

# Temperature effects on fecundity, development and survival of the benthopelagic calanoid copepod, *Pseudocyclops xiphophorus*

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**Abstract** The shallow-living, benthopelagic copepod species *Pseudocyclops xiphophorus* Wells (R Soc Edimburg 67:1967), collected over a yearly cycle from the fouling material in the brackish water Lake Faro (North-eastern Sicily), showed marked seasonal fluctuations in population abundances, with maximum numbers recorded in autumn. Highest in situ egg production rates coincided with periods of low adult and juvenile densities and vice versa, except in autumn when peaks in egg production and adult population densities were coincident. In this period, mean daily egg production rates reached a maximum of 4–5 eggs per female, when surface water temperature was 17–18°C. Egg production rates declined drastically in winter and were completely arrested when surface temperatures dropped to 10–12°C. In March, daily egg production rates began to increase again with an increase in ambient temperatures, reaching a maximum at the end of August. In the laboratory, as in the field, mean daily egg production rates were positively correlated with temperature, with values ranging from  $2.2 \pm 0.3$  (16°C) to  $8.9 \pm 2.6$  (30°C) (mean  $\pm$  S.D.) eggs per female per day. At 32°C, *P. xiphophorus* females

survived but did not reproduce. At 34°C, all specimens died after a few days. In terms of total egg production for the entire female lifespan, maximum values occurred at 16°C and minimum at 24°C. Temperature also dramatically affected female life span, which was shorter at higher temperatures. Development time of eggs decreased with increasing temperature, as also development time from egg to adulthood. Remating was necessary for the continued production of fertile eggs at 16°C because female life span was longer. The unique egg-laying behaviour in this species may ensure higher survival rates of egg stages compared to free-spawning and egg-carrying calanoid species. After releasing the egg pair, the female swims over the eggs with a rotatory motion, secreting a substance which facilitates the adhesion of the eggs to the bottom; she then continues to swim over the eggs until they are attached. Although egg production rates in this species are low compared to other pelagic copepods, they are within the range of values reported for egg-carrying species. The greater fecundity at higher temperatures compared to other subtemperate species indicates that the species is well adapted to the higher temperatures of coastal lagoons and brackish water lakes where it contributes to the biofouling community.

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## Introduction

Seasonal fluctuations in copepod fecundity are one of the major factors affecting seasonal oscillations in copepod abundances at sea. Over the last 50 years (Uye 1981; Abou Debs and Nival 1983; Runge 1984; Kimoto et al. 1986; Sullivan and Mc Manus 1986; Van Rijswijk et al. 1989; Nival et al. 1990), many field and laboratory studies on copepod egg production rates have demonstrated a positive correlation between fecundity and temperature up

to a maximum level beyond which egg production is arrested and females may die. Egg production rates are also positively correlated to female body size (Durbin et al. 1992), reproductive condition (Ianora et al. 1989), and food concentrations/food quality (Kiørboe et al. 1985; Arnot et al. 1986; Ianora and Poulet 1993). Furthermore, egg viability and female fertility may largely depend on female age and remating success (Parrish and Wilson 1978), as shown for *Calanus finmarchicus* by Marshall and Orr (1952).

These studies refer only to the most common planktonic copepod species occurring in north temperate to polar regions (Ianora 1998). Few studies have considered “rare” species even though these represent the majority of the 2000 and more species of identified copepods. For example, nothing is known of the reproductive biology of benthopelagic copepods such as the calanoid copepod group recently reported by Zagami et al. (2003). Species of this group live at the interface between the bottom and the overlying water column, from shallow to deep oceanic environments. This layer is often richer in organic material than the water column above and is generally associated with an increase in the abundance and biomass of zooplankton, thereby representing a potential biodiversity “hotspot” for the discovery of new copepod species. Studies on the feeding and reproductive biology of copepods that inhabit this layer may give new insights into the functioning and resilience of this habitat.

The benthopelagic copepod *P. xiphophorus* was discovered by Wells (1967), along the Inhaca Island coast in the Indian Ocean and recently reported for the first time, in the Mediterranean Sea, in the brackish water Lake Faro (North-eastern Sicily) (Zagami et al. 2005). In Lake Faro, *P. xiphophorus* (body length ranges from 0.624 to 0.671 mm, mean and standard deviation are  $0.664 \pm 0.027$ ,  $n = 10$ ) was found attached to submerged ropes and mooring-posts as a fouling organism, during the day. At night, this species migrates into the water column, becoming part of the plankton community (Zagami et al. 2008). Effects of three food types on egg production, hatching success and naupliar survival in *P. xiphophorus* were studied recently by Brugnano et al. (2008) demonstrating different responses to diatom and flagellate diets.

In this paper, egg production rates of *P. xiphophorus* were studied in the field and in the laboratory at different temperatures under food-satiated conditions. We also monitored development and recruitment rates as well as remating behaviour in laboratory experiments. These findings are considered in relation to natural seasonal fluctuations in population abundances of this species in this area and also in relation to what is known on temperature effects and reproductive patterns of more abundant pelagic copepod species.

