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*

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).

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

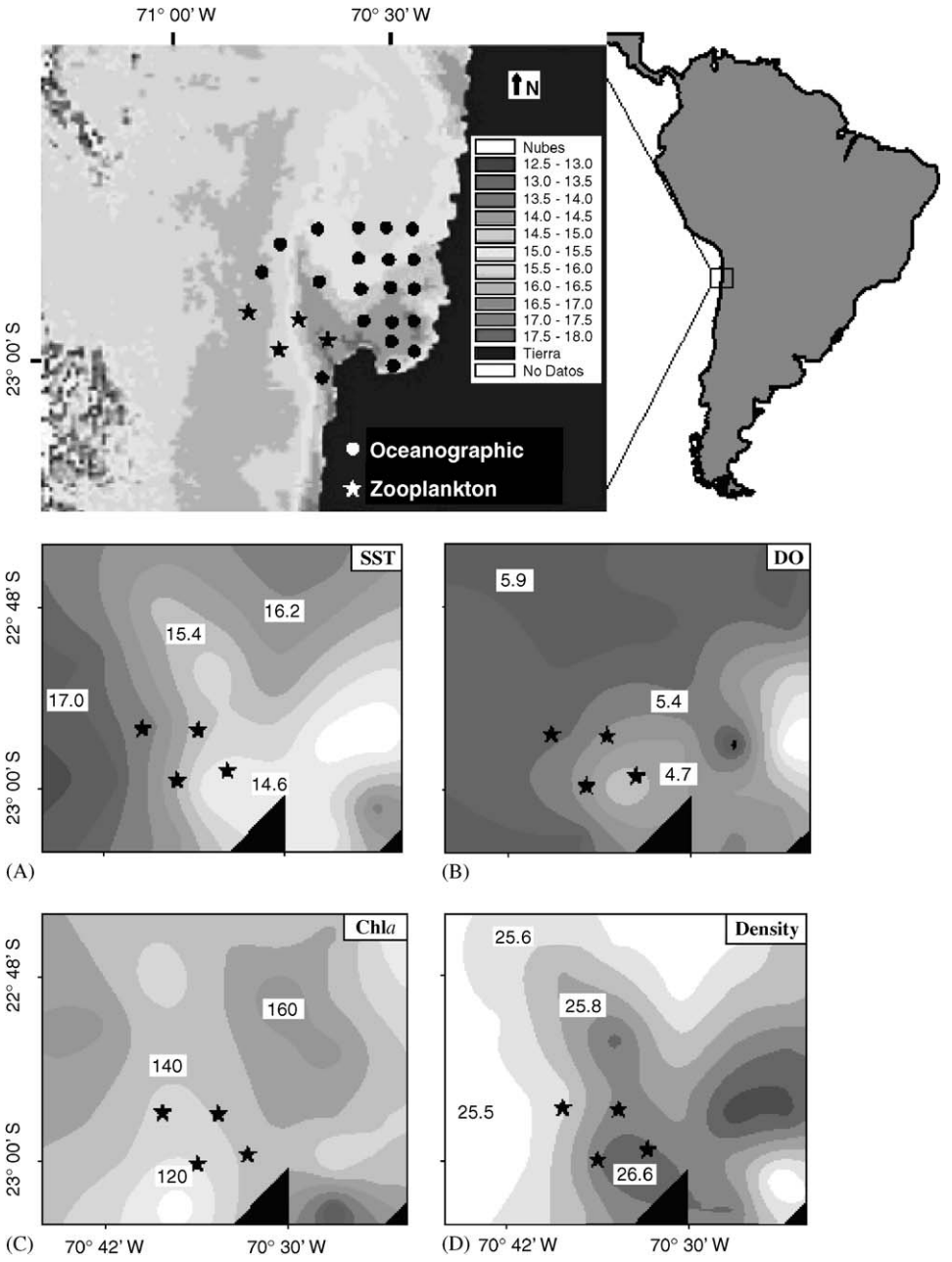

Fig. 1. NOAA satellite image of SST off Mejillones Peninsula, northern Chile, on 7 November 1999 (upper panel), illustrating the oceanographic and zooplankton sampling stations used to survey the cold-upwelling plume and surrounding areas during November 1999, and spatial distribution of in situ measurements of (A) sea surface temperature (SST) (°C), (B) dissolved oxygen (DO) (ml L^{-1}), (C) integrated (0–100 m) chlorophyll-*a* concentration (Chl-*a*) (mg m^{-2}) and (D) water density (Sigma-T, kg m^{-3}).

