

Reproductive biology of freshwater prawn *Macrobrachium vollenhovenii* (Herklot, 1857) caught in Warri River

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SUMMARY

A total number of 338 specimens of *Macrobrachium vollenhovenii* harvested from Ubeji, Jala and Soroghagbene creeks, were purchased from fisher folks at Ubeji, on monthly basis, March to November, 2011. Male and female specimens were differentiated by visual (observation of an open or close closet on the first pair of cheliped) and by microscopic examination of gonads. This resulted in 31 % male and 69 % female specimens. The size at first maturity was identified between 100.0 -120 mm for males and between 130.0 - 150.0 mm for females. The length-weight measurement revealed an increase in total length as body weight increased. The regression coefficient 'r' for length/weight relationship was significant ($p < 0.05$) as a value of (0.901) was recorded for males while that for females was (0.644). The value (0.003) recorded as mean condition factor were similar for male and female specimens. Gonado-somatic-index (GSI) was generally low, resulting in low peak in March for males (0.17) and females (0.29) and a higher peak in July for females (0.60) than males (0.50). Distinct histological changes were observed in the gonads, revealing five developmental stages of gonads for both sexes. Mean fecundity ranged between 6,140 - 20,113 eggs, and was correlated with total length (0.979) but not with body weight (0.185). It could be concluded that matured specimens probably spawned, in March and July, when GSI were at their peaks, and where recruits became evident in subsequent months. This pattern of breeding suggests multiple spawning within a reproductive season.

Keywords: biology, freshwater, prawn, *Macrobrachium vollenhovenii*, river, Warri

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INTRODUCTION

The biology of prawns attracts attention of biologists, not because of their economic importance but because its detailed scientific study, is still at its infancy (Sharma and Subba, 2004). *Macrobrachium vollennovenii*, of the family *Palaemonidae* is among the largest genus in the Nigeria waters. A maximum size of 135.0 and 195.0 mm attainable by this specie has been reported (Marioghae, 1995 and Holthius, 1980). The species grows bigger than *M. macrobrachion* whose maximum size is 125.0 mm. According to Marioghae, (1982) *Macrobrachium vollennovenii* accounted for 60 % of prawn landings from Lagos Lagoon.

Reproduction is important in the life of organisms, because through it, ripe females give birth to their young. Knowledge on gonad development and reproductive performance was important for culture programs and could be used to estimate their length at first maturity. This parameter which was used for management procedures indicate ecological processes when monitored through time and space (Irece et al., 2009). Spawning was linked to seasons of the year, being influenced by environmental factors such as food availability, temperature and photoperiod (Ismeal and New, 2000). According to Springate, (2002), prawns require food to grow and reproduce; hence food deprivation was reported to reduce their rate of growth, gonad development and total fecundity.

The successful culturing of any animal requires a basic understanding of its key biological processes. The most important of these biological processes was the development of gonads. In addition to the limited information available on prawn fisheries in Warri environ, is youth activity, in an area where oil vandalism has become a lucrative venture. The study investigates the length/weight relationship, condition factor, gonado-somatic index, fecundity and histological presentation of gonads at different maturity stages.

MATERIALS AND METHODS

Description of study area

Warri River is one of the most important coastal rivers of the Niger-Delta region of Nigeria. It lies within longitude $5^{\circ}.30^1$ to $5^{\circ}.40^1$ E and latitude $5^{\circ}.27^1$ to $5^{\circ}.32^1$ N (Figure 1). Taking its source few kilometres away from the first station at Ubeji, the river flows' south-west as a main channel into Forcados Estuary, and finally empty into the Atlantic Ocean. The river covers a surface area of about 255 km² with a length of about 150 km², located in the rain forest region of Nigeria. There are two recognizable seasons of variable durations: the sunny and the rainy seasons (Olomukoro and Egborge, 2004). The study area is not entirely fresh water most periods of the year. During the sunny months

(November-April) the water becomes brackish due to the incursion of marine waters from Forcados River. The reverse condition is the case during the rainy months May - October. The region is surrounded by tropical rainforest vegetation, while the shrimp landing stations (Ubeji, Jala and Soroghagbene) are presently secretly subjected to fishing activities, due to frequent youth clashes whose pre-occupation is oil vandalism.

Specimen collection and analysis

Specimens were purchased from fisher folk's at Ubeji, sorted and packed into a collecting ice-chest cooler provided. There were transported to the laboratory located at the Aquaculture and Fisheries Department of the Delta State University, Asaba Campus. Sampling was carried out once a month between 0900-1200 hours on each sampling day, for a period of nine months (March to November, 2011). In the laboratory, specimens were dissected, while gonads were isolated from the visceral region.