## Materials and methods

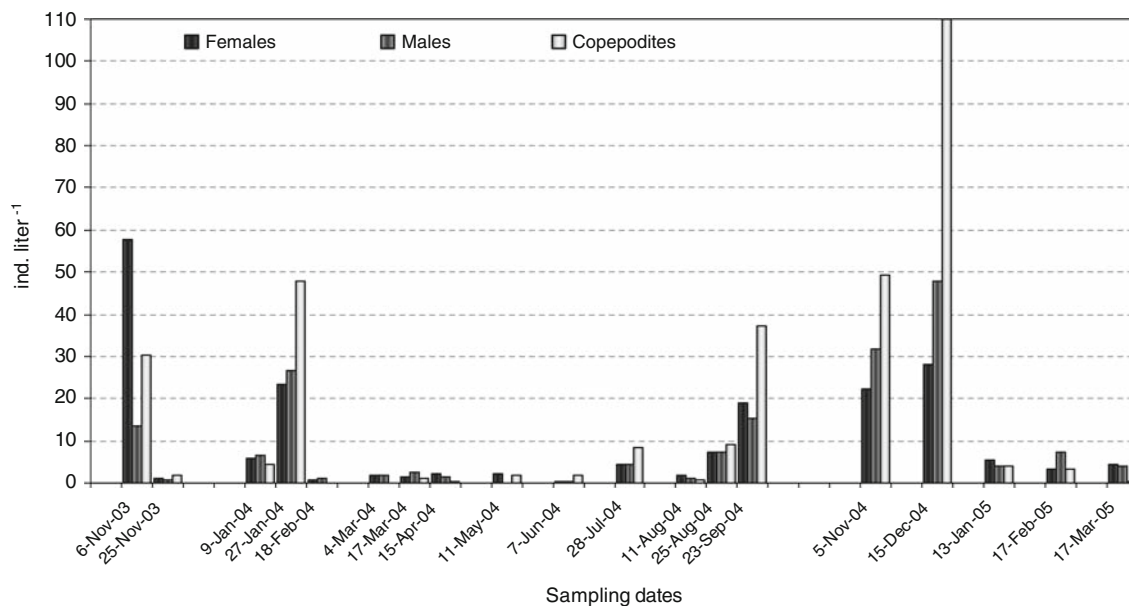
### Sampling area

Lake Faro (Surface area 263,600 m<sup>2</sup>, max depth 28 m) is a coastal basin located on the north-eastern tip of Sicily (Central Mediterranean). It has typical features of a meromictic basin, i.e. an oxic epilimnion and an anoxic hypolimnion, characterized by large fluctuations in physico-chemical parameters, especially temperature (10–28°C), salinity (34–37 psu) and dissolved oxygen (ranging from absent, near the bottom in the central area, to 8.3 mg/l at the surface along the shore). These layers are separated by a metalimnion, within which strong blooms of anoxygenic phototrophic bacteria cause the periodic development of a red water layer (Genovese 1963; Truper and Genovese 1968).

### Sampling methods and experimental plan

The “fouling” material, generally represented by organisms such as ascidiaceans, polychaetes, bryozoans, and copepods, attached to submerged ropes (max 0.5–1 m length), was collected manually, about once or twice a month, from November 2003 to March 2005 (with a gap between Nov. ‘03 and Jan. ‘04) at a fixed station situated in the centre of the lake. Submerged ropes to which fouling organisms were attached were directly put in a plastic container with environmental water and whole ropes were subsequently cut upon arrival to the laboratory a few hours later. In the laboratory, specimens of *P. xiphophorus* were counted and sorted from “fouling” washing-water by a stereoscopic microscope and transferred to an aquarium with 100 ml of filtered sea water. The aquarium was placed in a thermostatic-cell at 18°C. In the aquarium, specimens of *P. xiphophorus* were reared with a mixed diet given in excess concentrations and constituted by three phytoplankton species: *Tetraselmis suecica*, *Pavlova lutheri* and *Isochrysis galbana*. The volume of fouling samples was estimated by a gravimetric method: i.e. calculated by immersing the fouling material in a graduated beaker containing a known volume of distilled water and measuring the displacement. Abundance values of *P. xiphophorus* were expressed as individuals per liter of fouling samples (ind. l<sup>-1</sup>).

In a first set of experiments, a significant number, (ranging from 2 to 16 females depending on their abundance in the samples), of freshly caught adult *P. xiphophorus* females were sorted from fouling washing water and pipetted individually into 50 ml crystallizing dishes containing lake water filtered through 0.45 µm mesh net to remove all eggs and nauplii; females were then incubated at the same environmental temperature measured at the time of sampling. After 24 h, the number of eggs released by each female was counted to estimate in situ egg production,



**Fig. 1** Temporal fluctuations in *P. xiphophorus* female, male and copepodid abundances

according to the method used by Dagg (1978), Kimmerer (1984), Runge (1984), and Beckman and Peterson (1986) for studying in situ egg production. Studies by Tester and Turner (1990) have shown that short-term incubations (i.e. 24 h) with ambient bay water will not be affected by the potential artefact caused by a lag in conversion of food to eggs.

In a second set of experiments, groups of five female and male couples were placed as individual pairs into 50 ml crystallizing dishes containing filtered sea water enriched with three phytoplankton species, *T. suecica*, *P. lutheri* and *I. galbana*, given in excess concentrations. Couples of females and males were taken from the aquarium when they reached the CIV-CV stage and placed individually in crystallizing dishes. These dishes were checked frequently for moults in order to monitor the initial fertilization and spawning of females. Groups of five replicates were incubated at the following different temperatures: 12, 16, 20, 24, 28, 30, 32 and 34°C for each replicate. Each couple was monitored daily during its entire life span to measure egg production rates and hatching success in relation to temperature, and in order to observe egg-laying behaviour.