oceanographic grid, two daytime and two nighttime periods were sampled over the next two days. Upwelling/non-upwelling conditions were the main treatment variable, but daytime/nighttime effect, as well as short-term temporal changes, could also be examined. In addition, diurnal changes in the vertical distribution of copepodids were evaluated by sampling three depth strata each time: 200–80, 80–20 and 20–0 m. The upper 20 m was considered to represent the Ekman layer, the 80–20 m stratum a reversing flow and the 200–80 m as a deep, potentially more stable layer (Marin et al., 2001).

Zooplankton were captured with a vertically towed Hensen net with 0.5 m opening, 200 μm mesh, equipped with a double opening–closing system and a calibrated General Oceanic flowmeter. This mesh size efficiently captures all copepodid stages of *C. chilensis* in this zone (Escribano and McLaren, 1999). Zooplankton samples were preserved in 4% buffered formalin. To detect eventual changes caused by mixing and advection during zooplankton sampling, the CTD and fluorometer were also deployed as described above at each of the four stations during the two-day sampling period.

2.2. Zooplankton analysis

C. chilensis were removed from the 48 zooplankton samples after 3–4 d of preservation. Depending on abundance, about 10 individual copepodid stage C5, and 10 adult females were chosen randomly from all the samples of the upper 20 m layer. The prosome lengths (PLs) of all individuals were measured. As fixed specimens often had a curved body, only PL, from the anterior end of the cephalosome to the posterior lateral edge of fifth metasome segments, was measured. The size of the lipid store was estimated by obtaining linear measurements of the oil sac. We measured length and two widths of the oil sac, so that oil-sac volume (OSV) could be estimated assuming the shape of a spheroid (Escribano and McLaren, 1992). All measurements were made to the nearest 0.01 mm under a microscope at 40× magnification with a calibrated micrometer. After the oil sacs were measured, the individuals were quickly rinsed in distilled water, placed in pre-weighed aluminium pans and dried to constant weight (~12 h) at 70 °C. Dry weight was recorded to the nearest 10 μg with a Denver microbalance and correcting for preservation by assuming a 25% loss. From measurements of lengths and weights we estimated a condition index as, CI = ln(DW/length), where CI = condition index ($\mu g\,mm^{-1}$), DW = dry weight (μg) and length is prosome length (mm). This CI could indicate nutritive conditions of individuals. Before weighing, the adult females were examined for ovary development (gonadal index—GI), following the classification of Runge (1987). Runge's GI considers an initial stage of ovary development when anterior and posterior diverticula are empty. In the following development stage, oocytes are located in anterior portion of diverticula, and change successively from pre-vitellogenic oocytes (size between 60–140 μm), lightly opaque vitellogenic (>140 μm) and medium brown. In the last stage brown oocytes moves to the posterior portion of diverticula. Since samples had been fixed recently, there was no need for staining, although in some cases we used a 1:1 glycerin:alcohol solution to clarify the tissue. From the rest of the samples, all copepodid stages were sorted, identified and counted.

We used an analysis of variance (ANOVA) to test differences in body size measurements whenever possible. Homogeneity of variances between treatments was first verified using the Barlett test; log-transformations of variables were necessary for dry weights and CIs. When homogeneity could not be achieved we used the non-parametric one-way Kruskal–Wallis (KS) test. In the ANOVA design, we tested for the upwelling/non-upwelling factor as a treatment effect, and day of sampling as another effect, while data from day/night sources and sampling stations were considered as replicates of the main treatments, i.e. two stations × day/night = four replicates per two treatments (upwelling/non-upwelling and sampling day).

