Distribution and life cycle of *Calanus chilensis* and *Centropages brachiatus* (Copepoda) in Chilean coastal waters: a GIS approach

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ABSTRACT: *Calanus chilensis* and *Centropages brachiatus* are 2 of the most abundant species of copepods (Crustacea) off the Chilean coast. However, knowledge of their life cycle and distribution is fragmentary. We have analysed the distribution of both species in Chilean coastal waters by means of a Geographic Information System (ARC/INFO). We studied vertically integrated (0 to 100 m) zooplankton samples and ancillary physical oceanographic data collected during 1989 by the Instituto de Fomento Pesquero, Chile. Point estimates of abundance and physical data were transformed to a grid format in ARC/INFO. We show that both species are abundant within 10 km from shore, and that high abundances further offshore may be interpreted as the result of advection. We also show that both species remain year-round in the upper water column with no evidence of seasonal vertical migration. We then discuss potential life cycle mechanisms that might explain their dominance in the coastal area of the Humboldt Current ecosystem.

KEY WORDS: Crustacea · Calanidae · Marine ecosystems · GIS · Pelagic ecology · Plankton distribution · Eastern South Pacific

INTRODUCTION

Copepoda (Crustacea) comprise the most abundant taxa of the marine zooplankton (Omori & Ikeda 1984). They are particularly important in marine ecosystems dominated by large zooplankton species, e.g. *Calanus*-dominated systems (Runge 1988). There they act as an efficient and direct path for energy transfer to higher trophic levels (Bond 1994, Williams et al. 1994).

Calanus chilensis and *Centropages brachiatus* (Copepoda) are among the most important contributors to the secondary production of the Humboldt Current ecosystem (Heinrich 1971, Boyd & Smith 1980, Pepe et al. 1989, Sherman 1995), eastern South Pacific. This marine ecosystem is one of the world's most productive fish-producing upwelling regions (Alheit & Bernal 1993, Sherman 1994). *C. chilensis* appears to be an endemic

species (Marín et al. 1994), whereas *C. brachiatus* is a coastal species widely distributed in the Southern Hemisphere (Bradford 1979). There is little information regarding the spatial and temporal distribution, life cycle and population strategies of these 2 species in the Humboldt Current ecosystem (Gonzalez 1993). Lack of zooplankton sampling programs in some areas of the world's oceans, such as the eastern South Pacific, has led global change programs such as GLOBEC (Global Ocean Ecosystem Dynamics), IOC (The Intergovermental Oceanographic Commission of UNESCO), and SCOR (The Scientifc Committee for Oceanic Research) to implement plans for the use of plankton collections. An example of the use of such collections in the study of the life cycle of copepods can be found in Marín (1986). In this paper, we report the results of the analysis of the spatial and seasonal distribution of *C. chilensis* and *C. brachiatus* off the northern Chilean coast in relation to the hydrography, using a Geographic Information System (GIS) approach. For this purpose, we have used part of the zooplankton sample collection of the Instituto de Fomento Pesquero (IFOP), Chile. This collection represents a highly valuable dataset for the study of large-

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scale biological features of the Humboldt Current ecosystem.

METHODS

Sampling. Integrated zooplankton samples (0 to 100 m) were collected by IFOP using a Nansen net (1.0 m diameter, 200 μm mesh) during 1989 in 4 cruises off the northern Chilean coast (Fig. 1). All cruises covered the study area with similar station coverage. Cruise 1 sampled the area between March 20 and April 10, Cruise 2 between May 5 and May 26, Cruise 3 between July 15 and August 1 and Cruise 4 between August 21 and September 11. A total of 140 samples, fixed in 5% formaldehyde, were analysed in this study. Males, females and copepodites stage V, were counted using either the whole sample or a fraction of it. The Folsom splitter was used for subsampling (McEwen et al. 1954). For the purposes of this paper, we have concentrated our analysis in the adult portion of the populations. Seasonality in the reproduction of both species was studied using the male/female ratio (Mullin & Evans 1976, Marín 1986).

Temperature and salinity at depth (depths = 0, 10, 25, 50, 75, 100 m) were available from the IFOP database for 3 of the 4 studied cruises (Cruises 2, 3 and 4).
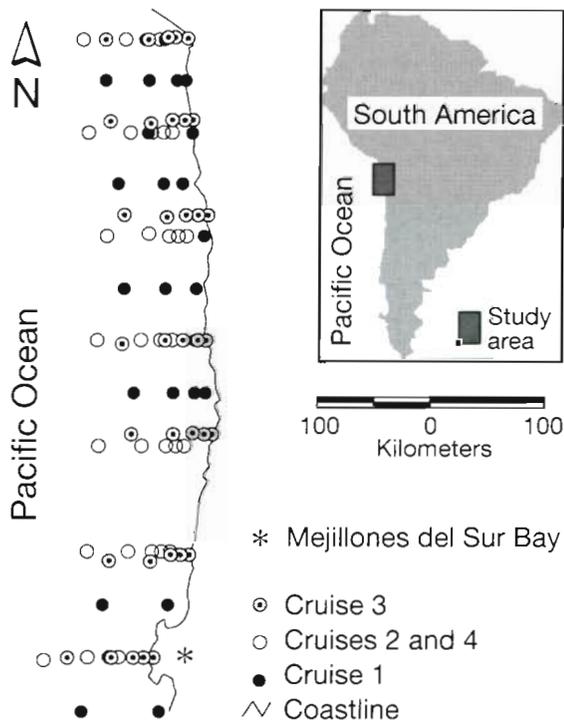

