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What triggers *Acartia* species egg production in a Mediterranean lagoon?

S. Boyer*, M. Bouvy, D. Bonnet

Laboratoire Ecologie des Systèmes Marins Côtiers, UMR5119, Université Montpellier 2, CNRS, IRD, Ifremer, Université Montpellier 1, CC 093, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France

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ABSTRACT

Environmental conditions triggering egg production and hatching success of copepod species are essential to better understand their population dynamics and consequently their contributions to the production of higher trophic levels. A monitoring station was sampled during 2 years in the Thau lagoon (Mediterranean Sea) to study temporal successions of 3 *Acartia* congeneric species (*Acartia clausi*, *Acartia discaudata* and *Paracartia grani*). Seasonal patterns defined the dominance of one *Acartia* species over the two others. There were two perennial species *A. clausi* and *A. discaudata* with maximum abundance in winter and in spring, respectively. The third species *P. grani* occurred in summer and was absent from the water column from February to April. Egg production and hatching success experiments were conducted at each sampling date to determine the different reproductive strategies of the *Acartia* species. Maximum egg productions (~25–31 eggs fem^{-1} d^{-1}) and mean hatching success (~65%) were similar between species but occurred at different periods depending on environmental triggers. Model averaging based on field data showed that temperature prevailed over other variables and that *Acartia* responses were different regarding the species. Temperature was the main trigger for egg production of *A. clausi* (negative effect) whereas temperature and salinity should be considered jointly to predict *A. discaudata* egg production. *P. grani* egg production described an uni-modal relationship with temperature. The effect of temperature on hatching success explained strongly the three species dynamics, especially the production of *P. grani* resting eggs.

1. Introduction

Copepods egg production represents an important life history trait to understand *in situ* population dynamics. Indeed, contribution of copepods to pelagic trophic relations depends on the production of viable eggs, together with their development times and growth rate (Koichi, 2001). However, some other processes such as predation (Tiselius et al., 2008) or natural mortality (Hirst and Kiørboe, 2002) also affect population recruitment. In general, copepod egg production is the result of ovigerous female responses to environmental conditions in which they have developed (Uriarte and Villate, 2005). Thereby, to understand and predict copepod spawning, it is fundamental to know and understand the contribution of physical and biological factors of the ecosystem controlling egg production (Uriarte and Villate, 2005).

Temperature is known to play a key role in copepods egg production seasonality (Ambler, 1986; Kiørboe et al., 1988), influencing the eggs hatching rate, their development time (Rivero et al., 2008) and the female prosome length (Liang and Uye, 1996). On short time scales, food availability and salinity can explain fertility changes of copepods (Ambler, 1986; Kiørboe et al., 1988; Huskin et al., 2000). Salinity changes may also influence the distribution of species (Cervetto et al., 1995) affecting growth and development time of estuarine species (Gaudy et al., 1988). Consequently, temperature and salinity are important parameters that allow defining the dimensions of the ecological niche (Hutchinson, 1957) for the species regarding the reproduction. The realized niche that takes into account predation, completion or fluctuation in food resources, describes the preferenda and the ecological position of the species in the natural environment (Begon et al., 2006).

The Thau lagoon, located in the Mediterranean Sea, is characterized by the dominance of the genus *Acartia* in the mesozooplankton community (Fatemi, 1938; Lam Haoi, 1985). The Acartiidae family constitutes a major component of mesozooplankton communities in semi-enclosed areas such as estuaries, harbours, bays and lagoons (Alcaraz, 1983; Lakkis, 1994; Boyer et al., 2012). In the Mediterranean Sea, the numbers of species reported

* Corresponding author.
E-mail address: severine.boyer@univ-montp2.fr (S. Boyer).

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varies from 2 in the harbours of Naples (Yamazi, 1964) and Marseille (Arfi et al., 1981) to 6 in the small port of Jounieh (Lakkis, 1994). To our knowledge, 6 congeneric species have now been identified in the Thau lagoon: *Acartia clausi*, *Acartia bifilosa*, *Acartia discaudata*, *Acartia margalefi*, *Paracartia latisetosa* (Fatemi, 1938; Mathias and Euzet, 1962; Lam Haoi, 1985) and recently the species *Paracartia grani* (Boyer et al., 2012). At our study site, *A. clausi* can contribute up to 65.5% to total mesozooplankton in winter, *A. discaudata* 36.2% in spring and *P. grani* 53% in summer (Boyer et al., 2012). It is not surprising to encounter such a high diversity and abundance of *Acartia* species as they have been shown (1) to coexist and show spatial and seasonal segregation patterns associated with hydrological conditions, seasonal variability, trophic status and pollution (Alcaraz, 1983; Uriarte and Villate, 2005), (2) to colonize many coastal areas and estuaries by propagation or introduction (Seuront, 2005; David et al., 2007; Aravena et al., 2009) and (3) to resist toxic algal blooms (Costa(da) and Fernández, 2002).

Most of *Acartia* species egg production (EP) and hatching success (HS) studies were conducted in estuaries (e.g. Sullivan and McManus, 1986; Koichi, 2001; Kimmerer et al., 2005; Uriarte and Villate, 2005; Tiselius et al., 2008) whereas to our knowledge, these topics have only been twice studied in lagoons (San Juan Island lagoon – Landry, 1978; Venice lagoon – Sei et al., 2006). Lagoons and estuaries could be considered as food non-limited ecosystems compared to other coastal waters (Smith et al., 1999; Bec et al., 2011), even if Kimmerer et al. (2005) reported from the San Francisco estuary that unusually low chlorophyll concentration could limit *Acartia* sp EP. *Acartia* species are known to be omnivorous and to graze both on phyto- and protozooplankton (ciliates, heterotrophic dinoflagellates, flagellates) (Rollwagen-Bollens and Penry, 2003; Dutz and Peters, 2008; Fileman et al., 2010). Temperature and salinity are therefore the main environmental parameters driving *Acartia* diversity and biological processes in estuaries and lagoons. In general, strong gradients of salinity are observed in estuaries while temperature ranges influence lagoons functioning. It is of note that comparative studies on *Acartia* species processes are scarce.

