Hydrobiologia **439:** 21–42, 2000.

The occurrence of Calanidae species in waters off Argentina

F.C. Ramírez[1,2] & M.E. Sabatini[1,2,*]
[1]*Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). Paseo Victoria Ocampo No 1. Escollera Norte. C.C. N° 175. 7600 - Mar del Plata. Argentina*
*E-mail: marsab@inidep.edu.ar (*Author for correspondence)*
[2]*Consejo Nacional de Investigaciones Científicas y Técnicas CONICET, Argentina*

Received 6 December 1999; in revised form 20 July; accepted 22 August 2000

Key words: copepods, *Calanus, Neocalanus, Calanoides*, southwestern Atlantic

Abstract

As food of planktivorous fish and likely good predictors of natural perturbations, members of the family Calanidae are recognised to be key species in ecosystems worldwide. The distribution and seasonal relative abundance of the Calanidae species occurring in the Argentine Sea were reviewed from published and unpublished data collected over the last three decades. Species are also figured in order to elucidate any possible taxonomic uncertainty. *Calanoides* cf. *carinatus, Calanus australis* and *Calanus simillimus* are the most abundant calanids in the region. The former two species typically inhabit inner and middle shelf waters decreasing offshore, while *Calanus simillimus* is distributed in the middle and outer shelf, its abundance increasing towards the shelf-break. The southern limit of the distribution of *Calanoides* cf. *carinatus* appears to be $\sim 46°$ S. *Calanus australis* is the most common large copepod in coastal and inner shelf waters off southern Patagonia. *Neocalanus tonsus* and *Calanoides patagoniensis* are a much rarer species. The latter is recorded in the southwestern Atlantic, for the first time, immediately east of Magallanes Strait and the Beagle Channel. The taxonomic status and worldwide biogeographic distribution of the region's calanids are briefly described and the patterns identified off Argentina are discussed in relation to the major hydrographic characteristics.

Introduction

Members of the family Calanidae are major components of the zooplankton of shelf seas and oceanic waters. Mainly because of their large size, they are normally significant contributors to biomass and thus a crucial link between primary and fish production (e.g. Runge, 1988). In terms of both food of planktivorous fish, and as indicators of natural perturbations (e.g. Heath et al., 1999), calanids are recognised to be a key species in ecosystems worldwide. As compared to the oceans of the Northern Hemisphere that have been studied more, there is a special need for information about the species distributed in the Southern Hemisphere.

Representatives of the Family Calanidae in waters off Argentina have been reported extensively in the current local literature on zooplankton taxonomy and ecology (Ramírez 1970 a,b, 1971, 1977, 1981; Björnberg, 1981; Fernández Aráoz et al., 1991; Ramírez & Santos, 1991, 1994; Viñas et al., 1992, Fernández Aráoz, 1994; Fernández Aráoz et al., 1994; Saito & Kubota, 1995; Santos & Ramírez, 1995; Bradford-Grieve et al., 1999). Nevertheless, the species list has surprising omissions given what is known about global distribution, and the identity of other species is not clear when examined in detail. Even though a large amount of information on the occurrence and distribution of Calanidae in the region has been gathered over years, this is quite scattered or remains unpublished.

Therefore, the aims of this paper are: (1) to synthesise existing knowledge on the taxonomy, distribution and relative abundance of the calanid copepods in Argentinian waters, (2) to identify both their areas of occurrence and patterns of relative abundance and (3) to relate them to the main hydrographic characterist-