Eggs, nauplii and copepodites from each parental couple were monitored until adulthood. Recruitment rates were calculated by estimating the percent ratio between the copepods that survived to adulthood and nauplii that hatched from eggs.

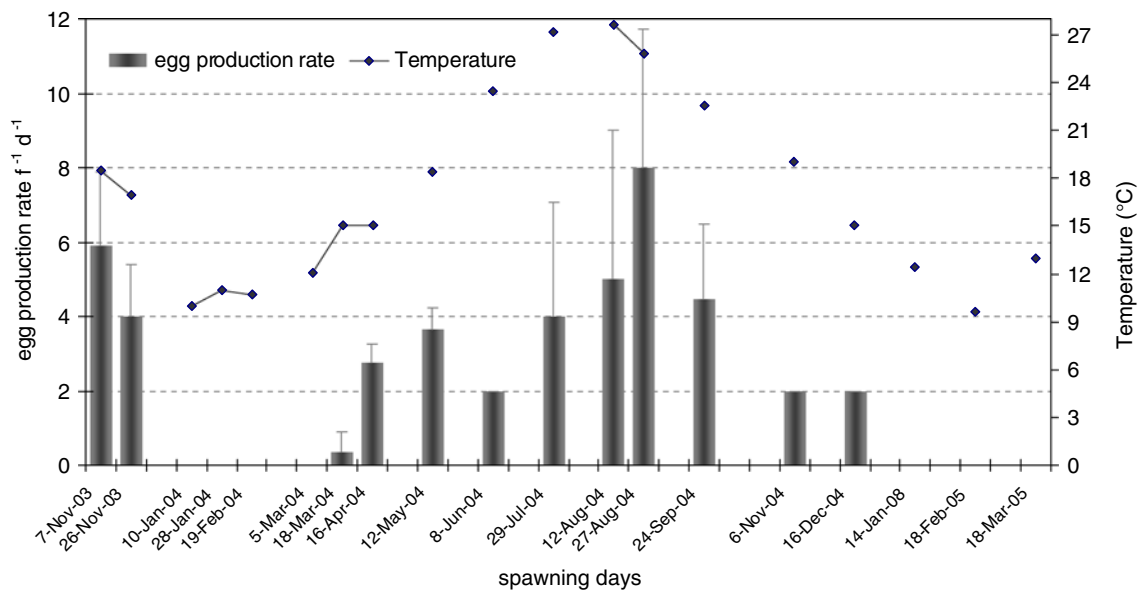
In order to study remating behaviour of *P. xiphophorus*, another group of five replicates was incubated under the same experimental conditions and diet, and incubated at 16°C. In these replicates, each male was immediately

removed after the first fertilization (when the first spermatophore was attached by males to the first abdominal segment of females). In these experiments, egg production and hatching success of females maintained in the absence of males were monitored daily. When females had completely stopped producing eggs, males were replaced into cultures containing females. Egg production rates and hatching success measured for these groups of replicates were compared to ones obtained from females maintained in the presence of males during their entire spawning period at 16°C.

## Results

*Pseudocyclops xiphophorus* showed marked seasonal fluctuations in population abundances. The timing of low- and high-density phases for adult females, males and juveniles are shown in Fig. 1. Peak abundances of adults and copepodites were recorded in November 2003 (72.8 and 31.7 ind. l<sup>-1</sup> of fouling samples, respectively) and December 2004 (76.0 and 110.0 ind. l<sup>-1</sup> of fouling samples, respectively). After January, population abundances showed a sharp decline, excluding a slight increase in March, with very low adult abundances and an almost complete absence of copepodites in spring and early summer. Population densities began increasing again in the second half of July.

In situ seasonal fluctuations in daily egg production rates (Fig. 2) were clearly different compared to abundance oscillations in that highest rates coincided with periods of low adult and juvenile densities and vice versa. However, higher mean daily egg production rates were coincident with



**Fig. 2** Temporal fluctuations in in situ mean daily egg production rates female<sup>-1</sup> day<sup>-1</sup> in relation to environmental temperatures

higher abundances of adults and juveniles in November. In this month, in situ mean daily egg production rates reached a maximum of 4–5 eggs female<sup>-1</sup> day<sup>-1</sup>, when the surface water temperature was 17–18°C. Mean daily egg production rates declined drastically in winter and were completely arrested when surface temperatures dropped to 10–12°C. In the second half of March, mean daily egg production rates began to increase again with an increase in ambient temperatures, reaching a maximum (8 ± 3.7 eggs female<sup>-1</sup> day<sup>-1</sup>) at the end of August.