The aims of this study are to determine the contribution of 3 environmental parameters (temperature, salinity, chlorophyll *a* concentration) to the EP of 3 *Acartia* congeneric species (*Acartia clausi*, *Acartia discaudata* and *Paracartia grani*) in Thau lagoon, and to define their reproductive strategies by experiments performed during a 2 years survey.

2. Material and methods

2.1. Study site, sampling

The Thau lagoon is a shallow Mediterranean lagoon with a surface of 70 km^2 and a depth average around 4 m. The lagoon is connected to the sea by a channel in Sète, and exposed to a large catchment (60 000 ha). Rainfall also shows a large interannual variation (from 200 to 1000 mm per year) and the wind plays an important role in the lagoon hydrodynamics (Plus et al., 2003). The regional climate imposes a wide range of water temperatures (5–29 °C), and a less contrasted salinity window (27–40 psu) (Plus et al., 2003).

Mesozooplankton samples were collected at a fixed station (43°25 N; 03°40 E) in the Thau lagoon, close to the Sète channel (Fig. 1). Sampling occurred over a 3-year period. Between February 2008 and March 2009, 21 mesozooplankton samples were collected monthly or bi-monthly (when possible). Unfortunately, the only sample recorded in July 2008 was lost hence the missing point in Fig. 3-A. In 2010, 24 samples were collected twice a month, except in February due to bad weather conditions. A WP2 plankton net with a 200 μm mesh size was used to collect mesozooplankton by two horizontal hauls in the inner surface water (maximum 1 m depth). The first sample was fixed with buffered formaldehyde to a final concentration of 4% and used to determine the biodiversity and abundance of *Acartia* populations. Formalin samples represent a seawater filtered volume ranging from 8 to 95 m^{-3}. Indeed, very short hauls (a few minutes) were processed in summer to avoid clogging the net. The cod-end contents of the second mesozooplankton haul were placed in insulated containers and brought back to the laboratory within 1 h after collection to conduct EP experiments on *Acartia* species. Triplicates of 50 ml water samples (0.5 m depth) for chlorophyll *a* analysis were passed through GF/F filters (Whatman, 25 mm diameter) and stored at −80 °C. Chlorophyll *a* was extracted in 90% acetone for 24 h and then concentration was determined with a spectrofluorometer (LS 50B Perkin Elmer). Surface (0.5 m depth) temperature and salinity were recorded with a probe (EC 300 VWR International/WTW model 350i).

2.2. Acartia species egg production and hatching success

In the laboratory, healthy females of *Acartia clausi*, *Acartia discaudata* and *Paracartia grani* were picked out. The physiological state of the female (ovigerous *versus* non-ovigerous) was determined with a binocular microscope. For each species, and for most of the EP experiments, 3 replicates of groups of 5 females were incubated during 24 h in 1 L beaker filled with 0.45 μm filtered seawater. However, depending on ovigerous female abundances in the field, up to 6 groups of 5 ovigerous females were incubated. In 2010, two experiments were run with just 1 female due to (1) the appearance of *P. grani* in May, and (2) the very low occurrence of *A. clausi* in July. The first EP experiments occurred in June 2008. In 2008–2009 and 2010, respectively, a total of 43 and 72 EP experiments were performed for *A. clausi*, 24 and 53 for *A. discaudata* and 30 and 48 for *P. grani*. Each beaker contained a Plexiglas insert with a 200 μm mesh false bottom to separate eggs from females and to avoid cannibalism. At the end of the incubation, the vitality of the females was checked with a binocular microscope and the individuals were fixed with formaldehyde at 4% (final concentration) for later prosome length measurements. A total of 480 *A. clausi*, 329 *A. discaudata* and 369 *P. grani* ovigerous females were used for the EP experiments and prosome length measurements over the entire study. The eggs produced were collected and counted. For a targeted species, eggs were pooled together. A total of 24 eggs (when possible) were randomly chosen and placed individually in 2 ml wells of a multiplate. HS was not considered when the pool of eggs was less than 10. Hatching was checked twice (after 24 h and a week), and the percentage of HS was derived accordingly. Eggs that did not hatch after 7 days were considered as not viable as they were damaged except for *P. grani* in October, which started to produce a second type of eggs at this time. These eggs were morphologically different with long spines on the chorion and were expected to be resting eggs (Guerrero and Rodríguez, 1998). All those spiny eggs were incubated and did not hatch even after 2 month of storage at *in situ* temperature. EP experiments were run with a 12 h:12 h dark-light cycle. Temperature of incubation was 16 ± 1 °C in 2008–2009, in the range of the mean temperature encountered at the sampling station over the year while EP and HS experiments took place at *in situ* temperature in 2010. Both Laabir et al. (1995) and Bonnet et al. (2009) have demonstrated that no significant influence of incubation temperature was noted on *Calanus helgolandicus* EP (on short time scale, 24 to 48 h and for temperature up to 10 °C difference from the average field temperature). Therefore, the incubations made at 16 °C in 2008–2009 should be representative of *in situ* EP.