

Spatial distribution of *Calanus chilensis* off Mejillones Peninsula (northern Chile): ecological consequences upon coastal upwelling

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ABSTRACT: The Mejillones Peninsula upwelling system (northern Chile) appears to be a natural laboratory, suitable to test hypotheses concerning variability of copepod growth in nature. In this zone, in January 2000, we collected zooplankton samples inside and outside of an upwelling plume to assess differential responses of copepodid *Calanus chilensis* to spatial distribution of temperature, chlorophyll *a* (chl *a*), current field and dissolved oxygen (DO). We studied variability of prosome length (PL), dry weight (DW), oil sac volume (OSV), ovary development (GI) and a condition index (CI) of females, and PL and OSV of Copepodid Stage C5. The sea temperature ranged between 14 and 20°C in the upper 10 m, whereas chl *a* varied between 3 and 14 mg m⁻³. We distinguished 2 zones according to temperature and the current field: a cold retention area coinciding with the upwelling plume, and a warmer highly advective zone, outside the plume. Abundance of most copepodids was associated with cold and chl *a*-rich waters, and positively correlated to current speeds. DW and CI of females and PL of Stage C5 were negatively correlated to temperature, but not to chl *a*. Within the cold retention zone, copepodids were more abundant, females and C5 copepodids were larger and heavier, and females had more developed ovaries, but there were no differences in lipid content or CI. We concluded that resulting circulation may act as an efficient mechanism to maintain copepodids within the chl *a*-rich upwelling center, but this also implies spatial heterogeneity in temperature and food, giving rise to variability in growth and development of copepods, which is then reflected in different-sized individuals in the late stages of development.

KEY WORDS: Advection · Humboldt Current · Northern Chile · Body size · Copepods · Temperature · Upwelling

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INTRODUCTION

The endemic calanoid copepod of the Humboldt Current, *Calanus chilensis*, has received increasing attention in the last few years, mostly because it is considered to be a key link between primary production and small pelagic fishes (anchovy and sardine) in the rich, northern Chilean upwelling ecosystem. Previous studies have suggested that this copepod may exhibit

continuous production year-round in northern Chile (Escribano & McLaren 1999), is very abundant and widely distributed along the coast off northern Chile (Gonzalez & Marin 1998), and their populations appear strongly associated with upwelling centres (Escribano 1998). Although previous laboratory experiments (Escribano et al. 1997) indicated that food may affect development and growth rates, more recent field data suggest that food might be sufficiently high to maintain high growth rates in nearshore areas at all seasons (Escribano & McLaren 1999, Escribano & Hidalgo 2000a, Ulloa et al. 2001). If this is true, then tempera-

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ture alone may suffice for understanding and modelling population growth on seasonal and annual bases (Escribano & Hidalgo 2000a). However, coastal upwelling systems in this zone may show much variability of food and temperature in time and space (Marin et al. 2001). Phytoplankton, the main food source for this species (Boyd et al. 1980), is highly patchy in its distribution during upwelling (Escribano 1998), such that there could be situations in which individuals are actually exposed to low quantities of food. In other words, at times, fractions of populations may be subject to distinct environmental regimes of food and temperature. If such distribution patterns persist for an extended period of time, then differential growth and development responses could arise among those fractions. Observed copepod growth rates and body size variation within populations in nature (Hirst & Lampitt 1998) might thus be explained in terms of regional environmental effects. Testing that hypothesis is certainly relevant when examining and modelling the population dynamics of zooplankton in coastal upwelling systems.

Off Mejillones Peninsula, wind-driven upwelling seems to occur year-round in the nearshore zone (Marin et al. 1993, Escribano 1998), and often dense aggregations of *Calanus*, associated with well-distinguishable patches of phytoplankton and water masses of different temperatures, can be observed (Escribano 1998). These patterns of copepodid distribution can

then provide a natural experiment to test the temperature/food effects on copepod growth.

In this work, using data from a cruise carried out during the summer of 2000, we examined responses of copepodid *Calanus chilensis* differentially distributed off the Mejillones Peninsula. We assumed that physiological state and body size of adult females and late-stage copepodids (C5) represent growing conditions of earlier stages exposed to distinct food/temperature regimes. Also, we made use of *in situ* information on the current field to evaluate the role of advection and retention processes in causing distinct fractions of the population to be subjected to differential food/temperature habitats for sufficient periods of time, so that different development and growth rates could arise and be reflected at terminal stages, such as C5 and adults. In addition, we assessed ambient effects on cohort development by analysing stage distribution throughout the study area.

