Seasonal variation of clutch size in the crangonid shrimp Philocheras trispinosus (Crustacea: Decapoda) in the western Mediterranean (Spain)

A. Sanz-Brau, J. A. Gil-Delgado, F. Mesquita-Joanes

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SEASONAL VARIATION OF CLUTCH SIZE IN THE CRANGONID SHRIMP *PHILOCHERAS TRISPINOSUS* (CRUSTACEA: DECAPODA) IN THE WESTERN MEDITERRANEAN (SPAIN)

A. SANZ-BRAU, J. A. GIL-DELGADO, F. MESQUITA-JOANES*

Dept. Microbiology and Ecology and ICBiBE, Univ. of València, Av. Dr Moliner, 50, E-46100 Burjassot, Spain
* Corresponding author: mezquita@uv.es

CLUTCH SIZE
SEASONAL VARIATION
PHILOCHERAS TRISPINOSUS
COASTAL ENVIRONMENTS
REPRODUCTIVE EFFORT
MEDITERRANEAN
SPAIN

ABSTRACT. – Seasonal variation in clutch size of multi-brooded vertebrates in intermediate latitudes follow a parabolic trend that could be coupled to seasonal variation in environmental factors so that maximal clutch size is attained at times of higher resources availability. To test whether this trend may be observed in aquatic invertebrates, we monitored the clutch size and related ecological traits of a crangonid decapod *Philocheras trispinosus* population on the Western Mediterranean coast of Spain for more than two years. Unlike other northernmost studies, the monitored population presented ovigerous females throughout the year without interruption. The analysis of sex-ratio, size-frequency distribution and percentage of ovigerous females allowed the period of maximum recruitment and reproduction to be assigned between April and June. Pooling all the samples analyzed into one theoretical reproductive year starting on 1 September (minimal clutch size) showed a second order polynomial (parabolic) trend with maximum sizes and clutch size corresponding to early spring. We suggest that the response of *P. trispinosus'* reproductive effort to habitat variability over time is similar to that of clutch size in birds. This could be a general trend in organisms living in habitats with strong seasonal habitat variability.

INTRODUCTION

The crangonid shrimp *Philocheras trispinosus* (Hailstone, 1835) inhabits the sublittoral zone from Morocco to North of Britain Islands (Zariquiey 1968, Lagardère 1971, Labat 1984, Falciai & Mimervimi 1992). Its presence has been recorded on eastern Spanish Mediterranean coasts (Sanz 1986, Guillén & Perez Ruzafa 1993).

Previous studies indicated that *Philocheras trispinosus* could have two reproductive periods per year (Labat 1984). Furthermore, ovigerous females were potentially consecutive breeders, capable of multiple spawning within a single reproductive season (Oh & Hartnoll 1999a). Both studies, carried out in distant areas of the Atlantic Ocean (Isle of Man, Oh & Hartnoll 1999a) and the Mediterranean Sea (Banyuls-sur-Mer, Labat 1984), show that ovigerous females were missing during a certain period of the year and, consequently, the breeding season was suspended. It was also noteworthy that the authors found a higher proportion of ovigerous females in spring-summer (Labat 1984, Oh & Hartnoll 1999a) than at other times of the year. Our aim was to test whether these patterns are consistent in populations located at lower latitudes given the numerous references to land and aquatic animals as to latitudinal trends in clutch size and length of breeding season (Lack 1954, Margalef 1974).

Many crangonid species show a wide variation in the egg load of ovigerous females (Allen 1960, 1966, Tiews 1970, Hong & Oh 1989, Oh & Hartnoll 1999a, b). Several factors related to food availability, season, geographic region, morphology and size of females have been proposed to explain the clutch size variation in shrimps (Boddeke 1982, Annala 1991, Mantelatto & Fransozo 1997).

This study describes i) clutch size, ii) seasonal variation of clutch size, iii) seasonal variation of ovigerous females relative abundance, iv) changes in sex-ratio and v) the effect that both female size and year period have on clutch size. Sizes of females and males are also presented. Finally, we discuss the factors that may be affecting temporal (seasonal) and spatial (latitudinal) variation of the studied population traits in comparison to previous studies (Labat 1984, Oh & Hartnoll 1999a).