Fig. 1. Geographic location of the study area and spatial distribution of the oceanographic stations along the Chilean coast (eastern South Pacific Ocean)

Temperature was measured with reversing thermometers while salinity was measured using an AUTO-LAB 601™ inductive salinometer. Using this database, and the characteristics of the water masses present in the area (Silva 1983), we calculated their proportion in the top 100 m for each station from T-S diagrams (Gonzalez 1993). Three water masses can be identified in the upper 100 m of the water column in the study area: Subtropical Surface Water (SSW), Subantarctic Water (SAW) and Equatorial Subsurface Water (ESW). The last of these was seldom present in the area (Gonzalez 1993). Thus, we analysed the hydrography in terms of 2 water masses: SSW and SAW. The SSW is characterised by a temperature between 17 and 20°C and by salinity higher than 35 PSU. The SAW has a temperature between 10 and 18°C and a salinity between 33.9 and 34.7 PSU. We used the thermosteric anomaly limits for each water mass (Silva & Sievers 1974) to define their vertical extent, in meters, and then transformed those to the percentage of the 0 to 100 m water column occupied by each.

Spatial analysis. We used a GIS, ARC/INFO version 7.0.3 for UNIX, for the display and analysis of spatial information (ESRI 1994a). We analysed our data using a raster or grid model (Bosque-Sendra 1992). Raster models define the geographic space in a simple and uniform fashion, i.e. cells of same size, and they have great analytical power (ESRI 1994b, Eastman 1995). We provide a brief account of the analytical steps taken in the generation of our grids.

Dbase™ files containing physical and biological attributes collected at each oceanographic station were converted to INFO files (the database management part of ARC/INFO). Point coverages for each cruise were then generated from those files (Fig. 1). Subsequently, we generated grids through surface interpolation methods, and analysed them using ARC/INFO's GRID module. Oceanographic stations in each cruise covered an area on the order of 59 000 km^2, with 7 transects 80 km from each other and separation between stations ranging from 4.5 km near the coast to 33 km offshore (Fig. 1). Thus, we generated grids with a distance of 10 km between mesh points using 2 surface interpolation techniques: *kriging* (Rossi et al. 1992) and *spatial weighted moving average* or IDW (Jongman et al. 1995). Kriging is an optimum interpolation method based on the estimation of an experimental semivariogram. The semivariogram describes the changes of the semivariance (one-half of the variance) as a function of the distance between points. The experimental semivariogram is estimated by fitting the calculated semivariances to a set of theoretical semivariograms or models (see Table 2). IDW, on the other hand, is a surface interpolation method that assumes that each point has a local influence that diminishes with distance and

it does not require fitting to a theoretical semivariogram (Jongman et al. 1995). We used the kriging method for the analysis of the distribution of water masses. However, when attempting to use it for copepod distribution, we failed to fit any theoretical semivariogram, a requirement of the kriging technique (Jongman et al. 1995). We therefore used the IDW interpolator to generate the copepod grids.

Aside from generating abundance grids for both species using the GIS, we analysed their distribution using classical linear statistical analysis (Sokal & Rohlf 1981). We tested, using a 2-way ANOVA with interaction, for differences in abundance between cruises, i.e. seasonality and distance from shore. We checked for homogeneity of variance and, as a result, we used $\log(x+1)$ transformed data. Correlation among variables was studied in 2 ways: first, we used linear statistics and calculated Pearson's r from the original point estimates (Sokal & Rohlf 1981); second, we calculated the spatial cross-correlation index from the resulting grids (Goodchild 1986, ESRI 1994a). This index measures the similarity between 2 grids. Its calculation is performed as follows: let n be the total number of cells in a grid (i.e. number of rows × number of columns, since grids mathematically are matrices), i any cell of the first grid, j any cell of the second grid, z_i the value of cell i, z_j the value of cell j and c_{ij} the similarity of i's and j's attributes given by: $(z_i - z_m) \cdot (z_j - z_m)$, where z_m is the average value. Then, the cross-correlation index, c, is calculated using the following formula (Goodchild 1986):

$$c = \sum_k^n c_{ij} / \left\{ \text{sqrt}\left[\sum_k^n (z_i - z_m)^2 \right] \cdot \text{sqrt}\left[\sum_k^n (z_j - z_m)^2 \right] \right\}$$

where sqrt = square root and $k = i$ or $j = 1$.

RESULTS

Water masses in the studied area

El Niño events (i.e. the warm phase of the El Niño Southern Oscillation, ENSO) have profound effects on the dynamics of the Humboldt Current ecosystem (Shermann 1995). Therefore, the analysis of ecological data in this region should make specific reference to whether samples were taken during a warm or a cold phase of the ENSO. According to the information available (Rutllant et al. 1992) 1989 corresponded to a cold phase of the ENSO in the Humboldt Current ecosystem.

