newly deposited spermatophore had mostly the

Fig.1a. *P. homarus homarus* female with a freshly deposited spermatophore covering two third of the sternum

Fig.1b. *P. homarus homarus* remnants of spermatophore ('tarspot') after repeated spawning

ovary in stage V_3 or V_4 indicating that spawning is imminent. In January and February nearly 35% of the spawned females had partially used spermatophore and among this 56% had re - developing or rematuring ovary. These females may spawn a second time using the remaining spermatophore.

The spawning time and frequency can be determined by following temporal changes in GSI of the female lobsters. GSI showed an increasing trend from August onwards and reached a peak in November (Fig.2). GSI values were low in April, May, June and July. The mean GSI increased from 0.15+ 0.27 in 30 - 39 mm CL size class (55 - 90 g) to 0.95+0.3 in 70 - 79 mm CL size class lobsters (345 - 480 g) (Table 1). The ovaries of 30 - 39 mm CL size class of lobsters were strap - like with a pale white colour and translucent and ovaries of lobsters in 40 - 49 mm CL size group were slightly swollen with a creamy colour and a mean GSI of 0.22+0.14. The ovaries were in different stages of development in lobsters measuring 50 mm CL and above. The ovary is swollen with a bright coral red colour (V_3) with a GSI of 0.6+0.27 in 50% of the lobsters in 50 - 59 mm CL size class. In 60 - 69 mm CL size group, the mean GSI was 0.85+0.1 and 72% of lobsters sampled had fully mature ovary with a deep coral red colouration and 18% were in spent - recovery stage (V_5). In 70 - 79 mm and 80 - 89 mm CL size class, 90% of the ovaries were in Stage $V_4$and 8 - 10% in spent - recovery condition (V_5).

Table. 1. Gonado - somatic Index (GSI) in different size groups of female lobsters

Carapace length (mm)	Weight (g)	No of lobsters	GSI (Mean)±SD
30 - 39	55 - 90	15	0.15±0.27
40 - 49	85 - 135	15	0.22±0.14
50 - 59	140 - 255	15	0.6± 0.27
60 - 69	220 - 340	15	0.85± 0.11
70 - 79	345 - 480	15	0.95± 0.32
80 - 89	475 - 660	15	0.75± 0.41

Size at sexual maturity

Estimates of size at first maturity based on maturity status of the ovary, presence of ovigerous setae on pleopods and 'window' were not significantly different. The estimates derived from presence or absence of eggs was significantly greater than that calculated from observations on development of setae. The smallest *P. homarus homarus* with a stage V_3 ovary (developing) observed during the study was 45.5 mm CL. However, the CL at which 50% physiological maturity attained by female lobsters was estimated to be 55.0 mm (Fig.3). The size at maturity based on 50% of females mated but non - berried and berried females were estimated at 61.0 mm CL (Fig. 4).

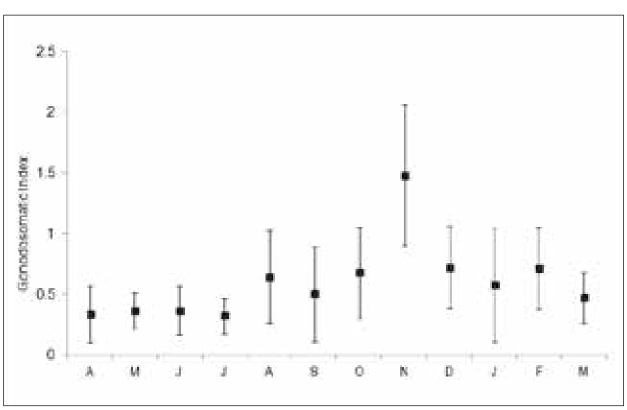

Fig. 2. Monthly variation in Gonado - somatic index (GSI) in the spiny lobster *P. homarus homarus* (April 2006 to March 2007)

