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Distribution pattern and population structure of *Calanus australis* Brodsky, 1959 over the southern Patagonian Shelf off Argentina in summer

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In the southwest Atlantic Ocean, *Calanus australis* is widely distributed in waters of the inner and middle shelf off Argentina. Along the coast of southern Patagonia it is the most abundant large copepod through all seasons, typically occurring at higher densities over the inner shelf <100 m deep. Its concentration decreases offshore as it is replaced by *Calanus simillimus* and *Neocalanus tonsus.* The abundance, vertical distribution, and population structure of *Calanus australis* off Patagonia were examined during a summer survey (March 1998) in order to study the ecological response of the copepod to hydrographic conditions. Differences in population densities were related to geographical difference in water-column stability. Higher numbers were recorded inshore at 51°S in strongly stratified coastal waters, where a well developed thermocline was present at 50 m. A sharp decline in abundance was evident southwards, coinciding with the occurrence of highly mixed, coastal, isothermal, and isohaline waters. Very low concentrations were also found at the most offshore, thermally stratified stations influenced by transitional waters between shelf and Malvinas waters. The population consisted mainly of stage 5 copepodites and fewer adult females. The scarcity or absence of younger stages cannot be attributed to the mesh size employed (150 µm). The population dynamics of *Calanus australis* are discussed and compared with other *Calanus* species.

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Introduction

Waters off southern Patagonia constitute one of the most productive fishing grounds off Argentina. The region sustains high production of mainly demersal and midwater fish, such as longtail hake, southern blue whiting, Argentinian common hake, austral hake, Patagonian toothfish, austral cod, and kingklip (Otero *et al.*, 1981; Bertolotti *et al.*, 1996; Wöhler *et al.*, 1999). Pelagic species such as squid (Brunetti and Pérez Comas, 1989) and Patagonian sprat (Sánchez *et al.*, 1995, 1997) are also present. All these species consume micro- and mesozooplankton during their early life history, and some feed on zooplankton exclusively, even as adults. Among them, the Patagonian sprat is also recognized as a link between trophic levels, because it is a main food item for many of the commercially targeted species. Hence, copepods play an important part in the trophodynamics of both adult and juvenile fish in the region.

Calanus australis is virtually the sole large copepod occurring year-round over the inner and middle shelf off Argentina south of 46°S (Ramírez, 1970; Ramírez and Sabatini, 2000) and it constitutes a major component of the larger fraction of mesozooplankton biomass (Sabatini and Alvarez Colombo, 2000). In common with several other members of the *helgolandicus* lineage to which it belongs (Bucklin *et al.*, 1995), the species is

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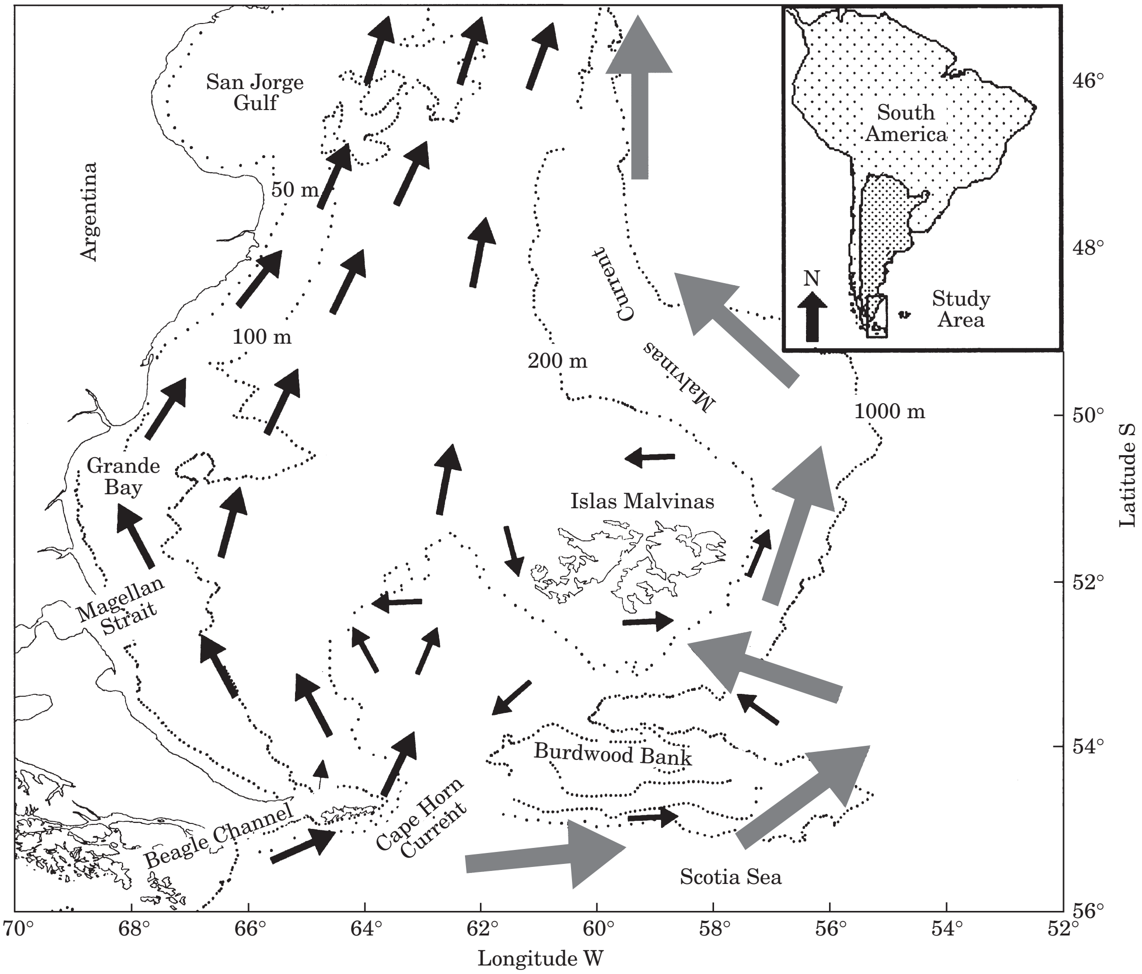