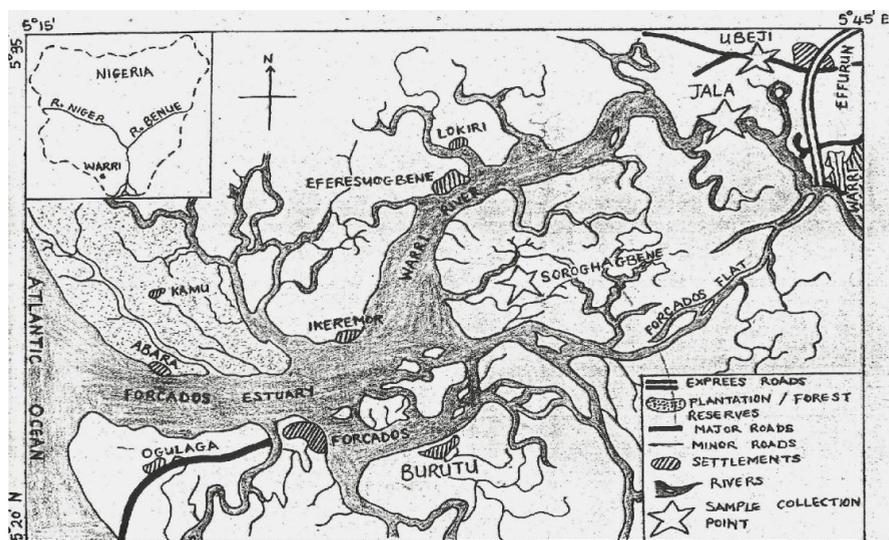


Fig. 1. Map of Warri River and its environs showing the regions (Souaroagaene, Jala and Ubeji) where prawn samples were purchased

They were preserved in Bouin's fixative, in readiness for histological preparations. When eggs were observed in matured females, they were neatly collected into different vials and preserved in 5% formalin for fecundity estimation. Total length measurements of specimens were recorded in millimetres using a measuring board, while weight measurements were conducted with an electronic balance, Model LP 302A LARK C. R.). Weighed specimens were recorded in grams (Sharma and Subba, 2004).

Sex determination

Sex was differentiated by visual (observation for open or close closet on the first pair of cheliped) and also by microscopic examination of gonads. The first pair of cheliped was either joined together at the abdominal segment (in males) or separated (in female) specimens. Sex ratio was determined through chi-square.

Length/weight relationship

The length weight relationship was calculated from the equation: $W=aL^b$ according to Okayi and Lorkyaa (2004). However, because body weight increase more rapidly than total length, the formula was linearized for the purpose of regression analysis by using logarithm transformation thus: $W= \text{Log } a + b \text{ log } L$ where W =body weight in gram, a = regression constant, b = allometric coefficient and L =total length in millimetres.

Condition factor

The wellbeing of the specimens otherwise known as the condition factor (Bernacsek, 1984) was determined by the formula: $K = 100W/L^3$, where K = Condition factor; W = Weight of prawn in gram (g) and L = Length of prawn in millimetres (mm)

Maturity stages

In order to determine the total length at which the prawns attained maturity, it was essential to ascertain that total length where 50 % and above of the prawns had gonads at maturity stage 111 and above. That length was taken as the maturity stage for both sexes (Dumont et al., 2007).

Gonad histology

Transverse sections of gonads preserved in Bouin's fixative were dehydrated in several changes of alcohol (70, 80, 90, 95 and 100 %) for 45 minutes each. Gonad sections were cleared in two changes of Xylene for 45 minutes each. Paraffin wax was prepared at a temperature of 56°C in the oven and the molten wax poured into Lucas boxes. Tissue sections were embedded inside molten wax and immersed in ice to solidify. Five microns (5.0µm) section of tissue was sliced out with the aid of rotary microtome. Flakes of sliced tissue sections were floated in warm water bath. Each flake was picked with and allowed to stick on cleaned slides. Such slides were placed on hot plate to dry and stained with Haematoxylin and Eosin. They were dried thoroughly again, in the air and viewed under the binocular microscope (at X 10 magnification) connected to a digital photomicrograph whose magnification was adjusted to X 5000 before each mounted gonad was snapped.

Gonado somatic index

The gonado-somatic-index was calculated from the formula:

$$\text{GSI} = 100(\text{GW})/\text{BW};$$

where: GW = Gonad weight and BW = Body weight after (Fernandez et al., 1998).

Fecundity estimation

Fecundity is the number of ripened eggs in the Ovary. Ripe ova were used for fecundity estimation by the gravimetric method. Eggs preserved in 5 % formalin were dried on layers of filter paper while the ovarian tissues were physically removed by hand. Sub-samples of eggs were taken with the aid of Bran Scientific weighing balance (LA 164 Model) and recorded. The total number of eggs in the ovary (absolute fecundity) were calculated by the formula of Fernandez et al., (1998), written thus: $F = nG/g$, where F = Fecundity; n = number of eggs, G = ovary weight in (g) and g = weight of sub samples in (g). Relative fecundity (F) was calculated by the formula: $F = \text{Total no of eggs in the brood pouch} / \text{Total weight of prawn}$ (Fernandez et al., 1998).