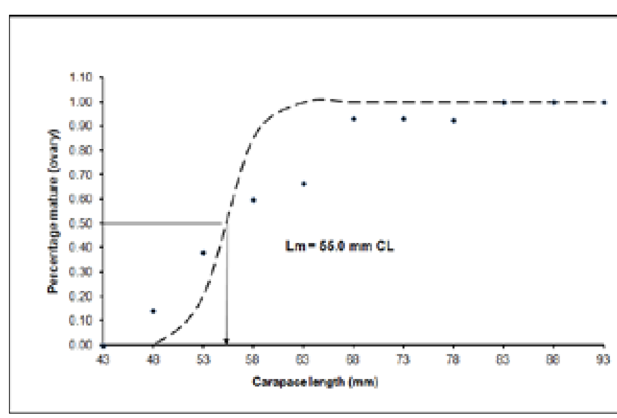

Fig. 3. Logistic relationship between carapace length and the onset of maturity (percentage of females with mature ovary) in *P. homarus homarus*

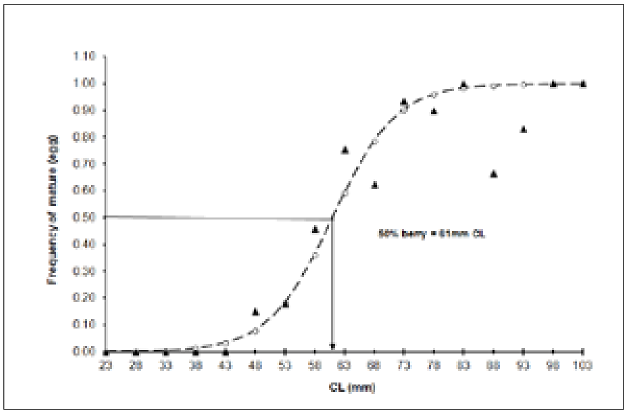

Fig. 4. Logistic relationship between carapace length and onset of maturity (percentage of egg bearing females) in *P. homarus homarus*

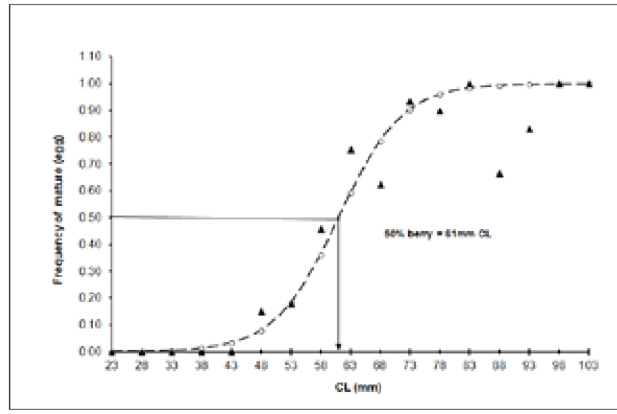

Fig. 6.a. *P. homarus homarus*: An ovigerous seta of a mature female with seteoles b) View of a single seteole with lumen

Setae were absent on the endopods of pleopods of females up to 19 mm CL. Presence of setae was first observed in lobsters measuring 20 - 24 mm CL and the setae had a length of 1 - 2mm. Setal growth was proportional to the carapace length upto 50.0 mm CL. Further growth was allometric up to a carapace length of 60 mm. Dramatic changes occurred in setal length and morphology. Regression slopes of relationships between carapace length and setal length differed significantly ($p<0.05$) in lobsters among the size range from 20mm to 100 mm CL (Fig.5). Three regression lines were obtained (Y_1, Y_2 and Y_3). The regression slopes for Y_1 (non - ovigerous) and Y_2 (ovigerous) differed significantly ($p<0.002$) and the intersection of the two regression lines occurred at 50.0 mm CL ($p<0.002$) with the length of seta at 5.2 mm. The intersection of the regression lines Y_2 (ovigerous) and Y_3 (fully ovigerous) was at 60.0 mm CL and the length of seta was measured at 11.5 mm. The seta develops seteoles and a lumen at a length of 5 - 6 mm and was considered as ovigerous (Fig.6a & 6b). Females in the size range of 20 - 40 mm CL had only either an undeveloped or developing setae (non - ovigerous), whereas ovigerous