MATERIALS AND METHODS

A NOAA satellite image of sea surface temperature (SST) on 14 January 2000 was the basis to establish 27 oceanographic stations covering areas inside and outside of a well-defined upwelling plume in the coastal area off Mejillones Peninsula, northern Chile (23° S) (Fig. 1). The cruise was carried out in the shortest time

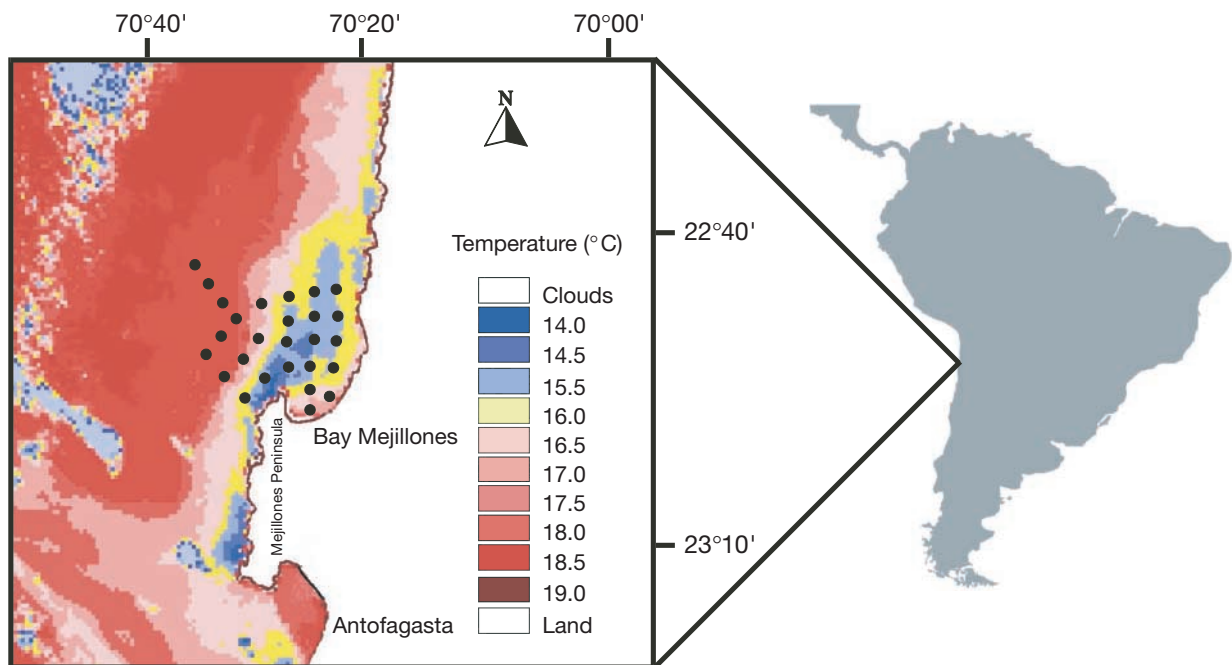


Fig. 1. The Mejillones Peninsula upwelling system as shown by a NOAA satellite image of sea surface temperature on 14 January 2000. The map shows the 27 sampling stations used to survey oceanographic conditions and collect copepodid stage *Calanus chilensis*

possible to avoid short-term changes in oceanographic conditions, on board the RV 'PuriHaalar' from the University of Antofagasta. All surveys were completed over a 30 h period. At each station a Doppler sensor current meter profiler (Aanderaa RCM-9), equipped with calibrated conductivity, temperature, oxygen and depth sensors (CTDO), was deployed down to 200 m or near the bottom. We thus obtained the current field in the upper 200 m, covering at least 2 tidal cycles. To remove eventual tidal effects on the east (u -axis) and north (v -axis) components of currents, the mean vector of the whole water column (200 m) was subtracted, although surface circulation in this area is well correlated to wind-driven upwelling, such that tidal currents may be less important (Marin et al. 2001). In addition, a WetStar fluorometer attached to a CTD ocean sensor (OS200) was used to obtain vertical profiles of the chlorophyll a (chl a) concentration down to 100 m. Fluorescence units were converted to chl a through an *in situ* calibration performed as described in Escribano & McLaren (1999).

Zooplankton at each of the 27 stations was captured through vertical tows of a Hensen type net (50 cm diameter opening), equipped with a calibrated General Oceanics flowmeter. The net had a mesh size of 200 μm , which has been shown to efficiently capture all copepodid stages of *Calanus chilensis* (Escribano & Rodriguez 1994, Escribano & McLaren 1999). The net tows were made from 80 m to the surface at a mean speed of about 1 m s^{-1} . We sampled the upper 80 m, independent of time of the day, assuming that this copepod may not make diel vertical migrations in the nearshore area off Mejillones Peninsula, and because the population appears to concentrate mostly within the upper 80 m (Escribano 1998, Escribano et al. 2001). Zooplankton samples were preserved with buffered 5% formalin.

In the laboratory all copepodid stages of *Calanus chilensis* from C1 to adults were sorted and counted from the samples after 3 to 4 d of preservation. From each sample, about 10 individuals in Copepodid Stage C5 and 10 adult females were randomly chosen. The apparently small sample size of individuals resulted from the variable abundance of Stage C5 and adults in each sample. However, because there were 27 samples and 2 treatments (upwelling vs non-upwelling conditions), the final sample size was indeed >260 individuals per stage ($n > 100$ per treatment) to assess the population responses. All these individuals were measured for prosome length, and the size of their lipid store was estimated by linear measurements of the oil sac. We measured length and 2 widths of the oil sac, so that oil sac volume (OSV) could be estimated assuming the shape of a spheroid (Escribano & McLaren 1992). All measurements were made to the nearest 0.01 mm under

a microscope at 40 \times with a calibrated micrometer. Thereafter, individuals were quickly rinsed in distilled water, placed in preweighed aluminum pans and dried to constant weight (~ 12 h) at 70 $^{\circ}\text{C}$. Dry weight was thus obtained after repeated readings to the nearest 10 μg using a Denver microbalance. From measurements of lengths and weights we estimated a condition index as:

$$\text{CI} = \ln(\text{DW}/\text{length}) \quad (1)$$

where CI represents the condition index ($\mu\text{g mm}^{-1}$), DW is dry weight (μg) and length is prosome length (mm). This CI was used to indicate the nutritional condition of individuals. Also, before weighing, adult females were examined for ovary development, following the classification criteria of Runge (1987). Since samples had been recently fixed, ovaries were usually visible under the microscope, although in some cases we used 1:1 glycerin:alcohol solution to clarify the tissue.