Figure 1. Area of investigation and schematic major circulation pattern off southern Patagonia (adapted from Piola and Rivas, 1997). Arrows indicate the direction and relative mass transport of the water flux.

abundant nearshore and over the adjacent continental shelf off southern Patagonia. Other examples of the group include *Calanus chilensis* (Escribano and Rodríguez, 1994), *Calanus helgolandicus* (Söhr *et al.*, 1996), *Calanus agulhensis* (Verheye *et al.*, 1994), *Calanus pacificus* (Osgood and Frost, 1994), and *Calanus sinicus* (Huang *et al.*, 1993). As a crucial link between primary production and fish, it most likely plays a similar role in austral Patagonia to that of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic and North Sea (e.g. Matthews and Bakke, 1977; Cushing, 1984; Williams and Conway, 1984; Franz *et al.*, 1991; Tande, 1991; Meise and O'Reilly, 1996; Runge and de Lafontaine, 1996), *Calanoides carinatus* in the southeast Atlantic ecosystem (e.g. Verheye *et al.*, 1992) and in the upwelling area off Cabo Frío, Brazil (e.g. Campaner and Honda, 1987; Valentin *et al.*, 1987), and *C. agulhensis* in southern South African waters (e.g. Verheye *et al.*, 1994).

The species was first described in the study area, and it is strictly restricted to the southern hemisphere (Brodsky, 1959). At present, despite its implied importance, no population studies have been conducted on it, and little is known beyond its overall distribution. In the southwest Atlantic Ocean, *C. australis* is widely distributed in shelf waters off Argentina, presumably related to the overall drift northwards of subantarctic waters. Its abundance decreases offshore as it is gradually replaced by *Calanus simillimus* and *Neocalanus tonsus.* Abundance of *C. simillimus* starts to increase in an offshore direction from the middle shelf, whereas *C. australis* is the typically dominant species in inner- and middle-shelf waters. *N. tonsus* becomes abundant towards the outer shelf and slope (Ramírez, 1970; Ramírez and Sabatini, 2000).

Two main currents transport subantarctic waters onto the austral Patagonian shelf (Figure 1), the Cape Horn Current (salinity ± 33.5 PSU) flowing over the shelf in a

N–NE direction towards the Atlantic Ocean, and the Malvinas Current (33.75 PSU) flowing also N–NE but along the continental slope (Lusquiños and Valdés, 1971; Piola and Rivas, 1997). The former waters are measurably diluted in the northern Drake Passage by an excess of rainfall in the southeast Pacific and by continental discharge from the Fueginian Channels. The cold, nutrient-rich Malvinas Current originates as a branch of the Antarctic Circumpolar Current, and it is the major boundary current influencing the region. Run-off from the Magellan Strait creates a tongue of water of low salinity (<32.5 PSU) that also flows N–NE, but along the Patagonian coast (Piola and Rivas, 1997). Three water masses can be recognized over the shelf off southern Patagonia: Malvinas Water, characterized by salinities of 33.8–34.2 PSU, Coastal Water, <33.2 PSU, and Shelf Water, produced by mixing of the other two, with salinities of 33.2–33.8 PSU (Bianchi *et al*., 1982). Stratification over the Patagonian Shelf depends largely on the seasonal variation of solar radiation. The influence of salinity is limited exclusively to the area of discharge of diluted waters from the Magellan Strait (Guerrero and Piola, 1997). The increasing solar warming during spring is stored in the upper layer of the water column, generating a seasonal thermocline between 30 and 50 m depth (Blanc *et al*., 1983; Glorioso, 1987; Scasso and Piola, 1988; Martos and Guerrero, 1992). The southernmost limit for the occurrence of the seasonal thermocline appears to be ca. 52°S, and it vanishes completely at 53°S. The southern Patagonian coast is characterized by high tidal amplitude, which in turn generates high energy dissipation caused by bottom friction (Simpson and Bowers, 1981; Glorioso, 1987). The high tidal energy, along with the seasonal thermal stratification, leads to the formation of tidal fronts along the coast (Glorioso, 1987; Glorioso and Flather, 1995; Martos and Sánchez, 1997).