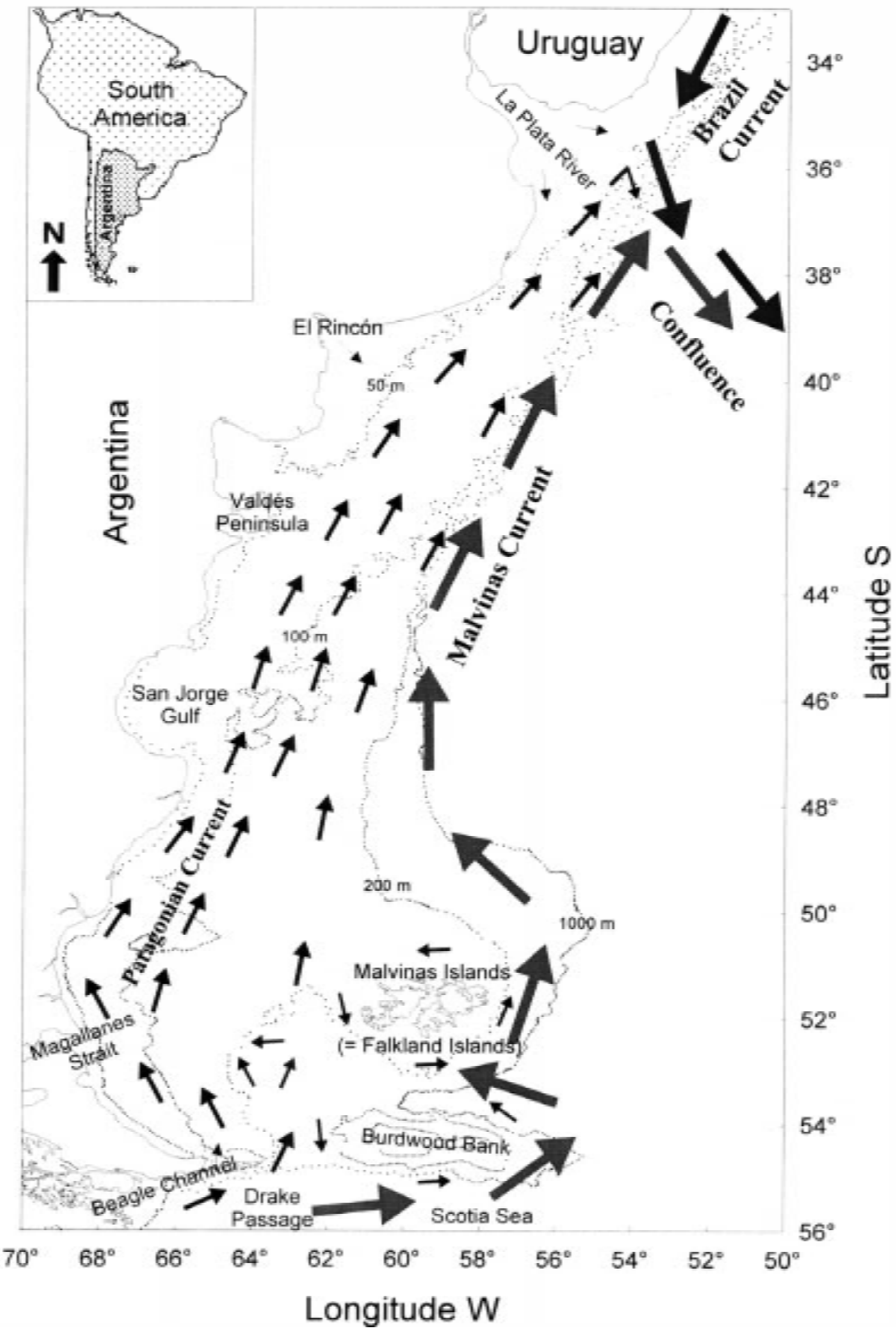

Figure 1. Major circulation pattern over the Argentinian Continental Shelf (adapted from Piola & Rivas, 1997). Thin arrows indicate runoff from La Plata River, El Rincón area and Magallanes Strait. Black arrows: Shelf waters; light grey arrows: Malvinas Current (= Falkland Current); dark grey arrows: Brazil Current.

ics of the region. These results constitute an overall baseline to focus future work on individual species.