Profiles of current speed and direction were used to describe zones of intense advection and retention areas with reduced current speeds. This information, along with SST distribution illustrating the position of the upwelling plume, was utilised to define *in situ* food/temperature habitats. We distinguished between sampling stations from a cold retention zone and those from a warmer highly advective area, and then compared copepodid abundance, stage distributions, sizes and the condition of C5 copepodids and adult females in both zones. To examine copepodid stage distribution we estimated a population index as:

$$\text{PI} = \frac{\sum_{i=1}^6 in_i}{N} \quad (2)$$

where PI = population index, i is copepodid stage (1, 2, ..., 6), n is abundance (number m^{-2}) of the copepodid stage (i) and N is total abundance of copepodids (number m^{-2}) in the 0 to 80 m depth layer. Since older stages are longer lived (Escribano et al. 1998), they are expected to be more abundant than younger ones, such that PI is biased toward older stages. To avoid this bias, stage-specific abundance (n) was weighted by its corresponding temperature-dependent stage duration, estimated according to the development function for this species (Escribano et al. 1998), and modified by Escribano & McLaren (1999) as:

$$D_i = p_i [5887 (T + 11.0)^{-2.05}] \quad (3)$$

where p_i is the proportion of time occupied by each copepodid stage, relative to the time from hatching to C1, and assuming the 'equiproportional rule' of Corbett et al. (1986), and T is the temperature measured in the field at 10 m depth. Since adult abundance also

needs to be weighted by adult development time, we arbitrarily used the C5 development time increased by 20% for adults, due to a general lack of knowledge about the life span of adult *Calanus chilensis*.

To test the influence of oceanographic conditions on abundance and copepodid responses we used step-wise multiple regression on log-transformed variables, whereas comparisons between zones were made with 1-way ANOVA on normalised variables.

RESULTS

Oceanographic conditions

At the time of sampling the upwelling plume was oriented northward, extending up to 50 km alongshore, and covering an area of about 200 km². Presence of cold, upwelled waters can be seen in the distribution of *in situ* measured temperature at 10 m (Fig. 2a), whereas less-oxygenated waters coincided with the upwelling plume (Fig. 2b). Chl *a* was in the range of 3.0 to 14.0 mg m⁻³ at the surface, and maximum peaks were usually found at about 15 m in the water column. Chl *a* maximum values were aggregated inside the upwelling plume, having maxima inside Mejillones Bay and at the northern end of the plume (Fig. 2c).

Vertical profiles of current speed and direction revealed that circulation was dominated by a single layer in the upper 200 m. Vector averaging in the upper 50 m showed current speeds in the range of 0.18 to 0.60 m s⁻¹, with maximal speeds at the northern end of the plume and inside Mejillones Bay, and a well-distinguishable median zone with reduced current speeds. Spatial distribution of the *u*-component (likely to cause offshore advection) clearly showed a retention zone at the front and inside of Bay Mejillones, in which the flow was mostly directed to the coast (positive values) and an advective zone dominated by an offshore (negative values) flow. According to temperature distribution (Fig. 2a), stations in the retention zone mostly corresponded to those inside the upwelling plume; thus, this could represent a zone of cold, recently upwelled waters. Therefore we grouped locations into 2 major habitats: a retention zone of cold, chl *a*-rich water, including stations at the southern end of the cold plume, and a zone of offshore advection characterised by low chl *a* concentrations, outside the upwelling plume. Distribution of the *u*-component and distinction of both zones are shown in Fig. 3. When oceanographic variables were grouped into these retention and advection zones, significant differences arose (Table 1). The retention area was colder and had greater values of chl *a* compared to the advective zone. The oxygen minimum layer, here defined as depth at which the oxygen

concentration is 0.5 ml l⁻¹, was shallower inside the retention zone and the east component was positive (flow to the east) in contrast to the advection area (Table 1).