RESULTS

Sex ratio

Two hundred and thirty-five females and one hundred and three males making up 338 specimens of *Macrobrachium vollenhovenii* were examined between March and November 2011. Of this number, the male specimens accounted for 31.0 % while the female specimens accounted for 69.0 %. The monthly composition of sample size, mean monthly composition for total length, body weight, condition factor for both sexes and sex ratio are shown in Table 1.

Length - weight relationship

The length weight measurement revealed that the biggest male specimen harvested measured 198.00 mm in total length and 72.70 g in body weight. The smallest specimen was in the size class of 10.00 - 60.00 mm. It measured 45.20 mm in mean total length and 12.16 g in mean body weight. The mean total length in the size class of 130.0 to 180.0 mm for females was 138.30 mm in mean total length and 44.95 g in mean body weight. In the size class of 70.00 to 120.00 mm for females a mean total length of 80.40 mm was recorded, while the mean body weight was 25.60 g. The highest numbers of specimens (305) were caught in the size class 70.0 - 120.0 mm for combined sexes while the least number (01) was caught in the size class 190.0 to 240.0 mm for both sexes (Table 2). The regression coefficient 'r' for length weight

relationship was less significant for females (0.644) than males (0.901) (Figures 2 and 3).

Table 1. Monthly sample size, mean monthly composition for total length, body weight, condition factor and sex ratio of *M. vollenhovenii*

Time in month	Sample size	\bar{X} T _L mm	\bar{X} B _w (g)	\bar{X} K-Factor	Sample size	\bar{X} T _L mm	\bar{X} B _w (g)	\bar{X} K-Factor	Sample size	\bar{X} T _L mm	\bar{X} B _w (g)	\bar{X} K-Factor	Sex ratio
March	10	117.50	41.71	0.003	20	106.90	33.70	0.002	30	112.20	37.71	0.003	1:2
April	17	95.90	34.11	0.004	16	82.70	14.93	0.002	33	89.30	24.52	0.003	1:1
May	14	93.50	26.20	0.003	20	88.80	18.99	0.002	34	91.15	22.60	0.003	1:1.4
June	12	134.70	47.80	0.002	18	114.60	36.15	0.002	30	124.65	41.98	0.002	1:1.5
July	17	149.90	66.30	0.002	16	88.70	22.90	0.003	33	119.30	44.60	0.002	1:1
August	12	119.50	51.80	0.003	28	75.60	21.77	0.005	40	97.55	36.79	0.004	1:2.3
Sept.	07	93.60	44.19	0.005	18	94.60	25.10	0.006	25	94.10	34.65	0.004	1:2.6
October	11	90.20	22.98	0.003	39	72.80	18.50	0.005	50	81.50	20.74	0.004	1:3.5
Nov.	03	86.30	16.30	0.003	60	115.50	43.60	0.003	63	100.9	29.95	0.003	1:20
Total	103	981.10	351.39	0.031	235	840.20	235.64	0.03	338	910.65	293.54	0.025	
Mean, \bar{X}	11.44	109.01	39.04	0.003	26.11	93.36	26.18	0.003	37.56	101.18	32.62	0.003	1:2.28

\bar{X} T_L= Mean Total Length in mm, \bar{X} B_w= Mean Body Weight in gram

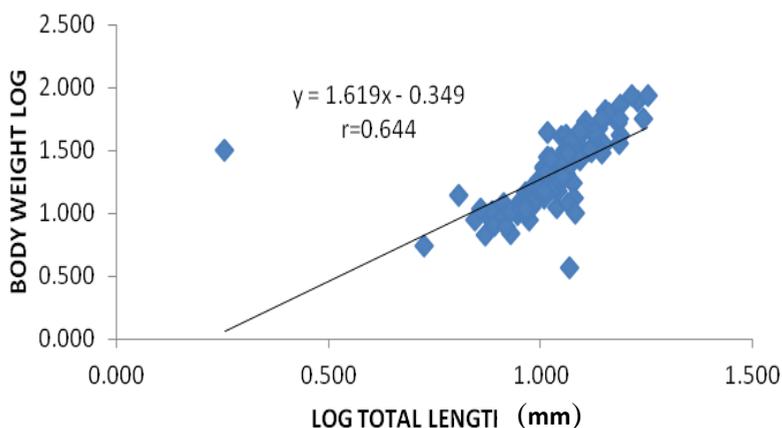


Fig. 2: Log of total length versus body weight for female *Macrobrachium vollenhovenii*

Condition Factor

There were variations in mean condition factor for male and female specimens used for the study. Variations in condition factor was generally low but were higher in females than in male specimens, (Table 2) with the mean data for both sexes remaining the same (Table 1). Generally, the mean condition factor (K) was higher in juveniles than adult specimens (Table 2). The

range in condition factor for male specimens is 0.002-0.012 while that of the females was 0.002-0.008 (Table 2).