As a first step in investigating the population dynamics of *C. australis* in the region, the aims of this work were to examine the horizontal and vertical distribution of the copepod and its population structure during a summer survey carried out off southern Patagonia, and to relate them to the major hydrographic features of the region.

Materials and methods

The research was conducted in the southern region of the Argentine Sea from 10 to 22 March 1998. At all stations (Figure 2), profiles of temperature and salinity were recorded with a Sea-Bird 19 CTD. Data were calibrated for salinity by salinometer measurements of discrete water samples and for temperature by reversing thermometers.

Stratification of the water column was estimated by calculating the vertical stability parameter φ, which is a measure of the amount of mechanical work, in J m^{-3}, required to vertically mix the water column and is derived from vertical profiles of density (Simpson, 1981). The parameter is defined as

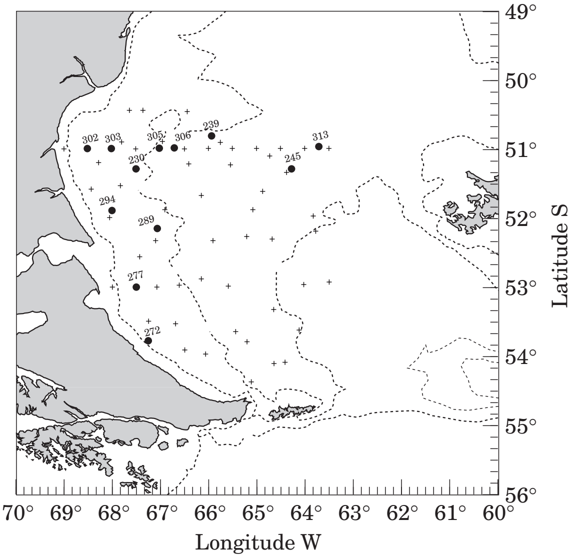

Figure 2. Hydrographic and biological sampling in the study area. Dots and numbers correspond to stations where zooplankton and CTD sampling were performed and crosses refer to those where only a CTD was used.

$$\phi = gh\int_{-h}^{0}(\rho-\rho_0)z\ dz$$

where g is the gravity acceleration, h the total depth, ρ the density, ρ_0 the mean density of the water column, and z is the depth. It was derived from vertical profiles with a depth interval of 1 m.

Zooplankton sampling was performed along a cross-shelf transect at 51°S and in waters along the Patagonian–Fueguinian coast. Samples (n = 44) were collected using a multiple opening/closing Hydrobios Multinet, 0.25 m^2 mouth opening and 150 μm mesh size. Sampling was carried out by horizontal tows of 5–10 min at each of 3–4 discrete depths covering the total water column in ca. 25-m steps. Filtered volume was estimated from the mouth area and towing time and speed. The samples were preserved in 4% buffered formaldehyde solution immediately after capture for later analysis ashore.

Developmental stages were counted from subsamples consisting generally of at least 200 *C. australis*, which were all staged and the adults sexed. Total samples were enumerated on occasions when animals were very scarce. The numbers of individuals per cubic meter obtained at each towing depth were quantified to the abundance of animals per ca. 25 m stratum (number m^{-2}) by multiplying those values by their respective

