Journal of the Marine Biological Association of the United Kingdom, 2012, 92(3), 531–538.
doi:10.1017/S002531541100107X

An investigation on ovarian development of grooved shrimp *Melicertus kerathurus* in Izmir Bay, Turkey

AYSUN KÜCÜKDERMENCI AND AYNUR LOK

Ege University, Faculty of Fisheries, Department of Aquaculture, 35100 Bornova, Izmir, Turkey

In the current study, commercially valuable penaeid shrimp, Melicertus kerathurus*, were attained approximately monthly in the Izmir Bay, southern Aegean Sea from May 2004 to April 2005. For each specimen, we measured body length, body weight and ovarian weight, and calculated gonadosomatic indices (GSI). GSI values results pointed out that the GSI in* Melicertus kerathurus *increased during vitellogenesis (2.03 ± 0.24%) but sharply decreased after spawning (0.53 ± 0.35%) to reach levels similar to those in immature females. We also examined oogenesis in* Melicertus kerathurus *by histological observation of the ovary to determine reproductive cycle for future domestication. The observation on the gonads leads us to conclude that there are five stages of development for the females: (I) previtellogenic; (II) early vitellogenic; (III) late vitellogenic; (IV) mature; and (V) spent. Histological characteristics showed that the best time to capture adult shrimps for breeding purposes was between the months of April and June. The numbers of each oocyte type that were present were also counted, measured, and used to evaluate the following traits: total oocyte number; mean oocytes diameter; and maximum oocyte diameter. Oocyte diameter was significantly different at all stages ($P < 0.05$) and the largest diameter was observed as 163.92 ± 4.51μm at stage IV.*

Keywords: *Melicertus kerathurus*, grooved shrimp, reproductive cycle, gonadosomatic index, histology, ovarian development

Submitted 20 August 2010; accepted 28 March 2011; first published online 31 August 2011

INTRODUCTION

The east Atlantic–Mediterranean prawn *Melicertus kerathurus* (Forskal, 1775) lives in coastal marine and brackish waters but it has nearly disappeared from Israel, southern Turkey and up to the Southern Aegean Sea (Galil & Kevrekidis, 2002), its habitat being overrun mainly by *Marsupenaeus japonicus* (Kevrekidis & Thessalou-Legaki, 2006).

Reproductive pattern is a major factor determining the reproductive potential of a species. Therefore, it is very important to understand the reproductive biology (ovarian development) for future domestication of this species in local waters. Increased attention has been paid in recent years to the ovarian development of penaeid shrimp and macroscopic, histological characterization of penaeid shrimp maturation has been studied on various species such as *Melicertus japonicus* (Yano, 1988), *Melicertus vannamei* (Arcos *et al.*, 2005), *Melicertus semisulcatus* (Badawi, 1975), *Melicertus kerathurus* (Medina *et al.*, 1996), *Melicertus monodon* (Tan-Fermin, 1991; Quinitio *et al.*, 1993), *Litopenaeus setiferus* (King, 1948), *Penaues indicus* (Subrahmanyam, 1965), *Melicertus aztecus* (Duronslet *et al.*, 1975), *Melicertus duorarum* (Caillouet, 1972), *Fenneropenaeus merguiensis* (Crocos & Kerr, 1983), *Lucifer orientalis* (Oka & Sirahata, 1965) and *Melicertus plebejus* (Kelemec & Smith, 1980) in the world. Medina *et al.* (1996) have also stated that the ovarian histology of *M. kerathurus* is typical of that described previously for other penaeids and based on their histological features, five distinct stages have been identified throughout ovarian development: previtellogenic, early vitellogenic, late vitellogenic, mature and spent or degenerating.

There are many studies on this species in the Mediterranean but very little is known about the seasonal cycle of gametogenic development, spawning periodicity and length at sexual maturity in Turkey. Until now, there have been many systematic studies of ecology (Geldiay, 1969; Geldiay & Koçataş, 1973; Alpbaz, 1978; Özden, 1989) and cultivation (Köse *et al.*, 1999; Kumlu *et al.*, 2001; Aktaş *et al.*, 2004). The present study represents the first documentation of the gametogenic cycle of shrimp in Turkey. Therefore, the current study aimed to refine the existing methods of staging by further characterizing reproduction in *Melicertus kerathurus* using: (1) qualitative techniques such as histology of the ovaries; and (2) quantitative parameters such as morphometry (carapace length, body length, gonad weight, body weight, gonadosomatic index and average/maximum oocyte diameter) and oocyte frequency as they occur in wild specimens.

MATERIALS AND METHODS

Wild specimens of *Melicertus kerathurus* (Forskal, 1775) were captured monthly (from May 2004 to April 2005) from Izmir Bay (032°32′00N 026°46′00E) (Figure 1). All individuals (N = 60) were weighed to the nearest 0.01 g and measured for their body length (BL, distance between the post orbital margin and

