Life history and population dynamics of the marine cladoceran *Penilia avirostris* (Branchiopoda: Cladocera) in the Catalan Sea (NW Mediterranean)

D. ATIENZA[1]*, E. SAIZ[1], A. SKOVGAARD[2], I. TREPAT[1] AND A. CALBET[1]

[1]INSTITUT DE CIÈNCIES DEL MAR (CSIC), PASSEIG MARÍTIM DE LA BARCELONETA 37-49, 08003 BARCELONA, SPAIN AND [2]DEPARTMENT OF BIOLOGY, SECTION OF PHYCOLOGY, UNIVERSITY OF COPENHAGEN, ØSTER FARIMAGSGADE 2D, DK-1353 COPENHAGEN, DENMARK

*CORRESPONDING AUTHOR: datienza@icm.csic.es

Penilia avirostris is a cosmopolitan marine cladoceran that inhabits coastal and shelf waters of most low and mid latitude ecosystems. In this study, we describe the life history and population dynamics of P. avirostris at a fixed coastal station in the NW Mediterranean Sea. This marine cladoceran was very seasonal, having population maxima in summer (2500–3000 ind m⁻³), and being practically absent from the water column for the rest of the year. The population typically collapsed in late summer–early autumn, and this decline was accompanied by a shift to gametogenetic reproduction, allowing the production of resting eggs to ensure the continuity of the species in the following season. Estimated birth rates of P. avirostris in the Catalan Sea ranged between 0.097 and 0.46 day⁻¹ and seemed to be decoupled from changes in P. avirostris standing stocks. Birth rates were mainly dependent on the changes in abundance of embryo-carrying females and their brood size, because during the period of population plateau the temperature-dependent embryonic developmental time was rather similar (2.3–2.7 days). Neonates are like miniature adults and need a very short period of growth and moulting to reach the reproductive stage. This life-history trait can explain the fast blooming and dominance of plankton communities by P. avirostris under suitable conditions. Finally, the causes for the seasonal decline of P. avirostris populations are also discussed.

INTRODUCTION

Cladocerans play a major role in freshwater ecosystems (Richman, 1958; Lampert, 1987), but have not been very successful in colonizing the marine environment. Such colonization requires the evolution of adaptation mechanisms at the morphological, physiological and behavioral level (Critescu and Hebert, 2002). The acquisition of a closed brood pouch to keep the embryos in a suitable nourishing environment, the presence of a resting egg provided with a thick wall instead of an ephippium and the predatory grasping mode in most species instead of filter-feeding seem to be essential features linked to this colonization by cladocerans (Lochhead, 1954; Aladin and Potts, 1995; Critescu and Hebert, 2002). In this sense, *P. avirostris* is a rarity within marine cladocerans for being the only filter-feeding representative, in clear contrast to the broad presence of this feeding strategy in freshwater cladocerans.

Penilia avirostris is a seasonally abundant and widely distributed cladoceran in neritic tropical and subtropical waters, expanding its distribution towards northern temperate latitudes since the mid-20th century (Lochhead,

1954; Della Croce and Venugopal, 1973; Johns *et al.*, 2005). When abundant, *P. avirostris* may play an important role in marine food webs by concentrating organic energy of small plankton and making it available to consumers at higher trophic levels (Paffenhöfer and Orcutt, 1986; Turner *et al.*, 1988; Atienza *et al.*, 2006a). In this regard, previous field work showed that *P. avirostris* feed on a wide range of prey, mostly nanoplankton (2–20 μm), but also larger cells such as dinoflagellates and diatoms (Atienza *et al.*, 2006a). Moreover, *P. avirostris* plays an important role in the recycling of nutrients in the upper water column, actually contributing to the limitation by P to phytoplankton growth by excreting only N derivatives (Atienza *et al.*, 2006b).

In spite of the relevance of this species in the biogeochemical cycles, the information about its population dynamics is mostly limited to their abundance and seasonal distribution (Della Croce, 1964; Onbé and Ikeda, 1995; Tang *et al.*, 1995; Marazzo and Valentin, 2003a; Valentin and Marazzo, 2003; Wong *et al.*, 2004). These studies revealed that the temporal distribution of marine cladocerans is discontinuous during the year, with peaks of very high abundance followed by rapid decline and eventual absence from the plankton. Until now, the factors controlling this pattern remain unclear. Some authors suggest that temperature may play an important role in the population dynamics of *P. avirostris* (Onbé and Ikeda, 1995); however, other factors such as food availability, chemical composition of seston and photoperiod might be also relevant (Egloff *et al.*, 1997).

Although the general pattern of its population seasonal cycle is known, the difficulty of rearing these organisms in the laboratory has complicated the estimation of most of their reproductive parameters (Della Croce, 1964; Tang *et al.*, 1995; Marazzo and Valentin, 2003b; Wong *et al.*, 2004). The life cycle of *P. avirostris* is characterized by an alternation between gamogenesis and parthenogenesis. Their populations are initiated by the hatching of resting eggs, followed by peaks of high abundance when parthenogenetic females reproduce (Onbé, 1973, 1978). In marine cladoceran populations, gamogenetic individuals usually appear immediately after population maxima, coinciding with decreasing parthenogenetic reproduction. Gametogenetic reproduction produces resting eggs, which sink and remain on the sea bottom during the seasonal disappearance of the parental population from the water column (Onbé, 1985; Egloff *et al.*, 1997).

The general trend of population dynamics of *P. avirostris*, briefly described here, resembles that of many freshwater cladocerans (Threlkeld, 1987). However, in contrast to them, we lack deep knowledge about the reproductive characteristics of *P. avirostris* at each of the different phases of its seasonal cycle. Consequently, our objective was to study the seasonal distribution of the population of *P. avirostris* in the Catalan Sea (NW Mediterranean), taking special care to describe in detail the reproductive condition of the females during the seasonal cycle. We believe that certain aspects of *P. avirostris* life cycle should contribute to explain the explosive growth and sudden disappearance of this species from the water column. We also discuss here the influence that some biological and physical factors could have on the temporal variation of this species.