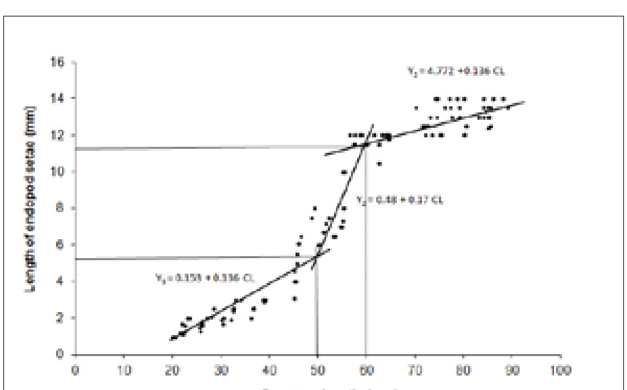

Fig. 5. Regression of pleopod endopodal setal length versus carapace length in *P. homarus homarus*

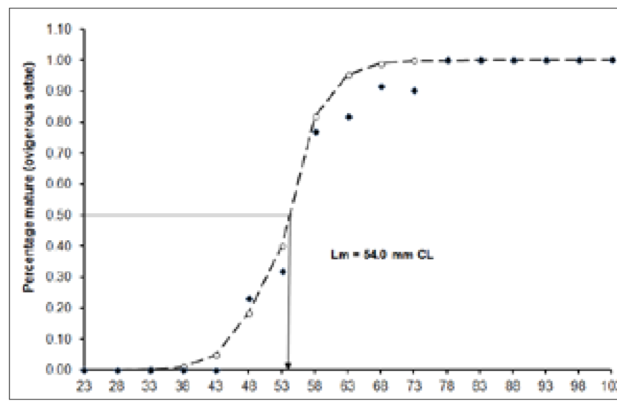

Fig. 7. Logistic relationship between carapace length and the onset of maturity (presence of ovigerous seta) in *P. homarus homarus*

setae were recorded in 40 - 60% of females in the size range of 45 - 60 mm CL. Almost all lobsters above 60 mm CL had well developed endopod setae with an average length of 13.5 mm. The logistic curve of CL versus proportion of females with ovigerous setae shows 50% maturity at 54.0 mm CL (Fig. 7). The estimated mid - point of the two intersections of the regression lines Y_1 and Y_2 and Y_2 and Y_3 i.e. $50+60/2=55.0$) is 55.0 mm CL.

An attempt was made to relate the appearance of 'windows', a secondary sexual character in *P. homarus homarus*, as a sign of sexual maturity. The first 'window' (posterior) appears as a decalcified circular zone on the last sternal plate and changes into an oval shape as the females grow (Fig.8a). In juveniles, all the sternal plates are hard with no soft decalcified areas (Fig.8b). The smallest female with a pair of first pair of 'windows' was 46.5 mm CL and the largest female without a 'window' measured 73.0 mm CL. A second pair of round - shaped 'windows' appears anterior to the first 'window' on a later stage. *P. homarus homarus* lobster with a well - developed first pair of 'windows' is

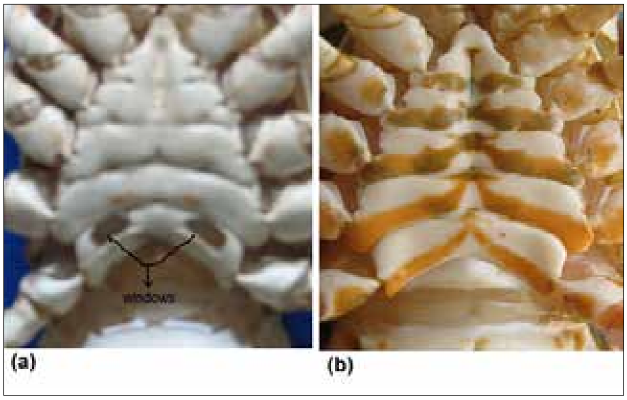

Fig. 8. *P. homarus homarus*: a) The sternal plate of a mature female lobster showing the first (posterior) pair of 'windows' at the base of the fifth pereiopod b) An immature female without 'windows'