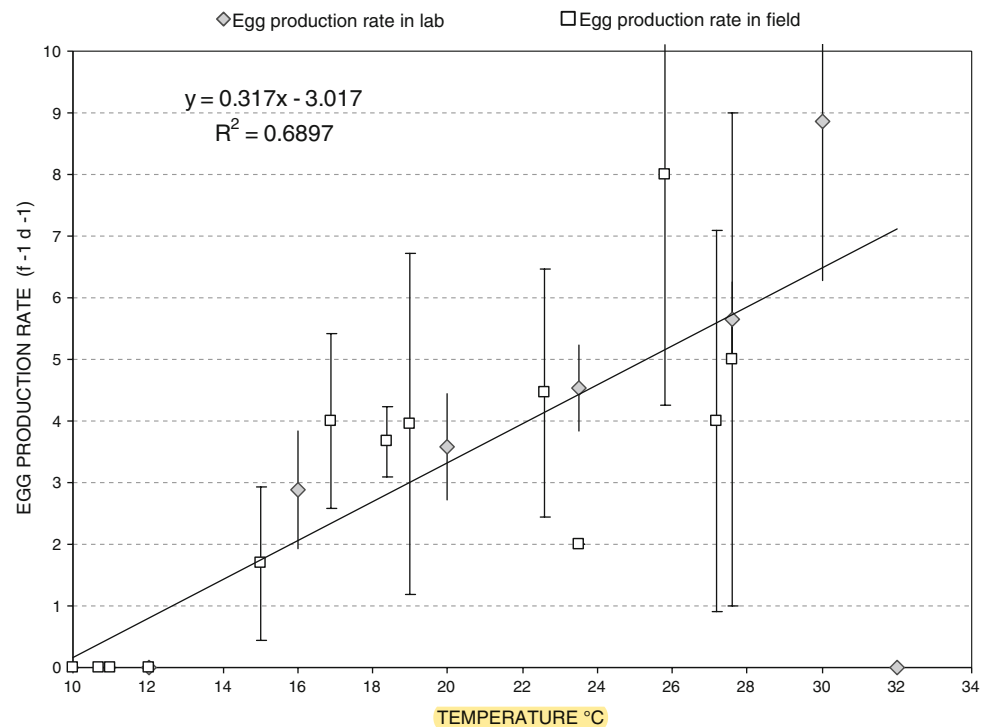
In the laboratory, as in field, mean daily egg production rates were positively correlated with temperature (Fig. 3) and significantly different at each temperature (1-way ANOVA,  $F = 49.35$ ,  $p < 0.01$ ). Mean daily egg production rate was  $2.2 \pm 0.3$  (16°C),  $3.6 \pm 0.9$  (20°C),  $4.5 \pm 0.7$  (24°C),  $5.6 \pm 0.6$  (28°C) and  $8.9 \pm 2.6$  (30°C) (mean ± S.D.) eggs female<sup>-1</sup> day<sup>-1</sup>. At 12 and 32°C, *P. xiphophorus* females survived but did not reproduce. At 34°C, all specimens died after a few days. Mean daily egg production rates showed marked oscillations throughout the spawning period (Fig. 4). At almost all tested temperatures, spawning rates could be characterized by three phases: a first phase with low initial daily egg production rates; a second phase in which fecundity reached maximum levels allowed by each temperature, and a last phase characterized by a more or less slow decline in daily egg production (Fig. 4). The same figure also reports mean daily egg production rates and percentage hatching success at different temperatures. In general, hatching success was very high and ranged from 99.7% at 20°C to 94.6% at 16°C. Hatching success was lower at 16°C but never decreased below 50%.

Under laboratory conditions, mean daily egg production rates were considerably lower than those observed in the field. In August, females produced a mean of eight eggs per day in situ, compared to in the laboratory where 5.6 eggs per day were produced at the same temperature (Fig. 3, August temperatures = 27.6–25.8°C). Maximum values for mean life time egg production occurred at 16°C ( $391.0 \pm 109.3$  eggs female<sup>-1</sup>) and minimum at 24°C ( $192.6 \pm 31.6$  eggs female<sup>-1</sup>). At the other temperatures, life time egg productions showed an increasing trend:  $225.5 \pm 3.59$ ,  $240.7 \pm 5.64$  and  $269.3 \pm 8.89$  eggs female<sup>-1</sup>, respectively at 20, 28 and 30°C.

Temperature dramatically affected female life span, which was  $178 \pm 24.30$  days at 16°C,  $79.0 \pm 1.15$  days at 20°C,  $52.0 \pm 4.16$  days at 24°C,  $46 \pm 6.08$  days at 28°C and  $28 \pm 6.43$  days at 30°C (Fig. 5).

Development times of eggs decreased with increasing temperatures: eggs hatched after 96 h at 16°C, 72 h at 20°C, 48 h at 24°C, 24 h at 28°C and 12 h at 30°C (Fig. 6a). Development time from egg to adulthood showed a similar trend. *P. xiphophorus* reached adulthood in  $43 \pm 6.8$ ,  $38.7 \pm 5.5$ ,  $19.3 \pm 3.2$ ,  $14.3 \pm 1.5$  and  $12 \pm 1.0$  days, at 16, 20, 24, 28 and 30°C, respectively (Fig. 6b). Longevity was inversely correlated to temperature and increased with decreasing temperatures: 224.7, 120.3, 73.7, 61.3 and 40.8 days at 16, 20, 24, 28 and 30°C, respectively (Fig. 6c). Development time and longevity at 12 and 32°C were not obtained during laboratory experiments but interpolated from the straight regression line (Fig. 6a–c). In the laboratory, recruitment rates were very low but showed a positive correlation with temperature (Fig. 6d). Values ranged from

**Fig. 3** Relationship between mean egg production rates female<sup>-1</sup> day<sup>-1</sup> in field and laboratory experiments and temperature



a maximum of  $28.5 \pm 13.2\%$  at  $28^\circ\text{C}$  to a minimum of  $7.1 \pm 3.8\%$  at  $16^\circ\text{C}$ . High recruitment rates ( $17.0 \pm 6.9\%$ ) were also obtained at  $30^\circ\text{C}$ , but lower values ( $8.7 \pm 1.73$  and  $8.8 \pm 3.8\%$ ) occurred at  $20$  and  $24^\circ\text{C}$ , respectively.