Corresponding author:
A. Kücükdermenci
Email: aysun.kose@ege.edu.tr

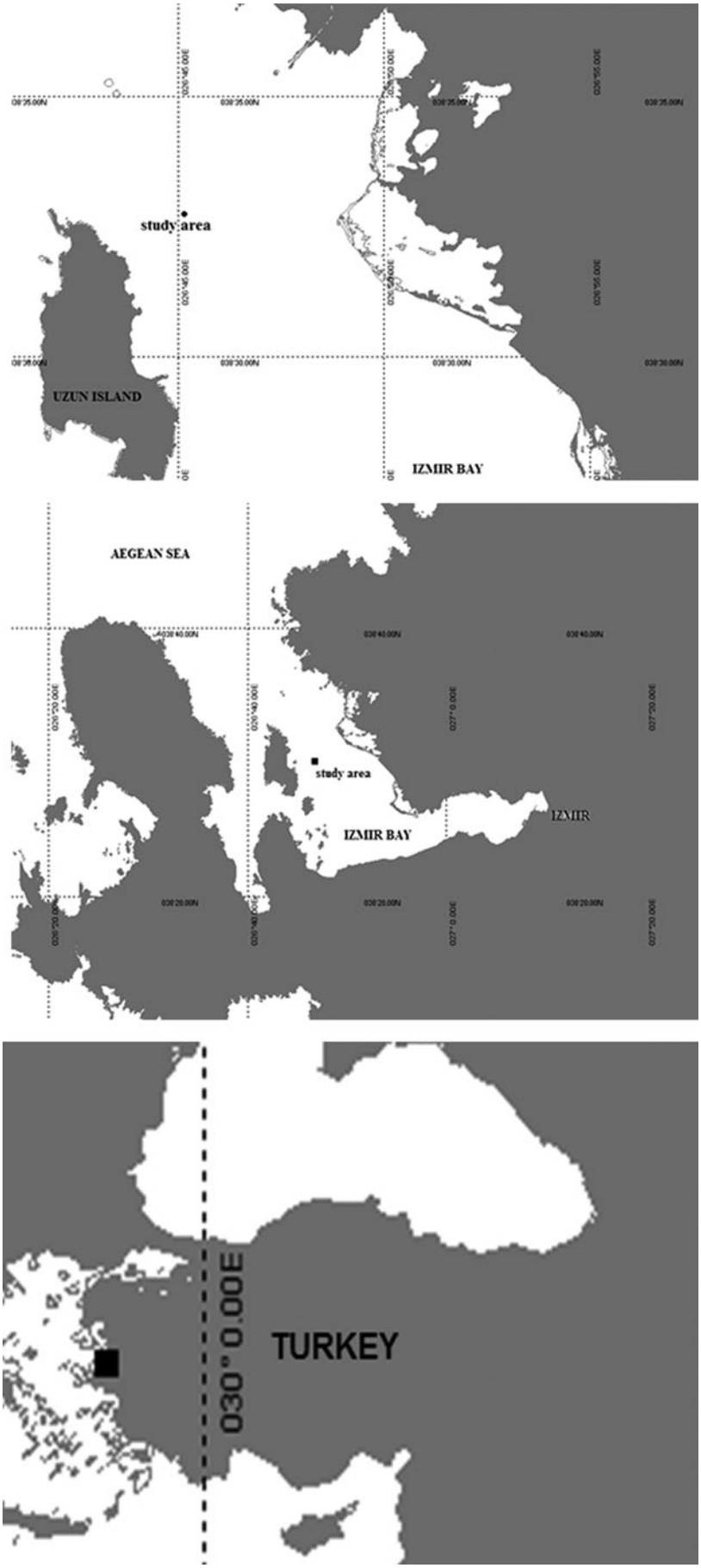

Fig. 1. Shrimp (*Melicertus kerathurus*) sampling area in Izmir Bay, Turkey.

https://doi.org/10.1017/S002531541100107X Published online by Cambridge University Press

Table 1. Summary of data on the quantitative parameters of wild *Melicertus kerathurus*. Data are presented as mean ± SEM.

	Stages				
Parameters	**Stage I**	**Stage II**	**Stage III**	**Stage IV**	**Stage V**
BL (mm)	158.10 ± 0.9	145.80 ± 0.52	166.30 ± 0.66	189.80 ± 0.50	164.0 ± 0.42
CL (mm)	5.85 ± 0.34	5.00 ± 0.18	5.77 ± 0.85	5.49 ± 0.4	6.22 ± 0.25
BW (g)	27.30 ± 5.58	21.45 ± 2.65	25.44 ± 4.04	47.35 ± 3.02	27.75 ± 2.46
GW (g)	0.46 ± 0.05	0.21 ± 0.00	1.69 ± 0.35	2.53 ± 0.63	0.48 ± 0.04
GSI (%)	1.32	0.9	3.97	4.65	1.38
AOD (mm)	–	49.8 ± 8.89	66.65 ± 18.86	125.12 ± 38.79	98.01 ± 1.4
MOD (mm)	–	88.8	152.2	229.4	140.6
			Duncan statistics $P < 0.05$		

CL, carapace length; BL, body length; BW, body weight; GW, gonad weight; GSI, gonadosomatic index; AOD, average oocyte diameter; MOD, maximum oocyte diameter; SEM, standard error of the mean.

the end of the telson extended in a straight line) and also carapace length (CL, from the posterior margin of the orbit to the posterior margin of the carapace) using Vernier callipers. The ovaries were dissected out and weighed. Since the different regions of the ovary exhibited similar oocyte stages and size–frequencies at all stages of development, only the mid-region of the abdominal lobe of the ovaries was analysed. The diameters of about 30 oocytes and follicles from each animal were measured using an ocular micrometer. Mean diameter was calculated from the long and short axes of the oocytes. The gonadosomatic index (GSI) was expressed as the percentage of the ovarian weight in relation to the total body weight (Medina *et al.*, 1996). Temperature (with a mercury thermometer that ranged −10 to 100 ± 0.5°C), salinity (with a hand refractometer, ‰) and pH (with pH meter) levels were monitored regularly throughout the study.