The study area

As recently reviewed by Piola & Rivas (1997), two major currents influence the general circulation in the Argentine Sea: the warm Brazil Current flowing southwards, and the cold, nutrient rich Malvinas Current (= Falkland Current) flowing northwards (Figure 1). The latter originates as a branch of the Antarctic Circumpolar Current in the Drake Passage and enters the region through the channels east and west of Burdwood Bank. Water with low salinity due to the contribution of continental runoff and to the interchange of mass and heat with the atmosphere in subantarctic regions flows through the shallow west channel in a N–NE direction. The east channel allows the access of the denser Antarctic Intermediate Waters which originate under strong Antarctic influence. This main flow of the Malvinas Current maintains its trajectory northwards along the continental slope. Between 45° and 48° S, the western subantarctic shelf waters converge with the axis of Malvinas Current. Both flows proceed with a N–NE direction until they meet the Brazil Current at 36°–39° S. This wide eddy-rich area in the Argentinian Basin is known as the Brazil/Malvinas Confluence. Immediately adjacent to the southern coast of Argentina, runoff from the Magallanes Strait mainly, and from the Beagle Channel is the source of a low salinity water tongue referred to as the Patagonian Current. It flows also with N–NE direction, but along the Patagonian coast, until it separates from shore at 47° S and flows along in the middle continental shelf.

Therefore, shelf waters over most of the southern Argentinian shelf are of subantarctic origin, resulting from the mixing between the waters of the Malvinas Current and coastal waters highly diluted by continental runoff (Bianchi et al., 1982; Guerrero & Piola, 1997). On the other hand, to the north of 45° S, shelf waters are the result of the mixing of subantarctic waters, coastal waters off El Rincón and runoff from La Plata River. The La Plata River, flowing onto the wide shelf, forms an extended coastal plain estuary, the effects of which can extend seasonally either to the coastal area located to the south of the river (spring–summer) or extends to the mid-shelf region (fall–winter) (Guerrero et al., 1997). Depending on the continental drainage and the meteorological conditions, the influence of the estuarine waters extend even as far as the continental slope and contact Brazil Current waters (Provost et al., 1995), Malvinas Current waters (Negri et al., 1992), or may be found between both currents (Provost et al., 1995). These highly dynamic features make the hydrography of the region particularly complex.

As a consequence of such water mass diversity, the strong tidal influence, the large extent of the Argentinian shelf and slope and overall topography, diverse frontal systems have been identified in the Argentine Sea (reviewed by Guerrero & Piola, 1997). Several fronts are of the shelf sea type, and one is a shelf-break front. The latter occurs at the meeting of shelf waters and the Malvinas Current. Among the former, three main fronts are formed at the confluence of shelf waters and continental runoff: the front of the La Plata River estuary between 34° and 37° S, the front off El Rincón area between 39° and 41° S and the front that extends along the coast of southern Patagonia from the Magallanes Strait to the southern extent of the San Jorge Gulf. Another major frontal system, created by tidal mixing, occurs off northern Patagonia off the Valdés Peninsula and extends southwards close to shore.

Materials and methods

Published and unpublished information on the seasonal occurrence and abundance of Calanidae species was used in this study (Table 1). Only records of adults were considered since this is the stage at which the species identification is reliable. An exception was *Neocalanus tonsus* that normally was found as copepodid V (see Results). All the available quantitative and semi-quantitative data were pooled together for each species and plotted. Five categories were used in order to homogenise the data set when abundances were originally available as ind m^{-3}: rare= species represented by 0 -10 ind m^{-3}; scarce= species represented by 11–100 ind.m^{-3}; frequent= species represented by 101–1000 ind m^{-3}; abundant= species represented by 1001–10 000 ind m^{-3} and very abundant= species represented by >10 000 ind m^{-3}. These categories were chosen as they have been commonly used in the literature.