### Egg-laying behaviour

Egg-laying behaviour in this species is unique. *P. xiphophorus* females release eggs more or less continuously throughout the day, 2–3 days after achieving maturity, almost until the end of their life. Females do not release eggs directly into the water; instead, after a pair of eggs is extruded from the paired gonopores, the female swims with a pair of eggs attached on either side of the genital double-somite until the eggs are released by a rapid urosome stroke. After releasing the egg pair, the female swims over them with a rotatory motion, probably secreting a substance, which facilitates the adhesion of the eggs to the bottom of the Petri dish or to any hard surface, such as wood fragments, nylon filaments, filamentous algae, leaves, etc. The female continues to swim over the eggs until they are attached.

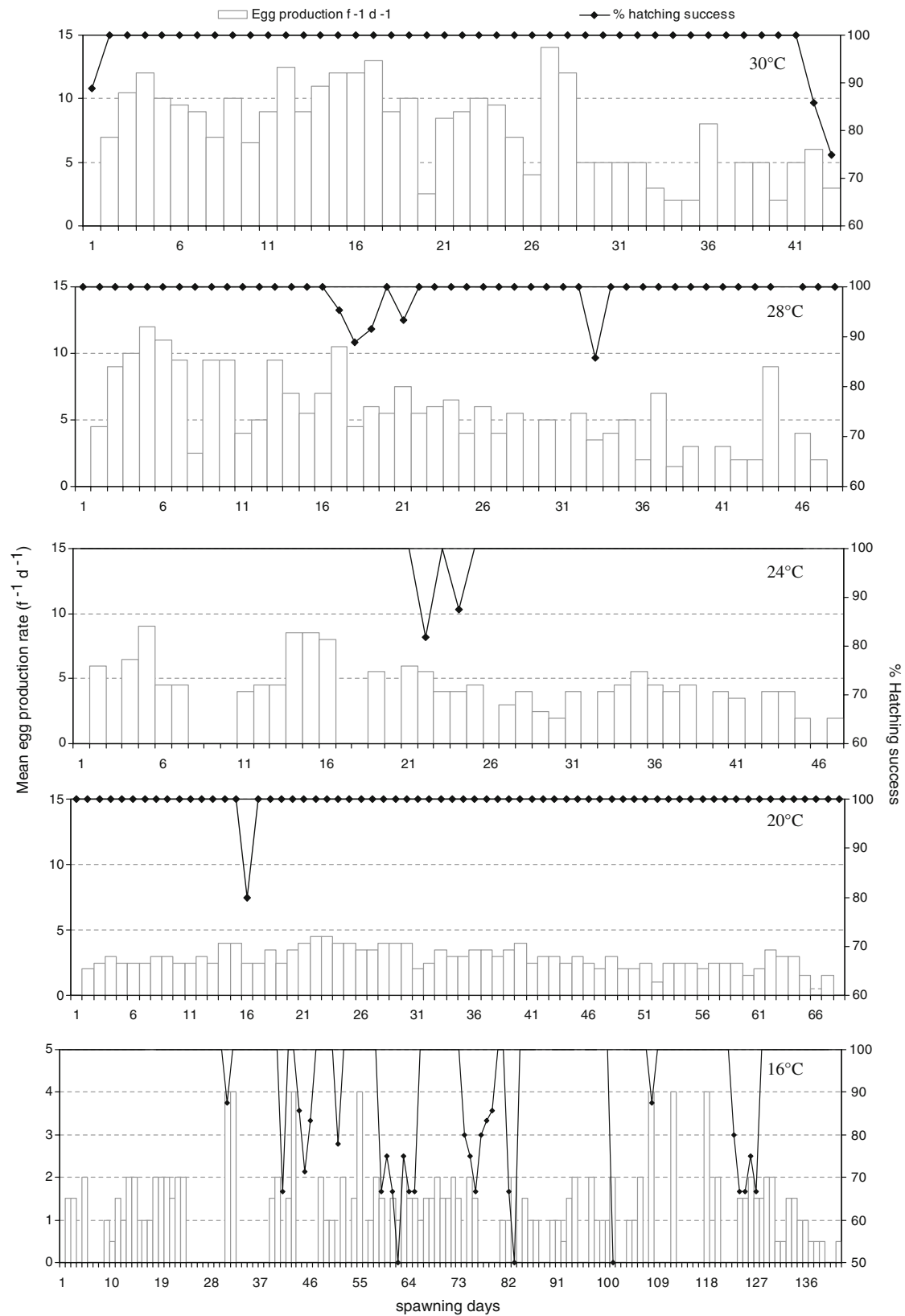
### Remating behaviour at $16^\circ\text{C}$