3. Results and discussion

In situ observations of sea surface temperature (SST), dissolved oxygen (DO) and Chl-*a* are shown in lower panel of Fig. 1. The upwelling plume at the beginning of the survey was about 10 km long and oriented northward from its origin near the north point of the Mejillones Peninsula. In situ SST revealed a difference of about 2.6 °C between the sites inside and outside the upwelling plume (Fig. 1A). Inside the cold plume and associated with lower SST, surface DO was low ($<5\,ml\,L^{-1}$), confirming the upwelling of subsurface waters (Fig. 1B). Integrated (0–100 m) Chl-*a* did not seem to be associated with the cold plume, although greater concentrations were found in frontal areas of the plume (Fig. 1C). The horizontal distribution of density revealed a strong physical gradient, suggesting that mixing and advection between upwelled and nearby waters during the study was no substantial (Fig. 1D). Differences in oceanographic conditions between upwelling/non-upwelling conditions are illustrated in Fig. 2. When comparing upwelling vs. non-upwelling conditions, there were significant differences in SST ($KS_{0.05,1} = 11.3, P<0.001$), in temperature at 10 m depth ($F_{0.05,1} = 80.1, P<0.001$), and also in mean temperature of the water column ($F_{0.05,1} = 13.9, P<0.001$) (Fig. 2A and B), but surface