The SAW occupied, on average, more than 80% of the water column and dominated the study area (Table 1). During Cruise 2, May (Fig. 2A), the largest percentage of the SAW occurred close to shore in sectors that have been characterised as coastal up-

Table 1. Average water mass composition for Cruises 2, 3 and 4 in the 0 to 100 m water column. SAW = Subantarctic Water, SSW = Subtropical Surface Water, ESW = Equatorial Subsurface Water. Data correspond to the mean (standard deviation) percentage of each water mass in the study area

Water mass	Cruise 2 (n = 33)	Cruise 3 (n = 15)	Cruise 4 (n = 35)
SAW	83.3 (17.3)	88.0 (12.0)	80.5 (17.6)
SSW	13.6 (15.7)	12.0 (11.1)	9.9 (10.5)
ESW	2.8 (7.5)	0	9.0 (15.0)

welling areas (Fonseca & Farias 1987). This same trend, i.e. dominance of SAW close to shore, was observed at some locations during Cruise 3, July-August (Fig. 2B), which corresponds to the austral winter. However, the SSW largely dominated the area during Cruise 3; that is, lower percentages of SAW (red in Fig. 2B) occurred. The presence of warm subtropical water has been previously recorded in this same area of the Chilean coast (Brandhorst & Cañon 1967). During Cruise 4, August-September, at the beginning of the austral spring, the whole area was almost homogeneously dominated (minimum percentage of 73%) by the SAW (Fig. 2C). This condition can be attributed to the intensification of coastal upwelling during spring, which brings this water mass to the surface (Rodriguez et al. 1991, Strub et al. in press).

Seasonal changes in the structure of the physical environment were also detected while calculating the semivariograms for each grid (Table 2). The results of the semivariograms show that the range, a, increased from 190 km during Cruise 2 to over 500 km during Cruise 4. That is, the area over which there is correlation among properties of the physical environment increased during seasons, with its maximum during the spring period.

Table 2. Parameter values of the spherical semivariogram used to interpolate the percentage of SAW in Cruises 2, 3 and 4 (Fig. 2). Parameters correspond to the following formula: $\gamma(h) = c_0 + c_1[(3h/2a) - 0.5(h/a)^3]$ for $0 < h < a$, and $\gamma(h) = c_0 + c_1$ for $h \geq a$. Where $\gamma(h)$ is the semivariance for each spatial lag h, a is the range [above which $\gamma(h)$ remains theoretically stable], c_0 is the nugget or random variance and $c_0 + c_1$ equals the sill, or maximum theoretical semivariance. This is a commonly used theoretical semivariogram model and the default in many geostatistical software. The use of other models (e.g. linear, Gaussian) did not change the resulting grids

Parameter	Cruise 2	Cruise 3	Cruise 4
c_0	162.8	0.0	165.7
c_1	540.7	3155.0	0.0
a (km)	190	332	>500

Cruise 2 / May 1989   Cruise 3 / July-August 1989   Cruise 4 / August-September 1989

0–10
10–30
30–50

50–80
80–100
No Data
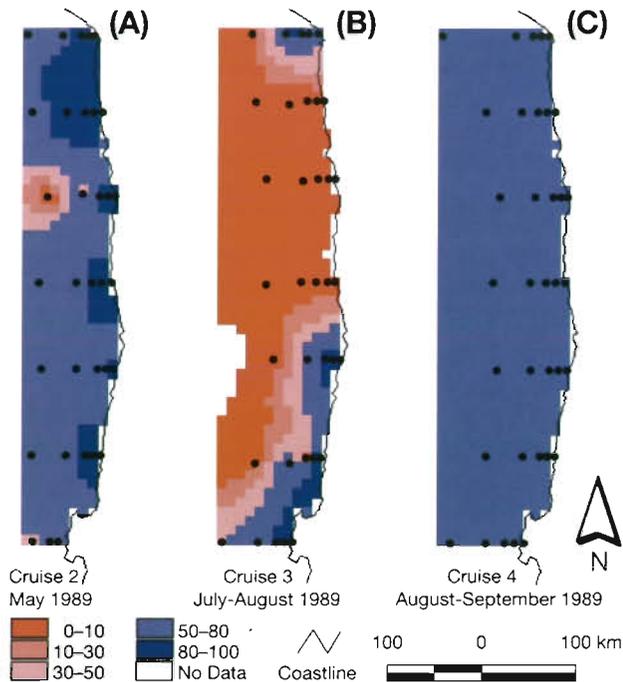
100   0   100 km

Coastline

Fig. 2. Spatial distribution of the Subantarctic Water Mass as a percentage of the water column (0 to 100 m) occupied. Grids were generated by spatial interpolation of data points (oceanographic stations in each cruise) using kriging (for details see 'Methods: Spatial analysis')

Distribution of *Calanus chilensis* and *Centropages brachiatus*

The largest abundance of *Calanus chilensis* was found in the northern part of the study area (Fig. 3). Data from Cruises 2 through 4 showed that those large abundances occurred predominantly close to shore. The 2-way ANOVA (Table 3), however, showed that there is no general linear cross-shelf trend in the abundance of this species. It also showed significant differences in its abundance among cruises. Finally, the interaction between Cruise and Distance was marginally significant (p = 0.085, Table 3), suggesting that the relationship between abundance and distance from shore changes seasonally. The distribution of *Centropages brachiatus*, on the other hand, showed differences to that of *C. chilensis*. The largest average abundance of *C. brachiatus* (247 copepods m^{-3}) was found in Cruise 1, March-April, when *C. chilensis* was at its lowest (Fig. 4). *C. brachiatus*, contrary to *C. chilensis*, showed a significant cross-shelf linear trend in its abundance, i.e. higher values close to shore (Table 3). It also showed significant differences among cruises and no significant interaction between Cruise and Distance. Thus, the abundance of *C. brachiatus* tends to decrease offshore and this pattern does not change seasonally.