Histology

Following the removal and weighing of the ovaries, fragments of the middle region of the ovary were fixed for 24 hours in 10% formaldehyde. Thereafter, the ovarian tissues were dehydrated in increasing concentrations of alcohol. Ovarian tissues in paraffin wax were embedded at 6 μm and stained with haematoxylin and eosin. Oocyte diameters were measured from stained sections. The stained tissue glass slide was then examined, photographed (Olympus PM-C3566) under an optical microscope (Olympus CH-2) and qualitatively classified into a stage of development.

Statistics

Means of body weight, carapace length, GSI and oocyte diameter were compared by one-way analysis of variance (ANOVA) followed by the Duncan multiple comparison test at $P = 0.05$, in order to determine significant differences in each sample of shrimp separately. Statistical analyses were performed using SPSS 11.0 software.

RESULTS

Data on the quantitative parameters from shrimps are presented in Table 1. All parameters showed significant differences over the five stages ($P < 0.05$). The mean body length and body weight of the shrimps in stages I to IV was significantly different from each other but stage IV individuals were significantly larger. Mean gonad weight was significantly increased through stages previtellogenic and mature and decreased at stage spent to a weight similar to stage previtellogenic. GSI mean values also increased significantly from stage previtellogenic through stage mature but decreased at stage spent to the previtellogenic. Average and maximum oocyte diameter values were significantly different at all stages ($P < 0.05$) and were largest for stage mature individuals (Table 1).

Changes in the mean GSI are shown in Figure 2. The GSI values of females started to increase in January and reached maximum level in June (8.45%). GSI values abruptly decreased in September (0.53%) which corresponds with the spawning season. After spawning, GSI started to increase again gradually.

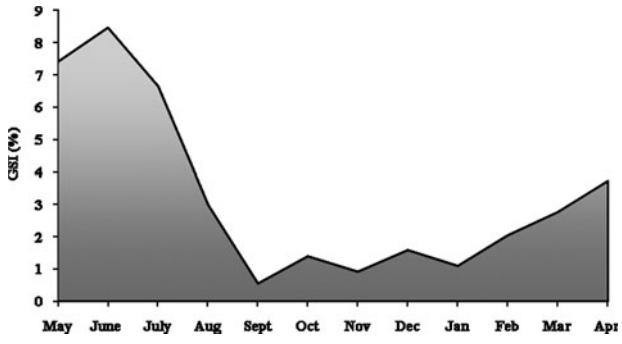

Fig. 2. Changes in the mean gonadosomatic index (GSI) of female *Melicertus kerathurus* during an annual reproductive cycle.

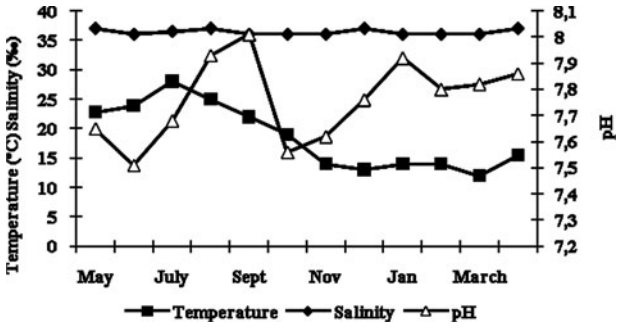

Fig. 3. Variation of temperature, salinity and pH in sampling area 2004/2005.

https://doi.org/10.1017/S002531541100107X Published online by Cambridge University Press