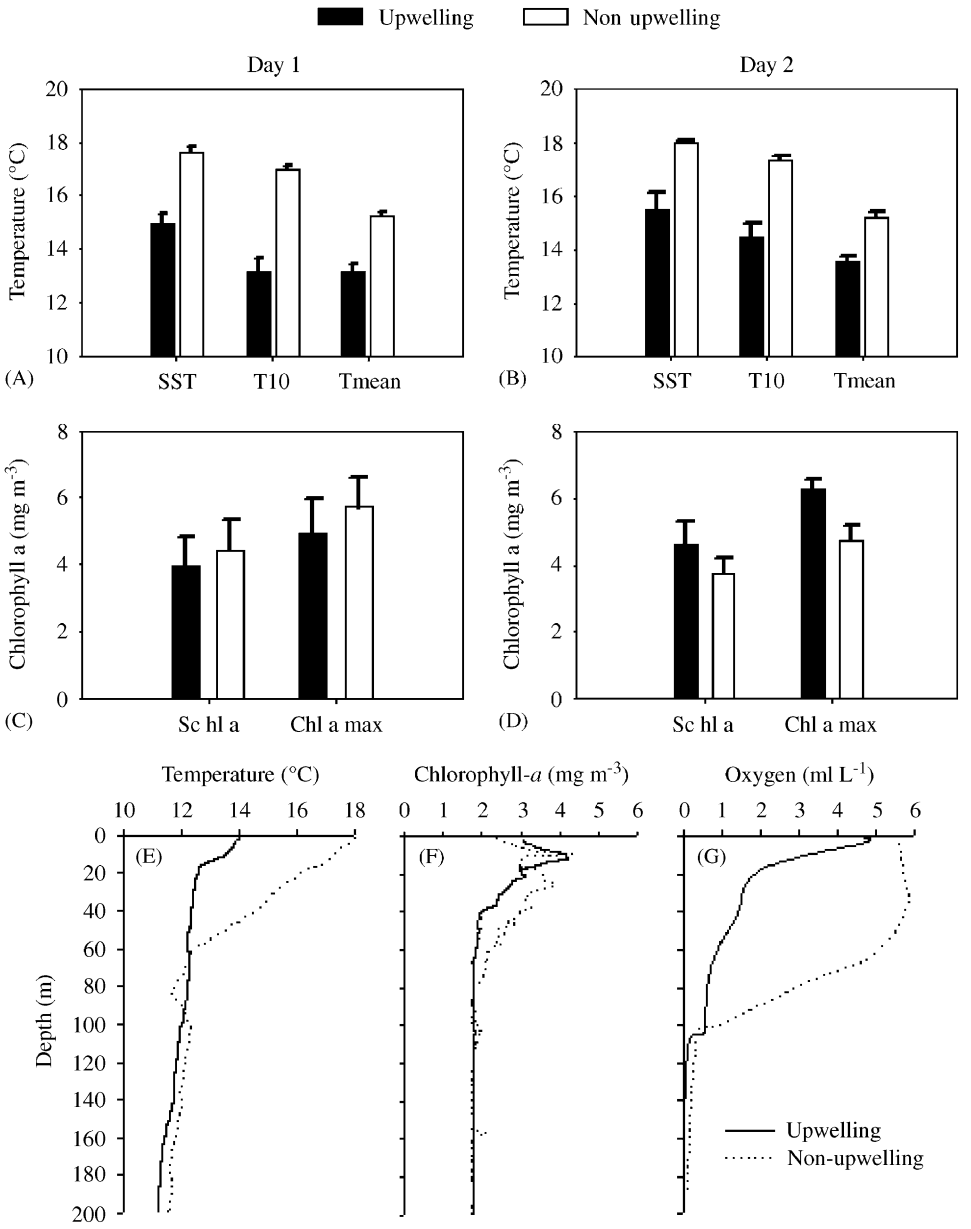

Fig. 2. Upper panel: comparisons of upwelling/non-upwelling oceanographic conditions for 2-d sampling off Mejillones Peninsula. (A) and (B) are mean values of in situ sea surface temperature (SST), temperature at 10 m depth ($T10$) and mean temperature of the water column (Tmean), (C) and (D) are mean values of surface chlorophyll-*a* concentration (Schl-*a*) and mean maximal chlorophyl-*a* levels (Chl-*a* max). Lower panel: vertical profiles of temperature (E), Chlorophyll-*a* (F) and dissolved oxygen (G) inside (upwelling) and outside (non-upwelling) of the upwelling plume.

Chl-*a* and Chl-*a* maximum were not significantly different ($F_{0.05,1}<1, P>0.05$) (Fig. 2C and D). No significant differences ($F_{0.05,1}<2, P>0.05$) between sampling days were found, except for temperature at 10 m depth, which showed a slight (0.5 °C in average), but significant ($F_{0.05,1}=5.3,\ P=0.039$) increase from day 1 to day 2 inside the plume. The lack of sampling day effects suggested that these conditions may have prevailed during our sampling.

Inside the upwelling plume the thermocline was very shallow (~10 m depth), while outside the plume the temperature gradient went beyond 50 m

(Fig. 2E). Chl-*a* was prominent in the upper 30 m and maxima (~4 mg Chl-*a* m^{-3} in average) were at about 10 m depth inside, and at nearly 20 m depth outside the plume (Fig. 2F). The oxycline, on the other hand, fell sharply with depth inside the plume, with oxygen concentration (<2 ml L^{-1}) at about 20 m depth, compared to the well oxygenated water column down to nearly 80 m outside the non-upwelling waters (Fig. 2G). This again confirms that deep, low-oxygen water was upwelling inside the cold plume.

The *C. chilensis* population was represented by all copepodid stages from C1 to adult males and females during our study. There were no significant day/night effects on copepodid abundance ($F_{0.05,1}<2, P>0.05$) and individuals were mostly concentrated in the upper 80 m layer. Using integrated abundances (200–0 m) of copepodids and pooling data from daytime and nighttime sampling, from both stations at each site, the relative abundance of copepodid stages was compared between the upwelling and the non-upwelling sites. Inside the plume copepodids were dominated by late C5 and adults males and females comprising about 70% of total copepodids, whereas outside the plume the population was mostly comprised of early C1 to C3 copepodids (nearly 60%). This stage frequency within sites remained nearly stable from day 1 to day 2, with a slight increase in females inside the upwelling plume on day 2. However, stage distribution was significantly different between sites (contingency $G_{0.05,5}=72.5, P<0.001$). This suggests that development of cohorts may not have been synchronous between the two sites as a result of either retarded development inside or accelerated development outside the plume, or both.

Fig. 3 illustrates individual measurements from both habitats. No females were found at station 3 in day 1, but they appeared in day 2. Ranges of PLs were 1.8–2.2 mm for C5 and 2.5–2.8 mm for adult females. Dry weights were more variable than lengths, in the ranges of 60–104 and 137–327 μg for C5 and adult females, respectively. The CI was higher (>4) in adult females compared to C5s, because of the presence in the former of fully matured ovaries, with gonadal indices >3 on average, according to the scale of Runge (1987). Two-way ANOVA and KS tests revealed that PLs of both C5 and females, and dry weights of females, were significantly greater inside than outside the upwelling plume (Table 1). The CI of C5 and females was also significantly greater inside the plume.

