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ORIGINAL ARTICLE

Reproductive biology of the prawn *Melicertus kerathurus* (Decapoda: Penaeidae) in Thermaikos Gulf (N. Aegean Sea)

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Abstract The reproductive biology including insemination frequency, ovarian maturation, gonadosomatic index (GSI), size at first maturity, and fecundity of *Melicertus kerathurus* were investigated using monthly samples from Thermaikos Gulf. Insemination was recorded by the presence of a spermatophore in the thelycum, and ovarian development was based on macroscopic ovarian staging (ST1–ST5). Inseminated females were found throughout the year with high percentages recorded from April to July. Although all ovarian stages were represented in mated females, insemination increased with size and ovarian maturation. High percentages of vitellogenic or mature ovarian stages were observed from May to July, while immature and developing ovaries were predominant mainly in winter. Spawned ovaries occurred from May to October. Carapace length at first maturity based on the presence of a spermatophore (CL_{50sp}) was estimated at 39.20 mm, while that based on the presence of vitellogenic and mature ovaries (CL_{50ov}) at 40.70 mm. The seasonal peak in the proportion of mature females (ST4) varied with size. Inseminated females at ST4 and GSI peaked in June–July. GSI varied in relation to insemination status and ovarian stage. In large females (>50 mm CL), the decline in mature ovaries and GSI increment with size indicates a relative reduction in the reproductive output. The number of oocytes ranged from 62,742 to 602,947 (mean ± SD: 268,000 ± 113,000). As the prawns are targeted during the spawning season, mainly by the artisanal fishery, and female size at first maturity is selected by artisanal net size, managerial measures toward artisanal fishery should be implemented.

Keywords *Melicertus kerathurus* · Penaeid prawn · Reproductive biology · Thermaikos Gulf · Aegean Sea

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Introduction

Penaeids exhibit a rather complex life history, with reproductive cycles that are affected by seasonal rainfall, temperature regime, and depth (Dall et al. 1990; Crocos et al. 2001). In contrast to tropical/subtropical penaeids, which mainly exhibit bimodal seasonal spawning patterns, penaeid species that inhabit temperate latitudinal zones spawning becomes unimodal, with only one well-defined recruitment period (e.g. Dall et al. 1990; Staples 1991; Crocos and van der Velde 1995). The interannual, seasonal, spatial (latitudinal), and size variations in spawning patterns of several penaeids have been documented (e.g., Crocos and van der Velde 1995; Courtney and Masel 1997; Minagawa et al. 2000; Aragón-Noriega and Alcántara-Razo 2005; Montgomery et al. 2007).

The prawn *Melicertus kerathurus* is an east Atlantic-Mediterranean species of major commercial significance. In 2009, its world fishery production approached ≈5,500 mt (FAO 2011). Intense exploitation rates in parts of the Mediterranean and eastern Atlantic, along with the replacement of the species by Eritrean penaeid prawns in the eastern

Mediterranean, have resulted in very low landings in most countries (e.g. Rodrígeuz 1977; Scordella and Lumare 2001; Kevrekidis and Galil 2003; Can et al. 2004; Galil 2007; Kevrekidis 2009). Thus, species-specific initiatives toward sustainable management of this resource should be implemented (Kevrekidis and Thessalou-Legaki 2011).

Information on the reproductive aspects of the species is available from the gulf of Cádiz in the eastern Atlantic and several Mediterranean localities (Heldt 1938; Ben Mustafa 1967; Abdel Razek 1985; Rodríguez 1985; Ben Meriem 1993; Türkmen and Yilmazyerli 2006; Türkmen et al. 2007; Lumare et al. 2011). In Greece, information is only available from Amvrakikos Gulf (Ionian Sea) (Klaoudatos et al. 1992; Conides et al. 2008).

In Thermaikos Gulf, the prawn is a target species for both the artisanal and trawl fishery. Otter-trawling is permitted for an 8-month period from 1 October to 31 May, at grounds at a 3 nm minimum distance from the shore (in the period under study minimum distance was 2 nm). In addition, a special regulation prohibits trawling in the inner part of Thermaikos. Thus, the main fishing ground is located in the northern part of the outer Gulf, mainly at a depth of 35–70 m. Otter-trawling mainly targets recruits and 1^+ age class. The artisanal fishery is conducted along the coasts of both the inner and outer gulf, usually for a 5-month period (May–September), during which there is a 2-month fishing ban (10 July to 10 September). The artisanal fishery targets at 1^+ and 2^+ age classes, mainly at a depth of 10–25 m (Fig. 1).

Information on otter-trawling fishery, growth, and population dynamics of the prawn stock in Thermaikos Gulf has recently been provided by Kevrekidis and Thessalou-Legaki (2006; 2011). In the present paper, intra- and interannual variations in the reproductive biology of *M. kerathurus* stock including insemination frequency, ovarian maturation, gonadosomatic index (GSI), size at first maturity, and fecundity are investigated.

Materials methods

Sampling

During two open fishing periods (October to May 2000–2001 and 2001–2002), a monthly sampling schedule was followed on board commercial otter trawlers (280–500 hp, 20.0–30.5 m, 40 mm cod-end stretch mesh size) in the fishing ground of Thermaikos Gulf. During the closed seasons (June and September 2001; July, August and September 2002), experimental hauls were conducted using commercial trawlers (265–425 hp, 23.5–29.0 m, mesh size as above) in both the outer (5–47 m depth) and the inner gulf (5–28 m depth), including areas and depths where commercial trawling is not permitted. In total, data from 94 hauls were obtained. Samples were also collected from the artisanal fishery (trammel net: 2,500 m length; 1.5 m height; 20 mm mesh size) in May and June 2002 (9–22 m depth). In May 2001 and July 2002, additional samples from the artisanal fishery were collected only for the identification of ovarian stages ($N = 59$, 18–20 m depth). To estimate fecundity, mature females (ST4) were selected from samples taken from the artisanal fishery in June and July 2005

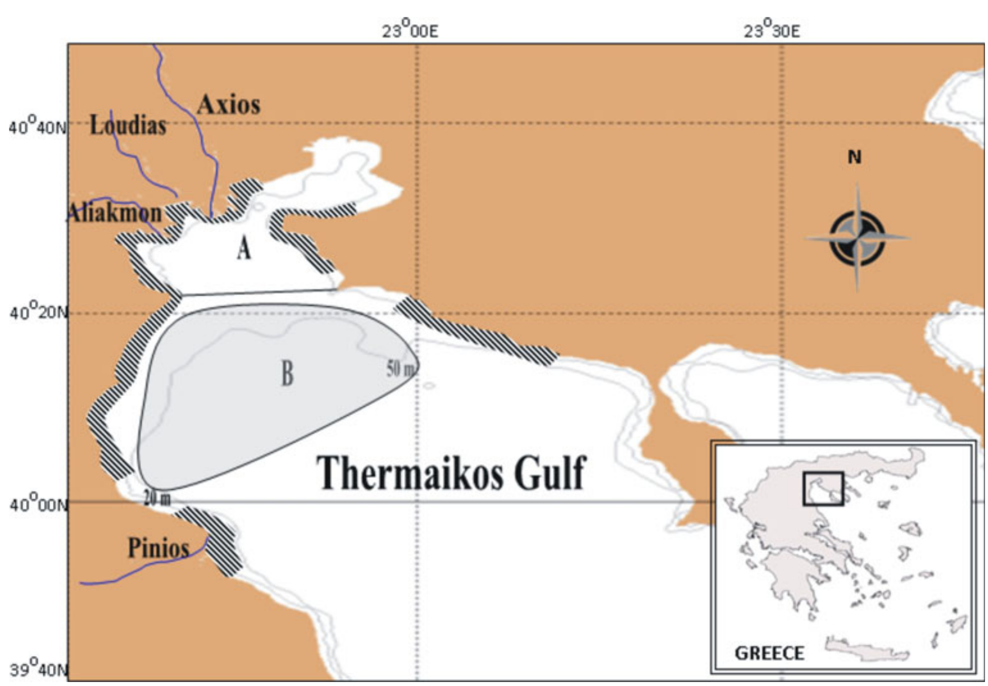

Fig. 1 Map of Thermaikos Gulf (North Aegean Sea). Inner (**a**) and outer part (**b**) are separated by a *line*, which also represents the northern allowable trawling limit. The main trawling ground of *Melicertus kerathurus* is marked in *light gray* and the areas where the artisanal fishery is mainly conducted are denoted by stripes

($N = 44$, 14–17 m depth). Each sample was placed in a plastic bag, frozen, and processed in the laboratory.