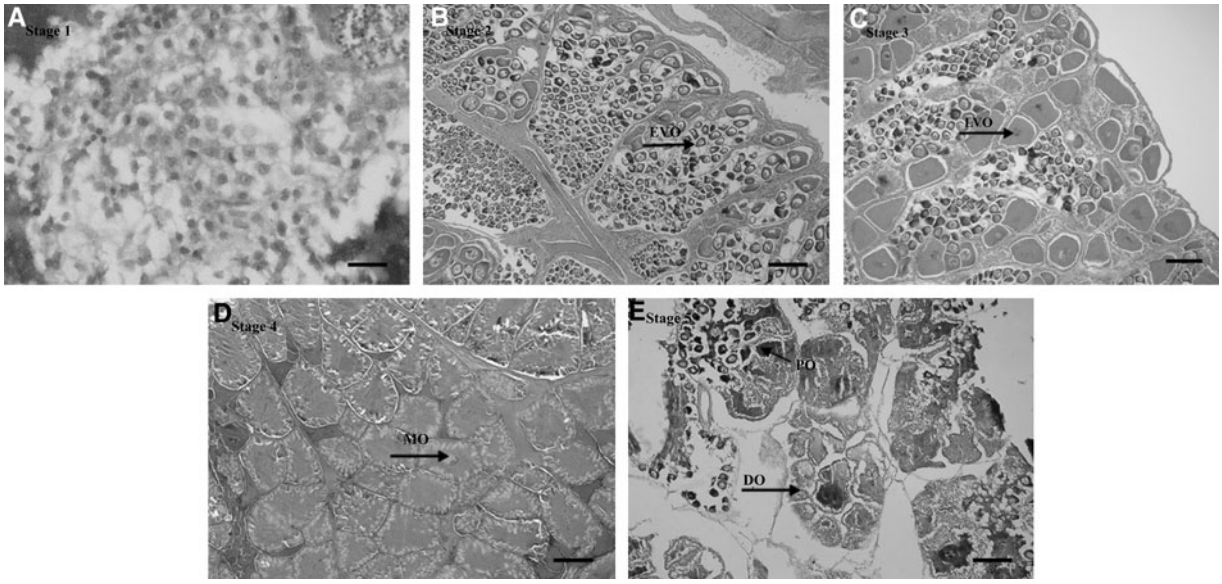

Fig. 4. Sections of wild-caught *Melicertus kerathurus* ovaries: stage I (4A) (December–January), stage II (4B) (June), stage III (4C) (February–May), stage IV (4D) (June–October) and stage V (4E) (September). EVO, early vitellogenic oocytes; LVO, late vitellogenic oocytes; MO, mature ooctyes; DO, degenerating oocytes. Scale bars: 100 μm.

Temperature showed a clear seasonal pattern with maximal values observed in July (28°C), and minimal in March (12°C) and December (13°C). pH ranged from 7.51 to 8.01 with a maximum in September and minimum in June. Salinity was not changed so much and ranged from 36‰ to 37‰ without seasonal variability (Figure 3).

Ovarian histology

Ovarian development of *Melicertus kerathurus* was classified into five stages based on the presence of the most advanced oocyte stage.

STAGE I (PREVITELLOGENIC): *M. kerathurus* captured from the wild in late December and January, the ovaries contained mainly previtellogenic oocytes (77.5%). The oogonia measured 34.53 SEM 1.88 indiameter (14–16 cm body length) μm. The GSI ranged from 1.57% to 1.08% ($P < 0.05$) (Figure 4A);

STAGE II (EARLY VITELLOGENIC): this stage consists mainly of previtellogenic oocytes (41.4%). Late vitellogenic oocytes were also present in this stage. The cytoplasm becomes more basophilic and undergoes a significant increase in size. These oocytes are gradually surrounded by follicle cells when they are relatively small. A basophilic nucleus lies

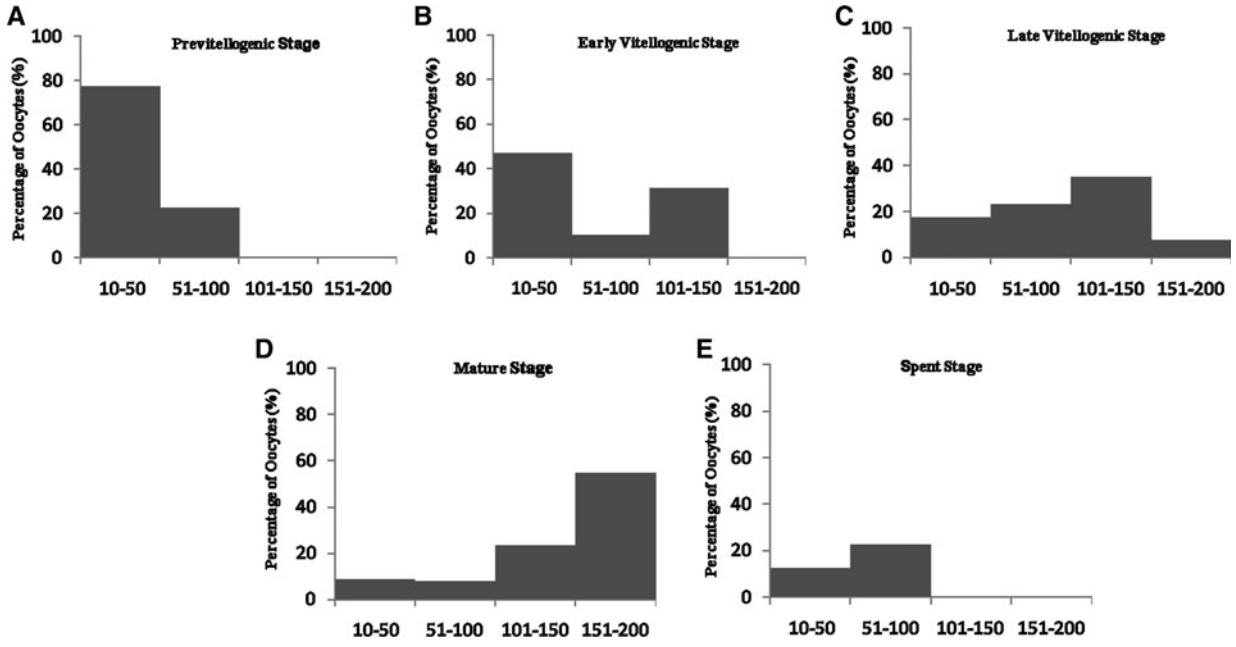

Fig. 5. Oocytes size–frequency histogram showing the development of the oocytes in wild *Melicertus kerathurus* as represented by the posterior abdominal region during the different stages of maturation.

https://doi.org/10.1017/S002531541100107X Published online by Cambridge University Press

Table 2. Monthly changes of vitellin in *Melicertus kerathurus* during the study.