MATERIALS AND METHODS

Monthly samples of *P. trispinosus* were collected at Vinaròs (40°28' N, 0°28' E) between April 2004 and October 2006. Vinaròs is located on the Mediterranean Sea coast, 10 km south of the Ebro River delta (Fig. 1). Water temperature varies between 12 °C in January-February and 29 °C in July-August (own data). In the upper infralittoral region of the Vinaròs shore, other 23 crustacean decapods belonging to 14 families were found (Sanz-Brau & Mezquita 1999).

A total number of 2004 individuals were collected on 28 sampling occasions between April 2004 and October 2006. We used a 2.0 mm mesh size hand net with a net mouth of 35 cm to collect specimens, sweeping it over the sandy substrate for a distance of about 1 m. The mean depth varied between 0.1 and 1.5 m.
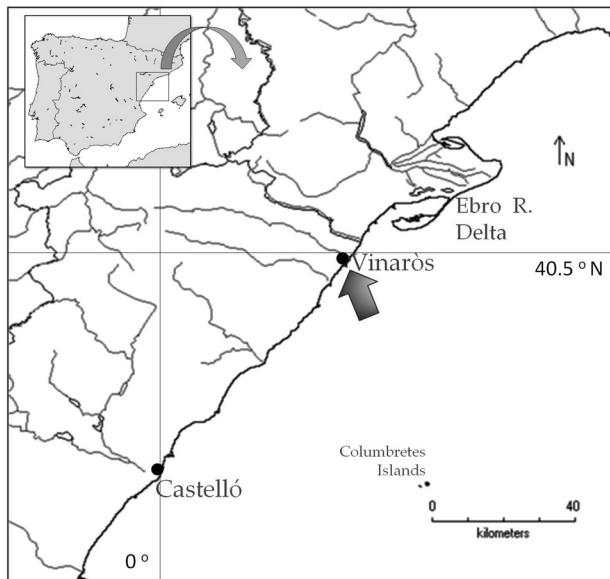
Fig. 1. – Location of the sampling site in Vinaròs (arrow), to the South of the Ebro River delta, on the eastern coast of Spain.

Collected animals were fixed in 70 % ethanol in the field. In the laboratory, individuals were sexed and the numbers of eggs (at any maturation stage, *i.e.* any embryonic development) were counted per ovigerous female. All the shrimps were sexed by examining the endopod of the first and second pleopods, and by the presence or absence of the appendix masculine using a stereomicroscope. Total length and carapace (cephalothorax) length were measured for each individual. Total length was defined as the distance between the anterior end of the rostrum and the distal point of the telson spines. Carapace length (CL) was measured as the distance between the anterior end of the rostrum and the posterior margin of the carapace. Both size variables were measured with a resolution of 0.1 mm, using a stereomicroscope.

In order to compare size differences between sexes and for any analysis that required a size variable, we chose the carapace length (CL) because the carapace is harder than the abdomen. Measuring the total length involves unfolding the abdomen. The measurement of carapace length was also used in previous studies (Oh & Hartnoll 1999a, b).

Data analysis: in order to test the seasonal effects on clutch size, we used quadratic polynomial regressions which have been previously shown to relate clutch size to time of the year in other organisms (Crick *et al*. 1993).

In order to check the significant relationships between carapace length of ovigerous females and the number of eggs, we performed a linear regression analysis with $log_{10}CL$ as the independent variable and the logarithm (base 10) of the number of eggs as the dependent variable, using the SPSS 14.0 software. The residuals resulting from this analysis were further analysed with a curvilinear regression versus time of the year as the independent variable to see whether any temporal pattern exists in the number of eggs that could not be related to the effect of individual size.

RESULTS

Size of **Philocheras trispinosus** *from Vinaròs*.