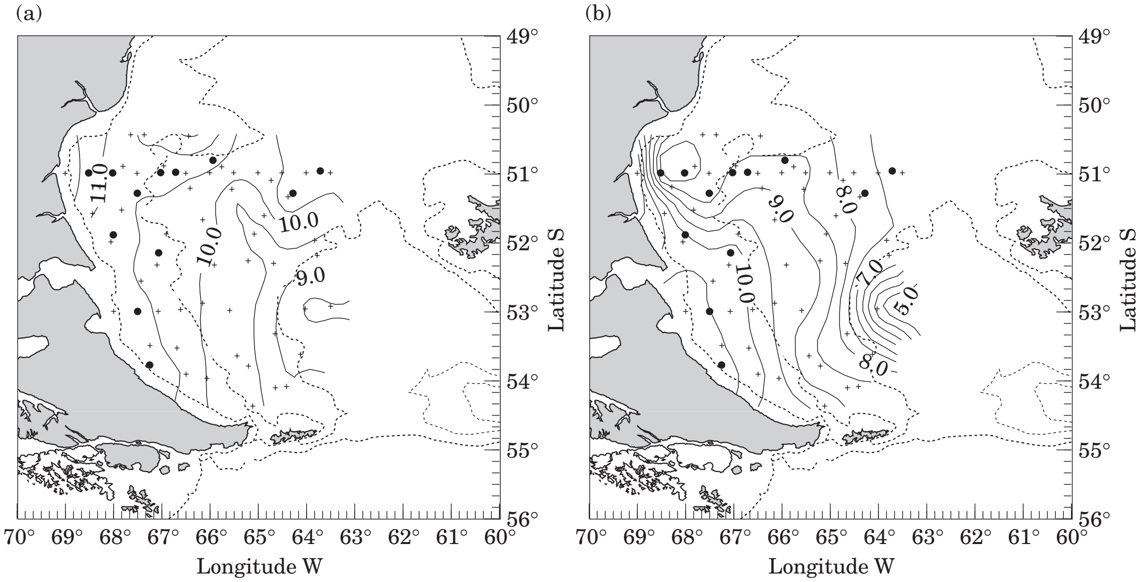

Figure 3. (a) Surface and (b) bottom temperature (°C). Dots indicate stations where zooplankton sampling was carried out.

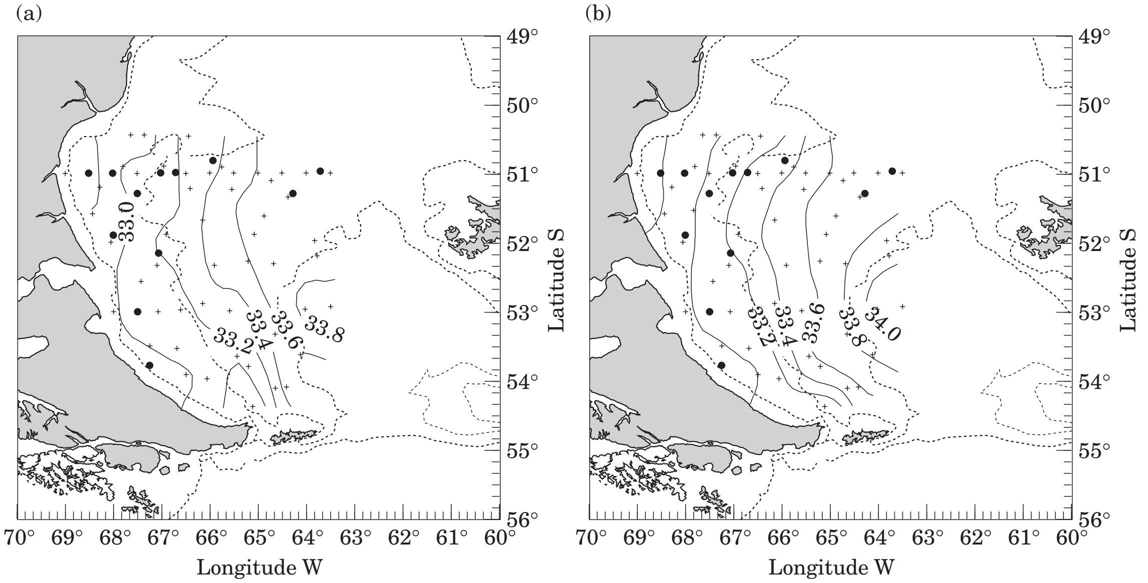

Figure 4. (a) Surface and (b) bottom salinity. Dots indicate stations where zooplankton sampling was carried out.

strata depths. The depth-integrated abundance for the total water column was estimated as the sum of all the 3–4 strata.

Results

Hydrography

Surface temperature was lowest (8.5°C) in the southeast of the area surveyed, whereas the highest values (11°C) were recorded in the coastal area of Grande Bay [Figure 3(a)]. Bottom temperature showed the same pattern, reaching minimum and maximum values of 5 and 10.5°C, respectively. There were two frontal zones, one located nearshore over the 50-m isobath in Grande Bay and the other at 53°S over the 200-m isobath. The former is a tidal front; the latter is produced by Shelf Water meeting the colder western subantarctic outflow [Figure 3(b)].

The salinity field revealed the typical water masses of the region. The 33.2 PSU isoline running over roughly