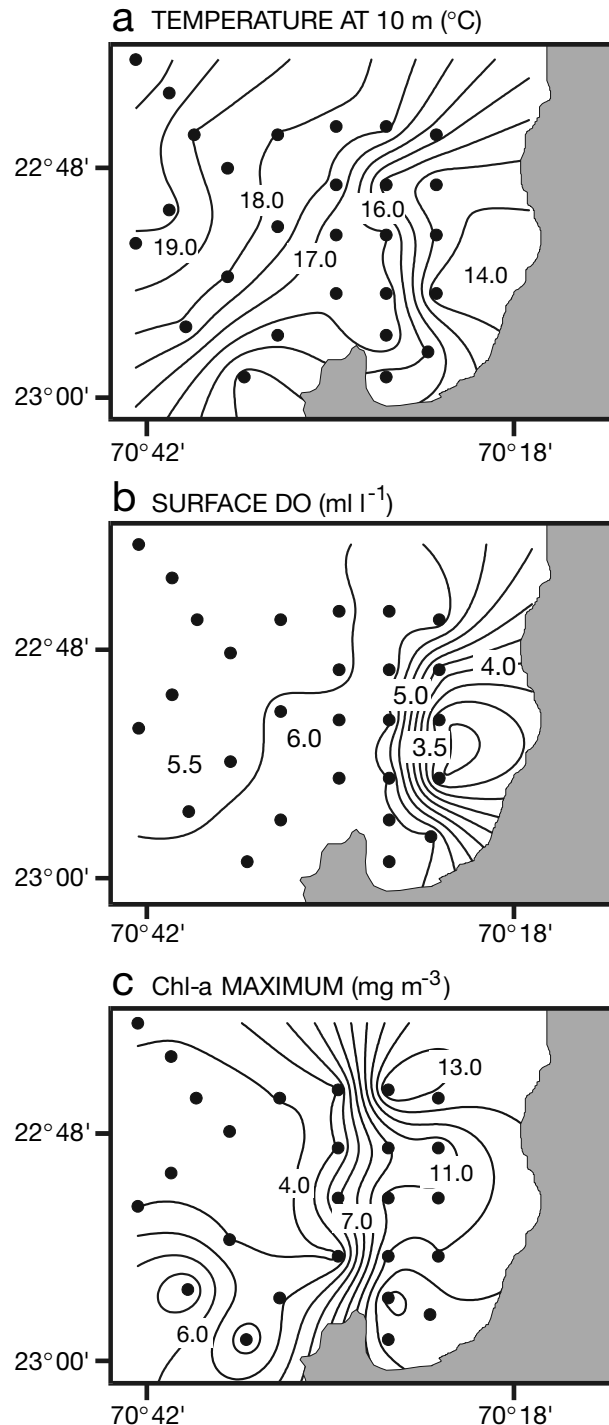


Fig. 2. Spatial distribution of (a) temperature at 10 m depth, (b) surface dissolved oxygen (DO) and (c) maximum chlorophyll *a* concentration in the water column, from *in situ* measurements over a 30 h survey, in January 2000, off Mejillones Peninsula

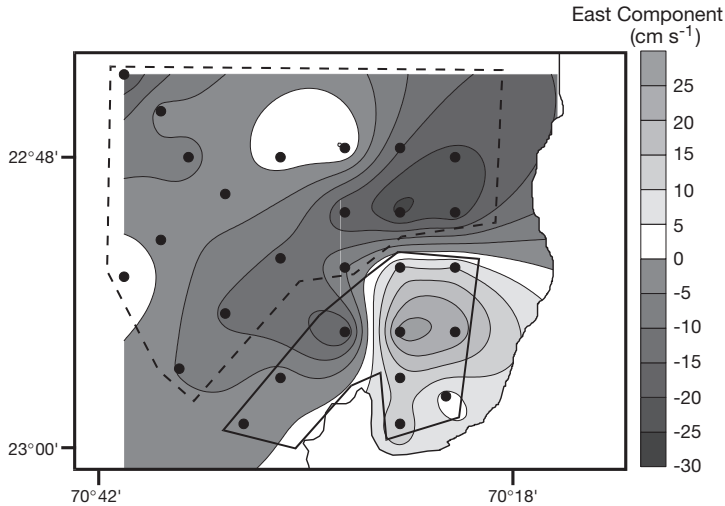


Fig. 3. Spatial distribution of the east component of current in the upper 50 m layer, off Mejillones Peninsula in January 2000. Distribution of the east component and position of the upwelling plume, as shown by sea temperature (Fig. 2a) were used to define 2 types of zones: a cold retention zone (inside the upwelling plume) with either low current speeds or eastward (to the coast) flow, as indicated by the continuous line; and a warmer offshore advective zone, defined by higher temperature and westward flow (outside the plume) as illustrated by the broken line

Oceanographic effects on copepodids

All copepodid stages from C1 to adult males and females were present at the time of sampling. The spatial distribution of copepodids showed greater concentrations inside and in front of Mejillones Bay. This pattern was similar for copepodid stages from C3 to adults, which appeared more concentrated in the cold retention area, but C1 and C2 copepodids seemed more dispersed and showed a secondary aggregation offshore, outside the cold plume (Fig. 4).

When looking at the influence of oceanographic conditions on copepodid abundance and individual sizes from the whole sampling grid, stepwise multiple regression yielded significant correlations between temperature and abundance of early stages, but not with abundance of Stage C5 or adults. Correlations were mostly negative, because of greater abundance in cold waters. Significant associations between abundance and chl *a* were found for most copepodids, except for C5 and C1 (Table 2). Also significant influences of currents were observed on abundance of copepodids, when testing the effect of current velocity and the east and

north components (Table 2). There was little influence of oxygen concentrations or depth of the oxygen minimum layer (OML) on abundance, except for the significant effect of OML depth on PI. Stepwise multiple regression did not detect significant temperature effects on female lengths, although there was a significant negative effect on their weight and CI. This negative effect of temperature on body size was also observed in the lengths of C5 copepodids (Table 2).