Prawn measurement

For each female, the carapace length (CL) was measured from the eye orbit to the rear dorsal end of the carapace with a digital vernier calliper with an accuracy of 0.01 mm. The body wet weight (BW) was measured to the nearest 0.01 g (electronic balance KERN 440–33 N) and that of dissected ovaries (OWW) at 0.0001 g (electronic analytical balance SARTORIUS 1801). For each female, the presence of a spermatophore in the thelycum was recorded. The ovarian development of 1,027 females was divided into five stages: immature (ST1), developing (ST2), vitellogenic (ST3), mature (ST4), and spent (ST5), based on the macroscopic ovarian staging of Rodríguez (1985). Gonadosomatic index (GSI) was calculated as GSI = (OWW/BW) × 100. To estimate fecundity, an ovarian subsample from the 1st abdominal segment was removed and weighed to the nearest 0.0001 g (electronic analytical balance SARTORIUS 1801). The method followed for the preservation of the ovarian subsample was that of Martosubroto (1974). Oocytes of the tissue sample were counted and the total oocyte number in the ovaries was calculated. Fecundity was correlated with CL, total length (TL, from the tip of the rostrum to the end of telson), BW, OWW, and 1st abdominal segment width (AW).

Data analysis

A Kolmogorov–Smirnov two-sample test was used to detect any difference between inseminated and non-inseminated female size frequency distributions and a Mann–Whitney test was used to compare medians. Size at first maturity (CL_{50}) was determined on pooled data from the two periods, based on the presence of spermatophores (CL_{50sp}) and of advanced ovary stages ST3 and ST4 (CL_{50ov}). CL_{50} (mm) estimated by a logistic equation as described by King (1995): $p = 1/1 + \exp(a + b \times \mathrm{CL})$.

For examination of temporal differentiation in insemination, ovarian maturation, OWW and GSI with size, females were separated into three CL groups: small (<30 mm CL), medium (30–40 mm CL) and large (>40 mm CL), using pooled data from the two periods. The relationship between monthly insemination and ovarian stages from the pooled data of the two periods was tested with χ^2. A two-way ANOVA was used to detect significant differences in ln-transformed data of OWW and GSI, using ovarian stage and female size (CL) as factors, followed by a Bonferroni pairwise test. The relationship between OWW and BW by ovarian stage was described by the equation $y = ax^b$, on ln-transformed data. ANCOVA was used to test for differences in regression lines among ovarian stages. A Mann–Whitney test was used to detect any significant difference in GSI between inseminated and non-inseminated females. The model with the highest correlation coefficient between ln mean GSI and CL was applied. Fecundity-female size (CL, TL, AW) and fecundity-weight (BW, OWW) relationships were assessed using the equation $y = ax^b$ on ln-transformed data.

Results

Insemination and ovary maturation in relation to female size

In total, of the 7,206 females examined, 51.09 % were found to be inseminated (Fig. 2a). Their size ranged between 25.31 and 57.70 mm CL, with a mean (±sd) of 41.33 ± 4.28 mm CL. Non-inseminated females showed a wider size range, but dominated the smaller size classes with a mean of 32.20 ± 5.42 mm CL. Medians and size frequency distributions differed significantly between these two groups (Mann–Whitney test: $U = 1212761$, $p < 0{,}001$; two-sample Kolmogorov–Smirnov test: $z = 29.960$, $p < 0.001$). The percentage of inseminated females increased in parallel with size (CL). The plot of the percentage of inseminated females in each size class resulted in a sigmoidal relationship: a sharp increase in insemination is recorded from 30 to 40 mm CL with, however, the highest frequency (100 %) observed only in large classes (>52 mm). Size at first maturity, determined by spermatophore presence (CL_{50sp}), was found to be 39.20 mm CL (Fig. 3a).

Size frequency distribution of ovarian stages is shown in Fig. 2b. Medium- and large-sized prawns presented all ovarian stages, whereas in small prawns immature ovaries dominated. On the contrary, in larger prawns, ST1 decreased by increasing size until its complete disappearance at >46 mm CL. Ovaries at ST2 appeared at 26 mm CL with higher percentages from 42 to 44 mm CL and >54 mm CL. Ovaries at ST3 appeared at 30 mm CL, whereas ST4 at 34 mm CL. The appearance of advanced stages (ST3 and ST4) increased gradually with size, up to 54 mm CL and declined in size classes larger than this. Females with mature ovaries ranged between 32.24 mm (May 2001) and 55.46 mm (June 2001) CL, while spawned females between 32.26 and 49.70 mm CL.

Size at first maturity determined from pooled vitellogenic (ST3) and mature (ST4) ovarian stages (CL_{50ov}) was estimated at 40.70 mm CL (Fig. 3b). Coefficients of the respective logistic models for CL_{50sp} and CL_{50ov} are presented in Table 1.

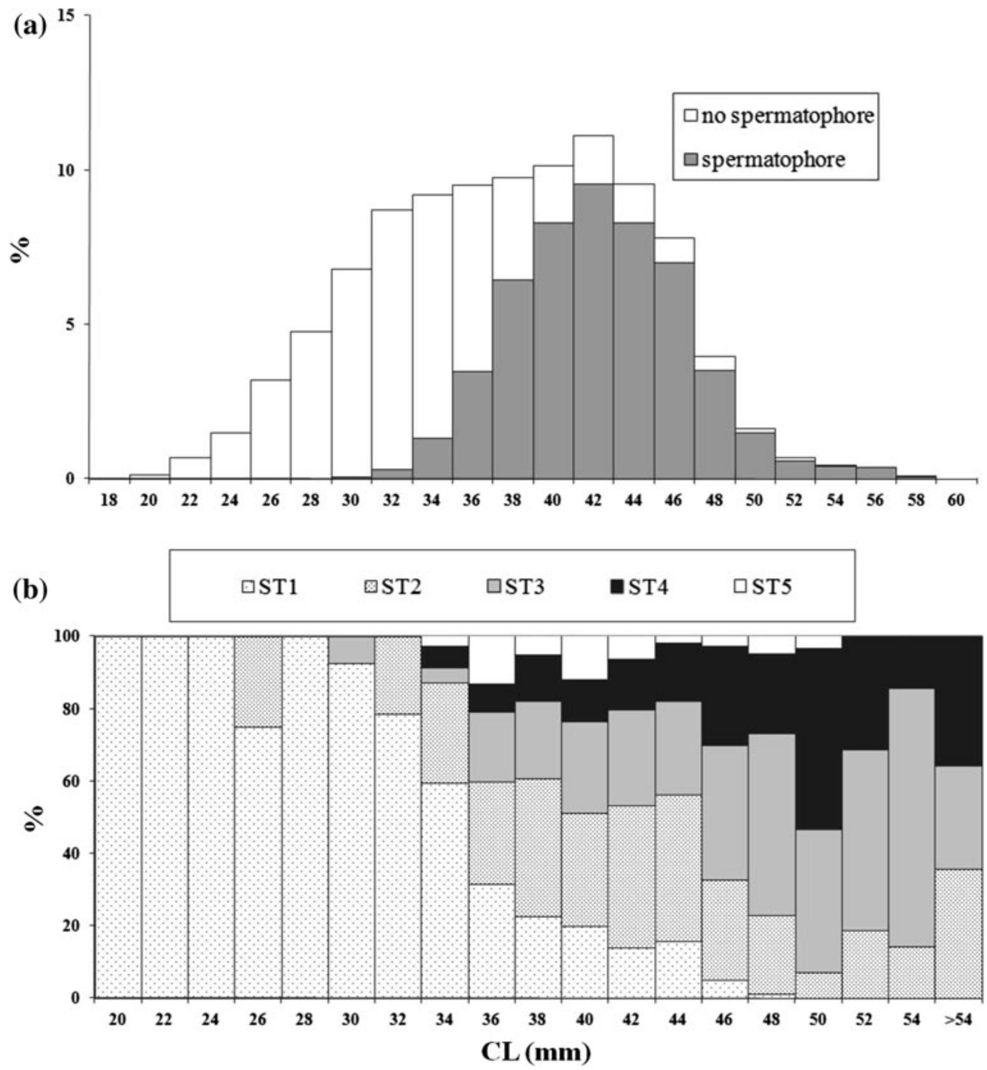

Fig. 2 Presence of spermatophore (**a**) and of ovarian stages (**b**) in relation to carapace length (*CL*) of female *Melicertus kerathurus* in Thermaikos Gulf for the study period 2000–2002. *ST1*: immature; *ST2*: developing; *ST3*: vitellogenic; *ST4*: mature; *ST5*: spent

Temporal variation of insemination and ovarian maturation

Monthly frequency of inseminated females is presented in Fig. 4a. The percentage of inseminated females was high throughout the study period, with the exception of August 2002 (4 %), September 2001 (20 %) and 2002 (35 %). The highest percentages of inseminated females (>80 %) were recorded from April to July, with peaks in April 2001 (93 %) and June 2002 (96 %). Insemination at a population level differs interannually: it was consistently more pronounced throughout the first period (>50 %), while it fluctuated largely during the second one.