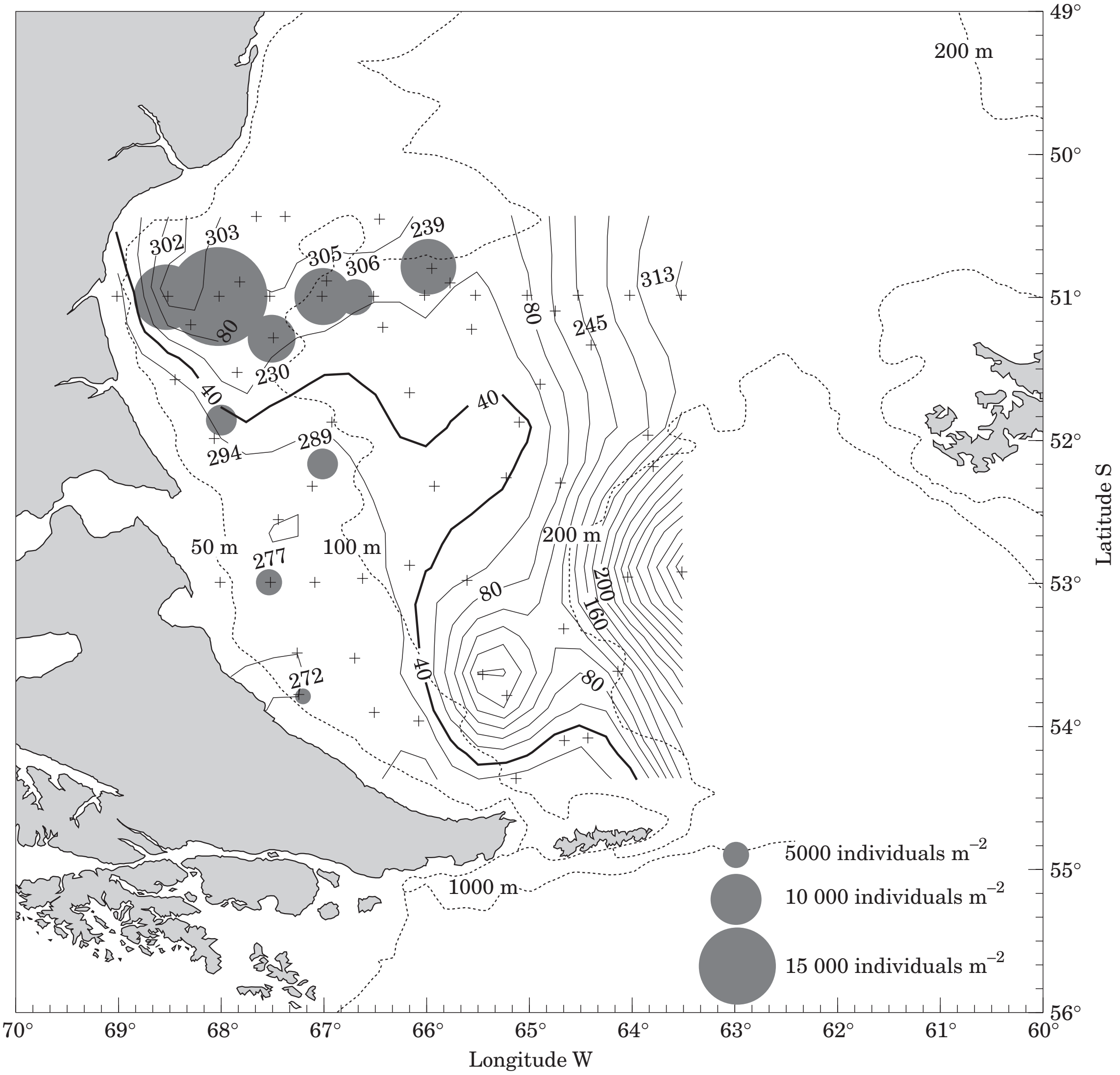

Figure 5. Stratification of the water column (isolines of stability parameter Φ) and depth-integrated population abundance of *Calanus australis* in the study area. Station numbers correspond to zooplankton sampling and crosses to CTD stations.

the 100-m isobath indicated the limit between Coastal and Shelf Waters. The 33.8 isoline denoted the external limit of Shelf Water [Figure 4(a), (b)].

The distribution of water column stability allowed the identification of distinct hydrological areas over the typical water masses of the region (Figure 5). A Φ critical value of 40 J m^{-3} separated well-mixed from stratified waters. North of 52°S, Coastal Water was associated with a tidal front separating the innermost waters (<50 m), which were tidally mixed, from strongly thermally stratified ones. Stability increased farther offshore over the Shelf Water, also as a result of the thermal stratification. South of 52°S, in contrast, Coastal Water was highly mixed without either thermal or haline stratification. In contrast, outer Shelf Water was strongly stratified because of the influence of the colder and heavier subantarctic waters entering the region west of the Burdwood Bank.