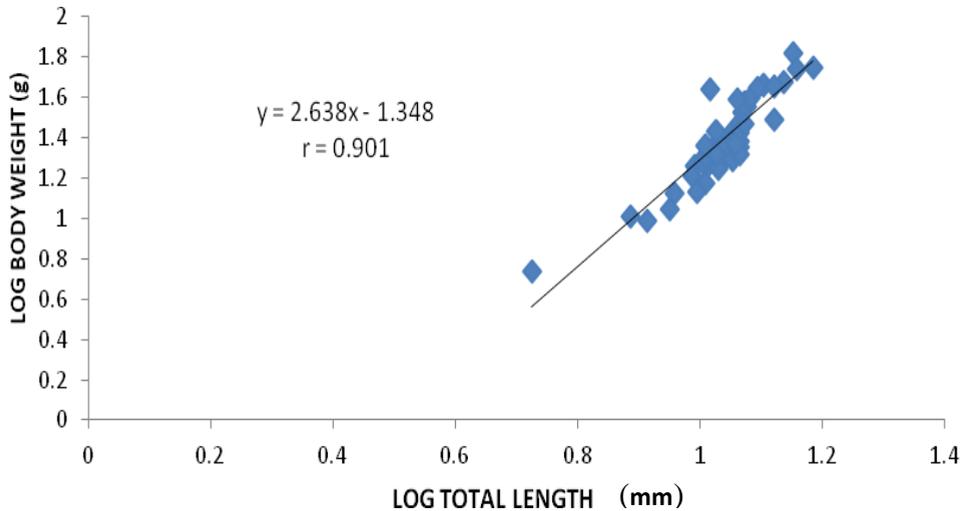


Fig. 3: Log of total length versus body weight for male *Macrobranchium vollehovenii*

Table 2. Size class, frequency of occurrence, total length, body weight and condition factor of specimens used for the study

Size class (mm)	Freq. of occ. for males	\bar{X} TL (mm) for males	\bar{X} BW (g) for males	K-factor for males	Freq. of occ. for females	\bar{X} TL(mm) for females	\bar{X} BW(g) for females	K-factor for females	Freq. of occ. for both sexes	\bar{X} TL(mm) for both sexes	\bar{X} BW(g) for both sexes	K-factor for both sexes.
10.0-60.0	05	50.20	15.61	0.012	012	60.10	18.30	0.008	017	55.15	17.00	0.25
70.0-120.0	89	118.00	41.30	0.003	216	80.40	25.60	0.005	305	92.20	33.45	0.003
130.0-180.0	08	140.40	48.41	0.002	007	138.30	44.95	0.002	015	139.35	46.68	0.002
190.0-240.0	01	188.00	72.70	0.001	-	-	-	-	001	198.00	72.70	0.001
	103	-	-	-	235	-	-	-	338	-	-	-

Maturity stages

Table 3 shows that the specimens were grouped into 20 mm total length size class interval, to enable the percentage of occurrence computation of various stages of maturity. Ovaries and testis in maturity stages 1 to 11 were classified as immature, while those in stages 111 to V were classified as matured. Going by this size classification, a size class of 40.0 to 90.0 mm recorded the highest number of juvenile male and female specimens (193). In the size class of 130.0 to 150.0 mm equal number of male and female specimens were encountered, while in the size class of 190.0 to 210.0 mm, no female specimen was encountered except one male sample caught in that class. The biggest/largest spent male specimen was caught in August. The total numbers of immature specimens were more than the matured ones. Specimen assessment at 50% maturity, revealed that only fewer specimens were in the

matured size class of 100.0 to 120.0 mm (11%) for males and 130.0 to 150.0 mm (18.1%) for females. The size at first maturity was therefore 100.0 mm for males and 130.0 mm for females.

Table 3. Size class distribution and percentage occurrence of specimens at different stages of maturity.