Laboratory studies at  $16^\circ\text{C}$  showed that *P. xiphophorus* females required remating for the continued production of fertile eggs. All females continued laying fertile eggs for

50–60 days after removal of males. Egg laying began to decline with the production of unfertilized eggs until spawning was completely arrested. Mean daily egg production rates were significantly different (1-way ANOVA,  $F = 76.89$ ;  $p < 0.01$ ) when females were maintained in the absence of males, or when females and males were kept as couples (Fig. 7a). Hatching success declined to zero after 60–61 days from the first fertilization, but returned to 100% upon reintroduction of a fresh male into containers on day 61 (Fig. 7b). Fecundity and hatching success of single females were significantly lower than female and male couples. When males were placed into containers with females (marked by arrows in Fig. 7a, b), all of the females reinitiated the production of fertile eggs even though the average number of eggs produced per female was lower than for females always maintained with males. After the reintroduction of males, the percentage of viable eggs was on average 96.6%. Female and male couples showed even higher egg viability (99.3%, Fig. 7b).

### Discussion

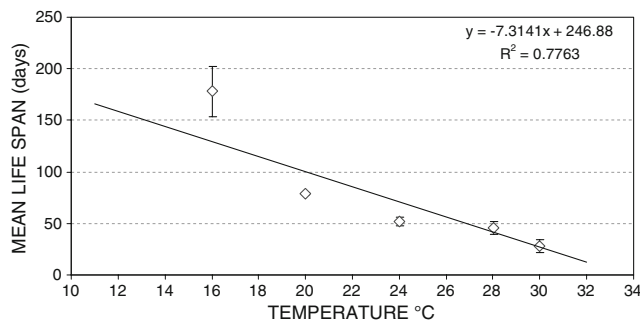
The present paper represents a detailed contribution to the understanding of mean daily egg production rates and several life cycle parameters of *P. xiphophorus*, reared in the laboratory and studied in situ. Highest abundances in this species were recorded in autumn and early winter. However, we found a mismatch between highest reproductive rates in summer and maximum population densities



**Fig. 4** Mean daily egg production rates and percentage hatching success at 30, 28, 24, 20 and 16°C. X-axes are different because the spawning period varies at different temperatures. In 16°C plot, also

principal and secondary y-axes are different to the others to make data better appreciable





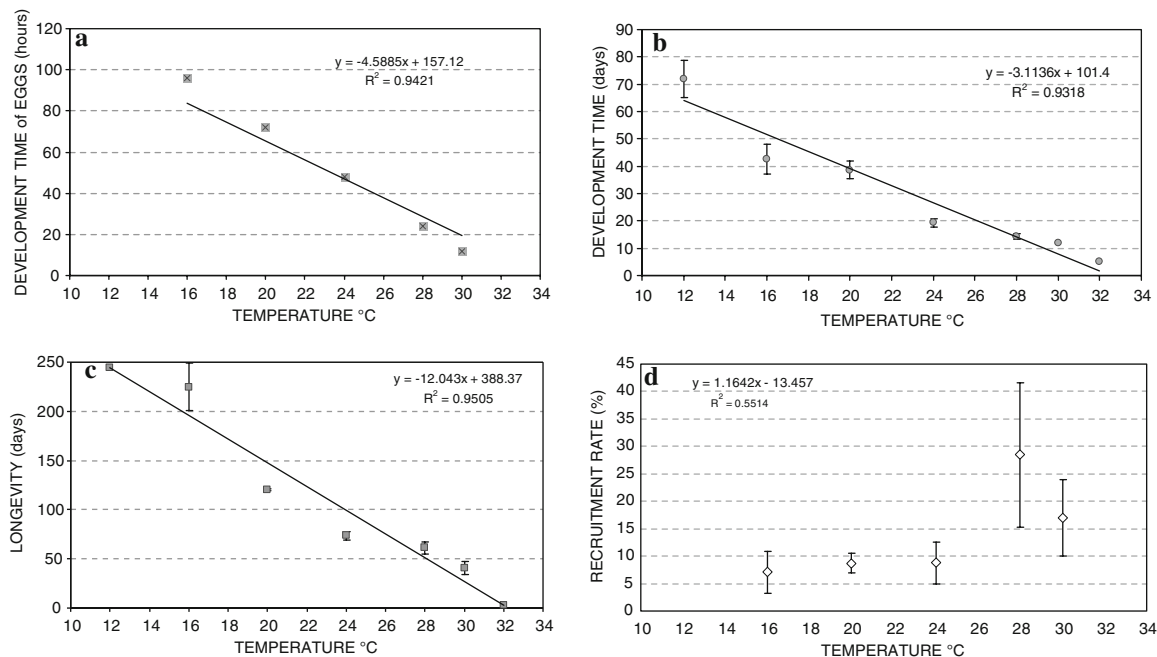
**Fig. 5** Relationship between temperature and mean life span (in days) of females reared in the laboratory

3 months later. These findings are similar to those reported for *Centropages typicus* in the Atlantic Ocean by Smith and Lane (1985), who observed a mismatch of  $\approx 2$  months between maximum egg production rates and adult female densities. Ianora and Buttino (1990) demonstrated an even stronger mismatch and quasi-inverse relationship between reproductive rates and population abundances of Mediterranean populations of *C. typicus* and *Acartia clausi*, with maximum daily egg production rates from autumn to spring when environmental densities of these species were low. In contrast, other authors have reported a concurrence between adult female abundances and daily egg production rates as in the case of Japanese populations of *A. clausi* (Uye 1982). We found such a concurrence only in November, when high fecundity coincided with high population densities of

*P. xiphophorus* females, possibly allowing this species to overwinter at low temperatures as adults or advanced copepodites. This life strategy would allow *P. xiphophorus* populations to survive without resting egg production which this species does not seem to produce, at least under our different experimental and temperature conditions. Smith and Lane (1985) demonstrated how *C. typicus* spends the cooler season as CV and that this temporal pattern is similar to that reported for *Rhincalanus nasutus*, *Pseudocalanus* sp., and *Paracalanus parvus* (Laundry 1983).