Monthly frequency of ovarian stages is presented in Fig. 4b. Immature and developing stages (ST1 and ST2) were predominant in winter and early spring, with a peak in February (63 %); ST1 decreased in spring to total disappearance in May and most of the summer; ST2 was consistently present throughout the two periods (except June 2001), with the highest percentage (60 %) recorded in December 2000. High percentages (50–92 %) of advanced stages (ST3 plus ST4) appeared at the end of spring and in summer (mainly from April to July for both periods); ST3 ranged from 4 to 58 % recorded in January and April 2002, respectively; ST4 ranged from 2 to 59 % with peaks in June 2001 (57 %) and July 2002 (59 %). In August, advanced ovaries decreased significantly (17 %), whereas in September and October, a new increase was recorded (>40 %). Spent ovaries (ST5) were most significant in autumn; they were observed from May to October (3–48 %), with the highest frequency recorded in September 2001.

Inseminated females presented all ovarian stages**.** Monthly frequency of inseminated females per ovarian stage showed that the highest percentage of inseminated females at ST4 appeared in June 2001 and July 2002, at 64 and 61 %, respectively. There was a significant positive correlation between percent inseminated and ovarian maturation: the highest proportion of insemination was found in

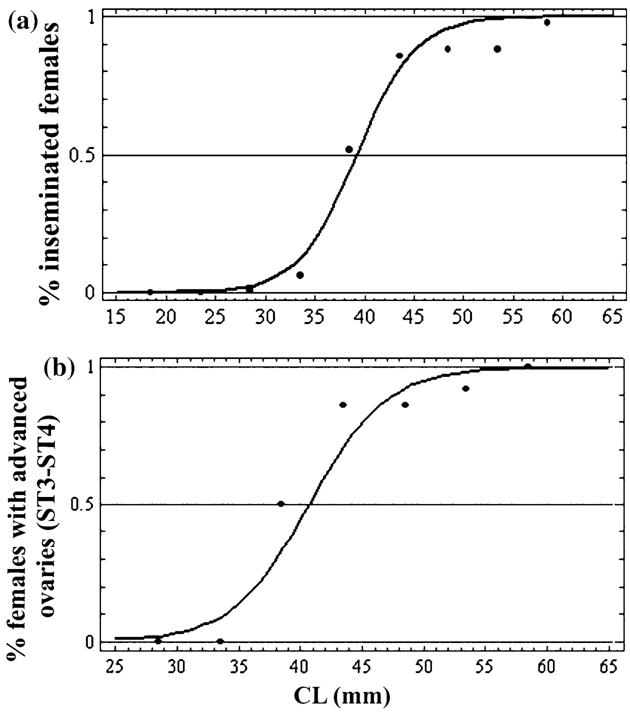

Fig. 3 Logistic curve for the estimation of length at first maturity based on the occurrence of insemination (**a**) and on the presence of advanced ovarian stages (vitellogenic and/or mature) (**b**) of female *Melicertus kerathurus* in Thermaikos Gulf for the study period 2000–2002

Table 1 Coefficients (a, b) of equations of the logistic model for the estimation of size at first maturity (CL_{50}) (mm) based on inseminated females, and females at ST3 and ST4 ovarian stages of *Melicertus kerathurus* in Thermaikos Gulf for the study period 2000–2002

	CL_{50}	a	b	R^2	p
Insemination	39.20	−13.314	0.339	92.50	<0.001
Ovarian maturation	40.70	−13.034	0.320	84.16	<0.001

females with ovaries at ST4 and the lowest at ST1 [χ^2 (4, 777) = 223.74, $p < 0.001$].

Monthly frequency of insemination and ovarian maturation in relation to size

Monthly frequency of inseminated females in relation to size for pooled data from the two periods is presented in Fig. 5a. In general, small individuals with a spermatophore were extremely rare (0.2 %), while large females presented a higher insemination rate (61 %) than medium-sized ones (39 %). Large-sized females exhibited high percentages (>60 %) of insemination throughout the study, especially from December to July, whereas medium ones only from April to June (in July no medium-sized females were sampled).

Monthly frequency of mature ovaries (ST4) in relation to size is shown in Fig. 5b. Throughout the study period, small-sized prawns did not reach maturity. In total, only 20 % of medium-sized females exhibited mature ovaries and were only sampled from May to October, in relatively low percentages (<40 %). Large females presented ST4 in all seasons, with the exception of the period November–December. Relatively high percentages were recorded in June–July (>50 %). In comparison with medium-sized females, large ones seemed to mature earlier and to present higher frequency of ST4 from June to September. However, comparable figures were observed for medium and large females in the time limits of reproductive activity (May and October).

Ovary wet weight and GSI

Two-way ANOVA showed that ovary wet weight (OWW) varied significantly with ovarian stage ($F = 272.026$, $df = 4$, $p < 0.001$), female size ($F = 118.138$, $df = 2$, $p < 0.001$), and their interaction ($F = 6.885$, $df = 4$, $p < 0.001$). Mean values of OWW per ovarian stage and size group and Bonferroni pairwise comparisons are shown in Fig. 6a. At ST1, OWW increased with female size. Moreover, between the two larger size groups, a significant difference was apparent in favor of large females at all ovarian stages, except ST3. In relation to ovarian stages, three groups were distinct in medium-sized (ST1, ST2 plus ST5, and ST3 plus ST4) and four (ST1, ST2 plus ST5, ST3, ST4) in larger prawns.

Regarding GSI, two-way ANOVA showed a significant effect of ovarian stage ($F = 228.447$, $df = 4$, $p < 0.001$), size group ($F = 7.072$, $df = 2$, $p = 0.001$), and their interaction ($F = 8.506$, $df = 4$, $p < 0.001$). Mean GSI values per ovarian stage and size group, together with the results of Bonferroni pairwise comparisons are shown in Fig. 6b. At ST1, small-prawn GSI did not differ significantly from that of medium and only slightly from that of the large-size group ($p = 0.056$). Similar to the OWW results, GSI at ST2 and ST5 was greater in large females than medium ones, whereas at ST3, it was greater in medium ones. Nevertheless, the two size groups showed equal GSI values at ST4. Regarding differences by ovarian stage, the same groups, as in OWW, of mean GSI were found in medium and large females.

Body weight-ovary wet weight regressions

The relationship between OWW and body weight (BW) for each ovarian stage and corresponding regression lines are shown in Fig. 7a–e. The relationship for all stages together was estimated as: $\ln OWW = -7.525 + 2.043 \ln BW$ ($R^2 = 0.491$, $N = 593$). All regressions were found to be significant ($p < 0.001$). ANCOVA has shown that there is a significant difference in BW-OWW regressions per ovarian stage (Table 2). Three groups of regression lines exist:

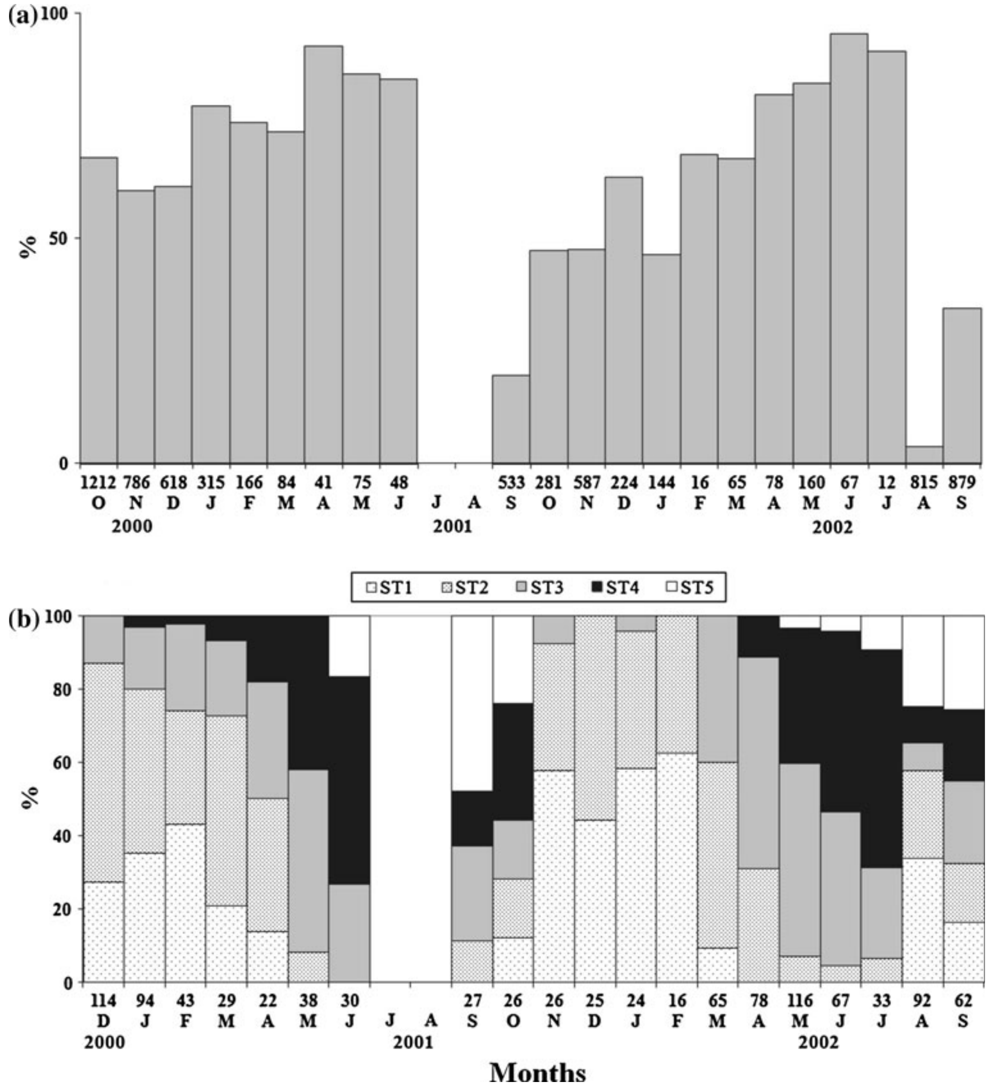

Fig. 4 Monthly frequency of insemination (**a**) and of ovarian stages (**b**) of female *Melicertus kerathurus* in Thermaikos Gulf for the study period 2000–2002. *ST1*: immature; *ST2*: developing; *ST3*: vitellogenic; *ST4*: mature; *ST5*: spent (Numbers along axis × represent total number of females sampled per month)

ST1–ST2, ST3–ST4, placed higher than the first group, and ST5 which differentiates from both other groups and is characterized by a higher slope.

Monthly variation of GSI

GSI exhibited a pronounced seasonal variation: it remained low in winter, with a minimum around 1, recorded in February for both periods. The trend increased in spring and peaked in summer, with highest values (4.41–6.78) from May to July, followed by a sharp decrease in August–September and by an increase in October (3.36 ± 2.00) (Fig 8).

Mean GSI (± sd) for inseminated and non-inseminated females was estimated at 2.88 (±2.25) and 1.58 (±1.41), respectively, a statistically significant difference (Mann–Whitney test, $U = 16756.5$, $p < 0.001$, $N = 593$). The relationship between lnGSI-CL is best shown by a reciprocal-x equation: $\ln\mathrm{GSI} = 3.2118 - (97.153/\mathrm{CL})$ $(R^2 = 0.840)$ (Fig. 9). GSI generally increased with increasing size, in the range 30–50 mm CL. However, in larger prawns (CL > 50 mm), GSI seems to reach a 'plateau' and further increase in size is followed by a lower increase in GSI.

Fecundity

Fecundity (F) in mature females (ST4) increased with size. In the present study, the number of oocytes ranged from 62,742 (37.31 mm CL, 135 mm TL) to 602,947 (47.78 mm CL, 182 mm TL). The mean (± sd) number of oocytes for the size range studied (35–49 mm CL) was 267,844 (± 112,703).

Coefficients (lna, *b*) of regressions of fecundity against CL, TL, AW, BW, and OWW are presented in Table 3. The relationship F–OWW showed the highest correlation, while there was a higher correlation in F–BW and F–TL than in F–CL and F–AW regressions.

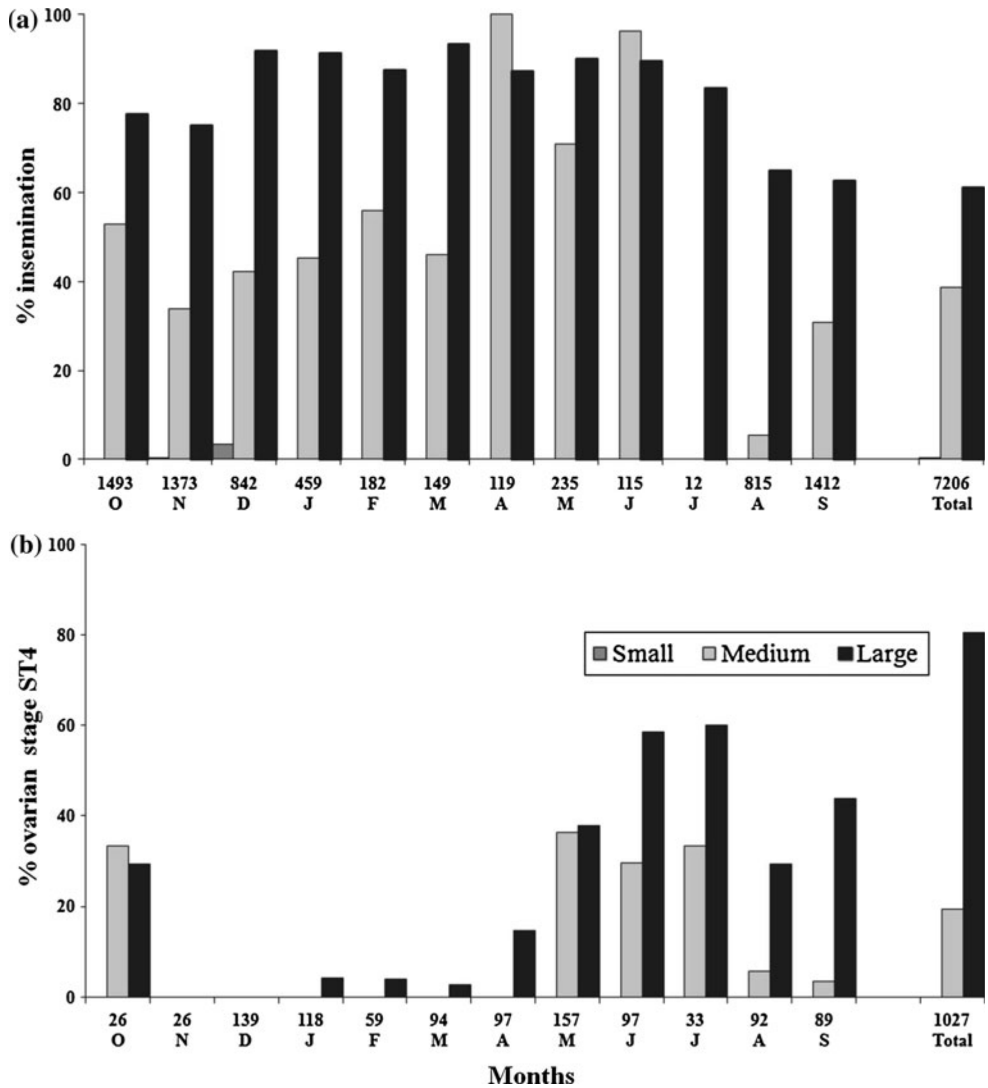

Fig. 5 Monthly frequency of insemination (**a**) and of mature ovaries (ST4) (**b**) of female *Melicertus kerathurus* per size group (small: <30 mm CL; medium: 30–40 mm CL, large: >40 mm CL) in Thermaikos Gulf for the study period 2000–2002 (Numbers along axis × represent total number of females from pooled data)

Discussion

Spawning period

Melicertus kerathurus exhibits a unimodal spawning pattern in Thermaikos Gulf. Monthly variation of spermatophore insemination, ovarian maturation, and GSI has shown that the spawning period of *M. kerathurus* extends from spring (late April–early May) to autumn (mid-October) with a peak in summer (June–July). Respective studies from other areas concur on a single spawning period for the species, with, however, variation in extent and number of peaks, even in the same locality (see Table 5). In temperate and subtropical areas, temperature and/or food supply variations may be responsible for the time limits of reproduction. Interannual and monthly variations in reproductive activity of many other penaeid species have been reported (e.g. Courtney and Masel 1997; Crocos and van der Velde 1995; Minagawa et al. 2000; Montgomery et al. 2007; Hossain and Ohtomi 2008).