Months	Stage	PO(%)	EVO(%)	LVO(%)	MO(%)	DO(%)
May	III	12.41	22.41	38.22	5.64	–
June	IV	–	24.0	24.0	32.0	–
July	IV	20.0	3.61	30.0	46.2	–
August	IV	–	3.66	–	96.0	–
October	IV	15.0	–	40.0	45.0	–
September	V	12.2	22.7	–	–	65.0
November	II	41.4	10.0	31.4	–	–
December	I	80.0	20.0	–	–	–
January	I	75.0	25.0	–	–	–
February	III	31.25	21.25	35.0	–	–
March	III	21.83	25.83	39.0	7.5	–
April	III	4.54	22.72	28.18	16.36	–

PO, previtellogenic oocyte; EVO, early vitellogenic oocyte; LVO, late vitellogenic oocyte; MO, mature oocyte; DO, degenerating oocyte; SEM, standard error of the mean.

centrally within the cytoplasm with one or two large, dark-staining nucleoli. Nucleoli appear around the periphery of the nucleus (perinucleus stage) and are stained slightly darker than the cytoplasm. This stage could be seen in June (Figure 4B);

STAGE III (LATE VITELLOGENIC): the ovaries contain large oocytes (90–150 μm in diameter) with cytoplasm filled with yolky substances. These yolky oocytes are preferentially located in the outer regions of the ovary, while previtellogenic is located in the cytoplasm of the ovary. The cytoplasm of previtellogenic oocytes is acidophilic, whereas the nucleolus is basophilic. This stage was observed from February to May (Figure 4C);

STAGE IV (MATURE): in this stage, from late June to October, ovaries are characterized by the presence of mostly mature oocytes that surpass 150–200 μm in diameter. As a typically distinctive feature, the cytoplasm of mature oocytes shows conspicuous cortical rods at the cell periphery (Figure 4D);

STAGE V (GVBD): in the middle of September, nucleus disappears (germinal vesicle breakdown, GVBD). Cortical rods elongate, extending radially inward. The GSI was very low, 0.53% ($P < 0.05$) (Figure 4E).

In September, ovaries are distinguished by the presence of atretic (degenerating) oocytes although in this month some animals will still have mature oocytes. It was observed that the ovaries were spent or had a resorbed appearance. Moreover, ovaries are characterized by the presence of empty oocytes when the shrimps are mating.

The oocyte size–frequencies for the posterior abdominal region of the ovary at the different stages of maturation are summarized in Figure 5. Oocytes at stage I (Figure 5A) were all in the size-range 10–100 μm and were mostly primary (previtellogenic) oocytes. At stage IV (Figure 5D), approximately 75% of the total number of oocytes per section had cortical rods with about 50% larger than 150 μm. The size-ranges of vitellogenic (yolky) oocytes with cortical rods overlap but their presence was mutually exclusive, that is, cortical rods were not observed at stage V (Figure 5E). Cortical rods occurred at stage V but were not counted since they were scattered singly and/or were without nuclei.

Percentages of vitellin in all stages are summarized in Table 2. In all *M. kerathurus* captured from wild in December and January the ovaries contained only previtellogenic and early vitellogenic oocytes (most ovaries were found at stage I). Stage III ovaries were predominant in shrimp sampled from February to May. Females samples collected between June and October showed stage IV ovaries with minimum percentages of previtellogenic oocytes (about 8%) and maximum percentages of mature (about 55%) oocytes.

Table 3 shows oocytes diameters of *M. kerathurus*. Changes in size of developing oocytes assist in differentiating between these stages. In stage II, diameter of oocytes ranged from 30.91 ± 1.19 μm to 68.69 ± 1.28 μm. In stage III, oocytes grew larger to 38–102 μm. In stage IV, cortical rods started to appear; oocytes varied from approximately 86–163 μm. In stage V, only late vitellogenic and degenerate oocytes could be seen (about 96–99 μm). The follicle size ranged from 468 to 858 μm (stages II–IV)

DISCUSSION

It has been believed that there is a close inverse relationship between reproduction (ovarian maturation and spawning) and growth (moulting) in penaeid prawns (Browdy, 1992), therefore, the understanding of reproduction is important for the development of a complete culture technology (Primavera, 1985). This study confirms the variability in *Melicertus kerathurus* reproductive performance at different times of the year. The results of the present study indicate that GSI peaked in June and after spawning decreased as pointed out by Medina *et al.* (1996) who observed that GSI and percentage of vitellogenic oocytes showed on upward trend from May to July. Türkmen & Yilmazyerli (2006) also reported that a seasonal reproduction pattern for *M. kerathurus* was observed from April to September in

Table 3. Oocyte diameters of grooved shrimp (*Melicertus kerathurus*) during developmental stages (the sample size was between 145.80 ± 0.50 and 189.8 ± 0.50 mm body length).

	Stage II Mean ± SE	Stage III Mean ± SE	Stage IV Mean ± SE	Stage V Mean ± SE
PO	30.91 ± 1.19	38.15 ± 1.57	0	0
EVO	68.69 ± 1.28	59.50 ± 2.59	0	0
LVO	0	102.32 ± 7.25	0	96.61 ± 9.48
MO	0	0	163.92 ± 2.25	0
DO	0	0	86.33 ± 6.86	99.41 ± 4.41
Follicle	468.31 ± 38.03	618.64 ± 29.19	858.40 ± 36.25	382.33 ± 53.75

PO, previtellogenic oocyte; EVO, early vitellogenic oocyte; LVO, late vitellogenic oocyte; MO, mature oocyte; DO, degenerating oocyte; SE, standard error.

https://doi.org/10.1017/S002531541100107X Published online by Cambridge University Press

Izmir Bay. Similarly, the GSI in *Fenneropenaeus indicus* also increased during vitellogenesis but decreased slightly after spawning to reach levels similar to immature females (Quinitio & Millamena, 1992). GSI values showed in *Pandalus kessleri* the same pattern with a rise during vitellogenesis and a sharp decrease after spawning (Quinitio *et al.*, 1989).

