Available online at www.sciencedirect.com
SCIENCE DIRECT®
Continental Shelf Research 26 (2006) 1307–1315
CONTINENTAL SHELF RESEARCH
www.elsevier.com/locate/csr

A field test of temperature effects on ecophysiological responses of copepodid *Calanus chilensis* during coastal upwelling in northern Chile

Alan Giraldo[a,*], Ruben Escribano[b], Victor Marín[c]

[a] *Grupo de Investigación en Ecología Animal, Departmento de Biología, Universidad del Valle, A.A. 25360, Cali, Colombia*
[b] *Center for Oceanographic Research in the South-Eastern Pacific (COPAS), Departamento de Oceanografía, Universidad de Concepción, P.O. Box 42 Dichato, Chile*
[c] *Laboratorio de Modelación Ecológica, Departamento Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile*

Received 5 July 2005; received in revised form 30 March 2006; accepted 11 April 2006
Available online 6 June 2006

Abstract

We assessed responses of late copepodid stages of *Calanus chilensis*, as subject to spatial heterogeneity in oceanographic conditions, during coastal upwelling off Mejillones Peninsula, northern Chile. An oceanographic survey conducted during 26 h prior to zooplankton sampling mapped upwelling conditions. Over the next 2 d, four zooplankton stations, two inside and two outside the cold upwelling plume, were sampled twice in the day and twice at night. We then tested the effects of upwelling/non-upwelling habitat (i.e. inside/outside the upwelling plume) on body length, body weight, oil-sac volume (OSV) and a condition index (CI) of stages copepodid C5 and adult female. We also compared ovary development of females and stage distribution from both habitats. C5 and females from inside the upwelling plume were heavier, larger, had a greater CI, and females had more developed ovaries, than those located outside the plume, although there were no significant differences in the OSV. Differences in stage distribution suggested that individuals outside the plume had developed faster under a higher temperature (17 °C) than those inside the cold (14 °C) plume. Chlorophyll-*a* concentration was uniformly high ($>4\,mg\,m^{-3}$), both outside and inside the plume. We concluded that distinct temperature regimes, persisting longer than 1 week, had caused different sized copepodids. We thus suggest that temperature alone may substantially explain variances in growth and development rates of *Calanus* in highly productive upwelling systems, with no need to invoke food and body size effects.

Keywords: Coastal upwelling; Humboldt current; Zooplankton; *Calanus*; *Calanus chilensis*; Growth; Body length; Body weight; Condition index; Temperature; Chile

1. Introduction

Laboratory and field studies have shown that temperature and food are the major causes of variability in growth, development and consequently body size of marine copepods. Experiments

*Corresponding author. Tel.: +57 2 3312234; fax: +57 2 3393243.
E-mail address: agiraldo@univalle.edu.co (A. Giraldo).

0278-4343/$ - see front matter
doi:10.1016/j.csr.2006.04.005

have shown that temperature affects growth by accelerating or retarding the rate of development (Vidal, 1980a; Klein Breteler and Schogt, 1994; Escribano et al., 1997), whereas low food quantity or quality may restrict the synthesis of somatic tissue, and therefore growth rate (Vidal, 1980b; Klein Breteler and González, 1988; Klein Breteler et al., 1990). These laboratory results, however, cannot readily be extrapolated to field conditions, as the actual history of copepods to combinations of food and temperature in nature is uncertain. Field observations, on the other hand, can only establish temporal or spatial correlations between growth, or other associated variables, and combinations of food and temperature in the field on short time scales (Landry, 1978; Peterson and Bellantoni, 1987; Richardson and Verheye, 1998). These positive or negative correlations are sometimes suggestive about the relative importance of food and temperature on copepod growth, but usually fail to separate highly correlated environmental variables and do not provide much detail on functional relationships or mechanisms involved. In the same context, shipboard incubations have proven useful to test food-temperature effects on some physiological rates, such as egg production (Ambler, 1985; Peterson et al., 1991), moulting rates (Burkill and Kendall, 1982; Runge et al., 1985), and growth rates (Richardson and Verheye, 1999). They still must depend on simulated conditions, however, and are often not prolonged enough to produce detectable effects (Miller et al., 1984). Controlled experiments may help reveal how temperature and food affect growth and hence body size. For instance, with high food and at high temperature, copepods develop more rapidly and the time available for growth shortens, such that size at any terminal stage is smaller compared to animals growing with high food at low temperature (Klein Breteler and González, 1988; Escribano and McLaren, 1992). These findings still need to be paralleled in the field and we propose that coastal upwelling systems, such as the eastern boundary Humboldt current system (HCS), may prove valuable for in situ experimental approaches. In the HCS, the endemic copepod, *Calanus chilensis*, has been found to be highly sensitive to temperature/food conditions when reared in the laboratory (Escribano et al., 1997). However, field data suggest that its growth might be primarily temperature-dependent in situ, because there is sufficient food year-round (Escribano and McLaren, 1999).Coastal upwelling in northern Chile may provide a rich environment for continuous growth of this copepod (Marin et al., 1993; Escribano and McLaren, 1999). Upwelling, however, also causes a spatially heterogeneous habitat. The ascent of cold, nutrient-rich waters generates cold upwelling plumes that associate with phytoplankton biomass (Rodriguez et al., 1991; Escribano and McLaren, 1999). Thus growth of copepodid *C. chilensis* may depend on their spatial location, i.e. inside or outside the persistent upwelling plumes. If this hypothesis is true, then spatial heterogeneity in development and growth rates should be expected, like that observed by Escribano and McLaren (1999) during the Spring of 1996 in this area. Since fractions of the population may locate either inside or outside the upwelling plume, field observations can be used to assess differences in copepodid body size, lipid-store and gonad development. All these variables may reflect the effects of ambient temperatures on growth and development rates. In this work we tested this hypothesis by examining copepodid stages C5 and adults obtained from inside and outside of the cold upwelling plume. We assumed that individual characteristics of these late-terminal stages reflect growing conditions during earlier development under different regimes of temperature. Temperature effects on development were also assessed by comparing stage distribution from both habitats.

2. Materials and methods

2.1. Sampling design and procedures

Daily satellite images from NOAA over a two-week period during November 1999 allowed us to establish a sampling grid of 24 stations that included zones inside and outside of a well-defined upwelling plume in the coastal area off Mejillones Peninsula (23°S), northern Chile (Fig. 1). The whole grid was sampled a 26-h period from the R/V Purihaalar of the University of Antofagasta. At each station vertical profiles of CTD and fluorometry were made from 200 m to surface, using a Seabird SBE-19 CTD and a Wetstar in situ calibrated fluorometer attached to an Ocean Sensor CTD.

The sampling design for zooplankton consisted of four stations: two inside and two outside the plume (Fig. 1). Locations of stations, as well as the distances between them, were selected so that all could be sampled within a single nighttime or daytime period. After completion of the