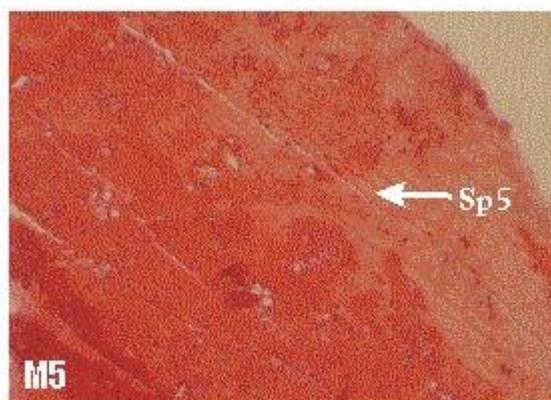
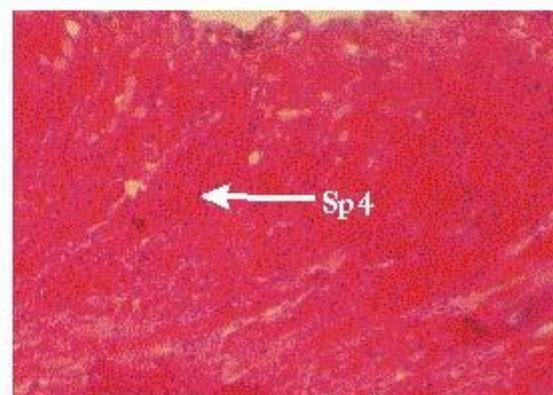
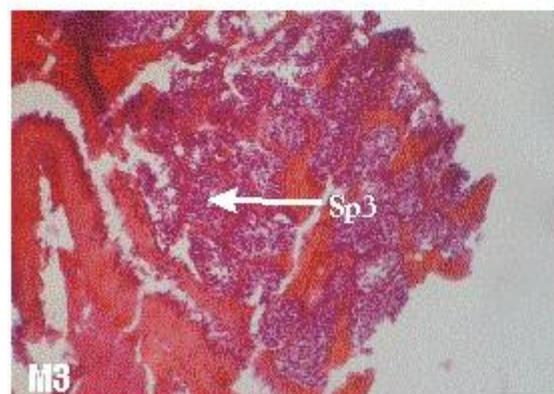
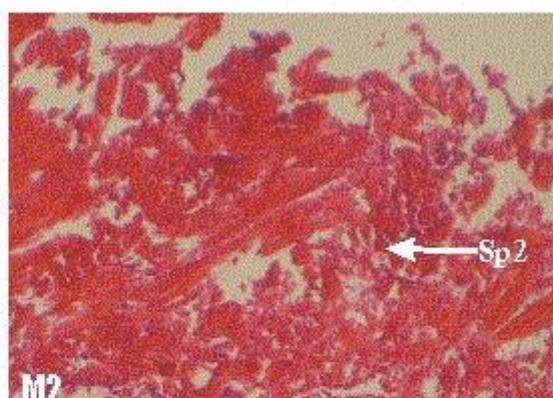
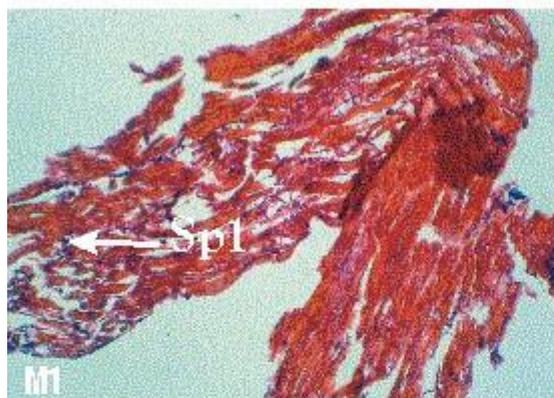
Size Class (T _L mm)	Male (%)						Female (%)					
	F	1	11	111	IV	V	F	1	11	111	IV	V
40-60	5	100.0	00	00	00	00	12	100.0	00	00	00	00
70-90	56	80.3	19.7	00	00	00	120	83.9	16.1	00	00	00
100-120	33	56.5	32.5	8.2	2.8	00	96	9.7	90.3	00	00	00
130-150	4	42.3	20.5	14.4	22.8	00	4	40.8	41.1	14.8	3.3	00
160-180	4	60.2	20.5	10.1	00	9.2	3	50.2	30.7	19.1	00	00
190-210	1	00	00	00	100.0	00		00	00	00	00	00
Total	103						235					

Key: F= frequency of occurrence. 1, 11, 111, 1V and V are the percentages of the maturity stages.