Spermatophore insemination

Non-inseminated females presented a wider size range as they included both young individuals recruited into the fishery from early autumn to winter (Kevrekidis and Thessalou-Legaki 2006, 2011), as well as adult females which had spawned from spring to autumn (October). Thus, low percentages of insemination (<40 %) were recorded in August and September. In the Adriatic, a very low percentage (2.4 %) of inseminated females was also recorded in September, followed by a gradual increase in winter (Lumare et al. 2011). At a population level, insemination status in Thermaikos differed between the two fishing periods: throughout the first period, it was higher than 50 %, whereas in the second, it presented a gradual increase from

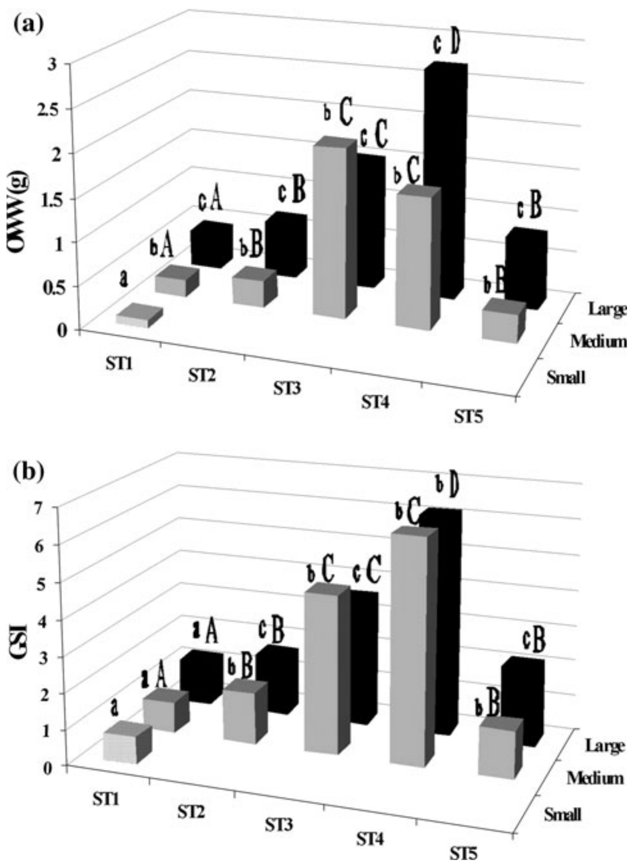

Fig. 6 Mean ovary wet weight (OWW) (**a**) and GSI (**b**) per size group and ovarian stage of female *Melicertus kerathurus* in Thermaikos Gulf. Bonferroni pair wise comparisons ($p < 0.05$) among size groups with *lower case letters*, among ovarian stages with *capital letters*

autumn to summer, with a peak in June. This may be due to the significant difference in size frequency distribution, with significantly smaller-sized individuals sampled in the second compared with the first period (Kevrekidis and Thessalou-Legaki 2006). Klaoudatos et al. (1992) and Ben Meriem (1999) reported that inseminated females are observed throughout the year.

In Thermaikos, high percentages (>80 %) of inseminated females were recorded for 4 months (April–July) in both periods. Similar high percentages (60–100 %) of inseminated females appeared for shorter or longer periods in other areas: in Adriatic for 2 months (June–July) (Lumare et al. 2011), in Cádiz for 3–4 months (June–July–September) (Rodríguez 1985), and in Cabès for 5 months (May–September) (Ben Meriem 1993). In contrast, in Amvrakikos Gulf, maximum insemination frequency seems to be significantly lower (56 % in June) (Klaoudatos et al. 1992) than in Thermaikos. High percentages of spermatophore insemination are recorded throughout the year for other closed thelycum species: *Melicertus longistylus, Melicertus latisulcatus* (Courtney and Dredge 1988), *Penaeus esculentus* (Crocos 1987b), *Marsupenaeus japonicus* (Minagawa et al. 2000).

Inseminated female *M. kerathurus* presented ovaries of various developmental stages, as copulation is not directly related to maturation in closed thelycum species, e.g., *Farfantepenaeus duorarum* (Kennedy and Barber 1981) and *M. japonicus* (Minagawa et al. 2000). However, according to our results, and the results for other species, e.g., *Penaeus semisulcatus* (Shlagman et al. 1986) and *Metapenaeus dalli* (Potter et al. 1989), insemination incidence is positively related to ovarian maturity.

Spermatophore insemination was also positively related to size, as inseminated females were larger than non-inseminated females. This is also shown by the monthly presence of inseminated females per size group, indicating higher participation of larger prawns in mating, but also by the proportion of inseminated females plotted against size, which formed a sigmoidal curve, with females >40 mm CL being inseminated at >90 %. It is known that in closed thelycum species, the plot of the percentage insemination in each size class results in a more or less sigmoidal relationship, e.g., *P. esculentus, P. semisulcatus* (Crocos 1987a, b), *M. longistylus, M. latisulcatus* (Courtney and Dredge 1988), *F. merguiensis* (Crocos and Kerr 1983). However, contrasting results are reported even for the same species, as sigmoidal curve is not presented in *P. esculentus* by Courtney and Masel (1997). Moreover, although insemination increases with size, a typical sigmoidal curve is not shown in *M. plebejus* (Courtney et al. 1995) and *M. japonicus* (Minagawa et al. 2000), since in these species, the frequency of insemination decreases in females with CL > 55 mm and body length > 179 mm, respectively. According to the above authors, this may be attributed to a decline in the incidence of mating in large (old) females and hence a decline in their capacity to produce fertilized eggs.

Ovarian stages

According to Minagawa et al. (2000), the ripe stage ovary is the most useful and accurate index to examine reproductive dynamics such as season, spawning ground, and reproductive cycle of a species. Courtney et al. (1995) proposed that the simplest and most logical alternative to using an index in reproductive studies would be to use a measure of mean ovary weight for specific size classes of females. In Thermaikos, high percentages of advanced (vitellogenic/mature) ovaries (83–91 %) were recorded from May to July, in accordance with the results from Amvrakikos Gulf (June, 85 % in Klaoudatos et al. 1992, or May, 80 % in Conides et al. 2008), the Adriatic (June, 90 %) (Lumare et al. 2011), Smyrni Bay (Türkmen and Yilmazyerli 2006) and Gulluk Bay (July, 80 %) (Türkmen et al. 2007). In a recent study from Amvrakikos, mature females comprised 59–73 % of the female population in the period May–August, with a