METHOD

Penilia avirostris population dynamics were studied from June 2003 to December 2004 at a near shore station located half a nautical mile off Port Olímpic, Barcelona (Spain, NW Mediterranean), characterized by shallow open sea waters. Zooplankton samples were collected biweekly, when it was possible, by hand pulling a microplankton net (53 μm mesh, 25 cm mouth diameter; without flowmeter) vertically from the bottom (38 m deep). The content of the cod end was preserved in borax-buffered formaldehyde at 4% final concentration. In addition, water was collected at a depth of 1 m with a transparent hydrographic bottle, temperature measured and the water transported in dark plastic jars to the laboratory for Chlorophyll *a* (Chl *a*) determination. Chl *a* was measured by filtering 75 and 150 mL onto GF/F Whatman and 5 μm pore-size polycarbonate nucleopore filters, respectively. The filters were analyzed fluorometrically after 24 h acetone extraction in darkness and cold. Further details on sampling and description of the zooplankton community can be found in Skovgaard and Saiz (Skovgaard and Saiz, 2006).

The total abundance of *P. avirostris* was determined by stereomicroscope counts of two 5 mL aliquots from each sample (sample volume: 250 mL), resulting in at least 300 individuals counted per sample. In addition, for each sample, 50 individuals of *P. avirostris* were randomly sorted, sized and staged. Organisms were classified into the following stages: juveniles (<500 μm), non-reproducing females, parthenogenetic female (with embryos), gametogenetic female (with resting eggs) and males. Body length (BL, from the tip of the head to the base of the caudal setae; Uye, 1982) was converted to dry weight (DW, μg C) using the length–weight relationship log (DW) = 2.66 log BL − 7.369 (Atienza *et al.*, 2006a) and assuming that carbon content was 50% of DW (Uye, 1982).

For each of the 50 individual sorted groups, all reproducing females (i.e. carrying embryos or resting eggs) were dissected carefully with thin needles under the

stereomicroscope, and the embryos or eggs in the brood pouch were removed, counted, examined and sized (BL for embryos; major axis for eggs). Resting eggs were easily identified because they are ovoid, flattened, with a thick chitinous membrane and are opaque (Fig. 1E), occupying the entire brood pouch. Parthenogenetic embryonic development was divided into four different stages based on the external morphology of the embryo, following the detailed description by Della Croce and Bettanin (Della Croce and Bettanin, 1965) and the simplified approach of Wong *et al.* (Wong *et al.*, 2004). Stage 1 corresponds to the parthenogenetic egg, ellipsoidal (although the posterior border of the head can be distinguished in the advanced phase), surrounded by an elastic membrane and almost completely filled with yolk granules (Fig. 1A). In stage 2, the cover membrane disappears, the second antenna starts to develop and the thorax region is differentiated (Fig. 1B). During stage 3, the embryo elongates, the second antenna is fully formed and the first antenna starts to elongate (Fig. 1C). At this stage, all the thoracic segments are visible, and sometimes rudiments of thoracic appendages are evident. Stage 4 embryos are similar to adults, with all the thoracic appendages completely formed, and the carapace and the eye fully developed (Fig. 1D).

Recruitment from parthenogenetical eggs was estimated from the population egg ratio (*E/N*, where *E* is

the number of parthenogenetic eggs and embryos recorded and N the total population size), using the Paloheimo (Paloheimo, 1974) equation for the instantaneous per capita birth rate (b, day^{-1}),

$$b = \ln((E/N) + 1)/D \qquad (1)$$

where D is the egg development time (in days). D was estimated from surface temperature in the water column using the equation of Bottrell (Bottrell, 1975) for freshwater cladocerans,

$$\log D = 0.847(\log T)^2 - 3.609 \log T + 3.796 \qquad (2)$$

where T is the temperature in degrees Celsius. The use of Bottrell's equation for *P. avirostris* seems to be warranted since Valentin and Marazzo (Valentin and Marazzo, 2004) compared field estimates of developmental time for *P. avirostris* at $24-26°C$ with Bottrell's equation predictions, and obtained similar values ($2-3$ days); other empirical estimations of embryo developmental time in the literature for *P. avirostris* embryos in natural conditions also fall in a similar range of values (ca. 2 days; Mullin and Onbé, 1992; Atienza *et al.*, 2007).
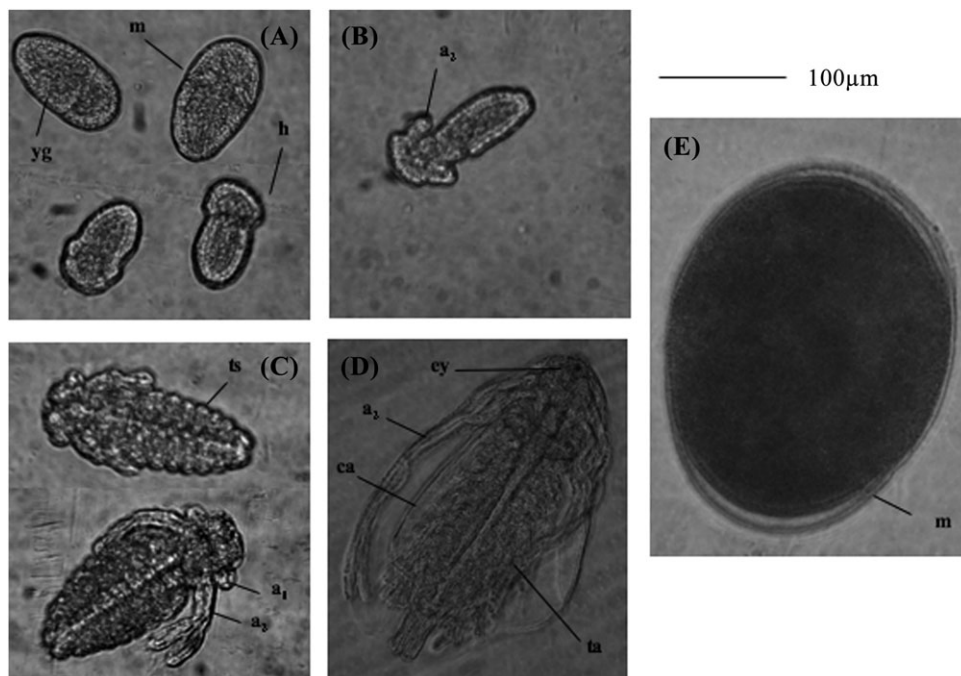
Fig. 1. Developmental stages of *P. avirostris* defined for this study. (**A**) stage 1; (**B**) stage 2; (**C**) stage 3; (**D**) stage 4; (**E**) resting egg. a₁, first antenna; a₂, second antenna; ca, carapace; ey, eye; h, head; m, membrane; ta, thoracic appendices; ts, thoracic segments; yg, yolk granules. Scale bar denotes 100 μm.