The distinction of the cold retention and warmer advective zones allowed us to sort and compare copepodid abundance and individual characteristics between the 2 habitats. Total copepodid abundance was 3 times greater in the cold area. Also, the cold area was dominated by late stages compared with the warmer zone in which early copepodids tended to dominate. In fact, the population index was significantly greater in the cold area (Table 3). Abundance for most stages is significantly greater in the cold retention area, except for the early stages C1 and C2, which did not show significant differences between areas (Table 3).

When comparing individual differences between habitats, we found that females from the cold retention zone were significantly larger, heavier and had more developed ovaries compared to those from the warmer zone (Table 4). Stage C5 copepodids from the cold retention zone were also significantly larger, whereas females from the warmer advective area had significantly greater amounts of lipids than those from the cold plume, but C5 copepodids did not show this difference (Table 4). The condition index (CI) was not different between areas, for either females or Stage C5 (Table 4).

ANOVA results from Table 4 can also be illustrated by the spatial distribution of the variables under study. The population index (PI) confirmed that older stages dominated the nearshore zone and early ones were located offshore (Fig. 5a). Also, within the cold upwelling plume adult females were larger (Fig. 5b), heavier (Fig. 5c) and

Table 1. One-way ANOVA to compare oceanographic variables between the cold retention zone (inside the upwelling plume) and the warmer advective zone (outside the upwelling plume), off Mejillones in summer 2000. SST, sea surface temperature (°C); T_{10} , temperature at 10 m (°C); Chl a_{0m} , surface chlorophyll *a* (mg m^{-3}); Chl a_{max} , maximum peak of chlorophyll *a* (mg m^{-3}) in the water column; Z_{min} , depth of the oxygen minimum layer (m); East, mean v-component of surface (0 to 20 m) current (m s^{-1})

Variable	Cold retention zone			Warm advective zone			ANOVA	
	Mean	SD	n	Mean	SD	n	F	P
SST	18.0	0.88	10	18.8	0.77	17	6.2	0.02
T_{10}	14.2	0.54	10	16.9	1.74	17	23.0	0.00
Chl a_{0m}	8.33	3.89	10	4.78	3.31	17	6.4	0.02
Chl a_{max}	9.30	3.79	10	6.10	3.37	17	5.2	0.03
Z_{min}	42	7.3	10	66	10.0	17	41.2	0.00
East	5.6	12.88	10	-9.0	8.79	17	12.3	0.00