Table 3. Two-way ANOVA with replication of the abundances of *Calanus chilensis* and *Centropages brachiatus*. Testing was done for 2 sources: time of the year (Cruise) and distance from shore (Distance). Data were transformed using $\log(x+1)$

Source	SS	df	MS	*F*-ratio	p
Calanus chilensis					
Cruise	8.60	3	2.87	8.87	0.000
Distance	1.31	4	0.33	1.01	0.404
Cruise × Distance	6.44	12	0.54	1.66	0.085
Error	32.21	109	0.32		
Centropages brachiatus					
Cruise	11.18	3	3.73	6.8	0.000
Distance	20.44	4	5.11	9.31	0.000
Cruise × Distance	2.81	12	0.23	0.43	0.950
Error	59.80	109	0.55		

Although the 2-way ANOVA showed that the 2 species differed in their cross-shelf abundance patterns, it only tested for log-linear trends. However, a visual analysis of the abundance grids (Figs. 3 & 4) suggested to us that large values of both species tended to occur close to shore. This analysis was performed using GIS tools. First, we defined 'large values' as those corresponding to the upper 10% of the range of abundance in each cruise. Table 4 shows the mean, standard deviation and the range of the abundances of *Calanus*
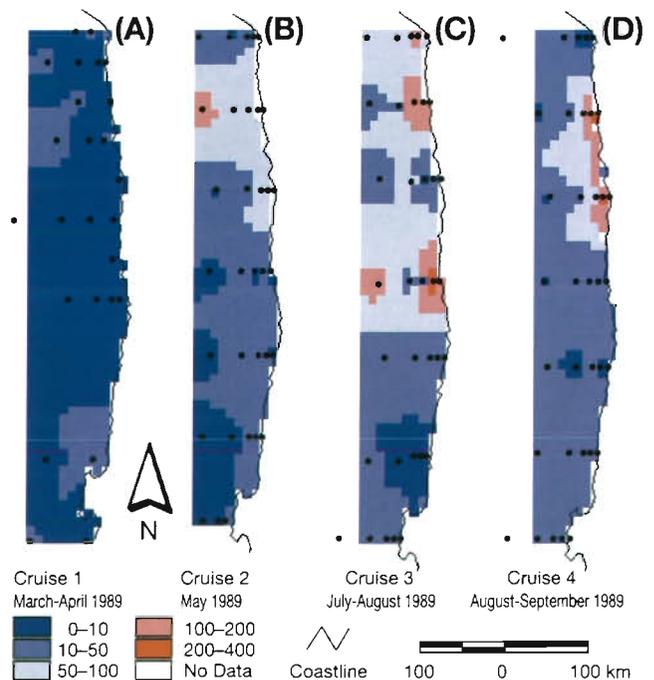

Cruise 1 March-April 1989   Cruise 2 May 1989   Cruise 3 July-August 1989   Cruise 4 August-September 1989

0–10
10–50
50–100

100–200
200–400
No Data

Coastline   100   0   100 km

Fig. 3. *Calanus chilensis*. Spatial distribution of the abundance (copepod m^{-3}) in the study area. Grids were generated using a spatial weighted moving average (IDW) technique (for details see 'Methods: Spatial analysis')
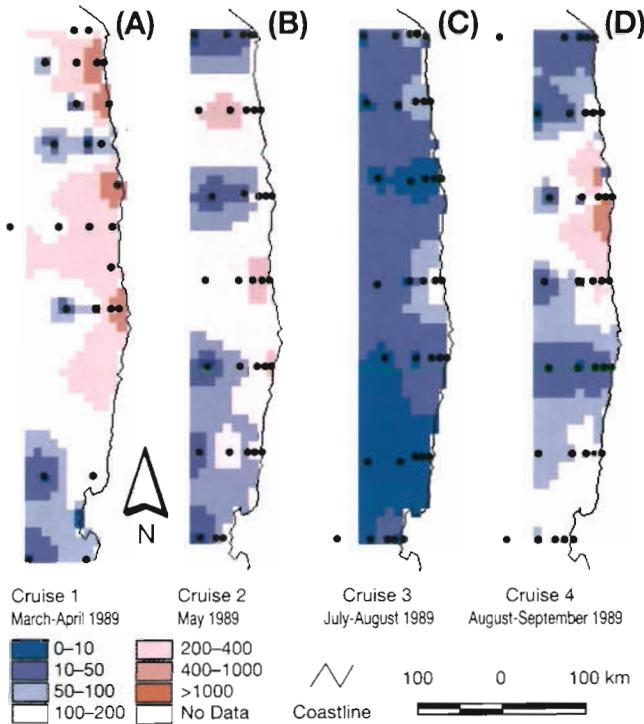
Cruise 1   Cruise 2   Cruise 3   Cruise 4
March-April 1989 May 1989   July-August 1989 August-September 1989

0–10	200–400
10–50	400–1000
50–100	>1000
100–200	No Data

/\/   100   0   100 km

Coastline

Fig. 4. *Centropages brachiatus*. Spatial distribution of the abundance (copepod m^{-3}) in the study area. Grids were generated using a spatial weighted moving average (IDW) technique

chilensis and *Centropages brachiatus*. Second, we queried all grids from Figs. 3 & 4, selecting those cells that would contain large values, as previously defined. The distribution of those values is shown in Fig. 5. With the exception of the data belonging to Cruise 2 (May 1989), large values for both species were located close to shore (within 10 km). Most of them occurred in the northern and central part of the study area, with the exception of *C. chilensis* in Mejillones Bay at the southern end of the study area. Large offshore values