RESULTS

Figure 2 shows the temporal variation of surface temperature and Chl a concentration and $P.$ $avirostris$ densities during the study period. Temperature ranged from ca. 12°C in winter up to ca. 28°C in summer, and Chl a concentration showed peaks in winter, spring and early summer, depicting the typical pattern for the northwestern Mediterranean (Calbet et $al.$, 2001; Ribera D'Alcala et $al.$, 2004). During most of the year, $P.$ $avirostris$ was absent from the water column, the first individuals starting to appear at the beginning of July and reaching
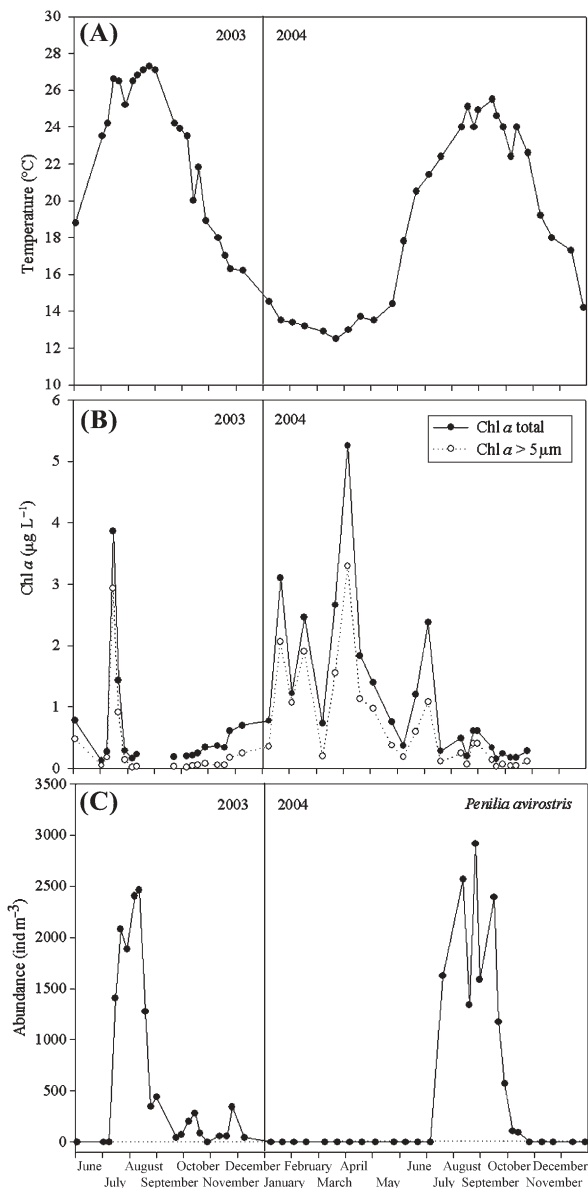

Fig. 2. Seasonal variation of surface water temperature (**A**), chlorophyll a concentrations (**B**) and $P.$ $avirostris$ abundance (**C**) in the coastal Catalan Sea during the study.

peak values by the end of the month (ca. 2500–3000 ind m^{-3}, Fig. 2C). This population of $P.$ $avirostris$ maintained until the end of August (2003) or September (2004), when suddenly declining in the water column to almost complete absence (followed in 2003 for sporadic low peaks, <500 ind m^{-3}, until December).

The temporal variation of $P.$ $avirostris$ population composition is shown in Fig. 3. During the phases of increase and the peaks of high abundance, the populations were evenly dominated by juveniles, non-reproducing females and parthenogenetic females (i.e. with embryos). When the populations were in the waning phase, males appeared followed by gametogenetic females (i.e. with resting eggs). This general pattern was common for both years, although in 2003 $P.$ $avirostris$ presence in plankton extended under very low levels until their complete disappearance (Fig. 3). During this period, juveniles represented a much lower fraction of the population compared with other periods, and the relative contribution of non-reproducing females was higher, indicating that recruitment during those peaks failed. Regarding females with resting eggs, they typically carried only one egg, except for two females carrying two eggs in 2003 (accounting for 12% of the gametogenetic females).

Table I and Fig. 4 show the BL of $P.$ $avirostris$ adults. Gametogenetic females were significantly larger than males and the other two female types. Mean sizes in 2003 were significantly larger (two-tailed t-test, Welch's correction, $P < 0.01$), partly as a consequence of the fact that the late autumn females in 2003 (absent in 2004) inhabited colder waters and were significantly larger than the summer ones (Fig. 4, Table II).

Brood size ranged from one to eight embryos per female and was positively correlated to female body size (2003: $r = 0.85$, $P < 0.001$; 2004: $r = 0.86$, $P < 0.005$; Fig. 5). Most females typically carried two to four embryos (Fig. 6), and the two-tailed t-test, Welch's correction confirms that there is no significant difference in mean brood size between 2003 and 2004 ($P < 0.01$). In terms of population dynamics, there was no clear change in the proportion of parthenogenetic females with embryos (relative to the total parthenogenic females) in the waning phases of $P.$ $avirostris$ populations (Fig. 7A), nor in female brood size through the population development (Fig. 7B). Interestingly, during the decllining phases, and even during the late peaks in 2003, a significant number of parthenogenic females were carrying embryos (Fig. 7C).