The significant differences in the mean values of gonad weight and GSI, but not in the mean values of body length and body weight, among the first three stages support the concept that energy is channelled to reproductive rather than somatic growth during the adult stage (Tan-Fermin & Pudadera, 1989). The current study shows also that significantly different GSI and gonad weight were accorded to the stages while there was not so much difference for the other criteria. The mean carapace length of stage spent (62.20 mm) was relatively higher, but not significantly different from the average of the other stages. Our results are in agreement with Tan-Fermin & Pudadera (1989) who found that the highest carapace length was in spent stage (73.0 mm).

While histology can precisely characterize oocyte development stages, classification schemes vary from one species to another. Based on light and electron microcopy, 5 stages of oogenesis were identified in *Farfantepenaeus. aztecus* and *Liptopenaeus setiferus* (Duronslet *et al.*, 1975), as demonstrated in a previous study with *M. indicus* (Subramanyam, 1965). Oka & Sirahata (1965) classified ovarian maturity in *M. orientalis* into 8 stages. Yano (1988) further demonstrated 10 stages of oocyte development in *M. japonicus*. Oocyte development was classified into 4 stages in *M. monodon* (Tan-Fermin & Pudadera, 1989) and *M. chinensis* (Matsuyama & Matsuura, 1983).

Medina *et al.* (1996) have stated that the ovarian histology of *M. kerathurus* is typical of that described previously for other penaeids. Based on histological features, five distinct stages have been identified throughout ovarian development: previtellogenic, early vitellogenic, late vitellogenic, mature and spent or degenerating. Similarly, the present results showed that 5 maturation stages were identified.

Cortical rods are supposedly the precursors of the jelly layer around penaeid eggs which have an important role in their activation (Clark *et al.*, 1990; Kruevoisayawan *et al.*, 2007). Subrahmanyam (1965) indicated that yolk started to appear in stage II oocytes, marginal bodies (cortical rods in this paper) were observed at stage IV and stage V, and ovaries were spent in *Penaeus indicus*. Results from the present study indicate that five maturation stages were followed starting from stages II and III, as categorized by Subrahmanyam (1965) these were similar in histological features except for the degree of yolk accumulation. Quinitio *et al.* (1993) have shown that *M. monodon* with stage V ovaries either spawned or resorbed their eggs before moulting, as was noted in *P. indicus*, like in *Melicertus kerathurus* in this study.

Medina *et al.* (1996) reported that in *Melicertus kerathurus* ovarian, as a typically distinctive feature, the cytoplasm of mature oocytes show conspicuous cortical rods at the cell periphery. Our results agree with this where cortical rods were seen in stage IV as indicated by the presence of mature oocytes with CO in their ovaries (Peixoto *et al.*, 2003).

According to Tan-Fermin & Pudadera (1989), investigation of the reproductive cycles of female *M. monodon* showed that almost 40% of the primary oocyte was recorded in vitellogenic stages (I–II), approximately 50% of the total number of oocytes per section had cortical rods in cortical rod stages (III–IV). Peixoto *et al.* (2008) found that PO frequency was 74 $\pm$ 2.6% and CO frequency was 25.9 $\pm$3.5% in the ovary. The present study found that females were reaching stages II, III and IV–V in November, February to May and June to September at a rate of 10%, 22%, and 12%, respectively. Our results agree with those of Medina *et al.* (1996), who also report over 10% (stage II in April), 20% (stage III in June) and 25% (stage IV or stageV in July).

The oocyte size–frequency and oocyte diameter are thought to be good indicators of the stage of ovarian maturity in wild *M. monodon* (Tan-Fermin & Pudadera, 1989). Undeveloped ovaries of *Melicertus semisulcatus* had 29–41 μm, vitellogenic stages had 110–281 μm and cortical rod stages had 356–380 μm oocyte diameters (Browdy *et al.*, 1990). Similar results have been reported for *M. monodon*. Tan-Fermin & Pudadera (1989) gave an average diameter of 250 μm for yolky and 340 μm for cortical rod oocytes. This trend was also reported by Vogt *et al.* (1989)—in the same species that the diameter of vitellogenic and cortical rod oocytes ranged from 150 to 300 μm and from 300 to 400 μm, respectively. It was measured in *Farfantepenaeus paulensis* that PO diameter was 69.7 $\pm$ 2.8 μm; CO diameter was 247.2 $\pm$ 3.5 μm (Peixoto *et al.*, 2008). In the current study, oocytes diameter ranged from 30.91 $\pm$ 1.19 to 38.15 $\pm$ 1.57 μm in previtellogenic stages, 102.32 $\pm$ 7.25 μm in late vitellogenic stages and 163.92 $\pm$ 2.25 μm in cortical rods stages.