Table 4. Mean, standard deviation and range of abundances (copepods m^{-3}) of *Calanus chilensis* and *Centropages brachiatus* in the study area

Cruise	Mean	SD	Range
Calanus chilensis			
1	8.1	4.2	0.0–25.0
2	40.0	49.0	0.0–164.0
3	52.0	27.0	3.0–390.0
4	96.0	192.0	1.0–349.0
Centropages brachiatus			
1	247.0	47.0	0.0–1035.9
2	121.0	31.0	0.0–184.0
3	30.0	17.0	2.0–174.0
4	134.0	71.0	11.0–1350.0

from Cruise 2 were located 40 km (*C. brachiatus*) and 73 km (*C. chilensis*) away from shore. We overlaid the 'large values' grid to the percentages of SAW during Cruise 2 to analyse if the spatial distribution of these values was related to the hydrography (Fig. 5). The result of this analysis showed that these high abundances occurred in an area with a large offshore extension of the SAW. Furthermore, the spatial cross-correlation index between the distribution of percentages of SAW and the abundance of copepods showed positive correlations for Cruises 2 and 4, and negative correlations for Cruise 3 (Table 5). This negative result may be partly due to the presence of coastal patches of high abundance of both species in the area of low percentages of SAW during Cruise 3 (Figs. 2, 3 & 4). Thus, our GIS analysis has shown that both species occurred predominantly close to shore, within 10 km, and that large abundances found further offshore tend to occur where offshore advection of coastal waters, dominated by the SAW, can be inferred.

A different way of analysing these results is to assume that both variables (percentage of SAW and

100   0   100 km

Cruise 2 legends:

_____ 80% SAW
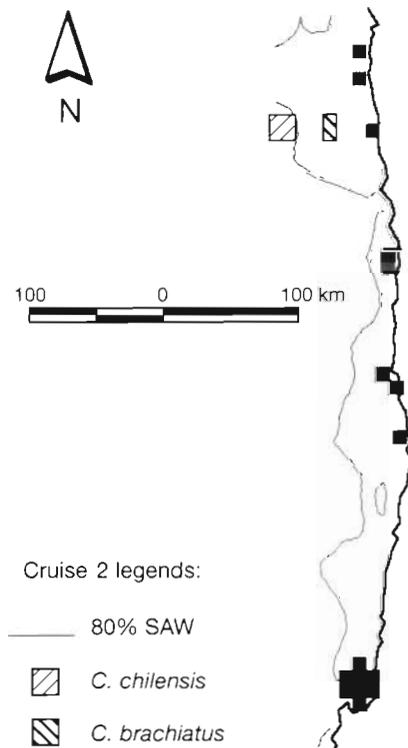
▨ C. chilensis

▧ C. brachiatus

Fig. 5. *Calanus chilensis* and *Centropages brachiatus*. Spatial distribution of large values (upper 10% of the range of abundance in each cruise) of abundance in the study area. A composite picture of the large values of both species in all cruises is shown. Gray cells: large values of *Centrophages brachiatus* in Cruises 1, 3, and 4; black cells: large values of *Calanus chilensis* in Cruises 1, 3, and 4. Other features of the map, those of Cruise 2, are explained within the figure

copepod abundance) are random variables, and analyse to see if the proportion of negative to positive correlations is higher than that expected by chance alone (a binomial test). The results of this test, p (n = 3, $x \geq 2$) = 0.5, show that from a purely statistical point of view, we cannot discard the possibility that water mass distribution does not play a role in the distribution of copepods.

Finally, the temporal distribution of the male/female ratio did not show evidence of seasonality in reproduction for both species. A 1-way ANOVA of male/female ratios with time (cruise) as the source of variability gave a probability of 0.56 for *Centropages brachiatus* and 0.47 for *Calanus chilensis*. Furthermore, the spatial distribution of the male/female ratio of both species did not show clear trends either in relation to distance from shore or with respect to latitude.

Relationship between species distributions

The available literature regarding *Calanus chilensis* and *Centropages brachiatus* suggests that they co-occur and belong to the coastal, distant-neritic, group of species (Heinrich 1971, Sameoto 1981). We tested this idea by performing a linear correlation analysis between the spatial distributions of the 2 species. For this test, we used the original sample estimates of abundance and calculated Pearson's r (Sokal & Rohlf 1981). When considered over all cruises, the spatial distribution of both species was positively correlated

Table 5. Spatial cross-correlation indices for the relationship between the percentage of the water column occupied by SAW and the abundance of copepods

Species	Cruise 2	Cruise 3	Cruise 4
Calanus chilensis	0.19	−0.36	0.11
Centropages brachiatus	0.47	−0.17	0.14

Table 6. Correlation analysis between the distribution of *Calanus chilensis* and *Centropages brachiatus* in the study area. Pearson's r correlation coefficients were calculated from the original data using $\log(x+1)$ transformation. Spatial cross-correlation indices are shown in the last column, these indices were calculated between species abundance grids for each cruise

Cruise	Pearson's r	p	Cross-correlation index
1	−0.45	0.02	−0.44
2	0.61	<0.001	0.39
3	0.55	0.001	0.84
4	0.65	<0.001	0.68

(r = 0.262, n = 129, p < 0.001). However, when the analysis was done cruise by cruise, results were different. We found significant correlations in all 4 cruises (Table 6). However, 3 were positive (Cruises 2 through 4) and 1 was negative (Cruise 1). We used again the binomial test on the proportion of negative to positive correlations. The result, p (n = 4, $x \geq 3$) = 0.31, showed that we cannot rule out the null hypothesis that both species occur independent of each other and that the observed correlations are the result of chance alone. The spatial cross-correlation indices between grids produced similar results (Table 6).