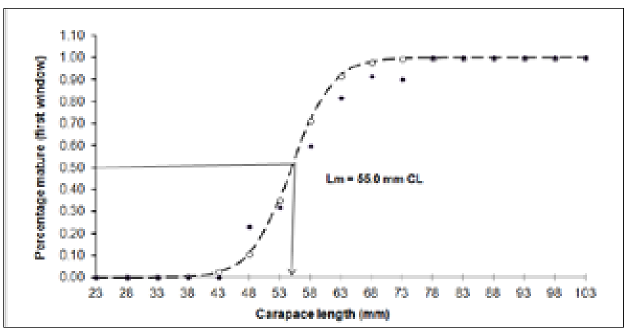

Fig. 9. Logistic relationship between carapace length and onset of maturity (presence of first pair of 'windows') in the spiny lobster *P. homarus homarus*

considered as mature. A logistic curve of the proportion of females possessing the first pair of 'windows' indicated 50% maturity at 55.0 mm CL (Fig.9).

Discussion

Reproductive cycle

The presence of developing, mature and re - maturing ovaries and egg bearing lobsters throughout the year indicate that breeding in the spiny lobster *P. homarus homarus* occurs continuously. However, the reproductive activity is maximum during October to December with a peak in November, which could be deduced from the presence of high percentage of ovigerous females (Table 2) and GSI values (Fig.3). A smaller peak in spawning activity was observed in June. *P. homarus* in the Kanyakumari district of south west coast of India is reported to breed throughout the year with peak breeding activity during November to January (George, 1965; Radhakrishnan *et al.*, 2005). High breeding activity during this period has been related to favourable oceanographic conditions and abundant food (brown mussel *Perna indica*) in the region (Joel and Ebenezer, 1989; Thangaraja and Radhakrishnan, 2012). In the southern coast of Sri Lanka, the maximum breeding activity of *P. homarus homarus* occurred from August to January (Jayakody, 1994) whereas on the west coast, breeding was at its peak in January (De Bruin, 1962). In the feral population of *P. homarus rubellus* in the east coast of South Africa, peak breeding activity was recorded in the summer months (November to February) (Berry, 1971). *P. homarus homarus* in the Oman waters has a protracted breeding period which stretches from May/June to January/February. Initiation of the breeding activity during May/June coincides with the onset of the southwest monsoon, and its continuation through to the January/February months probably take advantage of the cool seawater temperature and the availability of abundant food both for the breeding population and the hatched larvae (Al - Marzouqi *et al.*, 2007). Geographical variation in peak breeding period of the same species between regions may be due to differences in oceanographic conditions, especially the ocean temperature, currents and food.

Table 2. Monthly percentage of *P.homarus homarus* females with or without spermatophore and eggs

Months	Percent without spermatophore and eggs	Percent with spermatophore but no eggs	Percent with spermatophore and eggs	Percent with rudiment of spermatophore mass and no eggs
January	28.3	12.5	21.7	37.5
February	32.8	15.4	17.5	34.3
March	37.5	31	19.2	12.3
April	68.7	4.5	22.5	4.3
May	64.6	9.4	14.6	11.4
June	51.6	5.5	22.7	20.2
July	59.3	11	5.2	24.5
August	61.5	3.2	7.8	27.5
September	38	14.2	21.1	26.7
October	39.5	15.4	43.1	2.0
November	33.5	10.3	50.0	6.3
December	50.0	0.0	41.7	8.3

The high percentage of females with rudiment of spermatophore and spent - recovery ovaries in January and February (37.5% and 34.3%) (Table 2) and the high GSI values (0.5 and 0.59) (Fig.3) after the peak spawning intensity during November and December indicate possibility of repetitive breeding in *P. homarus homarus*. Tropical species of spiny lobsters may breed year round when they are not moulting (Chubb, 2000). Like other tropical species of palinurids, *P. homarus homarus* is capable of multiple spawning. Large females (70 mm CL and above) of *P. homarus rubellus* are capable of producing a maximum of four broods in an year, while the smaller sizes (50 - 59 mm CL) produce one brood in an year (Berry, 1971). A single female of *P. homarus homarus* has been reported to spawn seven times in a year under captive conditions (Vijayakumaran *et al.*, 2005).