The water column structure in the thermally stratified northern area is illustrated by a vertical profile along the cross-shelf transect at 51°S [Figure 6(a)]. There was a thermocline (0.4°C m^{-1}) approximately 50 m deep. A change from stratified to well-mixed water took place at the same depth, indicating the presence of the tidal front that was also evident from both bottom temperature and

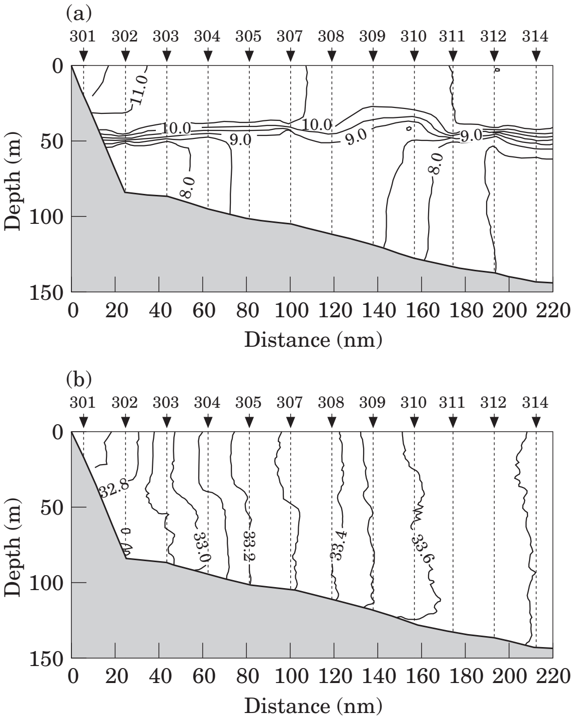

Figure 6. Vertical profiles of (a) temperature (°C) and (b) salinity along a cross-shelf transect at 51°S.

stability fields. Salinity was vertically homogeneous throughout the entire section [Figure 6(b)].

Calanus australis abundance, vertical distribution and population structure

Higher numbers of *C. australis* (Figure 5), ranging from 4000 to 8000 individuals m^{-2}, but up to 18 755 individuals m^{-2}, were recorded inshore <100 m deep at 51°S, mostly in thermally stratified Coastal Water. Values were highest in Grande Bay at the two innermost stations along the transect, both located on the stratified side of the tidal front. Lowest concentrations (∼200 individuals m^{-2}) were offshore in transitional waters between Shelf and Malvinas Waters. There was also a sharp decline in abundance southwards alongshore, coinciding with the occurrence of well-mixed Coastal Water. Peak densities of the copepod corresponded to a stability (Φ) range of 80–100 J m^{-3}. Only very low concentrations were found in water masses with stabilities <40 or >100 J m^{-3}.

The vertical distribution of *C. australis* was overall in accordance with the typical pattern of diel vertical migration known for planktonic organisms (Mauchline, 1998), even when there was strong thermal stratification (Figure 7). The bulk of the population was in the upper layer during darkness [Figure 7(a), (b), (c), (f)], from 21:00 to 22:30, probably exhibiting an evening ascent. On the contrary, animals were found at some distance from the surface [e.g. 07:30, Figure 7(e)] or at different levels [e.g. 06:00, Figure 7(d)] in daylight, likely descending to deeper waters (morning descent). The uniform distribution observed through the whole water column at a station sampled at 00:30 [Figure 7(b)] was probably due to sampling during the passive midnight sinking. Even though the observed patterns are largely suggestive of diel changes in behaviour, they cannot be considered conclusive. The day–night patterns could be confounded to some degree by changes in station location, so reflecting differences in space and time [e.g. Figure 7(g), (l)].

A distinct bathymetric pattern of developmental stages within the water column over the diel cycle was not found, implying no ontogenetic migration by *C. australis*. No pattern was evident corresponding to thermal stratification (Figure 7).

The population consisted mainly of stage 5 copepodites and a few adult females (Figure 8). On average, 74% ± 10 of the population was composed of C5 at the stations along the transect, whereas that fraction was much lower in the south (31% ± 10). Presence of C3 and C4 was occasionally significant at two stations located in this latter area, in coincidence with the lowest abundances. Adult males and stages younger than C3 were normally scarce or not found. This cannot be attributed to the mesh size employed, because the sampler had a 150-μm mesh and the length of *Calanus* spp. first nauplius is in the range 190–240 μm (Nichols and Thompson, 1991).

Discussion

Distribution of *C. australis* is presumably confined to the northern part of the West Wind Drift up to ca. 42°S (Marin *et al.*, 1994). As in the Southwest Atlantic, the species is found in coastal waters off southeastern Australia and New Zealand, normally in high numbers in bays and over the mid-shelf (Nyan Taw and Ritz, 1979; Bradford *et al.*, 1980; Bradford, 1985; Bradford-Grieve, 1994). It is a common species year-round in inshore coastal waters of southeastern Tasmania, where it is influenced by both estuarine and oceanic waters. Maximum abundance is during summer, C5s outnumbering the adults (Nyan Taw and Ritz, 1979). In the narrow continental shelf off western New Zealand, where onshore/offshore advection takes place as a result of major across-shelf exchanges of water, greatest numbers of adults and copepodites may be recorded subsurface in outer shelf waters or over the upper slope (Bradford, 1985). *C. australis* has been mentioned as also occurring in waters off Chile between 18 and 52°S (e.g. Brodsky, 1961; Bjönberg, 1973; Arcos, 1976; Marin