Embryo length increased with developmental stage (Table III), ranging from 86 to 315 µm. The latter stage set the smallest body size for the free living $P.$ $avirostris$ in
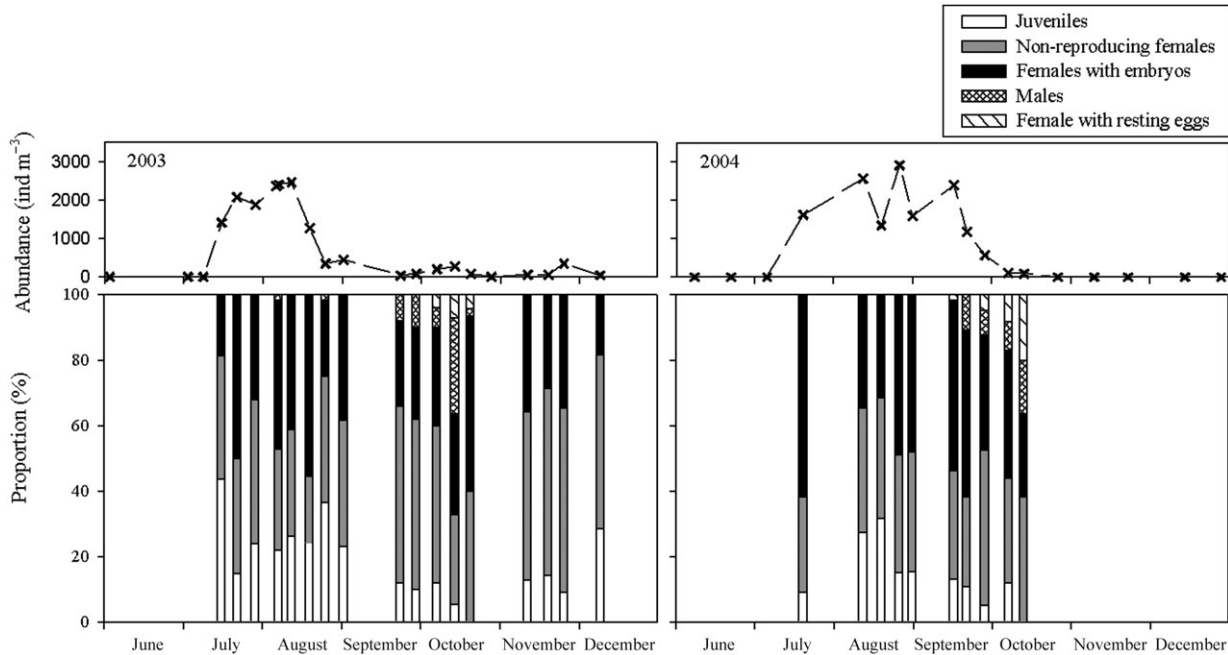
Fig. 3. Population composition (as %) of *P. avirostris* during summer 2003 (left panel) and 2004 (right panel). Abundance of *P. avirostris* from Fig. 2 is in the upper panels (dashed line) for the sake of the comparison.

the water column. No significant differences were found in embryo length between both years (two-tailed *t*-test, Welch's correction, $P < 0.05$). There was a negative correlation between embryo stage and brood size (2003: $r = -0.95$, $P < 0.001$; 2004: $r = -0.90$, $P < 0.001$; Fig. 8).

Finally, the estimated population egg ratios and the birth rates were very variable with values ranging between 0.54 and 3.64 embryos ind^{-1} and between 0.097 and 0.46 day^{-1}, respectively (Figs 9A and 9B). This variability reflected mainly the changes in abundance of embryo-carrying females and female brood size, whereas the embryonic developmental time, which

depended on the changes in surface water temperature during the seasonal occurence of *P. avirostris*, varied between 2.3 and 2.7 days. Birth rates were highest during the initial blooming period, thereafter showing diverse peaks not associated with changes in *P. avirostris* density (Fig. 9B). Actually, during the declining phases, the population birth rates were rather high.

Finally, we found that *P. avirostris* abundance, egg production, birth rates and mean brood size were positively correlated ($P < 0.05$) with temperature; also there was a negative correlation between temperature and the size of none-reproducing females and females with embryos. Chl *a* concentration was negatively correlated ($P < 0.05$) with *P. avirostris* abundance, size of none-reproducing females, egg production, birth rates and mean brood size (Table IV).

Table I: *Penilia avirostris comparative size (μm) of the different adult reproductive stages between years*

| Reproductive stage	2003			2004			
	Avg	SE	n	Avg	SE	n	
Non-reproducing females	632.3	5.01	353	606.03	5.31	188	*
Females with embryos	673.4	4.99	298	641.46	4.56	228	*
Males	651.1	8.93	31	629.05	16.71	23	
Females with resting eggs	799.8	16.66	8	721.92	11.41	19	*

Avg, average; SE, standard error; *n*, sample size.
*Significant at 0.01.

DISCUSSION

Penilia avirostris shows a pronounced seasonality in the Catalan Sea, with a sudden appearance in the water column in July due to rapid population growth until a dense population is established and maintained until the end of August–September, when standing stocks diminish. Whereas *P. avirostris* can be continuously present in the zooplankton community in tropical and subtropical latitudes (Della Croce and Venugopal,
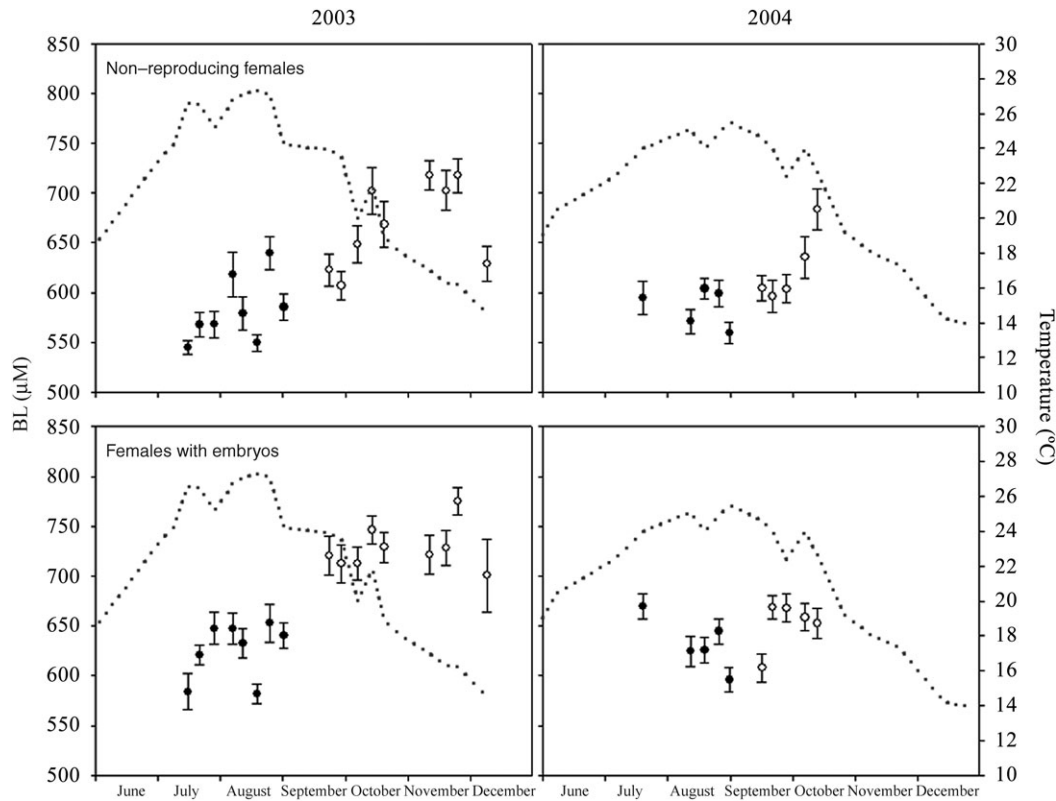
Fig. 4. Changes in BL of parthenogenetic females (non-reproducing and embryo-carrying) through the seasonal presence of *P. avirostris* in the Catalan Sea. Filled circles: summer samples (July–August); open circles: autumn samples (September–October–November). Dotted line is surface water temperature (from Fig. 2).