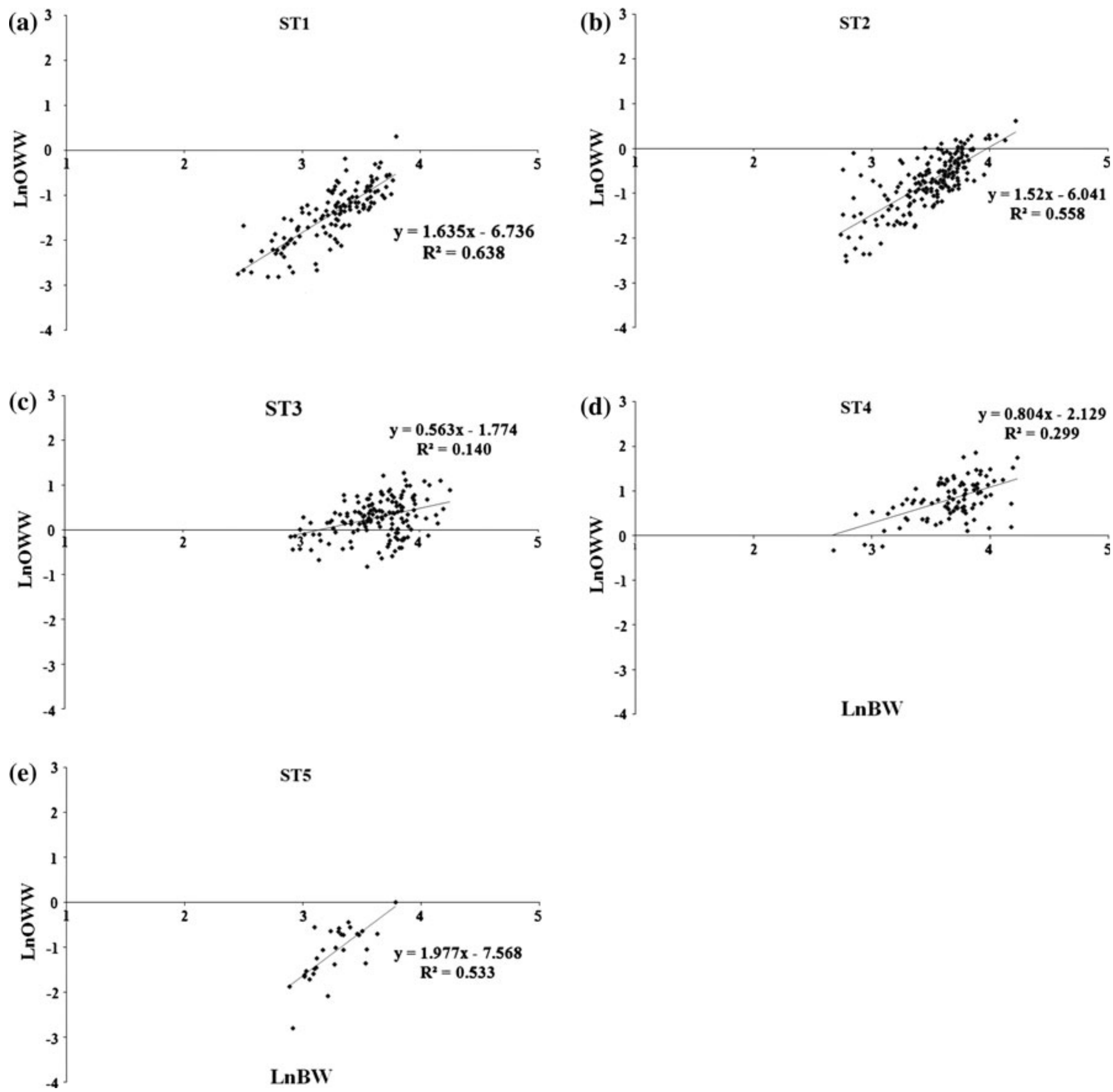

Fig. 7 Regression lines of the relationship ln ovary wet weight (*OWW*)—ln body weight (*BW*) of female *Melicertus kerathurus* by ovarian stage in Thermaikos Gulf

peak in August (Conides et al. 2008). In Thermaikos, the slight upward trend of advanced ovaries observed in autumn (October 2001: 48 %) is not recorded in Amvrakikos and in Smyrni, where low percentages are exhibited in the same period. In Thermaikos, high percentages (especially of vitellogenic ovaries) were observed earlier (April 2002: 70 %), compared with Smyrni (Türkmen and Yilmazyerli 2006) and Gulluk (Türkmen et al. 2007). In the present study, spent ovaries were found from May to October, with the highest frequency recorded in autumn (September 2001: 49 %), indicating that the bulk of potentially capable reproductive females spawned in the previous summer period.

It is known that closed thelycum penaeids can bear spermatophores for a relatively long time until ovarian maturation and subsequent spawning takes place in the specific intermolt period (Dall et al. 1990). Therefore, high spermatophore insemination recorded in March (especially in large prawns) and April, along with the prominent occurrence of advanced stages of ovarian maturation in the same period and the presence of females with spent ovaries observed in May for the first time, indicates that the beginning of spawning of *M. kerathurus* in Thermaikos should be placed in late April/early May.

In the easternmost Mediterranean, mature females of *P. semisulcatus* are present in all seasons, independent of temperature (Shlagman et al. 1986). In contrast, the frequency of mature female *M. japonicus* always comprised less than 30 % of the population in the same area, while developing stage predominate (>60 %) from April to November (Tom and Lewinsohn 1983). Minagawa et al. (2000) stated that the percentage of prawns with mature ovaries is considered

Table 2 ANCOVA results for comparison of the regression lines ln ovary wet weight (*OWW*)—ln body weight (*BW*) by ovarian stage of *Melicertus kerathurus* in Thermaikos Gulf for the study period 2000–2002

Pair wise comparisons	Slopes		Intercepts	
	F	*p*	*F*	*p*
ST1–ST2	3.64	NS	3.64	NS
ST1–ST3	47.37	*	83.81	*
ST1–ST4	25.51	**	58.30	**
ST1–ST5	6.96	**	4.97	*
ST2–ST3	40.08	**	65.60	**
ST2–ST4	18.22	**	43.73	**
ST2–ST5	9.55	**	8.91	*
ST3–ST4	3.64	NS	1.46	NS
ST3–ST5	40.90	**	53.70	**
ST4–ΣT5	28.76	**	44.61	**

NS non significant

** $p < 0.01$, * $p < 0.05$

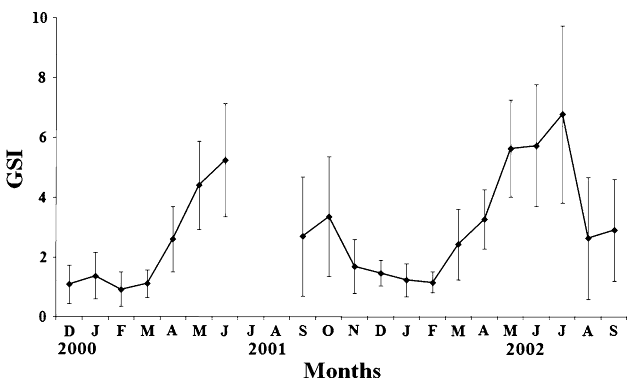

Fig. 8 Monthly variation of GSI (±sd) of *M. kerathurus* in Thermaikos Gulf for the study period 2000–2002

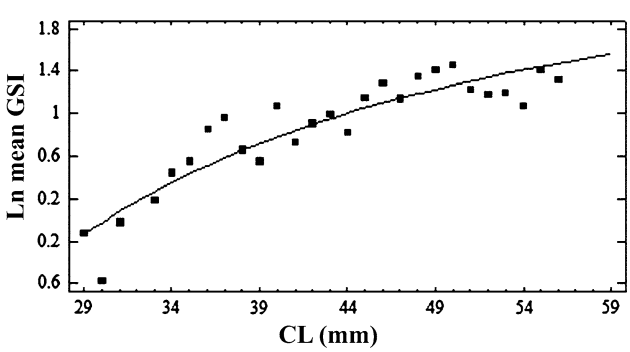

Fig. 9 Relationship lnGSI—CL of female *Melicertus kerathurus* in Thermaikos Gulf

to represent the relative reproductive activity of the species. Therefore, as inseminated females with mature ovaries are ready for immediate spawning (in ≈ 90 h) (Courtney et al. 1996), their seasonal variation may define the spawning period of a species. In Thermaikos, the percentage of inseminated females with mature ovaries was higher in June–July, indicating that peak spawning occurs in these months.

Table 3 Coefficients (lna, *b*) of the regressions of fecundity (*F*) against carapace length (*CL*), total length (*TL*), body weight (*BW*), ovary wet weight (*OWW*), and 1st abdominal segment width (*AW*) of *Melicertus kerathurus* in Thermaikos Gulf for the study period 2000–2002

Relationships	*b*	lna	$S.E_b$	R^2	*p*
lnF–lnCL	3.162	0.575	0.590	0.406	<0.001
lnF–lnTL	3.595	−5.832	0.639	0.429	<0.001
lnF–lnBW	1.128	8.413	0.199	0.434	<0.001
lnF–lnOWW	0.899	11.461	0.115	0.593	<0.001
lnF–lnAW	2.695	4.632	0.578	0.341	<0.001

According to Table 4, the smallest size at maturity fell within the small range recorded in most previous studies (27–32 mm CL), with the exception of that from Smyrni Bay (Türkmen and Yilmazyerli 2006). According to Heldt (1932), females begin to spawn at 106 mm TL with the majority at 125 mm TL, whereas according to Rodrígeuz (1977), the smallest inseminated female with mature ovaries had a TL < 115 mm. In the present study, the smallest female found at ST5 measured 32.26 mm CL (≈ 130 mm TL), similar in size to the smallest mature female (32.24 mm CL), implying that some mature smaller prawns may exist in the population.