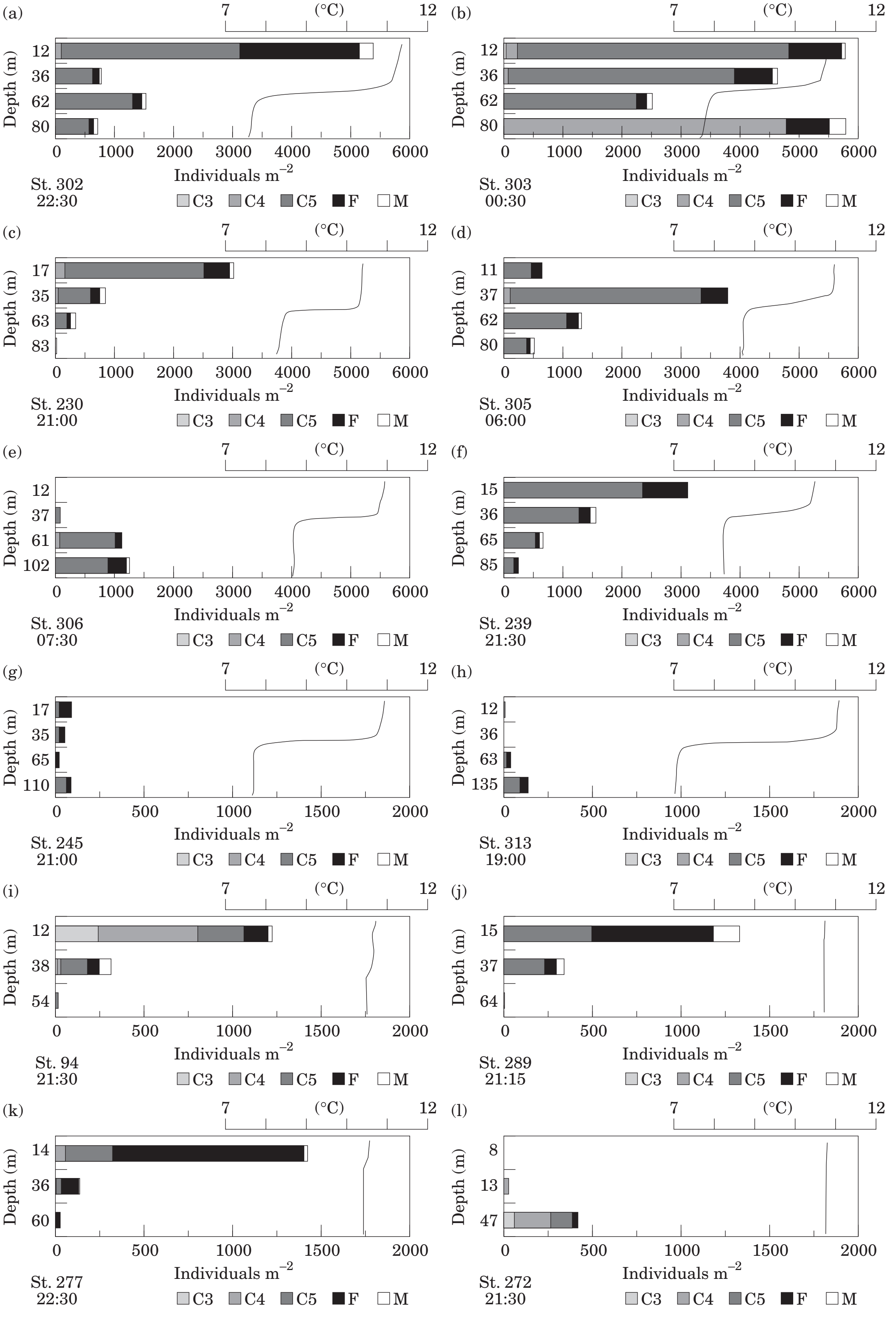

Figure 7. Vertical distribution of copepodite stages and adults of *Calanus australis* at each sampling station within the surveyed area. A schematic thermocline is also shown (for details on thermal stratification see text). Note different scale in panels (g)–(l).

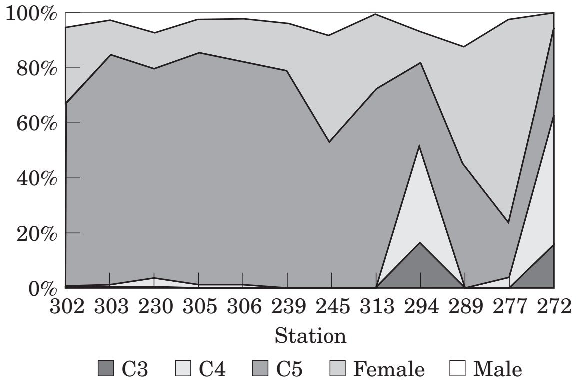

Figure 8. Depth-integrated population structure of *Calanus australis* over the investigated area. Stations 302–313 are along a transect at 51°S in an offshore direction and Stations 294–272 are ordered from north to south.

and Antezana, 1985) and in the Magellan Strait (Mazzochi and Ianora, 1991; Mazzochi *et al.,* 1995). However, its identity along the southern South American Pacific coast remains controversial given its striking similarity with *C. chilensis* (Marin *et al.*, 1994). In any case, to our knowledge, there is a complete lack of information on both species off southern Chile except for the records cited. In the Magellan Strait it has been reported as uniformly distributed with depth, with highest abundances in the upper 200 m (Mazzochi *et al.*, 1995).