The 1263 female *P. trispinosus* measured ranged between 1.6 and 8.0 mm of carapace length (CL, mean = 4.4, s.d. = 1.3). Males presented CL values (Table I) significantly smaller than females (t = 36.271, P < 0.001, d.f. = 1924.571). Ovigerous and non-ovigerous females also presented significant differences in CL (t = 28.715, d.f. = 1261, P < 0.001). Males were also smaller than non-ovigerous females and the difference between means was highly significant (t = 13.248, P < 0.001, d.f. = 1385). Total length presented a similar pattern: males were the smallest and ovigerous females the longest (Table I). In addition, the correlation coefficient between carapace length and total length presented values close to 1 in males (r = 0.992, P < 0.001, N = 741), ovigerous females (r = 0.994, P < 0.001, N = 617) and non-ovigerous females (r = 0.991, P < 0.001, N = 646).

The minimum CL value in ovigerous females was 3.4 mm. This length was shorter than the values of many non-ovigerous females. The CL of both female types presented overlapping frequency distributions (Fig. 2), thus we cannot discard that non-ovigerous females with sizes above 3.4 mm were sexually mature.

Males, but also ovigerous and non-ovigerous females, presented a seasonal variation in CL. In general, and despite some interannual variation, smaller sizes are presented between July and October and larger shrimps dominate between February and May (Figs 3, 4).

Table I. – Measurements of carapace length (CL) and total length (TL) of ovigerous females, non-ovigerous females and males (M) of the crangonid shrimp *Philocheras trispinosus*.

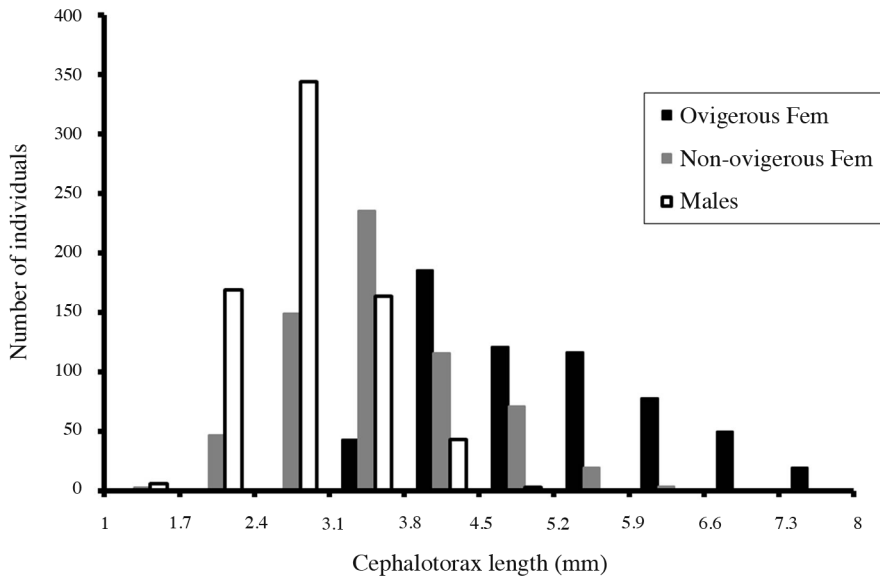| | CL | | | TL | |
	Ovigerous females	Non-ovigerous females	M	Ovigerous females	Non-ovigerous females
Mean	5.2	3.6	2.9	20.3	14.3
SD	1.1	0.9	0.6	4.1	3.3
Range	3.4-8.0	1.6-7.1	1.6-4.6	13.1-31.8	6.3-27.4
N	617	646	741	617	646