DISCUSSION

Spatial distribution of *Calanus chilensis* and *Centropages brachiatus*

Calanus chilensis and *Centropages brachiatus* occur at average abundances of 50 and 130 copepods m^{-3}, respectively, within 80 km of the northern Chilean coast. These abundances are within the same order of magnitude as those described by Heinrich (1971) for the Chile-Peru coastal zone for *C. chilensis* (25 copepods m^{-3}), but an order of magnitude larger for *C. brachiatus* (9 copepods m^{-3}). The highest concentration of both species (≥ 390 copepods m^{-3}) occurred close to shore (i.e. within 10 km from shore). The area of maximum abundance, or 'large values' as defined in the 'Results', corresponds to that most affected by coastal upwelling and having the highest primary production (Marín et al. 1993). This result also agrees with the observations by Heinrich (1971) and Escribano & Rodriguez (1994). Our analysis using GIS tools suggests that both species are more abundant under SAW conditions, the water mass associated with the upwelling dynamics (Strub et al. in press). This interpretation agrees with the coastal distribution of both species off the Peruvian coast, as shown by Heinrich (1971) and Semenova et al. (1982). However, if results are examined from a purely statistical point of view using the binomial test on expected proportions of positive and negative correlations, we cannot rule out the possibility that the relationship between the SAW distribution and copepod abundance is a result of chance alone. The same holds for the relationship between the spatial distributions of the 2 species. In this last case, however, both the GIS cross-correlation indices and Pearson's r produced the same result (Table 6). Furthermore, the ANOVA performed on abundance (Table 3) showed that, at least from the point of view of parametric statistics (Sokal & Rohlf 1981), the 2 species had different cross-shelf trends. Positive spatial correlation between *C. chilensis* and *C. brachiatus* has been

shown by some authors (Heinrich 1971, Sameoto 1981, Semenova et al. 1982), and these 2 species were put in the 'distant-neritic' group. Our results agree with these authors only in the sense that high abundances of both species occur close to shore, but we do not find firm evidence of positive spatial correlation between them. Alternatively, our GIS analysis may offer more clues on this statistical issue. Our preferred method for spatial interpolation was kriging. However, as stated in the 'Methods', we failed to fit any theoretical semivariogram for the copepod abundance distributions. The resulting semivariograms had the structure of 'noise', which would result from a process with structureless spatial variation (Jongman et al. 1995). One simple explanation for this result is that samples were taken too far apart to distinguish the statistical structure of the spatial distribution of copepods. Thus, it is possible that a finer scale distribution study is necessary to resolve this. Even in this situation, the methods used in this analysis allowed us to proposed general distribution patterns. Thus, we can conclude that the information presented here, as analysed through a GIS, strongly support the notion that *C. chilensis* and *C. brachiatus* are part of a group of zooplanktonic species especially abundant within 10 km from the coastline. Given the dominance of the SAW in that domain, the distribution of the species appears related to it. However, variability on smaller scales, which appear as random effects in our analysis, may be important.

Geographic Information Systems are powerful and complex computerised tools for the analysis and modeling of spatial data (Bosque-Sendra 1992). They are increasingly being used in ecology, especially for landscape analysis (Dunning et al. 1995). However, they have hardly been used in aquatic ecology, let alone plankton research. Only recently, ecologists have started using GIS's for the analysis of complex systems. Delgado & Marín (1997) show an example of the use of GIS's in the analysis and modeling of the Antarctic krill *Euphausia superba* fishery. Tishendorf (1997) discusses its use for the modeling of animal movements in heterogeneous landscapes. One important feature of GIS's is that they link spatial data models (a grid in our case) to database management systems. Thus, they support the combination and visualisation of different information layers, e.g. water mass characteristics and copepod abundance, improving our capacity for the description and modeling of the distribution of planktonic organisms. Another interesting feature of GIS's is that they include tools for surface generation from point estimates, a common problem in oceanographic studies, which incorporates the concept of autocorrelation among data (e.g. kriging, IDW). Furthermore, at least in grid data models, the cell-by-cell analysis allows for the testing of

hypotheses using, for example, Boolean evaluation of logical expressions. We used that feature to test the distribution of large values in relation to distance from the coast. GIS's include many other features that may be of interest to scientists working in plankton research, like watershed analysis, hydrological models, etc. In this paper, we have used just a small subset of the tools available in GIS's and for a rather limited dataset. Nevertheless, we are convinced, after using it, that this technology can be used effectively to study aquatic ecosystems, especially when dealing with large (e.g. global change) datasets on planktonic organisms.

Life cycle of *Calanus chilensis* and *Centropages brachiatus* in the Humboldt Current ecosystem

The problem of population regulation in marine animals is a recurrent issue in biological oceanography (Laevastu & Larkins 1981, Sinclair 1988, Angel 1994). Sinclair (1988), in relation to population regulation in the oceans, proposed the 'member/vagrant' hypothesis that emphasises the spatial constraints of the oceans to life cycle closure. The hypothesis proposes that, for species with complex life histories, populations are considered to be regulated, to a large degree, by physical oceanographic processes. Copepods in other marine ecosystems show life cycles tuned to the physical characteristics of that system (Marín 1986, 1988, Conover 1988).