In conclusion, in tropical countries, supply of mature broodstock may be possible throughout the year, but gravid females can only be obtained during certain seasons in subtropical Mediterranean countries (Aktaş *et al.*, 2003). Reproductive pattern is a major factor determining the reproductive potential of a species. Therefore, according to the GSI and ovarian development results in this study, the best period of capturing shrimp adults for breeding purposes from Izmir Bay is between April and June. At other times, although full ovary is seen in image, this time is not convenient for breeding. Ovarian histology has not been studied on the grooved shrimp *M. kerathurus* in Turkey until now. The results presented in this paper are additional information to help understand the reproductive biology of *M. kerathurus* important for the culture of shrimp which is captured at the spawning time from Izmir Bay, Turkey.

ACKNOWLEDGEMENTS

The authors of this paper thank Erol Hindioğlu, Selim Köseoğlu and Gülnur Metin for the supply of shrimps and assistance in the field.

REFERENCES

Alpbaz A.G. (1978) A study on larval development of shrimp (*Penaeus japonicus* Bate). *Journal of the Faculty of Science. Ege University* 15, 119–148. [In Turkish.]

Aktaş M., Kumlu M. and Eroldogan O.T. (2003) Off-season maturation and spawning of *Penaeus semisulcatus* by eyestalk ablation and/or temperature–photoperiod regimes. *Aquaculture* 228, 361–370.

Aktaş M., Eroldogan O.T. and Kumlu M. (2004) Combined effects of temperature and salinity on egg hatching rate and incubation time

https://doi.org/10.1017/S002531541100107X Published online by Cambridge University Press

Penaeus semisulcatus (Decapoda: Penaeidae). *Israeli Journal of Aquaculture—Bamidgeh* 56, 124–128.

Arcos F.G., Racotta I.S. and Palacios E. (2005) Ovary development at the onset of gametogenesis is genetically determined and correlated with reproductive traits at maturity in shrimp *Litopenaeus* (*Penaeus*) *vannamei*. *Marine Biology* 148, 339–346.

Badawi H.K. (1975) On maturation and spawning in some penaeid prawns of the Arabian Gulf. *Marine Biology* 32, 1–6.

Browdy C.L., Fainzilber M., Tom M., Loya Y. and Lubzens E. (1990) Vitellin synthesis in relation to oogenesis in *in vitro*-incubated ovaries of *Penaeus semisulcatus* (Crustacea, Decapoda, Penaeidae). *Journal of Experimental Zoology* 255, 205–215.

Browdy C.L. (1992) A review of the reproductive biology of *Penaeus* species: perspectives on controlled shrimp maturation systems for high quality nauplii production. In Wyban J. (ed.) *Proceedings of the Special Session on Shrimp Farming, Orlando, FL, USA*. Baton Rouge, LA: World Aquaculture, pp. 22–51.

Caillouet C.W. Jr (1972) Ovarian maturation induced by eyestalk ablation in pink shrimp, *Penaeus duorarum* Burkenroad. *Proceedings of the World Mariculture Society* 3, 23–26.

Clark Jr W.H. Yudin A.J. Lynn J.W. Griffin F.J. and Pillai M.C. (1990) Jelly layer formation in penaeoidean shrimp eggs. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 178, 295–299.

Crocos P.J. and Kerr J.D. (1983) Maturation and spawning of the banana prawn *Penaeus merguiensis* de Man (Crustacea: Penaeidae) in the Gulf of Carpenteria Australia. *Journal of Experimental Marine Biology and Ecology* 69, 37–59.

Dall W., Hill B.J., Rothlisberg P.C. and Staples D.J. (1990) The biology of the Penaeidae. In Blaxter J.H.S. and Southward A.J. (eds) *Advances in marine biology, Volume 27*. London: Academic Press, pp. 283–314.

Duronslet M.J., Yudin A.I., Wheeler R.S. and Clark W.H. (1975) Light and fine structural studies of natural and artificially induced egg growth of penaeid shrimp. *Proceedings of the World Mariculture Society* 6, 105–122.

Galil B.S. and Kevrekidis K. (2002) Exotic decapods and a stomatopod off Rhodes Island (Greece) and the Eastern Mediterranean Transient. *Crustaceana* 75, 925–930.

Geldiay R. (1969) A report on Natantia (Crustacea–Decapoda) along the coast of Turkey from the Eastern Mediterranean to the vicinity of Izmir. *Scientific Reports of the Faculty of Science, Ege University* 74, 1–17.

Geldiay R. and Koçataş A. (1973) Some biological and ecological characteristics of Natantia (Crustacea) Fauna in Türkiye. In *TUBITAK IV. Science Congress 5–8 November, Ankara*, p. 1–7.

Kelemec J.A. and Smith I.R. (1980) Induced ovarian development and spawning of *Penaeus plebejus* in a recirculating laboratory tank after unilateral eyestalk enucleation. *Aquaculture* 21, 55–62.

Kevrekidis K. and Thessalou-Legaki M. (2006) Catch rates, size structure and sex ratio of *Melicertus kerathurus* (Decapoda: Penaeidae) from an Aegean Sea trawl fishery. *Fisheries Research* 80, 270–279.

King J.E. (1948) A study of the reproductive organs of the common marine shrimp *Penaeus setiferus* (Linnaeus). *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 94, 244–262.

Kruevaisayawan H., Vanichviriyakit R., Weerachatyanukul W., Magerd S., Witnyachumnarnkul B. and Sabhon P. (2007) Biochemical characterization and physiological role of cortical rods in black tiger shrimp *Penaeus monodon*. *Aquaculture* 270, 289–298.