Size of the lipid store, here measured as OSV, was greater in females (mean $= 5.5\times10^{-3}$ mm^{-3}) than that of C5 (mean $= 3.8\times10^{-3}$ mm^{-3}). However, for both C5 and females, there were no significant differences between locations (Table 1). A visible lipid store (oil sac) has been mostly viewed as a characteristic of high latitude species, which accumulate lipids before entering diapause (Miller et al., 1998). As far as we know, *C. chilensis* do not diapause, but instead may reproduce continuously year-round (Escribano and McLaren, 1999). However, we observed considerable, although highly variable, amounts of lipids in C5 and females.

GI reflects the average frequency of ovary development of mature females. Mean GI was slightly, although significantly, greater inside the plume (Table 1), suggesting that females within the upwelling plume were reproducing more actively than those located outside the plume. The OSV, on the other hand, was related to body length in both C5s and females. The regression equation for C5 was, $OSV = 0.60PL^{2.99}$ ($r^2 = 0.38$), and for females was, $OSV = 0.16PL^{5.78}$ ($r^2 = 0.57$), where OSV = oil-sac volume (mm^{-3}) and PL = *prosomelength*(*mm*). The exponent of PL indicates that stage C5s had more lipids than females relative to their lengths, suggesting that females may have been using lipids for reproduction. This is consistent with mean frequency of ovary development (GI), which indicated that most females were undergoing egg spawning. Differences in body size between upwelling and non-upwelling habitats should arise during growth and development of individuals subjected to different regimes of temperature and food. However Chl-*a* levels seemed substantial (>4 mg m^{-3}) in both areas, suggesting that copepodids were well fed. In the laboratory, reduced rates of growth and development of late stages are obtained at Chl-*a* levels <2.8 mg m^{-3} on average (Escribano et al., 1997). High lipid contents in C5 and females, with no differences between locations, may also indicate that individuals had sufficient food at both sites (Hirche and Kattner, 1993), and greater variability of lipids in females than in C5s may have resulted from lipid utilisation for egg production (Hagen et al., 1993). Although we did not sample eggs or nauplii, presence of early copepodids at both sites indicated that reproduction had occurred or was occurring both inside and outside the plume. Moreover, values of GI, considered an index of female maturity, were high at both sites, suggesting that females were