1973), in temperate ecosystems and specifically in the Mediterranean, the observed unimodal seasonal pattern is the typical one (Alcaraz, 1970; Siokou-Frangou, 1996; Calbet *et al.*, 2001; Ribera D'Alcalà *et al.*, 2004).

Table II: Comparative size (μm) of P. avirostris parthenogenetic females (females with and without embryos) between different periods in the same year

| Reproductive stage	Summer			Autumn			
	Avg	SE	*n*	Avg	SE	*n*	
2003	Summer			Autumn			
Non-reproducing females	583.4	5.68	142	666.1	6.56	211	*
Females with embryos	624.7	5.16	161	730.6	6.08	137	*
2004	Summer			Autumn			
Non-reproducing females	585.5	5.69	96	627.5	8.57	92	*
Females with embryos	635.6	6.33	122	648.2	6.55	106	

Avg, average; SE, standard error; *n,* sample size.
*Significant at 0.01.

The abrupt appearance and disppearance of the populations is very characteristic for marine cladocerans and reflects a typical opportunistic life history. In this regard, the life cycle of *P. avirostris* is characterized by two modes of reproduction, parthenogenesis and gametogenesis, which follows the general pattern exhibited by other marine and freshwater cladocerans (Egloff *et al.*, 1997). Related to both types of reproduction, two kinds of eggs are also produced by this marine cladoceran, a parthenogenetic egg and a thick-walled resting egg. Parthenogenetic eggs are thin-walled and relatively small (86 μm), gametogenetic females lay resting eggs, which are larger (279 μm), fewer in numbers, and contain yolk (Egloff *et al.*, 1997). In agreement with previous evidence, gametogenetic females in our study generally carried only one resting egg, except for the observation of two individuals carrying two resting eggs in the brood pouch. The outer membrane of the resting egg is calcified, which may enhance survival through the digestive system of potential predators (Onbé, 1985), and facilitates its fast sinking after release, which might act as an adaptation to prevent predation in the water column and reduce dispersal by advection (Egloff *et al.*, 1997). Resting eggs are capable of undergoing diapause,
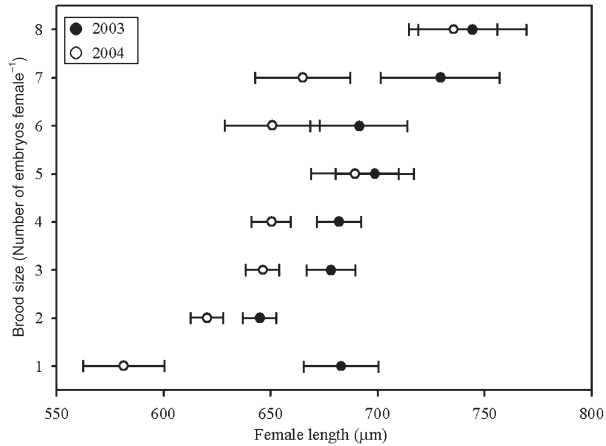
Fig. 5. Scatterplot of BL (µm) and brood size (number embryos female^{-1}) of *P. avirostris*.

carrying the populations through overwintering periods (Egloff *et al.*, 1997), and their distribution and abundance is a critical factor influencing the overall distribution, seasonal population dynamics, and long-term variations in the abundance of cladocerans (Viitasalo and Katajisto, 1994). In some regions, such as the Inland Sea of Japan, the seasonal fluctuations in the abundance of resting eggs of this marine cladoceran have been described in detail (Onbé, 1985), but data for the Mediterranean are more scarce. Moscatello and Belmonte (Moscatello and Belmonte, 2004) reported the presence of cladoceran resting eggs in Mediterranean sediments, and Sioko-Frangou *et al.* (Sioko-Frangou *et al.*, 2005) observed that *P. avirostris* resting eggs were more abundant (63–76 eggs m^{-2})
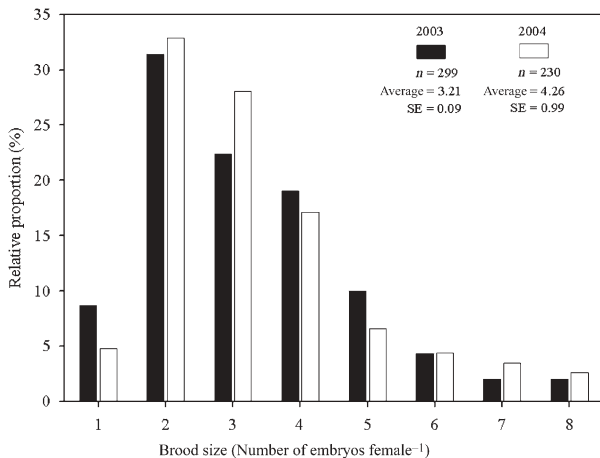

Fig. 6. Frequency distribution of brood size (number embryos female^{-1}) in the *P. avirostris* population in the Catalan Sea. Avg, average; SE, standard error; *n*, sample size.

in September and October, in agreement with the presence of gametogenetic females in the water column found in our study.