At the end of autumn, an increment in population numbers is followed by a drastic decline in daily egg production rates which continues into late spring. In winter and spring, low temperatures affect egg production which stops altogether at 12°C. This might result in the scarce abundance of copepodites and adults of *P. xiphophorus* recorded in spring and early summer. However, this scarce occurrence of adults could also be due to lower recruitment rates at lower experimental temperatures. This species shows maximum daily egg production rates in summer when environmental temperatures range from 26 to 28°C.

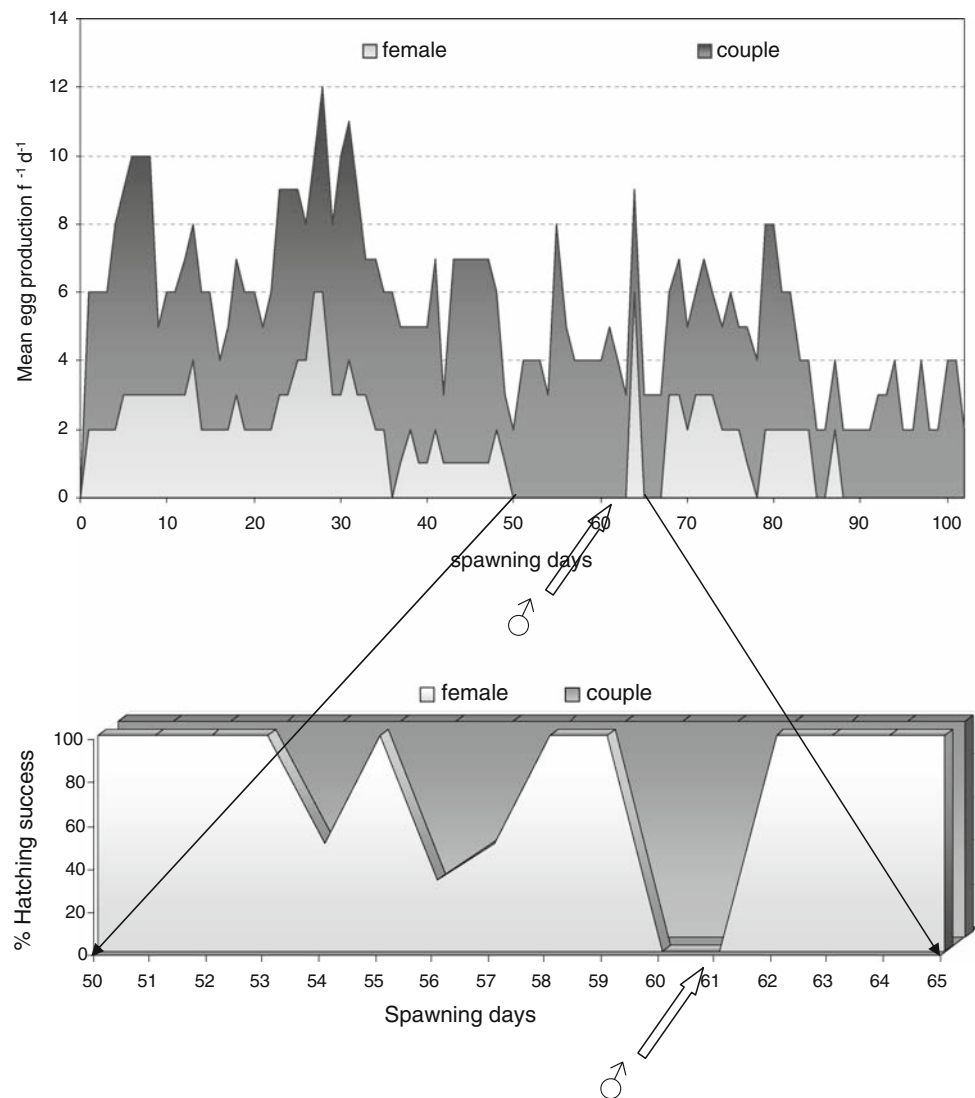
As demonstrated by Uye (1981) for *A. omorii*, at higher temperatures, although the average number of eggs produced per female per day of *P. xiphophorus* is higher, the period of egg-laying is reduced. Consequently, life time egg production is lower. Average number of eggs is higher because of the acceleration in the metabolic activity and accumulation rate of material in the developing oocytes so



**Fig. 6** Relationships between temperature and: (a) mean development time of eggs (in hours); (b) development time (in days) from naupliar stage to adulthood; (c) longevity (in days) and (d) recruitment rate (%)

in laboratory experiments at different temperatures. Development time and longevity at 12 and 32°C were not obtained during laboratory experiments but interpolated from the straight regression line

**Fig. 7** Comparison between (a) mean daily egg production rate female<sup>-1</sup> day<sup>-1</sup> and (b) percentage hatching success at 16°C in females maintained in absence of males and couples of female and male, for a 15-day egg laying period (from 50th and 65th days of the spawning period). Reintroduction of males is marked by white arrows



that egg production is higher and spawning intervals are shortened (Uye 1981).