GSI values are much useful as an estimation method for distinguishing between oocyte developmental stages of the ovary (Perez Gonzalez *et al.,* 2009). GSI values were found to be a reliable metric in distinguishing between inactive, developing and ripe ovarian stages, but not between the inactive and recovering stages in the Mexican spiny lobster *P. inflatus* (Perez Gonzalez *et al.*, 2009) and the Japanese spiny lobster *P. japonicus* (Minagawa, 1997). They also provide information on the reproductive potential of different sizes of females during peak season of breeding. The mean GSI values of *P. homarus homarus* in the present study ranges from 0.15+0.27 in 30 - 39 mm CL class to a maximum of 0.95+0.32 in 70 - 79 mm CL size class of lobsters (Table 1). The monthly mean GSI values of lobsters in the size range of 65 - 90 mm CL fluctuated from a minimum of 0.32 in July to a maximum value of 1.6 in November (Fig.3), indicating changes in reproductive activity with respect to the season. Rachel (2002) reported a GSI value of 4.9+1.0 in *P. homarus homarus* in V_4 (mature) stage with mature oocytes. The GSI values recorded in *P. homarus homarus* in the present study is well within the values (0.46 to 1.36) reported in the tropical spiny lobster *P. penicillatus* from Taiwan (Chang *et al.,* 2007). Macfarlane and Moore (1986) recorded GSI values ranging from 0.5 at the beginning of breeding migration to 4.0 in the breeding population of *P. ornatus*. Minagawa and Sano (1997) observed a GSI of greater than 11 in *P. japonicus* with mature oocytes. GSI can be influenced by a number of factors including variations in length - weight relationships, environmental conditions and food availability (Minagawa and Sano, 1997; Chang *et al.*, 2007).

Size at sexual maturity

The debate on the precise method of estimating sexual maturity in decapod crustaceans and specifically in spiny lobsters is continuing. Chang *et.al* (2007) considers physiological maturity based on histological examination of oocytes as the most accurate method to estimate size at sexual maturity in spiny lobsters, as non - berried but mature lobsters are indistinguishable from external morphology (DeMartini *et al.,* 2005). The sampling season and time also may influence the result (Chang *et al.*, 2007). The practical utility of this method is doubtful as it is cumbersome and may require a large sample size which is difficult to get, as in most fisheries, the lobsters are brought and exported live to fetch higher price.

The presence of maturing and mature ovary in a sampled population is a clear indication that the individuals are capable of producing viable eggs. However, the physiological maturity may not reflect the functional capability of an individual to hold eggs. A female is considered to be functionally mature only when it develops the secondary sexual characteristic, the ovigerous setae to hold the fertilized eggs. The size at functional maturity of *P. homarus homarus* at Khadiyapatnam was estimated at 46.5 mm (smallest egg bearing female), 55.0 mm (50% with maturing and mature ovary), 54.0 mm (50% possessing ovigerous setae), 55.0 mm ('window' method) and 61.0 mm (50% egg bearing). The estimate of physiological maturity in *P. homarus homarus* indicated by ovarian development stage - to - CL relation was about 11%smaller than the size at 50% functional maturity based on combined presence of eggs on pleopods and spermatophore. Such differences in size at maturity by these two methods have been reported in many species of spiny lobsters. In *P. homarus homarus* of Mambrui, Kenya, the difference in SOM based on 50% developing ovary and 50% egg bearing was 11.4 mm (Kulmiye *et al.*, 2006). In *P. penicillatus* from Taiwan, the estimated size at physiological maturity was 56.46 mm CL and functional maturity, 66.63 mm CL. The difference in size between the two estimates was 10.2 mm (18%) (Chang *et al.*, 2007). In *P. polyphagus*, the difference between the two estimates is 10 mm, which is higher than the difference obtained in *P. homarus homarus* in the present study (Kizhakudan and Patel, 2010). Groeneveld and Melville - Smith (1994) attributed these differences in size at 50% maturity between the two methods in *Palinurus gilchristii* to delay of one or more moults between the development of ovigerous setae and the attainment of functional maturity.