In upwelling systems the local maintenance of copepod populations seems to depend upon seasonal (ontogenetic) and/or diurnal migrations (Verheye et al. 1991, Angel 1994). The resolution of our sampling scheme did not allow us to distinguish diurnal vertical migrations. However, we did not find evidence for ontogenetic migrations. Indeed, our results show that adults of both species are found in the upper water levels (0 to 100 m) year-round. Furthermore, we found a lack of seasonal change in male/female ratios. This suggests that both species can reproduce throughout the year in the Humboldt Current ecosystem. In fact, Escribano & Rodriguez (1994) have shown year-round presence of nauplii and adults of *Calanus chilensis* in a coastal embayment within our study area. Our data and that of Heinrich (1971) support the idea that *C. chilensis* and *Centropages brachiatus* are especially abundant in areas of high biological production close to shore. Thus, the high abundance of both species more than 40 km away from the coast in some locations (Fig. 5) may be interpreted as the result of offshore advection. This interpretation would also agree with the idea, first introduced by Hutchinson (1953) and subsequently developed by Haury et al. (1978), that

the mesoscale (i.e. 10^2 km) distribution of zooplanktonic species is vectorial and reproductive. Vectorial patterns are those generated by external forces such as circulation and currents (Hutchinson 1953); while reproductive patterns are those generated by the biological dynamics (e.g. reproduction and growth) of each species. Thus, the spatial mesoscale distribution pattern of *C. chilensis* and *C. brachiatus* can be explained as the result of reproduction in coastal upwelling areas of the Humboldt Current ecosystem, followed by offshore advection. Consequently, if both species do not perform seasonal migration, the possibility of becoming vagrants from their local populations is high. On the other hand, they may have alternative mechanisms such as diurnal vertical migration, finely tuned to the upwelling circulation, as shown for other coastal calanoids (Angel 1994). Marín (1997) has shown that, at least for *C. chilensis*, the diurnal vertical migration pattern does not seem to be strong enough to prevent it from being advected offshore. Finally, it is also possible that the complex mixture of northward and southward flows that characterises the circulation of the Humboldt Current ecosystem (Silva 1983) produces enough 'residence time' to maintain local populations close to shore. However, discerning between these hypotheses will require a mixture of process-oriented sampling together with mathematical modeling of the circulation-migration dynamics.

LITERATURE CITED

Alheit J, Bernal P (1993) Effects of physical and biological changes on the biomass yield of the Humboldt Current ecosystem. In: Sherman K, Alexander LM, Gold BD (eds) Large marine ecosystems: stress, mitigation, and sustainability. AAAS Press, Washington, DC, p 53–68

Angel M (1994) Spatial distribution of marine organisms: patterns and processes. In: Edwards PJ, May RM, Webb NR (eds) Large-scale ecology and conservation biology. Blackwell Science, London, p 59–109

Bond WJ (1994) Keystone species. In: Schulze DE, Mooney HA (eds) Biodiversity and ecosystem function. Springer-Verlag, Berlin, p 237–253

Bosque-Sendra J (1992) Sistemas de Información Geográfica. Ediciones Rialp SA, Madrid

Boyd CM, Smith SH (1980) Grazing patterns of copepods in the upwelling system off Perú. Limnol Oceanogr 25: 583–596

Bradford JM (1979) Zoogeography of some neritic pelagic Crustacea and their close relatives. Proceedings of the

International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere, Auckland, New Zealand. NZ Dep Sci Ind Res Inf Ser 137:593–612

Brandhorst W, Cañon J (1967) Resultados de estudios oceanográfico-pesqueros aéreos en el norte de Chile. IFOP Publication no. 29

Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia 167/168:127–142

Delgado LE, Marín VH (1997) EIMS-Antarctica. An ecosystem analysis of the Antarctic krill fishery in the South Shetland Islands: a 2d (arcinfo based) cellular automata model of the krill fishery. In: Santibañez F, Marín VH (eds) Computer tools for the sustainable management of arid and antarctic ecosystems. Editorial Tecnográfica SA, Santiago, p II:25–80

Dunning JB, Stewart DW, Danielson BJ, Noon BR, Root TL, Lamberson RH, Stevens EE (1995) Spatially explicit population models: current forms and future uses. Ecol Appl 5:3–11

Eastman J (1995) Idrisi for windows. User's guide version 1.0. Clark University, Worcester

Escribano R, Rodriguez L (1994) Life cycle of *Calanus chilensis* Brodsky in Bay of San Jorge, Antofagasta, Chile. Hydrobiologia 292/293:289–294

ESRI (1994a) Understanding GIS. The ARC/INFO method. (Version 7 for UNIX). Environmental Systems Research Institute, Inc, Redlands

ESRI (1994b) ARC/INFO Data management. Concepts, data models, database design, and storage. Environmental Systems Research Institute, Inc, Redlands

Fonseca TR, Farias M (1987) Estudio del proceso de surgencia en la costa chilena utilizando percepción remota. Invest Pesq (Chile) 34:33–46

Gonzalez A (1993) Distribución espacial de dos copépodos Calanoideos *Calanus chilensis* (Brodsky) y *Centropages Brachiatus* (Dana) en el norte de Chile. Tesis de Grado para Licenciado en Biologia Marina, Universidad Austral de Chile

Goodchild MF (1986) Spatial autocorrelation, Catmog 47. Geo Books, Norwich

Haury LR, McGowan JA, Wiebe PH (1978) Patterns and processes in the time-space scales of plankton distributions. In: Steele J (ed) Spatial pattern in plankton communities. Nato Conference Series IV Marine Sciences, Plenum Press, New York, p 277–328