Fig. 2. – Size distribution of carapace length in ovigerous females, non-ovigerous females and males.
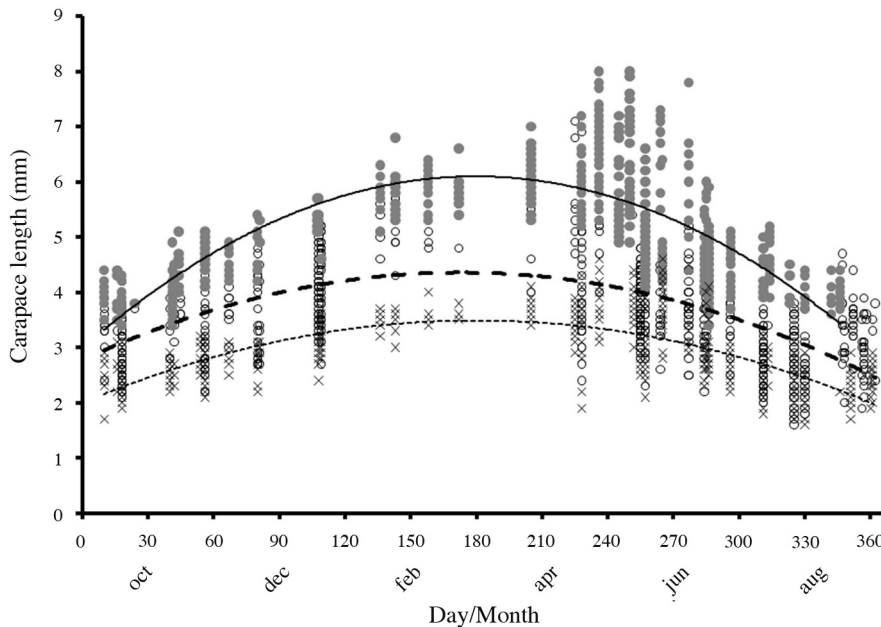

Fig. 3. – Carapace length variation throughout the year in ovigerous females (grey circles, solid line), non-ovigerous females (white circles, dashed line), and males (crosses, dotted line). All the sampling dates of several years were pooled in only one hypothetical year with day 1 = 1 September and day 365 = 31 August.

Sex ratio and the differential distribution of males and females

The number of males (N = 741) was smaller than that of females (N = 1263), resulting in a global sex ratio of 1.7 females per male. These values significantly differed from the ratio of 1:1 (X^2 = 135.97, d.f. = 1, P < 0.001). However, the sex-ratio varied seasonally between 0.5 and 4.5. Of the 28 samples, differences were significant in 18 (Fig. 5).

The ratio between ovigerous and non-ovigerous females

In general, there was no significant departure from a ratio of 1:1 between ovigerous and non-ovigerous females (X^2 = 0.7, n.s.). However, there were monthly variations in this ratio between 0 and 9 (X^2 = 407.66, d.f. = 27;

P < 0.001), and differences were significant in 17 of the 28 samples (Fig. 6).

Ovigerous females were always present, except for August 2004 (Fig. 6). Thus on the Mediterranean coast of Spain, the reproductive stage occurs all year round. We assumed that the increase of the percentage of ovigerous females indicated an increase of reproductive activity in April, May and July 2004, February, March and June 2005, and April, June and October 2006; that is, the periods with greater reproductive activity (Fig. 6).