The shelf off Patagonia can be divided hydrographically into an area down to 52°S, where thermal stratification as a result of increased solar radiation takes place during the warmer months of the year, and another area, thermally unstratified, south of 52°S. Both areas are largely influenced by Magellan Strait run-off. The development of different water masses and hydrographic structures in the region appears to lead to distinct patterns in the spatial distribution of *C. australis*. Therefore, differences in densities would be related to geographical differences in water column stability. Much of the area of highest copepod abundance was over the thermally stratified inner shelf, coinciding with a tidal front in Coastal Water. This is in striking contrast to the low densities recorded farther south in isothermal and isohaline Coastal Water and in stratified Shelf Water offshore, suggesting that *C. australis* approaches the southern boundary of its geographical distribution as the development of seasonal stratification vanishes with increasing latitude. Aggregation and likely enhanced primary production in the frontal area may explain its peak concentrations in Grande Bay.

The onset of stratification in spring is known to trigger the plankton production cycle in temperate seas (Cushing, 1975). Furthermore, seasonal thermal stratification is often closely related to the occurrence of frontal phenomena (Simpson and Hunter, 1974; Pingree and Griffiths, 1978; Le Fèvre, 1986). Tidal fronts are well known as highly productive hydrographic structures where phytoplankton accumulates by convergence, and other processes such as upwelling, cross-frontal flow, the spring/neap tidal cycle, and vertical mixing through the thermocline increase production (Cushing, 1995). Some evidence for the response of *C. australis* to upwelling events is available from studies in the area between New Zealand's North and South Islands, where a plume of upwelled water extending northeast is generally found during summer (Bradford-Grieve *et al.*, 1993). It appears that different parts of its life cycle occur in separate zones of the upwelling system, highest population abundance being reached in non-upwelled waters inshore in the eastern region of the plume corridor. A strategic vertical migration may be involved, ensuring that animals are carried inshore to breed. The closely related southern species *C. agulhensis* (formerly called *C. australis*), which largely dominates the mesozooplankton community over the eastern Agulhas Bank off South Africa, also appears to be associated with a subsurface ridge of upwelled water, particularly during spring and early summer (Verheye *et al.*, 1994).

Seasonal thermal stratification combined with the presence of a tidal front in Grande Bay may create an optimal environment for the development of a large endemic population of *C. australis*. The bay may constitute in turn a centre of dispersal for the species, supplementing neighbouring waters by advection of individuals in a north–northeast direction, following the mean flow in the region. The absence of thermal stratification and the lack of shallow-sea fronts in the southern coastal waters may be the reasons for the low population abundance of *C. australis*. In accordance with the present findings, large copepods of the genus *Calanus* appear to be associated with seasonally stratified waters over European shelves (Williams *et al.*, 1994).

By late summer, the bulk of the population of *C. australis* in Grande Bay was mostly C5s along with a few adult females and C4. Younger copepodites were scarce or totally absent. Such a population structure may correspond to an ageing summer generation that has finished reproduction, with C5s resulting from the summer breeding preparing to enter diapause in autumn. Even though C5s were not concentrated at any particular depth, i.e. evidence for diapause (Mauchline, 1998), animals at this stage were usually carrying large stores of lipid. Overwintering males of smaller *Calanus* spp. at high latitude in the northern hemisphere over shelves with winter temperatures >0°C moult earlier than females that spawn at the start of the spring phytoplankton bloom or shortly later (Conover, 1988). Boreal *Calanus* species usually spawn during a period of active phytoplankton growth (Marshall and Orr, 1955; Runge, 1984). This may also be the case for *C. australis* because, although there is not yet complete seasonal coverage of the phytoplankton cycle off southern Patagonia, there is typically a single long bloom during spring and early summer (Angelescu and Preński, 1987). The fact that males moult earlier to be ready to fertilize newly moulted females (Marshall and Orr, 1955) and have a shorter longevity than that of females (see Landry, 1983) may be the reason for the very low male : female ratios we found in late summer.

Further studies focused on the life cycle and dynamics of *C. australis* covering larger parts of the year, especially spring–summer, definitely need to be carried out to understand fully the role of the species in the ecosystem off southern Patagonia.

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