Köse A., Hindioğlu A., Özden O. and Alpbaz A.G. (1999) An investigation on larval growth and survival of shrimp, *Penaeus kerathurus*. *Journal of the Faculty of Science Ege University* 16, 131–140.

Kumlu M., Eroldogan O.T. and Saglamtimur B. (2001) The effects of salinity and added substrates on growth and survival of *Metapenaeus monoceros* (Decapoda: Penaeidae) post-larvae. *Aquaculture* 196, 177–188.

Matsuyama M. and Matsuura S. (1983) On the maturation of the korai prawn, *Penaeus chinensis* (Osbeck), in the Yellow Sea. *Science Bulletin Agriculture, Kyushu University* 38, 71–79.

Medina A., Vila Y., Mourente G. and Rodriguez A. (1996) A comparative study of the ovarian development in wild and pond-reared shrimp, *Melicertus kerathurus* (Forskal, 1775). *Aquaculture* 148, 63–75.

Menasveta P., Piyatiratitivorakul S., Rungsurpa S., Moree N. and Fast A.W. (1993) Gonadal maturation and reproductive performance of giant prawn (*Penaeus monodon* Fabricius) from the Andaman Sea and pond-reared sources in Thailand. *Aquaculture* 116, 191–198.

Oka M. and Shirata S. (1965) Studies on *Penaeus orientalis* Kishinouye. 2. Morphological classification of the ovarian stages and maturity of the ovary. *Bulletin Faculty of Fisheries, Nagasaki University* 18, 30–40.

Özden O. (1989) *An investigation on shrimp culture* (P. kerathurus, *Forskal 1775*.) PhD thesis. E.U. Institute of Science, Fisheries Department.

Peixoto S., Cavalli R.O., D'Incao F., Milach A. and Wasielesky W. (2003) Ovarian maturation of wild *Farfantepenaeus paulensis* in relation to histological and visual changes. *Aquaculture Research* 34, 1255–1260.

Peixoto S., Wasielesky W., Martino R.C., Milach A., Soares R. and Cavalli R.O. (2008) Comparison of reproductive output, offspring quality, ovarian histology and fatty acid composition between similarly-sized wild and domesticated *Farfantepenaeus paulensis*. *Aquaculture* 285, 201–206.

Preston N.P., Brennan D.C. and Crocos P.J. (1999) Comparative costs of postlarval production from wild or domesticated Kuruma shrimp *Penaeus japonicus* (Bate), broodstock. *Aquaculture Research* 30, 191–197.

Primavera J.H. (1985) A review of maturation and reproduction in closed thelycum penaeids. In Taki Y., Primavera J.H. and Llobrera J.A. (eds) *Proceedings of the First International Conference on the Culture of Penaeid Prawns/Shrimps; 1984 December 4–7; Iloilo City, Philippines*, pp. 47–64.

Quinitio E.T., Hara A., Yamauchi K., Mızushima T. and Fuji A. (1989) Identification and characterization of vitellin in a hermaphrodite shrimp, *Pandalus kessleri*. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry* 94, 445–451.

Quinitio E.T. and Millamena M. (1992) Ovarian changes and female-specific protein levels during sexual maturation of the white shrimp *Penaeus indicus*. *Israeli Journal of Aquaculture—Bamidgeh* 44, 7–12.

Quinitio E.T., Caballero R.M. and Gustilo L. (1993) Ovarian development in relation to changes in the external genitalia in captive *Penaeus monodon*. *Aquaculture* 114, 71–81.

Subrahmanyam C.B. (1965) On the reproductive cycle of *Penaeus indicus* (M. Edwards). *Journal of the Marine Biological Association of India* 7, 284–290.

Tan-Fermin J.D. and Pudadera R.A. (1989) Ovarian maturation stages of the wild giant tig prawn, *Penaeus monodon* Fabricius. *Aquaculture* 77, 229–242.

Tan Fermin J.D. (1991) Effects of unilateral eyestalk ablation on ovarian histology and oocyte size frequency of wild and pond-reared *Penaeus monodon* (Fabricius) broodstock. *Aquaculture* 93, 77–86.

Türkmen G. and Yilmazyerli H. (2006) Some biological aspects of *Melicertus kerathurus* (Forskal, 1775) (Decapoda, Penaeidae) inhabiting Izmir Bay (Aegean Sea), Turkey. *Crustaceana* 79, 583–591.

Vogt G., Quinitio E.T. and Pascual F.P. (1989) Interaction of the midgut gland and the ovary in vitellogenesis and consequences for the

breeding success: a comparison of unablated and ablated spawners of *Penaeus monodon*. In De Pauw N., Jaspers E., Ackefors H. and Wilkins N. (eds) *Aquaculture—biotechnology in progress*. Bredene, Belgium: European Aquaculture Society, pp. 581–592.

and

Yano I. (1988) Oocyte development in the Kuruma prawn *Penaeus japonicus*. *Marine Biology* 99, 547–553.

Correspondence should be addressed to:
A. Kücükdermenci
Ege University
Faculty of Fisheries
Department of Aquaculture
35100 Bornova, Izmir, Turkey
email: aysun.kose@ege.edu.tr

https://doi.org/10.1017/S002531541100107X Published online by Cambridge University Press