Fecundity and seasonal variation of the number of eggs

Ovigerous females were found on all the sampling occasions, suggesting that the reproductive stages of *Philocheras trispinosus* occurred continuously on the
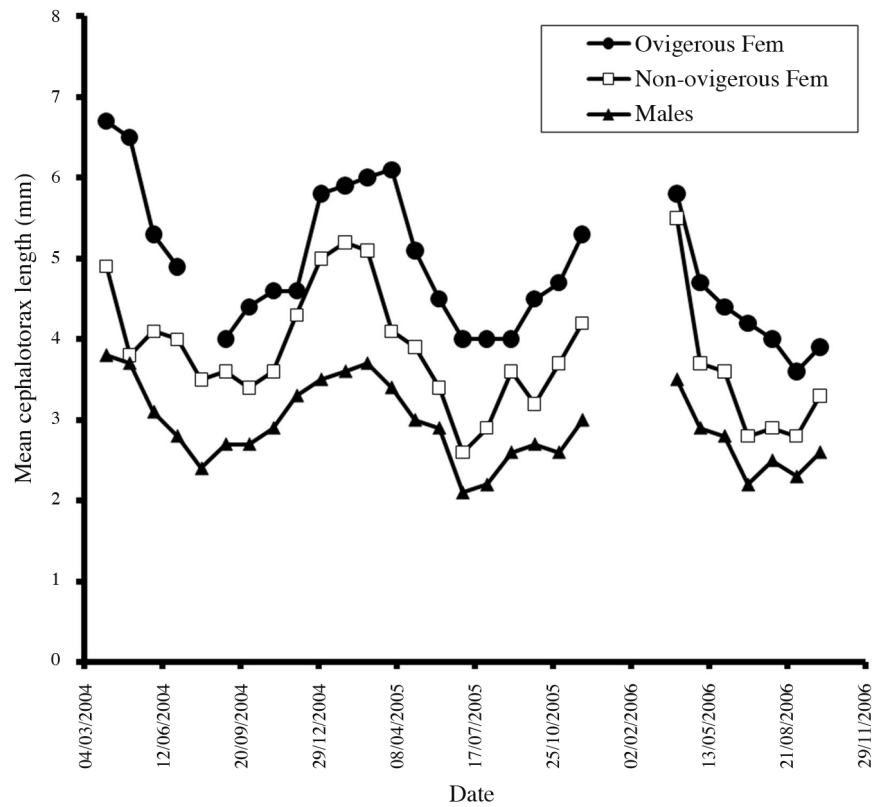
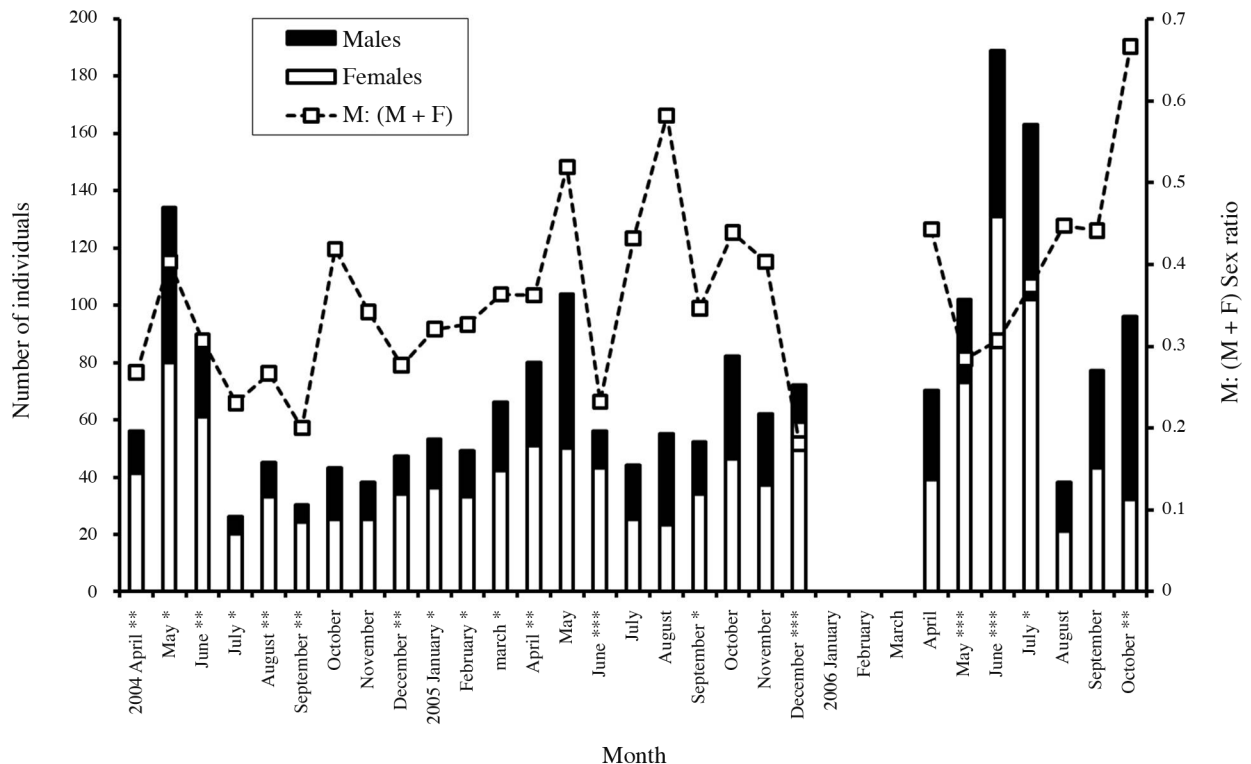Fig. 4. – Monthly variation of the mean carapace length of *P. trispinosus*.