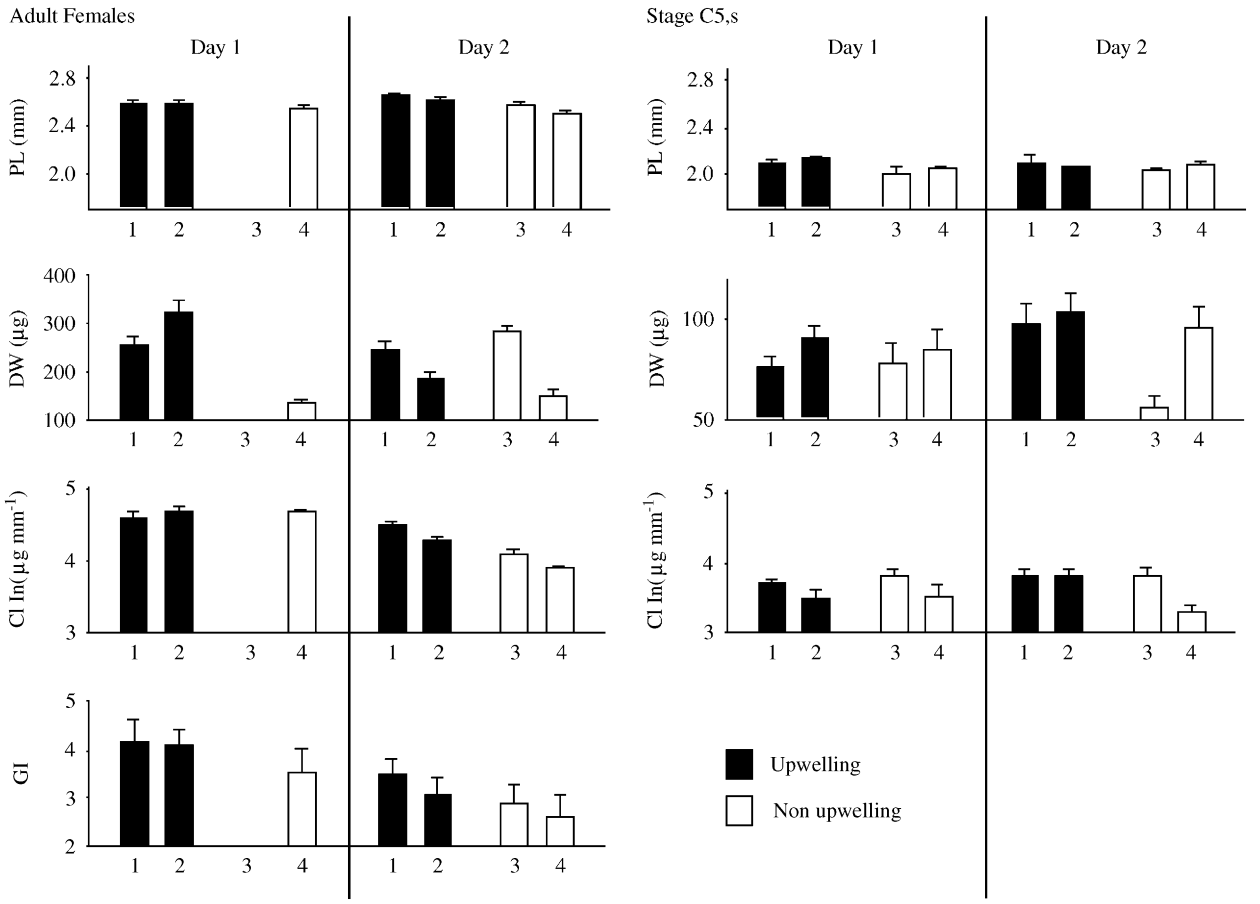

Fig. 3. Comparisons of body size measurements and gonad development of adult females (left panel) and stage C5 (right panel) of *Calanus chilensis* obtained in 2 d from stations 1 and 2 inside (upwelling) and stations 3 and 4 outside (non-upwelling) of the upwelling plume observed off Mejillones Peninsula in November 1999. PL = prosome length (mm), DW = dry weight (µg), CI = condition index (ln(DW/PL)) and GI = Gonad index. Females were absent in station 3 during day 1 of sampling.

indeed actively spawning and thus not experiencing low food.

If copepods were growing at satiating conditions of food, then temperature could have been the main cause of differences in growth and hence sizes of C5 and females. For these differences to develop individuals must be exposed to different temperature regimes for considerable fractions of their life cycles. In northern Chile, *C. chilensis* may have generation times as short as 20 d (Escribano and McLaren, 1999). Thus a week, or perhaps less time, might be sufficient to produce the results of different development and growth rates. Temperature-dependent development time of C1–C5 *C. chilensis* may be estimated following Escribano and McLaren (1999), who fitted the temperature-dependent development time of *C. chilensis* (Escribano et al., 1998) to the Bélehrâdek equation together with the equiproportional rule of development (Corkett et al., 1986). We estimated stage durations at each location (upwelling/non-upwelling), using mean temperatures at 10 m depth from both sites. Our estimated total times between C1 and adult females were 14.7 and 11.4 d at the upwelling and non-upwelling sites, respectively. This means ~22% longer inside the cold plume. Previous studies have shown that slow development at low temperature results in larger animals at a final stage (Klein Breteler and González, 1988; Escribano and McLaren, 1992). In our study, mean body lengths and dry weights of C5 were 2.6% and 14.8% greater, respectively, inside (at 13.9 °C) than outside the plume (at 17.2 °C). Such differences are even more remarkable in females: 2.8% greater in body length and 24.7% greater in dry weight for individuals inside the plume.

Table 1
ANOVA (F) and Kruskal–Wallis (χ^2) tests of location (upwelling/non-upwelling) effects on size measurements of stage C5 and adult females and ovary development of females, *C. chilensis*, obtained from inside and outside of the upwelling plume off Mejillones Peninsula

Size measurement	Stage	F	χ^2	P
PL	C5	—	4.19	0.041
	Adult ♀♀	8.24	—	0.005
DW	C5	3.41	—	0.067
	Adult ♀♀	—	11.65	0.001
CI	C5	4.40	—	0.038
	Adult ♀♀	—	13.78	0.000
OSV	C5	0.96	—	0.665
	Adult ♀♀	0.03	—	0.863
GI	Adult ♀♀	4.93	—	0.026

PL : prosome length (mm), DW: dry weight (μg),
CI: condition index ($\ln(\mu g\,mm^{-1})$),
OSV: oil-sac volume ($mm^{-3}\,10^3$) and GI: gonad index.