The observed brood sizes for parthenogenetic *P. avirostris* in the Catalan Sea are similar to previous reports for this species (Della Croce and Venugopal, 1973; Angelino and Della Croce, 1975; Tang *et al.*, 1993; Marazzo and Valentin, 2003a, b), although our highest values did not reach the 13 embryos per female recorded by Angelino and Della Croce (Angelino and Della Croce, 1975) in the Agulhas Bank and Knysna Lake (South Africa). Although brood size of marine cladocerans typically appears to be higher during the initial phases of population growth and decreases rapidly as population increases (Platt and Yamamura, 1986; Mullin and Onbé, 1992; Fofonoff, 1994), we did not find any clear relation during our study between either female brood size or population egg ratio and *P. avirostris* standing stocks. An interesting result was the negative correlation between the brood size and the brood stage of development (Fig. 8), which suggests the abortion and likely re-abortion of embryos, as described for podonids by Egloff *et al.* (Egloff *et al.*, 1997).

Fast recruitment of *P. avirostris* will depend on the actual birth rates, which in our study were rather variable and did not seem to be reflected in changes in population abundance (Fig. 9). However, one must be cautious with such interpretation, because much of the variability in *P. avirostris* abundance may merely reflect spatial variability (sampling was carried out at a single fixed station, see below). Evidence that spatial varibility exists was found in the data obtained by a parallel zooplankton survey study conducted during summer 2003 and 2004 covering the whole Catalan Sea shelf (four CACO cruises; Atienza *et al.*, in preparation). During those cruises, we found a high variability in *P. avirostris* abundance between station for the same sampling period, and, for example, through CACO-1 (July 2003) abundances ranged between 41 and 2491 ind m^{-3} between stations. The variability between stations was the same for the other three cruises and clearly indicated that spatial variability should be considered to explain the variation in the abundance of *P. avirostris*. For this reason, no attempt to estimate population growth and mortality rates has been made. In this regard, it is important to note that the observed variability in birth rates reflects essentially the variability in the population egg ratio, since during the periods of high standing stocks embryonic developmental times were rather similar (2.3–2.7 days).

Penilia avirostris must likely rely on the hatching of resting eggs to establish the new population annually because this marine cladoceran is practically absent
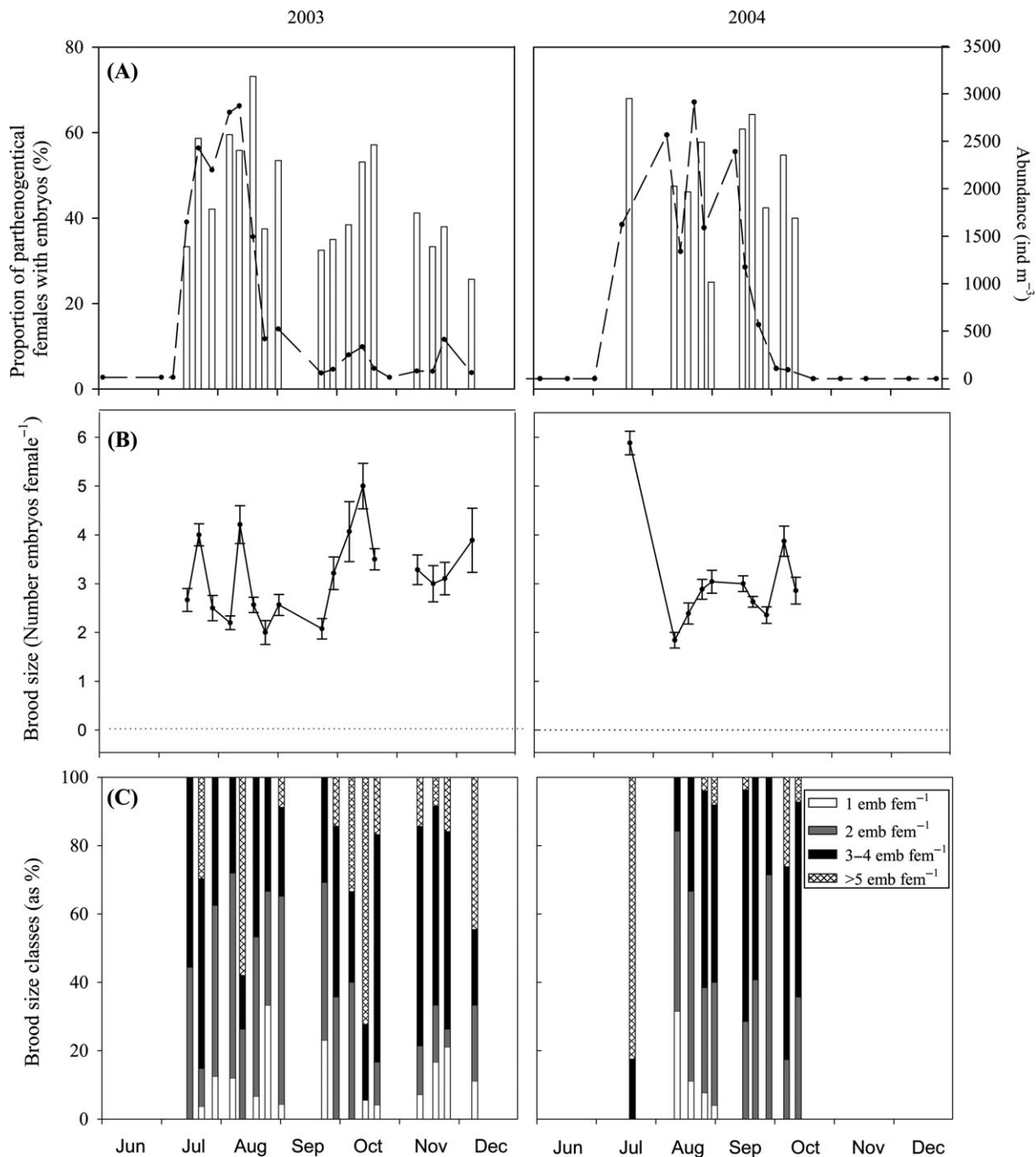
Fig. 7. (**A**) Proportion of parthenogenetic females carrying embryos in relation to total parthenogenetic females during the seasonal presence of *P. avirostris* in the Catalan Sea. Abundance of *P. avirostris* from Fig. 2 is overlaid (dashed line) for the sake of the comparison. (**B**) Variation of brood size (average ± 1SE). (**C**) Brood size class distribution (as %).

from the water column in winter and spring. Once certain threshold values in environmental variables are reached, parthenogenetic growth can explain the rapid development of the population. For instance, there is a 4-fold increase in volume between the egg (stage 1) and the neonate (stage 4), neonates being one-half to two-thirds to their eventual length as adults (Egloff *et al.*, 1997). This development allows the newly born *P. aviros-tris* to reach adulthood (reproductive period) in about 1 day (Atienza *et al.*, 2007). A simple calculation considering an average initial brood size of 4, an embryonic developmental time of 2 days (Mullin and Onbé, 1992;

Table III: Size (large axis, μm) of the different embryo stages of P. avirostris

Embryos stage	2003			2004		
	Avg	SE	n	Avg	SE	n
Stage 1	86.5	4.61	88	85.5	4.22	68
Stage 2	179.8	3.68	57	179.4	3.31	50
Stage 3	221.4	2.75	103	219.9	3.69	87
Stage 4	315.4	6.88	51	305.0	8.63	23
Resting eggs	282.3	14.97	8	277.2	2.99	1

Avg, average; SE, standard error; n, sample size. No significant differences were found.