Fig. 5. – Numbers of males and females captured throughout the study period (April 2004 to October 2006) (bars) and proportion of males in the population (dashed line). Months with significant deviations in M:F sex-ratio from 1:1 are noted (chi-square tests, * P < 0.05, **P < 0.01, ***P < 0.001).

Vinaròs coast. The mean number of eggs per female was 648.4 (s.d. = 533.84, range = 82-3138, n = 588). The number of eggs per female varied within the year. August

and September presented a smaller number of eggs per female. Therefore, we took the 1 September to be the first (Date = 1) and the 31 August to be the last (Date = 365)
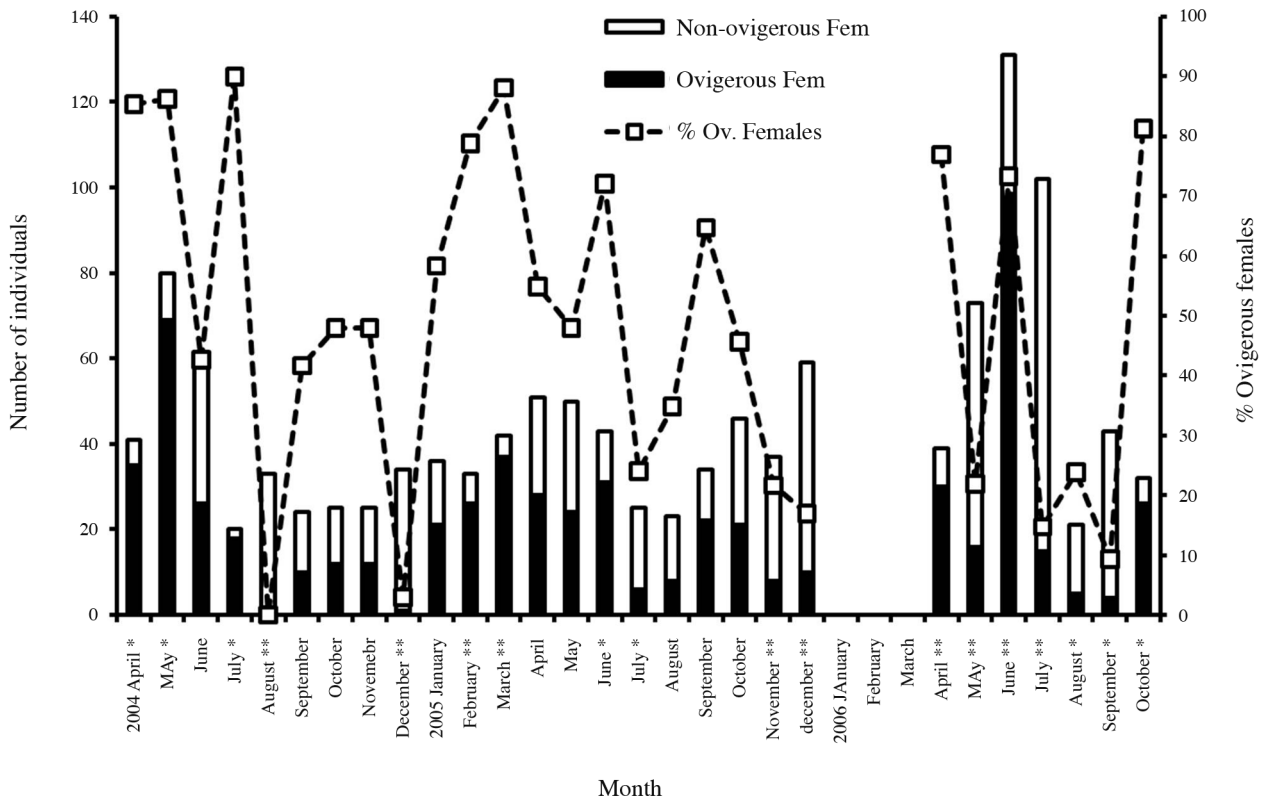
Fig. 6. – Numbers of ovigerous and non-ovigerous females captured throughout the study period (April 2004 to October 2006) (bars) and percentage of ovigerous females (dashed line). Months with significant deviations in ovigerous : non-ovigerous females ratio from 1:1 are indicated (chi-square tests, * P < 0.05, ** P < 0.01, *** P < .001).
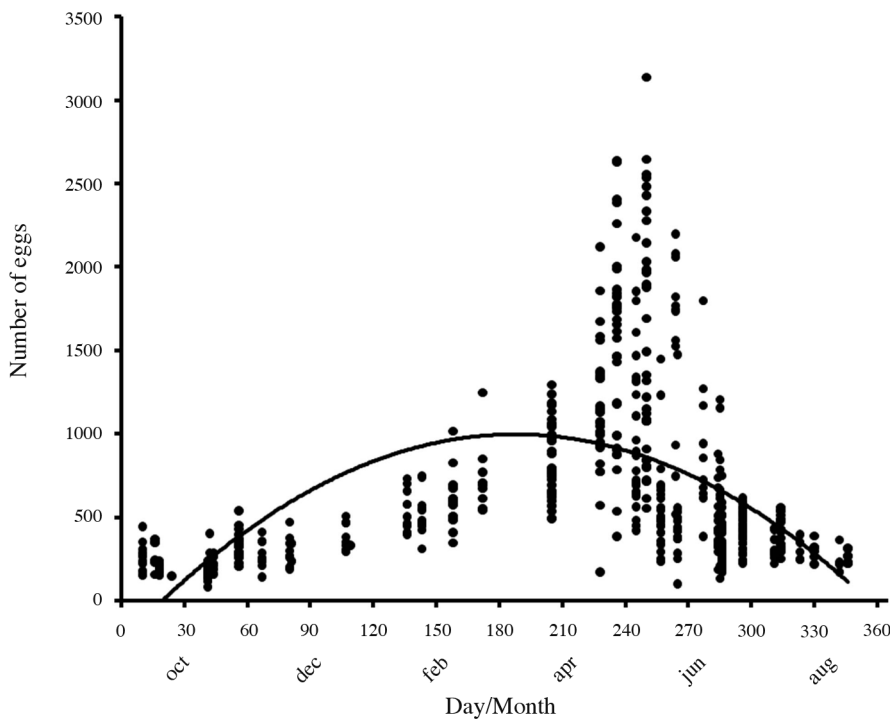
Fig. 7. – Changes in the number of eggs per ovigerous female throughout the year. Sample pooling as in Fig. 3.

