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Environmental boundaries of marine cladoceran distributions in the NW Mediterranean: Implications for their expansion under global warming

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ABSTRACT

We studied the horizontal and vertical distributions of marine cladocerans across the Catalan Sea shelf (NW Mediterranean) in July and September 2003, and in June and July 2004. At the seasonal scale, *Penilia avirostris* appears first in June in the southern region, where temperatures are warmer, and its populations develop northward during the summer. *Evadne-Pseudevadne* did not show a clear pattern, likely because several species were pooled. In 2003 successive heat waves affecting southwestern Europe resulted in surface seawater temperatures about 2 °C higher than usual across the whole study region. These high temperatures were associated with much lower abundance of *P. avirostris*. Overall, the mesoscale distributions of cladocerans were associated with the presence of low salinity, productive and stratified waters of continental origin, and negatively linked to the intrusion of offshore waters. On the vertical scale *P. avirostris* was located within or above the thermocline, whereas *Evadne-Pseudevadne* was much shallower; no evidence of diel migration was detected in either group. Our study provides new insights regarding the environmental limits for marine cladocerans in the NW Mediterranean; in the particular case of *P. avirostris* that knowledge can define the likely boundaries of its new distributions as it expands poleward under climate change.

1. Introduction

In contrast to their success in freshwater ecosystems, cladocerans have been regarded as an unsuccessful group in the marine environment; there are only 8 truly marine species according to Egloff et al. (1997). Despite that low diversity, marine cladocerans are a major component of mesozooplankton communities during the warmer months in many temperate and tropical coastal waters (Turner et al., 1988; Kim et al., 1989; Mazzocchi and Ribera d'Alcalà, 1995). The success of cladocerans in pelagic environments is tightly related to their particular life history (Egloff et al., 1997). Their capability to reproduce parthenogenetically, their high rates of embryonic and postembryonic growth, the large brood sizes and short generation times explain their high abundances and sudden population outbursts when environmental conditions become favorable (Egloff et al., 1997). Under unfavorable situations, both aquatic and marine cladocerans switch to gamogenic reproduction, producing resting eggs with a thick wall that can remain in bottom sediments until the next season of suitable conditions (Egloff et al., 1997). Most marine cladocerans are raptorial predators with well developed eyes (Mullin and Onbé, 1992; Onbé and Ikeda, 1995). An exception is the cosmopolitan species *Penilia avirostris*, which appears to be the only marine, filter-feeding cladoceran (Paffenhöfer and Orcutt, 1986; Atienza et al., 2006a, 2006b). It inhabits tropical to warm-temperate waters (e.g. Della Croce, 1964; Tang et al., 1995; Piontkovski et al., 2012).

Lochhead (1954) commented on the expansion of the habitat of *P. avirostris* since the end of the 19th century. However, it has not been until recently that its distribution in the Atlantic extended to more northern areas, presumably due to the warming trend linked to climate change (Andersen and Nielsen, 2003; Johns et al., 2005; Kane, 2013). Thus, cladocerans, and in particular the thermophilic species *P. avirostris*, could be used as indicator organisms to identify the extent of global warming effects in marine ecosystems. For that purpose, detailed knowledge of the responses of this planktonic group to marine physicochemical variables is needed.

The Catalan Sea (NW Mediterranean), with its notably active mesoscale circulation and wide range of environmental conditions (Alcaraz et al., 2007; Saiz et al., 2014), could serve as an ideal case for exploring the response of cladocerans to contrasting climatic conditions. Moreover, heterogeneities in phytoplankton, salinity and temperature, the most probable factors affecting cladoceran distributions (Paffenhöfer and Orcutt, 1986; Tang et al., 1995; Egloff et al., 1997), are found in the Catalan Sea at distinct spatial and temporal scales from meters to

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km, and from days to months (Calbet et al., 1996; Sabatés et al., 2013; Alcaraz et al., 2016). Thus, the Catalan Sea provides an array of environmental variables that can be used to depict the major factors controlling plankton distributions. The objectives of the present study were to determine the horizontal (at mesoscales) and vertical distributions of the marine cladoceran *P. avirostris* in the NW Mediterranean during spring and summer of 2003 and 2004, encompassing an array of different environmental conditions. We included in our analysis the cladoceran genera *Evadne* and *Pseudevadne* (pooled together and hereafter named *Evadne-Pseudevadne*) that are usually present in the region during the summer period, but in much lower numbers (Calbet et al., 2001). In the NW Mediterranean, cladocerans are important components of mesozooplankton and exhibit strong seasonality (Alcaraz, 1970; Calbet et al., 2001; Atienza et al., 2008).

Our study encompassed the 2003 summer heat wave that affected Europe and had significant consequences in marine and freshwater ecosystems (Garrabou et al., 2009; Anneville et al., 2010). The response of zooplankton populations to that extreme episode may help to understand the links of cladoceran success/expansion to biological and physico-chemical variables, thus enhancing the predictability of the impacts of climate change on aquatic ecosystems.