Table 4: Developmental stages of gonads

Maturity stages/Month	Male	Female
Immature dominant phase, undeveloped gonad encountered in March	Spermatogonia cells appear compact under the digital photomicrograph. Testis is physically translucent in colour. Plate M1	Ovary is small, translucent and difficult to distinguish through the carapace. Oogonia cells are aggregated, as seen through the microscope. Plate F1
Immature non-dominant phase. Developing gonad encountered between April and May	Cells are visible under the microscope. Gonads developing into spermatocyte stage. Note the presence of melanomacrophage centres and lacanae cells. Plate M2	Oogonia cells have advanced into oocyte stage. Developing ovaries are larger, opaque, and yellowish, with scattered melanophores over the surface, nucleolus is not visible. Plate F2
Pre-vitellogenic phase encountered between June to July	Dominated by black dots representing spermatocytes and spermatids. Gonad is physically light orange in colour. Plate M3	Vitellogenesis shown by eosin stained oocytes. Pre-vitellogenic oocytes with basophilic cytoplasm. Nucleus appears. Vesicular bodies appear with chromatin clumps. Ova are nearly ripe. Gonad is physically dark orange in colour. Plate F3
Mature spawning phase encountered between August to September	Dominated by Spermatids and spermatozoa cells. Gonad is physically light brown in colour. Plate M4	Numerous cortical rods shown. Follicle cells appear. This is the ripe spawning stage. Characterized by fully matured ovum whose centre region is opaque. It bears very thin cell wall. Ripe ova, filling virtually the whole space. This is the vitellogenic stage. Ovary is physically light yellow in colour. Plate F4
Hydrated/spent phase encountered between October to November.	This is the spent or hydrated phase, characterized by irregularly shaped/empty lumens that look flaccid after the release of spermatozoa. Gonad is physically dark brown in colour. Plate M5	Post vitellogenic stage is characterised by shrunken and irregularly shaped cells observed after ova release. Degeneration of oocytes by the appearance of vacuoles. Ovary is physically dark yellow in colour. Plate F5

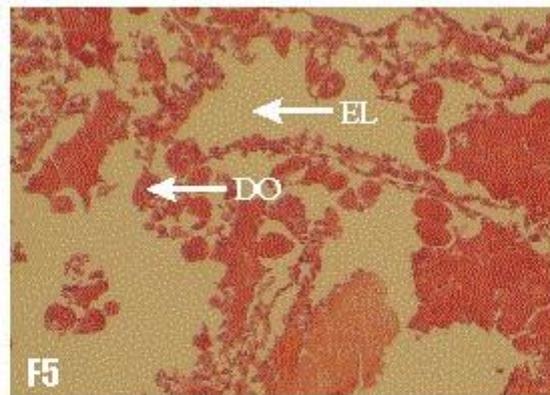
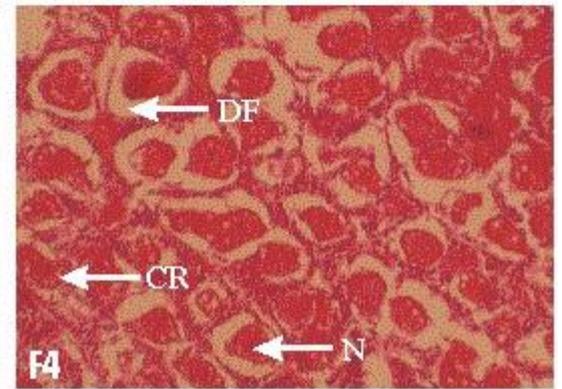
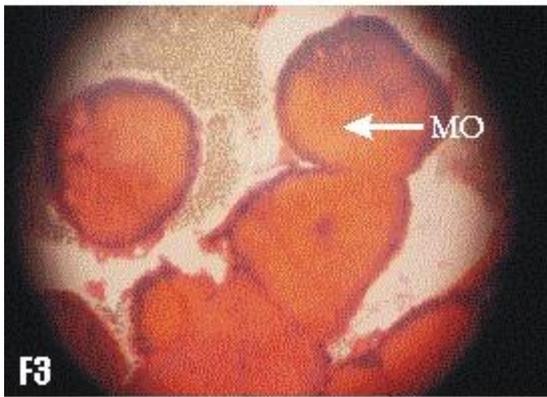
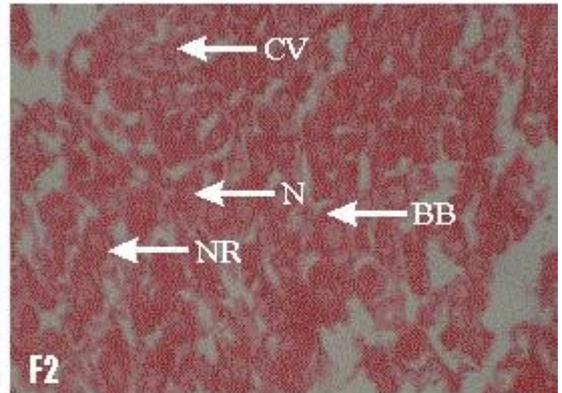
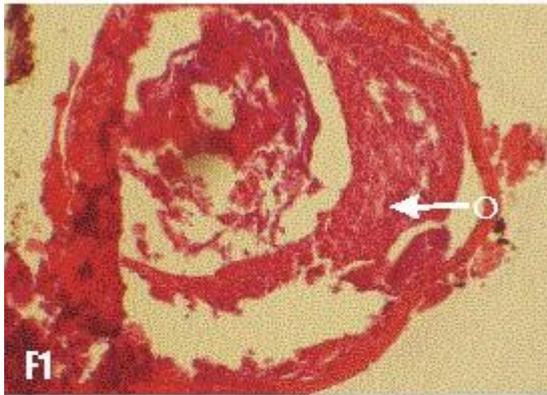
Male maturity stages



Mag. X 400

Sp1=Spermatogonia; Sp2=Spermatocyte; Sp3=Spermatid;
Sp4=Spermatozoa; Sp5=Empty irregular cells.