days of each annual reproductive cycle. Accordingly, a quadratic equation regression analysis was done which showed that the number of eggs per female varied seasonally ($Y_{egg\ number} = -178.89 + 11.42X_{Date} - 0.029X_{Date}^2$, $r^2 = 0.246$, $F_{587} = 95.201$, P < 0.001). The coefficient of determination r^2 is low, mainly due to the wide variation

in egg number per female during periods of maximum reproduction. The number of eggs in ovigerous *P. trispinosus* females initially increased with a peak in late April and May which then declined (Fig. 7).

The carapace length of ovigerous females correlated highly with the number of eggs per ovigerous female (log $Y_{egg\ number} = -178.89 + 3.35$ Log X_{CL} $r^2 = 0.841$, F = 3090, P < 0.001, N = 588). Therefore, we explored whether the seasonal variation of brood size was caused only by size increases or whether there were other additional effects. The analysis of the residuals of the last regression analysis showed a slight but significant quadratic relationship between the variation of the number of eggs, which was not accounted for by CL (residuals) and time of year ($Y_{residual\ number\ of\ eggs} = -6.30 + 1.33\ X_{Date} - 0.065 X_{Date}^2$, $r^2 = 0.348$, $F_{587} = 156.10$, P < 0.001).

DISCUSSION

Philocheras trispinosus females were larger than males, as is usually the case in Natantia decapods (Sanz 1987, García-Rodriguez & Esteban 1999, Oh & Hartnoll 2004). Females can lay eggs from 3.4 mm. This minimum value of ovigerous females captured in Vinaròs was lower than the size at sexual maturity of females from the Isle of Man estimated by Oh & Hartnoll (1999a) (CL = 3.7 mm).