2. Material and methods

2.1. Study area

The Catalan coast is located along the NW sector of the Mediterranean Sea (Fig. 1). The particular geomorphology of the area and its water circulation patterns make it a very dynamic and heterogeneous system (Saiz et al., 2014). The Catalan coast is characterized by a narrow continental shelf that only widens in its southernmost part, in the vicinity of the delta of the Ebro River and to the north between the main submarine canyons. The general surface circulation in the region is well established with a shelf-slope current, the Northern Current, from northeast to southwest along the whole continental slope (Millot, 1999).

The water column structure presents a marked seasonal cycle with strong stratification in summer, which restricts vertical water motion preventing surface nutrient renewal. Consequently, almost all the surface nutrients become depleted and primary production is restricted to the deep chlorophyll maximum (DCM), a thin layer at the deepest levels of the photic zone (Estrada et al., 1985). The only nutrient contribution to the surface during the fully stratified season comes from riverine runoff (Blanc et al., 1969). The southern shelf of the Catalan coast receives a significant inflow from the Ebro River, which in normal conditions accounts for around a 90% of the total fresh water discharges along the Catalan coast. The northern sector, which is more directly influenced by strong northerly winds, is generally colder than the central and southern parts, and a surface thermal front roughly coincides with the limit of frequent northerly winds (Sabatés et al., 2013).

2.2. Field sampling

Four oceanographic surveys were carried out in spring-summer, during two consecutive years: 18–26 July 2003 (Jul 2003), 10–19 September 2003 (Sep 2003), 23 June–July 2004 (Jun 2004), and 22–30 July 2004 (Jul 2004) on board the R/V García del Cid. In each survey, 66 sampling stations were located on transects perpendicular to the shoreline, from near the coast to the slope (Fig. 1). On each transect, the stations were placed 7.5 nautical miles apart and the distance between transects was 10 nautical miles. Vertical profiles of temperature, salinity, and fluorescence were obtained at each station with a Neil Brown Mark III-CTD (WOCE standard) equipped with a Sea Tech fluorometer. Chlorophyll *a* was obtained from the fluorescence profile calibrated for each cruise with nearly 200 samples (see Sabatés et al., 2009, for a methodological description). Mesoscale zooplankton sampling was conducted on selected transects (44 stations, see Fig. 1) using a 53-μm mesh net (40 cm mouth diameter) hauled vertically at 20 m min^{-1} from 100 m to the surface, or from 5 m above the bottom at shallower depths. The water volume filtered by the net was measured with a flowmeter. The contents of the cod-end were preserved with sodium tetraborate-buffered formalin (5% final solution).

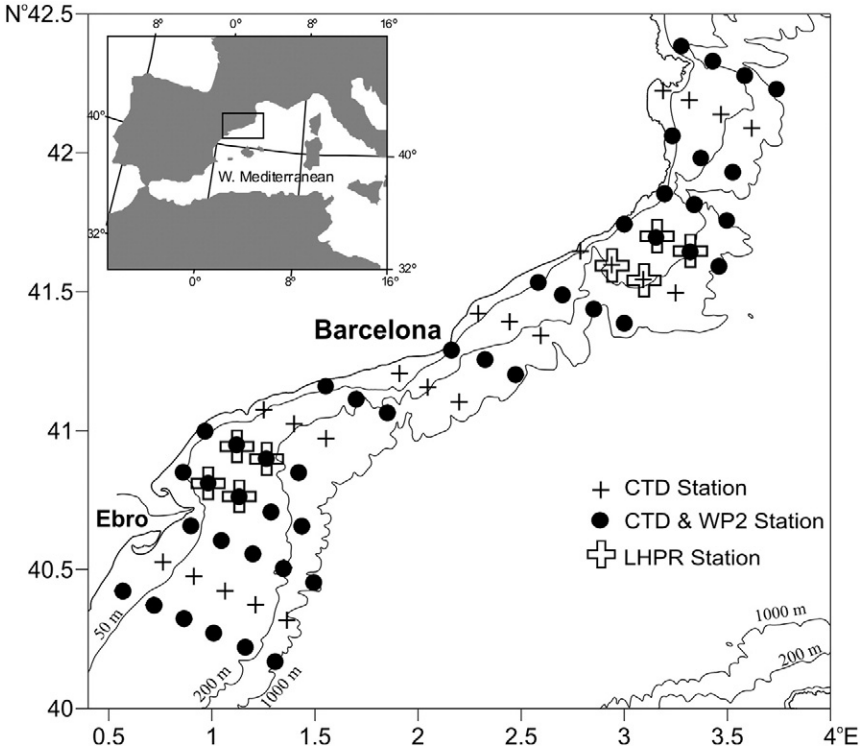

Fig. 1. Study area showing the sampling stations.