SOM estimates based on the presence of ovigerous setae (functional maturity) in this study is very close to the estimates of sizes at physiological maturity, suggesting that female *P. homarus homarus* are able to mate and carry eggs as soon as they attain physiological maturity. Stewart *et al.* (1997) reported slightly smaller size at physiological maturity compared to the size at physical maturity in the scyllarid lobster *Ibacus peronii*. In contrast, Jones (1988) found the size at physical maturity smaller than the physiological maturity in another scyllarid *Thenus orientalis*. Since the difference in size at maturity between these two estimates is not too wide, it can be reasonably assumed that the females are capable of mating and oviposition as soon as they attain physiological maturity (Stewart *et al.,* 1997). However, the SOM estimates based on presence of eggs (61.0 mm) is significantly different from all the other estimates. Gardner *et al.* (2005) could not find any significant difference between the SOM estimates based on presence of ovigerous setae and external eggs in Tasmania population of *Jasus edwardsii*. Although 50% of the *P. homarus homarus* acquire ovigerous setae at a carapace length of 54.0 mm, almost all females develop full complement of ovigerous setae at 60.0 mm CL. Thangaraja (2011) estimated the size at maturity of *P. homarus homarus* based on ovigerous setae at 53.0 mm CL. Kulmiye *et al.* (2006) obtained a much smaller size at maturity based on ovigerous setae (52.6 mm) than SOM based on external eggs (63.4 mm) in *P. homarus homarus* from Kenyan waters and Booth (1984) based on studies on the New Zealand populations of the spiny lobster *Sagmariasus* *verreauxi* attributed the difference in SOM between the two methods to the development of ovigerous setae prior to the development of functional maturity. However, Montgomery (1992) cautioned that classification of females as immature based on setose state may carry an element of subjectivity especially when comparing different results between studies.

The size at maturity based on the lobster carrying eggs shows wide difference within a subspecies and also between subspecies from different geographical regions (Table 3). The size at 50% maturity based on the presence of eggs in the present study (61.0 mm) is closer to the estimate (59.5 mm) made by Jayakody (1989) for the same subspecies from southern coast of Sri Lanka, but smaller than the estimated value (63.4 mm) for the same subspecies from Kenyan waters (Kulmiye *et al.*, 2006).George (1963) reported the size at maturity of *P. homarus homarus* (previously *P. homarus megasculpta,* see Lavery *et al.,* 2014) females to be between 60 mm and 70 mm at Aden (Yemen) and Johnson and Al - Abdulsalam (1991) found that the SOM estimates vary between 80 and 85 mm in the same species distributed off the coast of Oman. The estimated size at maturity of *P. homarus rubellus* from east coast of Southern Africa was 54.0 mm (Berry, 1971) and that of *P. homarus homarus* from Somalia at 58 mm (Fielding and Mann, 1999). Mohan (1997) reported significant variations in size at maturity in *P. homarus homarus* populations from Oman, ranging from 69 mm to 76 mm CL. Kulmiye *et al.* (2006) attributed the variations in size at maturity within a subspecies to extrinsic factors (temperature, food availability, population density) and the differences between subspecies to a combination of extrinsic factors and intrinsic genetic capacity.

Table 3. Estimated size at maturity by different methods in *P. homarus* subspecies from Western Indian Ocean

Authors		Setal method	Ovary (GSI)	Spawning method	Windows method	Country/ Location
Al Marzouqi *et al.*	2007	-	-	63.9 mm CL	-	Oman (Al - wasta)
		-	-	65.6 mm CL	-	Oman (Dhofar)
Kulmiye *et al.*	2006	52.6 mm CL	52.0 mm CL	63.4 mmCL	-	Kenya (Mambrui)
Mohan	1997	-	-	59.5 mmCL	-	Oman (Dhofar)
		-	-	69.2 mmCL	-	(Oman) Shuwamiyah
		-	-	75.9 mm CL	-	(Oman) Sudh
				72.8 mmCL	-	(Oman) Mugsyl
Berry	1971	-	-	54.0 mmCL		South Africa (Natal)
Jayakody	1989	-	-	59.5 mmCL	-	Sri Lanka (South coast)
De Bruin	1962	-	-	55 - 59 mmCL		Sri Lanka (West coast)
George	1963			60 - 70 mmCL		East Aden
Heydorn	1969			50.0 mm CL		South Africa
Present study	2016	54.0 mm CL	55.0 mm CL	61.0 mm CL	55.0 mm CL	(southwest coast of India)