Heinrich A (1971) On the near-surface plankton of the eastern South Pacific. Mar Biol 10:290–294

Hutchinson GE (1953) The concept of pattern in ecology. Proc Acad Nat Sci Phila 105:1–12

Jongman RHG, Ter Braak CJF, Van Tongeren OFR (1995) Data analysis in community and landscape ecology. Cambridge University Press, London

Laevastu T, Larkins HA (1981) Marine fisheries ecosystem. Its quantitative evaluation and management. Fishing News Books Ltd, Farnham

Marín V (1986) Distribution and life cycle of three antartic copepods (*Calanoides acutus, Calanus propinquus* and *Rhincalanus gigas*). PhD dissertation, University of California, San Diego

Marín V (1988) Independent life cycles: an alternative to the asynchronism hypothesis for antarctic Calanoid copepods. Hydrobiologia 167/168:161–168

Marín V (1997) A simple-biology, stage structured population model of the spring dynamics of *Calanus chilensis* at Mejillones del Sur Bay, Chile. Ecol Model 105:65–82

Marín V, Espinoza S, Fleminger A (1994) Morphometric study

of *Calanus chilensis* males along the Chilean coast. Hydrobiologia 292/293:75–80

Marín V, Rodriguez L, Vallejo L, Fuerteseca J, Oyarce E (1993) Efectos de la surgencia costera sobre la productividad primaria primaveral de Bahía Mejillones del Sur (Antofagasta, Chile). Rev Chil Hist Nat 66:479–491

McEwen GF, Johnson MW, Folsom ThR (1954) A statistical analysis of the performance of the Folsom plankton sample splitter, based upon test observations. Arch Meteorol Geophys Bioklimatol Ser A 71:502–527

Mullin MM, Evans PM (1976) Distribution, morphology and seasonal biology of the planktonic copepods *Neocalanus robustior* and *Neocalanus gracilis* in the Pacific Ocean. Pac Sci 30:119–130

Omori M, Ikeda T (1984) Methods in marine zooplankton ecology. Wiley-Interscience, New York

Pepe R, Oliva E, Toro J (1989) Importancia del zooplankton en los contenidos estomacales de *Sardinops sagax* en el norte de Chile para el verano de 1987. IX Jornadas de Ciencias del Mar, Chile, p 110

Rodriguez L, Marín V, Farías M, Oyarce E (1991) Identification of an upwelling zone by remote sensing and *in situ* measurements: Mejillones del Sur Bay (Antofagasta, Chile). Sci Mar 55:467–473

Rossi R, Mulla DJ, Journel AG, Franz E (1992) Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol Monogr 62:277–314

Runge JA (1988) Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. Hydrobiologia 167/168:61–71

Rutllant J, Aceituno P, Montecinos A (1992) Análisis comparativo de aspectos atmosféricos para los eventos de El Niño/ Oscilación del Sur de 1982–83, 1986–87 y 1991–92. Invest Pesq (Chile) 37:45–54

Sameoto D (1981) Distribution and abundance of six species of fish larvae in peruvian waters and their relationship with physical and biological environment. Bol Inst Mar Perú, Volumen extraordinario:171–179

Semenova TN, Timotin AG, Flint MV (1982) Characteristic features of the lateral and vertical distributions of abundant zooplankton species ner the Peruvian Coast. Oceanology 22:216–220

Sherman K (1994) Sustainability, biomass yields, and health of coastal ecosystems: an ecological perspective. Mar Ecol Prog Ser 112:277–301

Sherman K (1995) Large marine ecosystems and fisheries. In: Munasinghe M, Shearer W (eds) Defining and measuring sustainability. The biogeophysical foundations. The United Nations University and the World Bank, Washington, DC, p 207–233

Silva N (1983) Masas de agua y circulacion en la region Norte de Chile (Latitudes 18° S–32° S). Operación oceanográfica MARCHILE XI - ERFEN II. Cienc Tecnol Mar Cona 7: 47–84

Silva N, Sievers H (1974) Masas de agua, velocidad geostrófica y transporte de volumen entre Valparaíso e Isla Robinson Crusoe. Com Perm Pac Sur Cienc Derecho 2:103–120

Sinclair M (1988) Marine populations. An essay on population regulation and speciation. Books in Recruitment Fishery Oceanography, Washington Sea Grant Program, Seattle

Sokal R, Rohlf FJ (1981) Biometry, 2nd edn. WH Freeman and Company, San Francisco

Strub P, Mesías J, Montecino V, Rutland J (1998) Coastal ocean circulation off western South America. In: Robinson A, Brink K (eds) The sea, Vol 2. The global coastal ocean. First Workshop on Coastal Ocean Advanced Science and Technology studies (COASTS) IOC, Liege. John Wiley & Sons, Inc

Tishendorf L (1997) Modelling individual movenets in heterogeneous landscapes: potentials of a new approach. Ecol Model 103:33–42

Verheye HM, Hutchings L, Perterson WT (1991) Life history and population maintenance strategies of *Calanoides carinatus* (COPEPODA:CALANOIDA) in the Southern Benguela Ecosystem. S Afr J Mar Sci 11:179–191

Williams R, Conway DVP, Hunt HG (1994) The role of copepods in the planktonic ecosystems of mixed and stratified waters of the European shelf seas. Hydrobiologia 292/293: 521–530