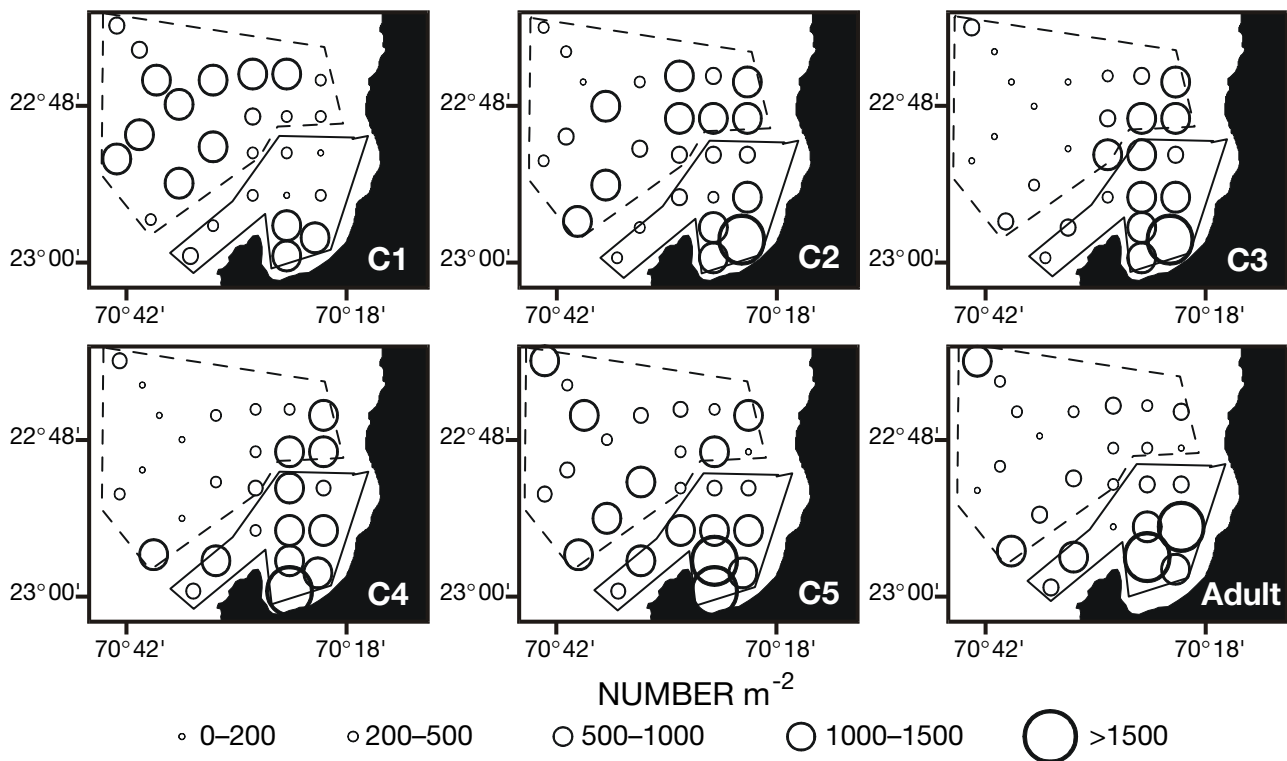


Fig. 4. *Calanus chilensis*. Spatial distribution of copepodid stages, during coastal upwelling, off Mejillones Peninsula, in January 2000. Adults include males and females. Values are integrated abundance (number m^{-2}) in the upper 80 m layer. The cold retention zone (inside the upwelling plume) is indicated by the continuous line, and the warmer offshore advective zone (outside the plume) is illustrated by the broken line

Table 2. *Calanus chilensis*. Probability values (ns, non-significant; $p > 0.05$) from stepwise multiple regression to test oceanographic conditions on copepodid abundance, stage distribution (PI), prosome lengths (PL) and oil sac volume (OSV) of C5 copepodids and adult females, and weights (DW) and condition index (CI) of females off Mejillones in summer 2000. Temp., temperature ($^{\circ}C$); Chl *a*, chlorophyll *a*; *V*, vector average current speed; east and north, *v* and *u* components of currents; DO, dissolved oxygen at surface ($ml\ l^{-1}$); Z_{min} , depth of the oxygen minimum layer ($0.5\ ml\ O_2\ l^{-1}$)

Dependent variable	Independent variables						
	Temp.	Chl <i>a</i>	<i>V</i>	East	North	DO	Z_{min}
Adult female	ns	0.00	ns	ns	0.00	ns	ns
Adult male	ns	ns	ns	ns	0.03	ns	ns
C5	ns	ns	0.01	ns	ns	0.04	ns
C4	0.00	0.00	0.03	0.00	ns	ns	ns
C3	0.00	0.00	ns	0.00	ns	ns	ns
C2	0.01	0.02	ns	ns	0.00	ns	ns
C1	0.01	ns	ns	0.03	0.00	ns	ns
PI	ns	ns	ns	ns	ns	ns	0.02
PL female	ns	ns	ns	ns	ns	ns	ns
PL C5	0.00	ns	ns	ns	ns	ns	ns
DW	0.04	ns	ns	ns	ns	ns	ns
CI	0.01	ns	ns	ns	ns	ns	ns
OSV female	ns	ns	ns	ns	ns	ns	ns
OSV C5	ns	ns	ns	ns	ns	ns	ns

had more developed ovaries (Fig. 5d), but those outside the plume showed greater oil sac volumes (Fig. 5e); no differences in CI distribution can be noted (Fig. 5f). Stage C5, also distributed in a similar manner to adults (Fig. 4), showed a similar pattern in their size distribution, i.e. larger C5 copepodids appeared concentrated near Bay Mejillones, inside the plume, and small ones in offshore zones (Fig. 5g), and their OSV did not show a clear pattern (Fig. 5h).

DISCUSSION

Off Mejillones Peninsula the population of *Calanus chilensis* had been previously reported as strongly associated with nearshore upwelling zones (Escribano 1998, Escribano & McLaren 1999). Upwelled waters concentrate high amounts of phytoplankton, sug-

Table 3. *Calanus chilensis*. Comparison of copepodid abundance (number m^{-2}) and stage frequency (PI) in the upper 80 m between a cold retention zone (inside the upwelling plume) and a warmer advective area (outside the upwelling plume), from samples obtained off Mejillones during the summer 2000. %, relative abundance with respect to total copepodids in each zone; p, probability value after 1-way ANOVA

Stage	Inside the plume			Outside the plume			p
	Mean	SD	%	Mean	SD	%	
Adult female	2 706	4 168.2	18	343	286.9	7	0.03
Adult male	1 593	1 942.1	11	119	92.8	2	0.00
C5	3 312	3 222.1	22	899	709.9	17	0.03
C4	2 600	2 759.7	18	744	961.4	14	0.00
C3	1 944	1 824.0	13	895	1 243.1	17	0.03
C2	1 712	2 030.0	12	921	578.0	18	0.24
C1	887	1 033.8	6	1 246	879.6	24	0.09
Total	14 754			5 167			
PI	3.30	0.63		2.14	0.64		0.00

Table 4. *Calanus chilensis*. Comparison of female and Stage C5 conditions between the cold retention area (inside the upwelling plume) and the warmer advective zone (outside the upwelling plume). PL, prosome length (mm); DW, dry weight (μg); GI, gonad index; OSV, oil sac volume ($mm^{-3} 10^{-3}$); CI, condition index ($\mu g mm^{-1}$); *F* and *p*, *f*-ratio and probability values after 1-way ANOVA