Female maturity stages



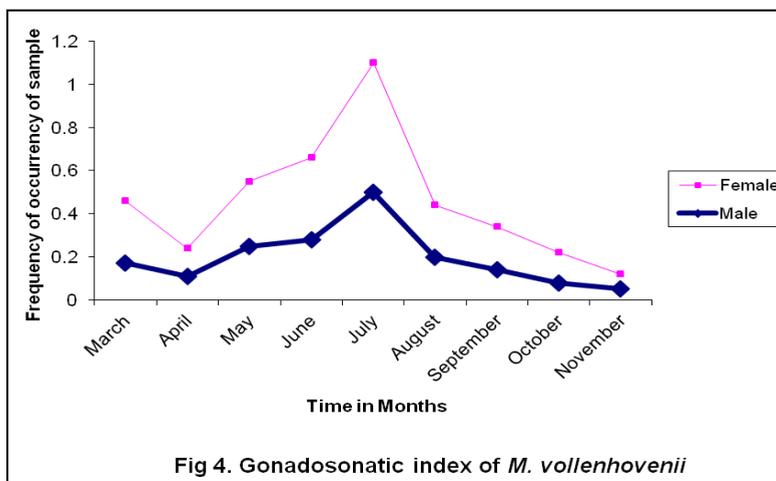
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O=Oogonia; NR=Nuclear ring; BB=Balbiani body; N=Nucleus;
 CV=Cortical vesicle; DF=Disintegrating follicle; MO=Matured oocyte;
 CR=Cortical rod and OC=Ovarian cavity.

The distinctions amongst different stages of maturity were based on the size/structure of the gonad, their staining affinity, presence/absence of yolk globules and the general changes in somatic development. Five stages of gonad developments were observed. The developmental stages are shown in Table 4 while the histology of the gonads is shown in plates M1 to M5 and F1 to F5.

Gonado-somatic index (GSI)

Data on the gonado-somatic index revealed that somatic activities in the cells were high in the month of March with a value of 0.17 for males and 0.29 for females, indicating not only the first peak period, but also continuation of yolk deposition and build-up of gonads. This activity decreased in the month of April with a value of 0.11 for males and 0.13 for females. Soon after these decreases, there was another gradual increase in gonad development in subsequent months. Somatic activities peaked again in the month of July as shown for both sexes with a value of 0.60 for females and 0.50 for males. There was a sharp decreased in gonado-somatic index during the months of April and August for both sexes, which characterised the months immediately after the release of ova/spermatozoa. From the pattern of somatic activity, it could be concluded that the specimens spawned in March and July and recovered in April and August respectively (Fig 4).



Fecundity estimation

Fecundity estimates varied between 6,140 to 20,113 eggs. The largest females had the highest body weight. The highest mean fecundity was recorded in the month of July. The reverse was the case in the month of

August, when the lowest mean (body weight/fecundity) were recorded (Table 5).

Table 5: Means of total length, body weight, absolute and relative fecundity

Month	Mean total length (mm)	Mean body weight (g)	Mean of absolute fecundity	Mean of relative fecundity
March	112.20	37.71	6,644	3,951
April	89.30	24.52	-	-
May	91.15	22.60	-	-
June	124.65	41.98	18,775	13,789
July	119.3	44.60	20,113	15,546
August	97.55	36.79	6,140	2,213
September	91.10	34.65	-	-
October	81.5	20.74	-	-
November	100.9	29.95	-	-

DISCUSSION

Sex ratio

The sex ratio observed during the present study, revealed that the females (235) were more than the males (103) in number. Similar sex ratio differentials were observed by George and Rao (1967) in respect of *Penaeus indicus*, *Metapenaeus dobsoni*, *Machrobrancium affinis* and *Parapenaeopsis stylifera* from the trawl catches off Cochin. These reports from aforementioned scientists were in line with that of the present study. However, the reports of (Menon, 1957; Inyang, 1981 and Marioghae, 1982) where males and females were of equal sex ratio is out of tune with that of present study. The reason for the disparity in sexes encountered in earlier and present study may be that the females were more vulnerable to catch in nature than the males that migrate into deeper waters soon after spawning. Again, season, species and the mere fact that different environs were sampled may be another reason for disparity in the number of specimens encountered. According to Tawari-Fufeyin et al., (2005), sex ratios may not always be static, as they vary from season to season and from year to year within the same population.

Length weight relationship

Weight increment revealed higher body weight gain in male than in female specimens. Also, the length weight relationship was more significant in males than in females. These observations agree with those expressed by Edokpayi, (1990). Differences in length weight relationships were attributed to sex, season and time of breeding (Marioghae, 1982).