The argument that temperature alone may explain differences in body sizes certainly requires that individuals are exposed for sufficient times to different temperatures. Our daily satellite information during 2 weeks prior to sampling showed that the pattern of upwelling (in Fig. 1) remained nearly the same for the preceding 10 d, with only slight changes in size and orientation of the cold plume (Marin et al., 2001). This means that the cold plume was a rather stable physical structure on a weekly time scale, preventing mixing with surrounding water masses. Thus, organisms advected within the plume may have indeed experienced a particular temperature regime, during several days, or perhaps weeks. Moreover, as the temperature-dependent model predicts higher development rates outside the plume, under no limitation of food, cohort development 22% ahead outside the plume, suggests that these individuals were developed ~3.3 d ahead. Since animals appeared in more advanced stages inside the plume, the young copepodids outside the upwelling plume could represent individuals produced earlier by females that have been largely replaced. They must therefore have been subjected to higher temperature for considerably longer than three days. In other words, when the cohort outside had developed to early copepodids, the one inside was still laying eggs. Such expectations are consistent with differences in age structure and also with greater GI of females inside the plume.

Hirst and Lampitt (1998) attempted to model global in situ growth rates of copepods incorporating temperature and body size effects. Their global equations however may not apply to some particular situations. For *C. chilensis*, at a temperature of 15 °C and median weights of 150 μg for stage C5 and 90 μg for C4 (Escribano and McLaren, 1999), equation 2 in Hirst and Lampitt (1998) predicts a growth rate of $0.032\,d^{-1}$ using 120 μg as median weight. If we assume exponential growth for this *Calanus* species (Escribano et al., 1997) and recalculate the time taken between C4 and C5 as, time $= [\ln(150) - \ln(90)]/0.032$, this yields 16 d. This duration is too much long for a single stage, compared to total generation time of this species at that temperature (Escribano and McLaren, 1999). Thus, at least for this species, the proposed equation of Hirst and Lampitt (1998) may greatly underestimate the growth rate. Certainly much of the variability of growth rates in very distinct habitats in nature may not be covered by single equations.

4. Conclusions

Spatial heterogeneity like that described here, involving discrete temperature habitats, might even increase confidence limits for any mathematical function that intend explain the copepodid growth-temperature relationship, as growth rates appear very sensitive to temperature in a short-term manner. It is relevant, however, that much variation of growth and corresponding changes in body sizes are associated solely with habitat temperature, with no need to invoke effects of food supply (Hirst and Lampitt, 1998; Richardson and Verheye, 1999). Coastal upwelling zones comprise large and highly productive marine ecosystems worldwide. Although the HCS may be considered a special case, as one of the most productive system of World Ocean, the influence of temperature on copepod growth, as reported here, might be a more general characteristic of other upwelling systems as well.

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References

Ambler, J.W., 1985. Seasonal factors affecting egg production and viability of eggs of *Acartia tonsa* Dana from East Lagoon, Galveston, Texas. Estuarine Coastal and Shelf Science 20, 743–760.

Burkill, P.H., Kendall, T.F., 1982. Production of the copepod *Eurytemora affinis* in the Bristol Channel. Marine Ecology-Progress Series 7, 21–31.

Corkett, C.J., McLaren, I.A., Sévigny, J.-M., 1986. The rearing of the marine calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jashnov and *C. hyperboreus* Kroyer with comment on the equiproportional rule. Syllogeus (Natural Museum of Canada) 58, 539–546.

Escribano, R., McLaren, I.A., 1992. Influence of food and temperature on lengths and weight of two marine copepods. Journal of Experimental Marine Biology and Ecology 159, 77–88.

Escribano, R., McLaren, I.A., 1999. Production of *Calanus chilensis* in the upwelling area of Antofagasta, northern Chile. Marine Ecology-Progress Series 177, 147–156.

Escribano, R., Irribarren, C., Rodríguez, L., 1997. Influence of food quantity and temperature on development and growth of marine copepod *Calanus chilensis* from northern Chile. Marine Biology 128, 281–288.

Escribano, R., Irribarren, C., Rodríguez, L., 1998. Temperature-dependent development and growth of *Calanus chilensis* from northern Chile. Journal of Experimental Marine Biology and Ecology 229, 19–34.