Variable	Cold retention zone (n = 100)		Warm advective zone (n = 161)		<i>F</i>	p
	Mean	SD	Mean	SD		
Adult female						
PL	2.517	0.098	2.484	0.139	4.80	0.03
DW	115.6	35.79	107.0	31.80	4.08	0.04
GI	4.08	1.45	3.31	1.46	16.05	0.00
OSV	3.33	3.95	6.63	55.71	8.62	0.00
CI	3.8	0.30	3.7	0.29	2.78	>0.05
Stage C5						
PL	2.00	0.095	1.94	0.114	18.44	0.00
OSV	3.29	2.195	3.46	4.078	0.04	>0.05

gesting an adequate environment to sustain continuous growth of this species year-round (Escribano & Rodriguez 1994, Escribano & McLaren 1999). However, aggregation of copepods inside the cold plume also implies reduced development rates at lower temperatures, compared to surrounding warmer areas. Slow development at low temperature and high food may give rise to a larger body size at maturity (Klein Breteler & Gonzalez 1988, Escribano & McLaren 1992, Escribano et al. 1997). Thus temperature could explain differences in sizes between cold and warm areas of the upwelling region, providing sufficient food for maximal growth rates. There are 2 shortcomings about such a conclusion. First, lower temperatures are correlated to higher phytoplankton levels, suggesting that small-sized individuals in the warmer zone may result not only because of a high temperature, but also they

may experience food shortage, which is known to affect growth and size at adulthood of this species (Escribano et al. 1997). Secondly, in order for differences to arise among individuals between areas, individuals must be exposed to a given temperature/food condition for a sufficient period of time during copepodid development.

Our data showed that phytoplankton levels were significantly lower in the warmer area, outside the upwelling plume than inside the plume. Surface chl *a* in the warmer area was nearly $5.0 mg m^{-3}$ and maximum chl *a* values were $>6.0 mg m^{-3}$ on average. In a laboratory study, Escribano et al. (1997) found that small-sized copepodids are obtained when food levels are $2.8 mg m^{-3}$ on average, whereas significantly larger females and C5 copepodids originate at food levels in the range of 6 and $24 mg m^{-3}$. Our field data of chl *a* concentrations may compare to the lower limit for development rates as high as those described by Escribano et al. (1997) under high quantities of food. This could also be true for attaining a larger body size. We do not consider, however, eventual effects of food quality, which may also influence copepod growth (Tiselius 1989, Klein Breteler et al. 1990). Nevertheless, it is relevant to note that in both sampled zones, inside and outside the cold plume, all copepodid stages were present, indicating that cohorts were indeed developing. Also

the condition index was the same in both habitats, and lipid content of females was even greater in the warmer, apparently low chl *a* zone, suggesting that individuals were well fed (Hagen et al. 1993, Hirche & Kattner 1993). This leads us to suggest that in both habitats food was not limiting for individual growth, and therefore differences in the sizes of C5 copepodids and adults would result from temperature effects.

We did not measure egg production or enumerate nauplii from both areas to assess the possibility that egg production could be food limited in the warmer zone. Indeed a greater gonad index in the cold area may reflect more intense reproduction within the retention area and this could also explain greater copepodid abundances.

If temperature alone caused size differences, the length of time to which individuals are exposed to a