Atienza *et al.*, 2007) and a period of 1 day from the neonate to the reproductive stage, suggests that every female may produce near 100 young individuals in 8 days. Atienza *et al* (2007) suggested that it was this short developmental time to the reproductive stage which allowed *P. avirostris* to rapidly appear and bloom in coastal environments in comparison with copepods, which have similar embryonic development times but much slower development to the reproductive adult stage.

The possible causes for the sudden disappearance of *P. avirostris* from the water column are not well understood. The decline in the annual population of cladocerans is typically accompanied by the onset of gamogenetic reproduction and the production of overwintering resting eggs. In natural populations, only a fraction of parthenogenetic females turn into gametogenetic females (i.e. *Evadne* spp.: 8–25%, *Pseudoevadne tergestina*: 5–10%, Onbé and Ikeda, 1995; *Pleopis polyphemoides*: 10–46%, Fofonoff, 1994; 20–23% *P. tergestina*: Onbé, 1978; 50–80% *Podon leuckarti*: Egloff *et al.*, 1997; and 25–60% *Evadne nordmanni*: Fofonoff, 1994).
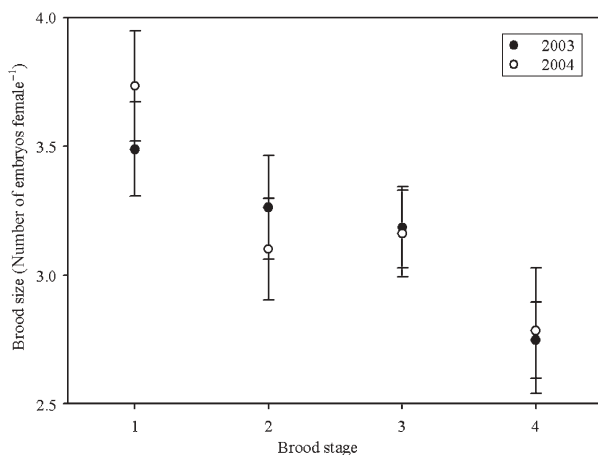

Fig. 8. Scatterplot of embryo stage and brood size of *P. avirostris*.

The fraction of gametogenetic *P. avirostris* females observed in our study is in the low range of values found for other marine cladocerans (4–8% in 2003; 1–20% in 2004), as also observed by Marazzo and Valentin (Marazzo and Valentin, 2003b) for *P. avirostris* in Brazilian waters (11–24%).

This shift from parthenogenetic to gametogenetic reproduction is an interesting phenomenon. In freshwater cladocerans, it is known that the appearance of males seems to be under hormonal regulation (Minelli and Fusco, 2006) and that crowding, photoperiod, temperature and food availability act as stimuli to induce gamogenesis in parthenogenetic females (Stross and Hill, 1968; Kleiven *et al.*, 1992; Carvalho and Hughes, 1983; Stross, 1987; Berg and Pálsson, 2001). Stross (Stross, 1965) suggested that at least two stimuli are necessary to induce gametogenetic reproduction. However, the causes that induce this shift from parthenogenetic to gametogenetic reproduction in marine cladocera are not fully understood (Fofonoff, 1994). Recent attempts to find evidence in freshwater cladocerans of the presence of the endobacterium *Wolbachia*, which is involved in the onset of parthenogenetic reproduction in many invertebrates (Stouthamer *et al.*, 1999) have failed (Fitzsimmons and Innes, 2005).

Environmental conditions seem to play a key role in the decline of populations at the end of the season (e.g. decrease in temperature, photoperiod, food availability, turbulence, crowding, predation; Frey, 1982; Fofonoff, 1994; Stross and Hill, 1968). *Penilia avirostris* populations in the Mediterranean Sea typically vanish in late summer–early autumn (Alcaraz, 1970; Lipej *et al.*, 1997; Calbet *et al.*, 2001; Ribera D'Alcalà *et al.*, 2004). The decline in *P. avirostris* population observed in 2003 (with some limited blooming in October and November) was premature in comparison with the 2004 data. Although *a priori* this fact could suggest variability in the timing of the onset of the factors triggering it, however, a parallel zooplankton survey conducted during summer 2003 and 2004 covering the whole Catalan Sea shelf (CACO cruises; Atienza *et al.*, in preparation) shows that the observed decline was a local event at our sampling station, associated with the intrusion of high saline oceanic waters into the central (and comparatively narrower) shelf of the Catalan Sea. Very likely the late peaks of *P. avirostris* in autumn 2003 reflect the receding of these oceanic waters in this area. Similar late peak events have been observed previously in the NW Mediterranean (Castellón waters, Alcaraz, 1970; Gulf of Trieste, Lipej *et al.*, 1997), although it is not known if the causes are similar.