The proportion of mature females increases with increasing size in *M. japonicus* (Minagawa et al. 2000), *P. semisulcatus* (Crocos 1987a), *P. esculentus* (Crocos 1987b), *Metapenaeus dalli* (Potter et al. 1989), *M. endeavouri,* and *M. ensis* (Crocos et al. 2001). On the contrary, according to Courtney et al. (1995), in *M. plebejus* the percentage of mature females > 60 mm CL decreases, as it may be a decline in the capacity of very large females to produce and fertilize eggs. In the present study, percentages of females in advanced ovarian stages increased with size from <20 % at 34 mm CL to 90 % at 50 mm CL. However, a slight decrease in ovarian maturation was observed in females > 50 mm CL, from which spent individuals are also absent. The above possibly indicates a decrease in their potential contribution to the population's total egg production or that they undergo an ovarian rematuration. On the contrary, all prawns with CL > 52 mm present only ST3 and ST4 in Smyrni, whereas in Gulluk Bay, all females with CL > 56 mm present only ST4, implying high participation of these classes in reproductive activity (Türkmen and Yilmazyerli 2006; Türkmen et al. 2007).

Two-way ANOVA has shown that mean OWW varied significantly with female size and ovarian stage. Pairwise comparisons showed that for those prawns participating in reproductive activity, spent and developing ovaries had

Table 4 Minimum size (CL, TL, in mm) at ST4 and size at first maturity based on the presence of advanced (vitellogenic and mature) or mature ovarian stages (CL_{50ov}, TL_{50ov} in mm) of female *Melicertus kerathurus* in Thermaikos Gulf and other geographical areas

Minimum size at ST4		Size at first maturity		Author (geographical area)
CL	TL	CL_{50ov}	TL_{50ov}	
	115.00			Abdel Razek (1985) (Southeastern Mediterranean Sea)
	110.00			Abdel Razek (1992) (lake Quarun)
		29.58–30.13[d]	120–122[a]	Rodríguez (1985) (Gulf of Cádiz, Atlantic Ocean)
		30.00[a]		Silva et al. (2003) (Gulf of Cádiz, Atlantic Ocean)
32.20	130.50	45.56	175.18	Lumare et al. (2011) (South Adriatic Sea)
27.50	117.00	30.30[c]	126.00	Ben Meriem (1993) (Gulf of Gabès, Mediterranean Sea)
39.00	141.00	46.00[b]	165.00	Türkmen and Yilmazyerli (2006) (Smyrni Bay, Central Aegean Sea)
31.00	123.00	48.00[b]	178.00	Türkmen et al. (2007) (Gulluk Bay, Southeastern Aegean Sea)
30.00	114.00	45.23[a]	156.20	Conides et al. (2008) (Amvrakikos Gulf, Ionian Sea)
32.24	129.00	40.70[b]	160.04	Present study (Thermaikos Gulf, North Aegean Sea)

[a] Estimated on the presence of ST4

[b] Estimated on the presence of ST3 and ST4

[c] Referred generally in mature ovarian stages

[d] Estimated from the relationship logCL = loga + *b*logTL (Rodríguez 1987)

equal mean OWW, indicating that in the former, as reported by Courtney et al. (1995) and Minagawa et al. (2000), there are mature oocytes that will begin reabsorption or that these ovaries are in an early stage of rematuration, or a combination of both. In the present study, mean vitellogenic OWW of medium-sized females is greater than that of the respective stage of large prawns. This may be attributed to large females having more spawnings and, as a result, some individuals may be at a phase of rematuration and/or reabsorption of mature oocytes.

Ovary maturation processes, as depicted by BW-OWW regression comparisons among ovarian stages, seem to be grouped into three phases: that of immature/developing, followed by a significant weight gain of the ovaries in vitellogenic/mature phase, and that of spent condition. The increased slope of the latter (in spent condition) suggests that, after spawning, the ovaries of larger females can retain a considerable part of their weight, a fact which would lead to respawning.

Penaeids are potentially capable of multiple spawning within a reproductive season (e.g. Penn 1980; Crocos and Kerr 1983; Minagawa et al. 2000; Yamada et al. 2007). Therefore, female *M. kerathurus* may have multiple spawnings during the extensive reproductive period observed in Thermaikos. More specifically, based on monthly variation of mature and inseminated females in relation to size, it seems that large prawns potentially spawn at least three times during the reproductive period. On the other hand, medium prawns seem to spawn two times and they exhibit a more constant contribution to spawning than larger prawns. Klaoudatos (1984) reported 2 peaks in *M. kerathurus* spawning in Amvrakikos: one in May and one in August. In the south Adriatic, the species may spawn at least twice, with the larger females the first to reproduce (in June) and the smaller ones later (in July) (Lumare et al. 2011). Rodríguez (1985) reported that in Cádiz the species spawns 2–3 times during the reproductive period, at 2-month intervals, while similar results are cited from Smyrni Bay and Gulluk Bay (Türkmen and Yilmazyerli 2006; Türkmen et al. 2007).

Monthly variation of spermatophore insemination and mature ovarian stage presence per size group showed that large prawns mature earlier than medium ones and are first to spawn, indicating a variation in spawning activity due to size. Ben Meriem (1993) reported that *M. kerathurus* large-sized females spawn earlier in Gabès (May–June), whereas prawns with CL < 40 mm spawn 3 months later. Variability in spawnings due to body size is also reported for *M. japonicus* by Minagawa et al. (2000) and attributed to the delayed vitelogenesis in small females. Moreover, they reported that prawns with TL > 170 mm exhibit a temporal maturation peak during the reproductive period, whereas small and medium prawns have a more stable participation in the reproductive process. In *Trachysalambria curvirostris* (= *T. palaestinensis*) higher frequency of mature ovaries was found in large and medium compared with smaller-sized prawns, which approach maturity in the middle of the reproductive period (Yamada et al. 2007).

A few small-sized inseminated prawns (CL < 30 mm) were collected at the end of autumn and early winter. They represent recruits (0^+) produced during the previous months (see Kevrekidis and Thessalou-Legaki 2011). However, the absence of mature ovarian stages in this size group excluded it from spawning activity during the reproductive period. Nevertheless, medium-sized prawns of the first 0^+ cohort (>30 mm CL), produced in late April–early May, possibly exhibit spawning activity in autumn, as they present mature ovaries. During experimental sampling (August 2001, September 2001 and 2002), medium-sized prawns at 34–36 mm CL size classes with mature and spent ovaries were collected. The above imply that a small number of recruits of the first 0^+ (spring) cohort may spawn once before they recruit to the offshore fishery (Kevrekidis and Thessalou-Legaki 2011).

Gonadosomatic index (GSI)

In Thermaikos, mean GSI ranged from about 1 (immature ovary) to 6.8 (mature ovary), recorded in February and July, respectively. The maximum mean monthly GSI was significantly lower than that reported from Cádiz (Rodríguez 1985) and the Adriatic (Lumare et al. 2011), where the highest GSIs were recorded in July and June–July, respectively. In Amvrakikos, GSI ranged from 0.66 (spent ovary) and 0.77 (immature ovary) to 9.6 (mature ovary) (Conides et al. 2008), with a mean GSI peak in May and August (≈7) (Conides et al. 2008). In the present study, the lowest mean GSI for both periods was observed in winter (February), similar to that reported in Amvrakikos (February–March) (Conides et al. 2008), Cádiz (Rodríguez 1985), and the Adriatic (Lumare and Scordella 2001), where it was recorded in January.

According to Courtney et al. (1995), GSI is likely to be a poor indicator of reproductive activity in penaeid prawns, as it is not independent of size, molt stage, histological stage, or insemination status, and that the effect of size must be taken into account. On the contrary, according to Tom and Lewinsohn (1983) and Ohtomi et al. (2003), GSI is independent of body size in *M. japonicus* and they proposed that it can be used as a useful index for the study of the reproductive aspects of the species.

GSI was not independent of insemination status in *M. kerathurus;* inseminated females had higher GSI than non-inseminated. In a 3-year study, Rodríguez (1977) reported that GSI and the proportion of inseminated females presented a similar monthly variation. Courtney et al. (1995) suggested that the absence of a spermatophore, due to a failure to copulate, is partially responsible for low GSIs observed in very large females (>60 mm CL). According to the same authors, this is attributed to an energy-saving mechanism, as it appears futile for females to develop ovaries, if no sperm is present to fertilize spawned eggs.