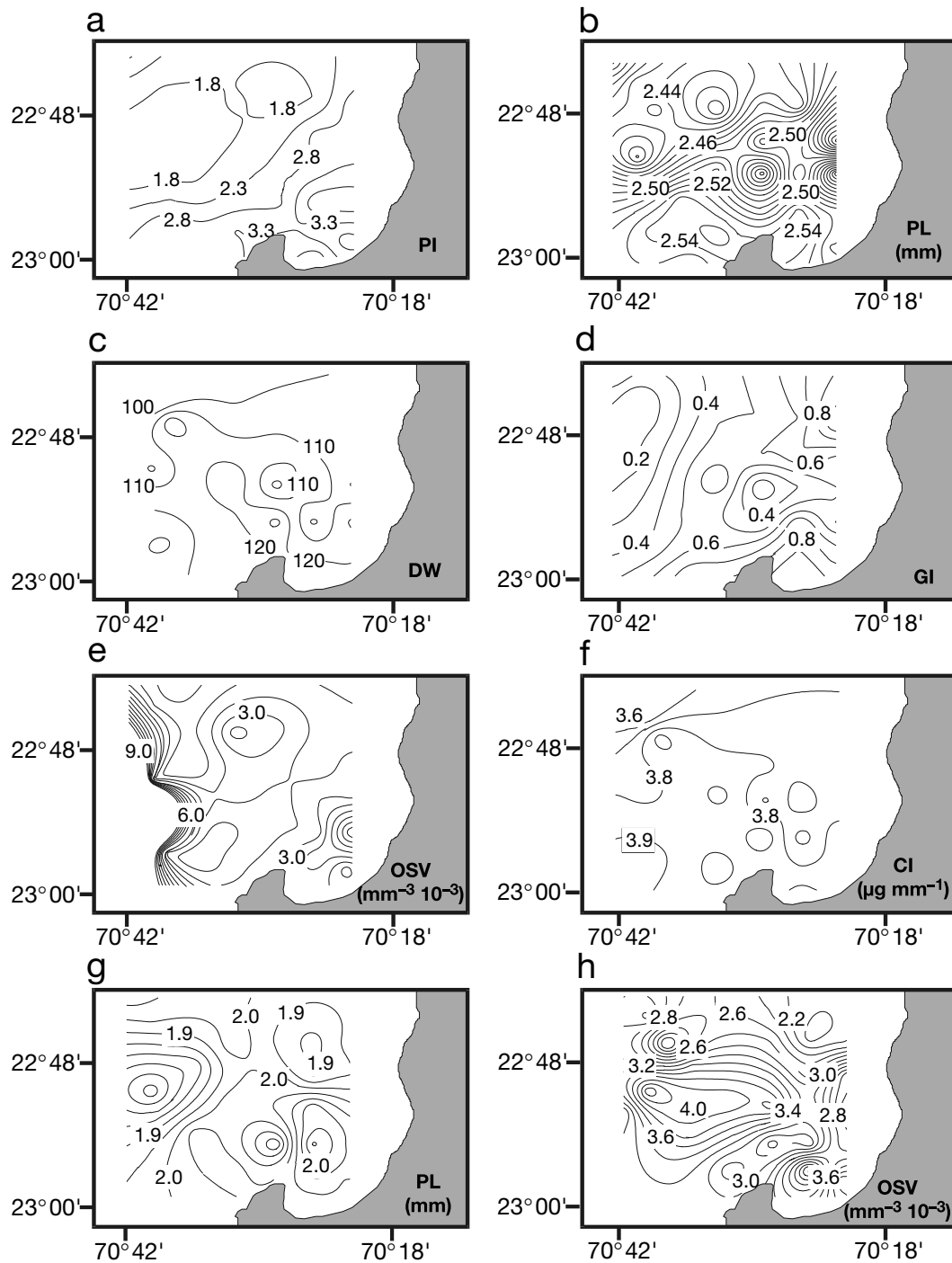


Fig. 5. *Calanus chilensis*. Spatial distribution of conditions of copepodids during upwelling off Mejillones Peninsula, in January 2000. (a) Stage frequency estimated as a population index (PI), (b) female prosome length (PL), (c) female dry weight (DW), (d) female gonad development (GI), (e) female oil sac volume (OSV), (f) female condition index (CI), (g) Stage C5 prosome length (PL) and (h) Stage C5 oil sac volume (OSV)

particular temperature regime will be an important parameter to consider. In this regard, our estimated current field suggested the presence of a retention area nearshore, the mean flow of which resulted in an eastward drift of about 10 km d^{-1} going into Mejillones

Bay due to the residual southward drift. This would induce a cyclonic gyre within and in front of Bay Mejillones (Marin et al. 2001). The possibility of being advected offshore once inside the gyre is rather low, allowing extended residence times within the reten-

tion zone. Escribano & McLaren (1999) estimated a generation time of *Calanus chilensis* as short as 20 d at 15°C, whereas copepodids may go from Stage C1 through adults within a few days. If we assume that temperature at 10 m depth adequately represents copepodid habitat (Escribano & McLaren 1999) and if development takes place at temperature-dependent rates, we can estimate stage duration using Eq. (3). This equation yields estimates of the time between C1 and adult stages of about 14 d at 14°C and 11 d at 17°C. Therefore 1 wk retention would mean development through at least 3 copepodid stages. This time might be sufficient to cause variability in adult size and condition, as shown by Escribano et al. (1997). On the other hand, by looking at age distribution in both zones and assuming differences in development times resulted from temperature, then it can be inferred that development of individuals in the warmer zone, dominated by early C1 copepodids, would be at least 10 d ahead of development in the cooler waters, suggesting a long residence time under a given temperature regime.

One of the key physical processes that dominate coastal upwelling systems is the offshore Ekman transport (Smith 1995). Zooplankton must cope with these advective forces to maintain their populations near phytoplankton-rich upwelling zones. Among the mechanisms proposed to help zooplankton retention, diel vertical migration (DVM) and ontogenetic layering have often been invoked (Pillar et al. 1984, Verheye et al. 1992). *Calanus chilensis*, however, show little or restricted DVM, possibly limited by the shallow OML (Escribano 1998, Escribano et al. 2001). Also, presence of alongshore currents and eddies induced by upwelling and protruding capes can act as retention areas (Lobel & Robinson 1986, Hutchings et al. 1995, Roy 1998). More recently secondary thermal fronts, present close to shore (termed 'upwelling shadow'), seem to efficiently concentrate and hence retain plankton (Graham et al. 1992, Graham & Largier 1997). Our data showed a well distinguishable retention zone with reduced current speeds, where *C. chilensis* appeared aggregated. Upwelling circulation is probably inducing an upwelling shadow inside Mejillones Bay in addition to the cyclonic eddy in front of the bay. This type of circulation may act as an efficient mechanism to maintain copepods nearshore. Therefore, the upwelling center of Mejillones Peninsula may not only serve as a location of high primary productivity, but also one inducing aggregations of phytoplankton and zooplankton, as our data showed for *C. chilensis*. Indeed, abundance of all dominant copepods in this zone was found closely associated with recently upwelled waters during the spring of 1996 (Escribano & Hidalgo 2000b), suggesting a significant role of circulation in structuring spatial distribution of passive, non-migrant copepods.

A major implication of the patchy distribution of zooplankton off Mejillones Peninsula is that spatial heterogeneity of temperature, food, or both may impose differential regional responses upon copepods. This finding should be considered when examining variability of *in situ* growth rates and hence production rates of zooplankton in other important upwelling ecosystems as well.

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