In the field, *P. xiphophorus* egg production showed a lower temperature limit (12°C) below which the species was unable to produce eggs and an optimal temperature range (16–30°C), at which *P. xiphophorus* daily egg production rate reached its maximum. This optimum temperature range seems to be higher than that reported for most common subtemperate copepod species, ranging from ca. 15°C for *C. typicus*, *Temora stylifera* and *Temora longicornis* (Abou Debs and Nival 1983; Van Rijswijk et al. 1989), to 20°C for *Acartia tonsa* and *Sinocalanus tenellus* (Kimoto et al. 1986). *P. xiphophorus* has lower daily egg production rates than most planktonic calanoid copepods in subtemperate regions (Ianora 1998), but these values are very similar to those of another benthoplanktonic congeneric species, *Pseudocyclops umbraticus*, described for this region (Zagami et al. 2003).

Although these calanoid benthoplanktonic species have low egg production rates, they are able to survive in restricted habitats where interspecific competition is high, mainly with harpacticoid copepods. The peculiar spawning behaviour of *P. xiphophorus*, whereby females could secrete a substance that favours the adhesion of eggs to the substrate, contributes to differentiate this species from free-spawning and egg-carrying calanoids. This egg-laying behaviour could represent an adaptation to a benthic habitat in order to guarantee higher survival rates of the egg stages compared to other planktonic free-spawning and egg-carrying calanoid species (Kiørboe and Sabatini 1994), thereby compensating for its low population abundance and reproductive rates. By carrying the eggs the female would be less susceptible to visual hunting predators (Webb and Weaver 1988). What makes the egg-laying behaviour in *P. xiphophorus* unique is that the female continues to swim over its eggs until they are attached to the substrate. To our knowledge



this egg laying behaviour has never been observed before for copepods.

Our data indicate that remating is necessary for the continued production of fertile eggs at 16°C. The egg-laying cycle may be longer at lower temperatures, so that a single insemination is insufficient to fertilize the total eggs produced by a single female. Hence, *P. xiphophorus* females are capable of producing viable clutches from a single insemination only at higher temperatures, but remating is necessary for continued reproduction at lower temperatures. These findings are therefore similar to those reported by Wilson and Parrish (1971) and Parrish and Wilson (1978) for female *A. tonsa* which requires remating at temperatures between 17 and 19°C. In a number of remated *A. tonsa* females, 70% of all eggs laid after 24 h were infertile. Egg viability reached values up to 100% for about 14 days before values began to decline again. *P. xiphophorus* females reinitiated the production of fertile eggs within 24–48 h after the reintroduction of males. Uye (1981) also reported that a single mating was not sufficient to maintain high egg viability for *A. clausi* and that remating resulted in the 100% hatching of the eggs. Also female *T. stylifera* maintained for longer than 3–4 days in the absence of males produced infertile eggs mainly (Ianora et al. 1989). Marshall and Orr (1952) and Runge (1984) demonstrated that a single insemination was sufficient to fertilize the total eggs produced by females of the species *C. finmarchicus* and *C. pacificus*, respectively.

Laboratory experiments generally, resulted in lower egg production rates than field conditions. It is reasonable to assume that temperature was not the only factor affecting egg production, but that food quality and availability may also have caused differences in fecundity between field and laboratory data. Because food was given in excess concentrations, such differences were probably due to a deficiency in the diet. Kleppel et al. (1991) demonstrated that mixed diets were more effective in increasing fecundity and that the combination of a dinoflagellate and ciliate diet contributed more than single diets to improved egg production, allowing nutrients lacking in one food source to be supplemented by others. In natural conditions, *P. xiphophorus* may benefit from a mixed diet consisting in planktonic diatoms, dinoflagellates and ciliates and benthic food types since this species migrates from its fouling habitat into the overlying water column at night (Zagami et al. 2008). Since the biology and ecology of this peculiar group of benthopelagic calanoid species is poorly known, further studies are currently under way to clarify its trophic requirements. Studies on the effects of different food items on egg production and hatching success of *P. xiphophorus* have already demonstrated different responses to different phytoplankton diets (Brugnano et al. 2008).

When compared to other more abundant pelagic copepods, this species is much less fecund even though maximum daily egg production rates (8 eggs female<sup>-1</sup> day<sup>-1</sup> at 30°C) are within the range of values reported for egg-carrying species (Mauchline 1998). The high hatching success and peculiar egg-laying behaviour of *P. xiphophorus* may also contribute to higher survival rates of egg stages compared to free-spawning species (Kiørboe and Sabatini 1994). The greater fecundity at higher temperatures compared to other subtemperate species which generally show maximum egg production rates at 15–20°C (Ianora 1998) indicates that the species is well adapted to the higher temperatures of coastal lagoons and brackish water lakes where it contributes to the biofouling community.

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