Hagen, W., Kattner, G., Graeves, M., 1993. *Calanoides acutus* and *Calanoides propinquus*, Antarctic copepods with different lipids storage modes via wax esters or triascylglycerols. Marine Ecology-Progress Series 97, 135–142.

Hirche, H.-J., Kattner, G., 1993. Egg production and lipid content of *Calanus glacialis* in Spring; indication of a food-dependent and food-independent reproductive mode. Marine Biology 117, 615–622.

Hirst, A.G., Lampitt, R.S., 1998. Towards a global model of in situ weight-specific growth in marine planktonic copepods. Marine Biology 132, 247–257.

Klein Breteler, W.C.M., González, S.R., 1988. Influence of temperature and food concentration on body size, weight and lipid content of two calanoid copepod species. Hydrobiologia 167/168, 201–210.

Klein Breteler, W.C.M., Schogt, N., 1994. Development of *Acartia clausi* (Copepoda, Calanoida) cultured at different conditions of temperature and food. Hydrobiologia 297/298, 469–479.

Klein Breteler, W.C.M., Schogt, N., Gonzalez, S.R., 1990. On the role of food quality in grazing and development of life stages, and genetic change of body size during cultivation of pelagic copepods. Journal of Experimental Marine Biology and Ecology 135, 177–189.

Landry, M.R., 1978. Population dynamics and production of a planktonic marine copepod, *Acartia clausi*, in a small temperate lagoon on San Juan Island, Washington. Hydrobiologia 63, 77–119.

Marin, V., Rodriguez, L., Vallejo, L., Fuenteseca, J., Oyarce, E., 1993. Efectos de la surgencia costera sobre la productividad primaria primaveral de Bahía Mejillones del Sur (Antofagasta, Chile). Revista Chilena de Historia Natural 66, 479–491.

Marin, V., Escribano, R., Rodríguez, L., Olivares, G., Hidalgo, P., 2001. Nearshore circulation in a coastal upwelling site off the Northern Humbodlt current system. Continental Shelf Research 21, 1317–1329.

Miller, C.B., Huntley, M.E., Brooks, E.R., 1984. Post-collection moulting rates of planktonic marine copepods: measurement, applications, problems. Limnology and Oceanography 29, 1274–1289.

Miller, B.M., Morgan, C.A., Prahl, F.G., Sparrow, M.A., 1998. Storage lipids of the copepod *Calanus finmarchicus* from Georges Bank and the Gulf of Maine. Limnology and Oceanography 43, 488–497.

Peterson, W.T., Bellantoni, D.C., 1987. Relationships between water column stratification, phytoplankton cell size and copepod fecundity in Long Island Sound and off central Chile. South African Journal of Marine Science 5, 411–421.

Peterson, W.T., Tiselius, P., Kiørbe, T., 1991. Copepod egg production, moulting and growth rates, and second day production, in the Skagerrak in August 1988. Journal of Plankton Research 18, 643–657.

Richardson, A.J., Verheye, H.M., 1998. The relative importance of food and temperature to copepod egg production and somatic growth in the southern Benguela upwelling system. Journal of Plankton Research 20, 2379–2399.

Richardson, A.J., Verheye, H.M., 1999. Growth rates of copepods in the southern Benguela upwelling system: the interplay between body size and food. Limnology and Oceanography 44, 382–392.

Rodriguez, L., Marin, V.H., Farias, M., Oyarce, E., 1991. Identification of an upwelling zone by remote sensing and in situ measurements, Mejilones del Sur Bay (Antofagasta-Chile). Scientia Marina 55, 467–473.

Runge, J., 1987. Measurement of egg production rates of *Calanus firmanchicus* from preserved samples. Canadian Journal of Fisheries and Aquatic Sciences 44, 2009–2012.

Runge, J.A., McLaren, I.A., Corkett, C.J., Bohrer, R.N., Koslow, J.A., 1985. Molting rates and cohort development of *Calanus finmarchicus* and *C. glacialis* in the sea off southwest Nova Scotia. Marine Biology 86, 241–246.

Vidal, J., 1980a. Physioecology of zooplankton. II. Effects of phytoplankton concentration, temperature, and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus* sp. Marine Biology 56, 135–146.

Vidal, J., 1980b. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Marine Biology 56, 111–134.