Temperature has been proposed as the main physical factor that controls *P. avirostris* populations (Gieskes,
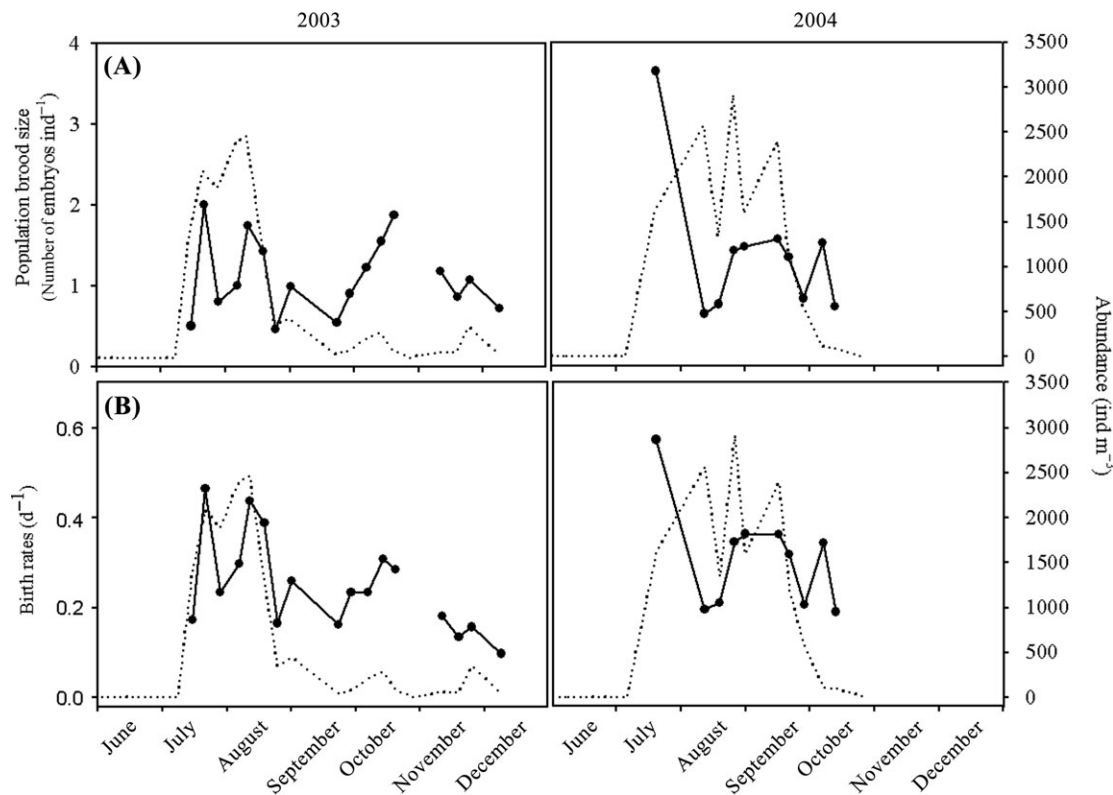
Fig. 9. (**A**) Population egg ratio (average number of eggs/embryos ind^{-1}) and (**B**) estimated birth rates (day^{-1}) of *P. avirostris* in the Catalan Sea. Dotted line, abundance of *P. avirostris*.

1971; Onbé and Ikeda, 1995). In general, populations of *P. avirostris* are often associated with warmer waters in the northern (Lipej *et al.*, 1997; Calbet *et al.*, 2001) and southern hemisphere (Resgalla and Montú, 1993), and we also found a positive correlation between the abundance of this marine cladoceran and temperature. However, this optimum range of warm temperatures where *P. avirostris* can reproduce and grow successfully appears to vary geographically. Some authors have

Table IV: Spearman's correlations between different P. avirostris population parameters and some environmental variables

	T	Chl *a* tot	Chl *a* > 5 μm
Abundance	0.78*	−0.43*	−0.46*
Size of non-reproducing females	−0.79*	−0.17	−0.56*
Size of females with embryos	−0.85*	−0.15	−0.43
Egg production	0.77*	−0.44*	−0.47*
Birth rates	0.72*	−0.51*	−0.51*
Mean brood size	0.44*	−0.43*	−0.47*

T, sea temperature; Chl *a* tot, total chlorophyll *a* concentration; Chl *a* > 5 μm, chlorophyll *a* > 5 μm concentration.
*Significant at $P < 0.05$.

pointed out that the distribution of *P. avirostris* is mostly restricted to waters above 18°C but can range between 12°C and 30°C (Kim *et al.*, 1994; Kim and Onbé, 1995), and it is known that this species has an optimum temperature around 25°C (China: Tang *et al.*, 1995; Japan: Onbé *et al.*, 1996). Recently, Johns *et al.* (Johns *et al.*, 2005) showed that this species is increasing in prevalence in the North Sea, where the sea surface temperature has been increasing over the last decade (more than 3°C, and reaching temperatures higher than 19°C).

Food availability has also been suggested to affect the seasonal dynamics of *P. avirostris*. Lipej *et al.* (Lipej *et al.*, 1997) and Calbet *et al.* (Calbet *et al.*, 2001) indicated that during warm periods (summer), the water column was stratified and the concentrations of nutrients and chlorophyll above the pycnocline are rather low, whereas pico- and nanoplanktonic autotrophs are abundant. *Penilia avirostris* is a filter feeder that ingests nanoflagellates preferentially (Atienza *et al.*, 2006a), and the higher abundance of these organisms results in a higher availability of food that is rapidly exploited. It is also important to notice that *P. avirostris* occurs mainly in coastal and shelf waters, where chain-forming diatoms

are typically an important component of autotrophic biomass during the non-stratified periods. *Penilia avirostris* is a typical filter feeder (Paffenhöfer and Orcutt, 1986), and even though it shows some degree of prey selection (Atienza *et al.*, 2006a), it most likely experiences detrimental effects and clogging when exposed to long chains of diatoms. It may well be that the preference for warmer waters exhibited by *P. avirostris* is not only related to temperature *per se* but also to the degree of stratification of the water column as pointed out by Alcaraz (Alcaraz, 1970); higher stratification in summer would be accompanied by a relatively lower abundance of long chain-forming diatoms and relatively higher abundance of nanoflagellates. This hypothesis agrees with the fact that in the Western Mediterranean the decline of *P. avirostris* populations is typically associated with a seasonal regime of thunderstorms and heavy rainfall in late summer−early autumn (Duarte *et al.*, 1999) with associated wind stress and increased run-off that must affect water column stability.

Finally, an additional cause for the disappearance of *P. avirostris* populations in late summer−early autumn could be predation pressure, which has shown to be very important in freshwater systems affecting cladocerans morphology, size, composition and abundance (Grant and Bayly, 1981; Thys and Hoffmann, 2005). The importance of predation in shaping marine zooplankton communities has been traditionally neglected (Verity and Smetacek, 1996). There is evidence that predators such as ctenophores, chaetognaths and fish larvae have the potential to decimate marine cladoceran populations (Canino and Grant, 1985; Duró and Saiz, 2000; Nip *et al.*, 2003; Barz and Hirche, 2005). However, in the NW Mediterranean, no studies have addressed the effects of predation on the population dynamics of *P. avirostris*.

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