At the study site, *P. trispinosus* females were more abundant than males, although there were seasonal variations in the sex ratio. Our results agree with previous studies in the same species in that males were in equal proportion to females, or at an even higher proportion, but only at the beginning of the reproductive period, that is, the end of summer to early autumn (Oh & Hartnoll 1999a). This may be related to a sexual bias in mortality in which males would die earlier than females, just after the mating periods. In other decapods, such as the intertidal prawn *Palaemon elegans* and the common shrimp *Crangon crangon* the number of females is usually higher than the number of male individuals (Sanz 1987, Oh & Hartnoll 2004).

This study shows the presence of ovigerous females of *P. trispinosus* all year round. Thus, this shrimp has a continuous reproductive pattern on the western Mediterranean Sea coastline. Oh & Hartnoll (1999a) already suggested the same pattern in *P. trispinosus,* although they failed to find ovigerous females between October and January. Therefore, they concluded that the reproductive period of *P. trispinosus* was interrupted in winter (Oh & Hartnoll 1999a). Many crangonid species show seasonal reproductive periods (Allen 1960, Corey 1987, Hong & Oh 1989). In the north-western area of the Mediterranean Sea, *P. trispinosus* presents two reproductive periods every year; the first in winter and the second in summer (Labat 1984). The studies by Labat (1984) and Oh & Hartnoll (1999a) show that reproductive seasons were interrupted.

Our results do not agree with these previous studies. The interruption in winter reproduction on the south British coast can be explained by latitudinal differences between the Isle of Man and the Mediterranean coast of Vinaròs. The lower temperatures on British coasts may account for these different patterns. In addition, the differences found between Labat's work (1984) and our results may also be related to similar causes because, even taking into account that both sites are located in the Western Mediterranean, the area of Banyuls-sur-Mer has a mean sea surface water temperature two degrees lower than average temperatures at the area of Vinarós (Arévalo 1991). However the differences observed in the reproductive biology are not so wide as compared with the Isle of Man, because Labat (1984) also detected ovigerous shrimps in winter. Seasonal variation of clutch size increases from September to spring and then decreases, and even if female size was the main effect to account for clutch size, the seasonal variation of clutch size is also in agreement with those of multi-brooded bird species (Crick *et al*. 1993, Gil-Delgado *et al*. 2005). Our study, however, do not take into account that brood loss can happen. In *P. trispinosus* brood loss averaged 30 % in egg number (Oh & Hartnoll, 1999), and occurred mainly during early and late incubation stages. Therefore, differences in the number of eggs can be also determined by the stage of embryonic development (incubation stages), that is, the time from egg laying. However the annual pattern of reproductive output would probably still be evident even with such a percentage of brood loss. In addition to this issue, Boddeke (1982) suggested that in *Crangon crangon* seasonal variation in brood volume was related to changes in both egg volume and number: few larger eggs in winter and many small eggs in summer. But no effect on number of eggs was detected by Oh & Hartnoll (2004). However, trade-off has been reported for other malacostracan taxa: mysids (Mauchline 1973), fairy shrimps (Belk 1977), stomatopods (Reaka 1979), and polar caridean shrimps (Clarke1993).

By taking into account the frequency of ovigerous females, seasonal changes are noted in reproduction intensity, which is minimal in August, at least in some years. Size distribution changes throughout the year are also indicative of reproductive activity since ovigerous females have a minimum carapace length. During January-March, all the females were larger than this minimum size boundary. All the data suggest that recruitment takes place gradually from September to May, attaining maximum population size in late spring, and mortality happening mainly in summer.

Since the largest females were found between January and May, we conclude that they must mostly die in summer. Another possible explanation could be differential migration towards deeper, non-sampled areas in summer, but there is no recovery of such large females afterwards. Consequently, those females with a reproductive capacity by the end of summer and in autumn must not only

attempt a first reproduction at this time, but must also present more breeding attempts between this time and the time when females reach their largest sizes. In conclusion, a continuous reproductive period exists, but with a reproductive and density minimum in summer: July to September, mainly in August, when highest mortality is expected due to high temperatures. An obvious maximum clutch size occurs in spring: April-May, period in which the maximum number and largest ovigerous females were also found, resulting in recruitment from July to May, which is observed in the field catches as a gradually increasing population density from autumn (September) to spring (May). The seasonal variation in clutch size is consistent with theoretical expectations observed in birds, with similar quadratic patterns of reproductive output through the year.

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