In the spiny lobster genus *Panulirus*, the appearance of 'window' on the sternal plate is considered to be an external sign of sexual maturity in females. This is considered to be a specialized receptive site for spermatophore deposition (George, 2005). Studies correlating appearance of the 'window' and size at sexual maturity in spiny lobsters is limited (Lindberg, 1955; Vega - Velaquez, 2003). Lindberg (1955) correlated the presence of soft and fleshy nature of the posterior segments of the sternum of female *P. interruptus* with maturity status and suggested that it was an adaptation for the reception and retention of the sperm case. *P. homarus homarus* females without a 'window' and spermatophore were rarely seen with a berry. The size at which 50% with first pair of 'windows' of 55.0 mm CL is in close proximity to the size at first maturity (54.0 mm CL) based on presence of ovigerous setae (Fig. 7).

The size at sexual maturity may be influenced by several biotic and abiotic environmental variables such as temperature (Chittleborough, 1976), food availability (Kanciruk, 1980), shelter (Polovina, 1989), population density (DeMartini *et al.*, 2003) and age (Fielder, 1964; Plaut, 1993; Chang *et al.*, 2007). Since size at maturity is related to age, the larger size at functional maturity of the female *P. homarus homarus* in Kenyan and Oman waters may be due to faster growth of the subspecies in these regions, compared to the same subspecies in India.

This study shows that estimates of size at physiological maturity (55.0 mm CL) and functional maturity based on 50% setose (54.0 mm CL) and appearance of first 'window' (55.0 mm CL) are in close proximity and therefore the maturity indices derived from ovigerous setae and 'window' method can be used as a reliable tool to estimate size at maturity in the spiny lobster *P. homarus homarus*. These methods are much easier to use in field studies without causing any damage to the live specimens.

The minimum legal size (MLS) should be fixed above the size at first sexual maturity so that the females may get an opportunity to reproduce at least once before being caught. In the present study, the size at 50% functional maturity of females was 54 - 55 mm CL. The current MLS fixed by Government of India is based on weight and for *P. homarus homarus,* the MLS for export of live/chilled/frozen whole lobster is 200 g (Radhakrishnan *et al.*, 2005). The total weight of a female equivalent to 55.0 mm CL (SOM) is 163 g, which is 37 g lower than the MLS for export and therefore the current MLS tends to be effective in protecting the sexually immature and maturing lobsters from export. The MLS recommended by the Central Marine Fisheries Research Institute for fishing *P. homarus homarus* (200g) within the maritime boundary of the State of Kerala is in tune with the existing MLS (200g) for export recommended by the Marine Export Development Authority, Government of India (Mohammed *et al.*, 2014). Since the standard practice for fixing MLS is in carapace length, the MLS for fishing *P. homarus homarus* from the wild may be fixed at 65.0 mm CL (equivalent weight 192 g). This size is even higher than the size at 50% maturity estimated on the basis of egg bearing lobsters (61.0 mm CL). Therefore, fixing the MLS at 65.0 mm CL will protect 60% of the egg production potential of the species. The lobster fishermen may be provided with a fixed scale of 6.5 cm, so that they can measure the carapace length of a doubtful size in the field itself and release the undersized lobster back to the sea. Further, the State Government of Tamilnadu may enforce a ban on using trammel net for fishing lobsters and introduce a closed season for lobster fishing during the peak breeding season of *P. homarus homarus* (November) in Kanyakumari district. The participatory management approach involving the lobster fishermen and the state governments may be the practical solution in conserving the declining lobster population and preventing a total collapse of the fishery.

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