Condition factor

In the present study, a number of berried prawns were found with empty stomachs. They had fat deposition in them, as well as yolk accumulation in the gonads. The wellbeing of any organism is dependent on the presence of food in the stomach. Food has influence on the wellbeing of fishes especially for fingerlings. This is because the fingerlings are more active and so scavenged for food more than mature specimens that are less active. This behaviour although presently observed in fishes could also be true for prawns. This could be the reason why juveniles were in a better condition than was otherwise the case for adult specimens, a confirmation of an earlier statement where the berried specimens were not active, because they had empty stomachs, and so were in poor condition. There was no disparity in the condition factor recorded for both sexes throughout the study period. This observation contrasts reports of earlier researchers (Inyang 1981, Marioghae 1982; Zar, 1984; Hla and Ohtomi 2005; Murphy and Austin 2005), who reported differences in the wellbeing of the sexes. It could be that biological interactions experienced for intra-species competition for scarce food and space were probable reasons for low values in condition factor in the present study. Variations of condition factor in respect to size class were uniform, indicating that their well-being did not depend on size. This was also the observation of (Hla et al., 2005 and Tawari-Fufeyin et al., 2005). Condition factor was generally low but slightly higher in female than in male specimens as a result of yolk deposition in the former sex.

Maturity stages

The size at maturity (100.0 – 120.0 mm for male and 130.0 – 150.0 mm for females) observed in the present study was comparable with those reported for female (157.0 mm) *P. semisulcatus* in the Bushehr area (King, 1995), but it is in contrast with the value of 172.0 mm reported in the same species at the Gulf of Carpentaria (Crococ, 1987). Fishing pressure was said to reduce the size of target species, especially the matured ones. According to (Sparre and Venema, 1992), fishing pressure apparently has influence on organisms, especially short-lived species as crustaceans or cephalopods.

Gonad histology

Increases were observed in the cyclical changes in gonad developments; evident in the monthly changes of gonado-somatic index, (Murphy and Austin, 2005) for both sexes as recorded throughout the study period. During the immature stage, the germ cells (oogonia and spermatogonia cells) were dominant but became gradually enlarged at the oocyte and spermatocyte stages and also in subsequent stages. This was the reason for the increase in gonado-somatic index which climaxed in March and July decreasing soon after

subsequent months. The variation in gonado-somatic index followed the same pattern in both sexes. The same observation was evident in the report of Hla and Ohtomi (2005). During this study, except between August and September, maturing as well as mature individuals were observed (especially from March to July). The spent specimens were encountered between October and November. The activities in the gonads during the period October to February accounted for happening during the resting/immature stage when they migrated towards shallower waters, for feeding.

Fecundity

Fecundity estimation in this study ranged between 6,140 and 20,113. This is an observation not comparable with those of (Marioghae, 1995) where fecundity was only 1,000 – 10,000 for *Macrobrachium macrobrachion* and 45,000 – 400,000 for *Macrobrachium vollenhovenii*. The reasons adduced for the differences in fecundity could be attributed to differences in season, size of the specimens and or differences in the habitat where they were caught (Inyang, 1981; Marioghae, 1982; Hla and Ohtomi 2005; Murphy and Austin 2005).

Few gravid females were caught in March (dry season) while an appreciable number of gravid specimens were caught between June and July during the rains. This observation suggests that they are partial spawners. Abundant food availability during the rainy season was probably the reason for appreciable number of spawners at that time. Only the rainy season spawning activity in the present study was in line with those reported (Inyang 1981, Marioghae 1982, Hla and Ohtomi 2005, Murphy and Austin 2005). In contrast to the present observation, Nagabhushanam et al., (1987) reported that rainy season reduced breeding activity in *M affini*. Again, Pillay and Nair (1971) reported that the rainy season was a constraint to breeding in estuarine and shore crabs. Observations by Gyananath (1982), Victor (1984) and Sarojini and Rajani (1987) (revealed that rainfall contributed very little to breeding activities of fresh water prawns) did not support those of present investigation. Spent ovaries were observed in April and August but the presence of only one size of oocytes in the ovary, suggests that breeding was not continuous as shown in gonad histological/observation suggesting probably that the species were not total spawner.

In the present study, spermatogenic tubules were observed to contain five or six developmental stages. This was the situation with *M. choprai*, in addition with different species of crab (Fasten 1926; Ryan, 1967 Sengupta and Chatterji 1976). However, Sengupta and Chatterji (1976) noted the presence of both spermatocytes and spermatids) in the tubule and reported that of all these cells, the spermatocytes were not always at different stages of differentiations.

Sarojini and Gyananath (1984) made a similar observation in *M. larnarrel*. This was not the situation in the present study.

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