According to our results, mean GSI is not independent of ovarian stage and female size. GSI of immature females is similar in all three size groups as an overlap may exist at that stage. Moreover, medium- and large-sized prawns with mature ovaries have similar GSIs, indicating a similar reproductive output in all reproducing females. Increase of GSI with increasing ovarian maturation is also reported in Amvrakikos (Conides et al. 2008) and the Adriatic (Lumare et al. 2011).

In general, GSI of *M. kerathurus* increases with size. However, in large classes (>50 mm CL), it seems to reach a 'plateau' and further increase in size is followed by a lower increase in GSI. Thus, a lower than expected contribution to oocyte production may exist in larger prawns. Courtney et al. (1995) recorded a decrease in mean GSI for very large female *M. plebejus* (>60 mm CL) with a parallel decrease in insemination (>55 mm CL), implying that there may be a reduction in the capacity of large females to fertilize and produce oocytes.

In the present study, the declines in mean GSI and the percentage of females at ST4, along with the absence of ST5 in females > 50 mm CL, may be indicative of a reduced capacity in very large females to produce eggs. However, this is not accompanied by a decline in insemination, as observed in *M. plebejus* (Courtney et al. 1995) and *M. japonicus* (Minagawa et al. 2000). We suggest that, older females continue to copulate, with, however, a reduced capacity to produce oocytes, which may be indicative that a gradual ovarian senescence takes place with age.

Size at first maturity

The smallest inseminated female in Thermaikos was of a similar size to that reported from Gabès (27 mm CL), whereas the CL_{50sp} varied considerably (29 mm CL, Ben Meriem 1993). Estimates on CL_{50ov} from other areas show a high variability, ranging from 30 to 48 mm CL, with that of the present study lying almost in the middle (Table 4). Differentiation in estimation method, use of different maturity ovarian stages, sample size range and sampling period, gear used, population abundance, structure and growth rate of the species in different areas may explain the divergence in estimates of CL_{50} in *M. kerathurus*. According to Ben Meriem (1993), CL_{50} may differ interannually. In Thermaikos, CL_{50sp} in *M. kerathurus* is smaller than CL_{50ov}. This is due to the fact that females in Penaeidae first mate and then begin the maturation process (e.g. Penn 1980; Dall et al. 1990). In the present study, $CL_{50ov} = 40.70$ mm corresponds approximately to a 1-year-old female (Kevrekidis and Thessalou-Legaki 2011).

Dall et al. (1990) stated that CL_{50} depends on environmental parameters that vary with season, latitude, and depth. More specifically, temperature is critical in defining CL_{50} (Crocos et al. 2001), and Aragón-Noriega and Alcántara-Razo (2005) reported that increased temperature and low seasonal variability allow *F. californiensis* to reproduce more frequently, but also to reach smaller size at maturity. This may, thus, explain why *M. kerathurus*

Table 5 Spawning period (and peaks) of *Melicertus kerathurus* in Thermaikos Gulf and other geographical areas

Geographical area	Spawning period (peaks)	Author
Tunisia (Mediterranean Sea)	Early May to mid November (June–September)	Heldt (1938)
Gulf of Tunis (Mediterranean Sea)	June–July to October–November	Ben Mustafa (1967)
Gulf of Gabès (Mediterranean Sea)	June–July to early October	Ben Meriem (1993)
Gulf of Cádiz (Atlantic Ocean)	May–September	Rodríguez (1985)
South Adriatic Sea	Late May to mid August (June, July)	Lumare et al. (2011)
Southeastern Mediterranean Sea	April–October (May, August, September)	Abdel Razek (1985)
Smyrni Bay (Central Aegean Sea)	April–September (May–July)	Türkmen and Yilmazyerli (2006)
Gulluk Bay (Southeastern Aegean Sea)	May–October (May–July)	Türkmen et al. (2007)
Amvrakikos Gulf (Ionian Sea)	May–August (May, August)	Klaoudatos et al. (1992)
Amvrakikos Gulf (Ionian Sea)	Late April to late September (August)	Conides et al. (2008)
Thermaikos Gulf (North Aegean Sea)	Late April to mid-October (June, July)	Present study

reaches first maturity at a smaller size in southern areas such as Tunisia, Egypt, and Amvrakikos (Table 4).

Fecundity

Our estimate on fecundity (F) of *M. kerathurus* is comparable to that of Rodríguez (1985) (81–670 × 10^3; size range: 32–46 mm CL, 130–179 mm TL) and Lumare et al. (2011) (112–606 × 10^3) and higher than that of Lumare (1979) (61–84 × 10^3; size range: 124–148 mm TL). It is much lower than that presented by Heldt (1938) (0.8–1.3 × 10^6) and Klaoudatos (1984) (170–800 × 10^3; size range: 135–123 mm TL). Conides et al. (2008) found that an individual at 53 mm CL (= 210 mm TL) produced 800 × 10^3 eggs. Based on F-CL relationship (see below), the number of oocytes at CL_{max} (59.97 mm, Kevrekidis and Thessalou-Legaki 2011) would be 744,993, and at CL_{50ov}, 218,673.

Fecundity may vary due to the estimation method, oocyte stage and sample size range, resulting in a significant difference in the number of oocytes counted. In this study, but also in Rodríguez (1985), the method followed for the estimation of fecundity differs from that of Klaoudatos (1984) and Lumare (1979), which was based on experimental spawning.

In Thermaikos, F is more tightly related to OWW compared with BW, as expected. A similar result has been reported for *P. duorarum* by Martosubroto (1974). In the present study, the *b* value in the relationship F–BW is similar to that in Cádiz ($b = 1.285$) (Rodríguez 1985). In contrast, a significant difference occurs in the relationship F–OWW, where a slightly negative allometry is present in Thermaikos compared with a positive one observed in Cádiz ($b = 1.207$) (Rodríguez 1985).

In Thermaikos, F–TL relationship is positively allometric, in accordance with that reported from Cádiz ($b = 3.709$, Rodríguez 1985) and Amvrakikos ($b = 3.476$, Klaoudatos 1984; $b = 3.557$, Conides et al. 2008). On the contrary, isometry is observed in the Adriatic ($b = 3.038$, Lumare et al. 2011). Nevertheless, this relationship does not seem to be very strong in the present study, with oocyte numbers exhibiting significant variation, especially in the larger female sizes. This may be attributed to multiple spawning during the reproductive period and/or intermittent spawning incidences occurring in the same ecdysian cycle. Rao (1968) reported a strong F–TL relationship in a series of species (*Fenneropenaeus indicus, Parapenaeopsis stylifera, Metapenaeus affinis, Metapenaeus dobsoni)*. In the present study, the F–CL relationship presents slightly positive allometry, whereas it seems to be slightly negative in *M. latisulcatus* ($b = 2.91$) (Penn 1980*)* and *M. longistylus* ($b = 2.92$) (Courtney and Dredge 1988). A very strong F–CL relationship is reported for *F. indicus* and *P. monodon* (Teikwa and Mgaya 2003).

Knowledge of the reproductive dynamics of a species is significant for managing its fishery and in particular for implementation of spatiotemporal measures for the maintenance of spawning stock and the conservation of nursery areas. Estimation of the exploitation rate of *M. kerathurus* stock in Thermaikos in the period 2000–2002 has shown that the stock was under intense fishing pressure, tending toward overexploitation (Kevrekidis and Thessalou-Legaki 2011). In the years that followed (2006–2010), landings declined significantly from 153 mt in the period 1995–2005 to a mean of 65 mt (data from Auction Agency of Greece 2011). As a causal relationship between spawning stock and recruitment exists in penaeids (Ye 2000), measures currently implemented should be reconsidered. In the light of the present findings, both medium- and large-sized spawners are fished by trawlers (open fishing period: October to May) at the beginning and the end of the reproductive period. Catches are most profitable in October at a depth < 50 m (Kevrekidis and Thessalou-Legaki 2006) and comprise new recruits and 1^+ old females (Kevrekidis and Thessalou-Legaki 2011) close to CL_{50} (present study), while they are minimal in May due to reproductive migration inshore. Thus, an issue arises concerning the advent of each trawling season (October) and/or the allowable trawling depth/distance from the shore, in the same month, as it has been shown that the period of high catch rates is significantly related to depth (Kevrekidis and Thessalou-Legaki 2006).

Moreover, as during the spawning period, the species is mainly a target species for the artisanal fishery and female size at first maturity is selected by artisanal net size, the existing closed period (10 July–10 September) for the artisanal fishery should be shifted to 1 June to 30 July, in order to conserve the spawning stock. In parallel, the effect of the artisanal fishery on the species' spawner abundance in the gulf must be assessed.

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