Results

Taxonomy

A description of each species and drawings emphas-

Table 1. List of the cruises that provided the data set and references to prior studies

Cruise	Area	Sampler mesh size	Depth tow	References
Spring				
Transección III/72	Transect 38° S	Hensen 330 μm	50 m	Ramírez et al., 1973
Transección IV/72	Transect 38° S	Hensen 330 μm	50 m	Roa et al., 1974
Walther Herwig V/78	Shelf 35°–55° S	Hensen 300 μm	100 m	Ramírez, 1981
Walther Herwig VI/78	Shelf 35°–55° S	Hensen 300 μm	100 m	Ramírez, 1981
Shinkai Maru VII/78	Shelf 35°–55° S	Hensen 300 μm	100 m	Ramírez, 1981
Eduardo Holmberg 04/82	Shelf 35°–41° S	Bongo 200 μm	bottom	Fernández Aráoz et al., 1994
Oca Balda 03/84	Shelf 42°–44° S	Hensen 200 μm	bottom	Santos & Ramírez, 1995
Oca Balda 06/86	Shelf 35°–41° S	Nackhai 400 μm	bottom	Fernández Aráoz et al., 1991
Oca Balda 09/94	Transect 47° S Transect 51° S	Nackhai 400 μm		Unpublished
Summer				
Pesquería III/67	Shelf 35°–45° S	Hensen 330 μm	100 m	Ramírez, 1971
Transección V/73	Transect 38° S	Hensen 330 μm	50 m	Unpublished
Oca Balda 01/86	Shelf 42°–44° S	Hensen 200 μm	bottom	Santos & Ramírez, 1995
Oca Balda 08/88	Shelf 42°–47° S	Small Bongo 150 μm	bottom	Viñas et al., 1992
Meteor/89	Shelf 42°–44° S	Biomoc 300 μm 8 strata 10m each	80 m	Unpublished
Oca Balda 03/95	Shelf 44°–51° S	Nackhai 400 μm	bottom	Unpublished
Oca Balda 04/95	Shelf 51°–55° S	Nackhai 400 μm	bottom	Unpublished
Oca Balda 04/97	Transect 47° S	Nackhai 400 μm	bottom	Unpublished
Autumn				
Pesquería XI/69	Shelf 44°–52° S	Hensen 330 μm	100 m	Ramírez, 1970b
Shinkai Maru I/78	Shelf 35°–55° S	Hensen 300 μm	100 m	Ramírez, 1981
Shinkai Maru II/78	Shelf 35°–55° S	Hensen 300 μm	100 m	Ramírez, 1981
Oca Balda 04/94	Transect 51° S	Nackhai 400 μm	bottom	Unpublished
Winter				
Transección I/72	Transect 38° S	Hensen 330 μm	50 m	Verona et al., 1972
Transección II/72	Transect 38° S	Hensen 330 μm	50 m	Carreto et al., 1972
Walther Herwig III/78	Shelf 35°–55° S	Hensen 300 μm	100 m	Ramírez, 1981
Walther Herwig IV/78	Shelf 35°–55° S	Hensen 300 μm	100 m	Ramírez, 1981

ising their salient features are given below in order to elucidate any possible taxonomic uncertainty.

Calanus australis *(Figure 2)*

This species is thoroughly described to facilitate comparison with the closely related species *Calanus agulhensis.*

Female. Total length = 3.03–3.53 mm, mean = 3.28±0.17, *n*= 15. Ratio of prosome length to maximum width= 2.75–3.14, mean 2.95±0.11, *n*=15. Ratio of prosome length to total length= 0.79–0.81, mean= 0.80±0.01, *n*=15. Slender body, forehead with rounded swelling in dorsal view. Corners of the last pedigerous somite rounded. Spermatheca in lateral aspect kidney-shaped. Antennae extending 1–1 1/2 segments beyond the tip of the caudal rami. Serrate inner edge of the coxa of leg 5 lyre-like, with 18–22 small triangular teeth. In leg 5, the outer distal projection of endopod segment 1 almost reaches the limit between exopod segments 1 and 2; endopod segment 3 extending as far as, or slightly beyond, the insertion point of the first inner seta of segment 3 of the exopod;

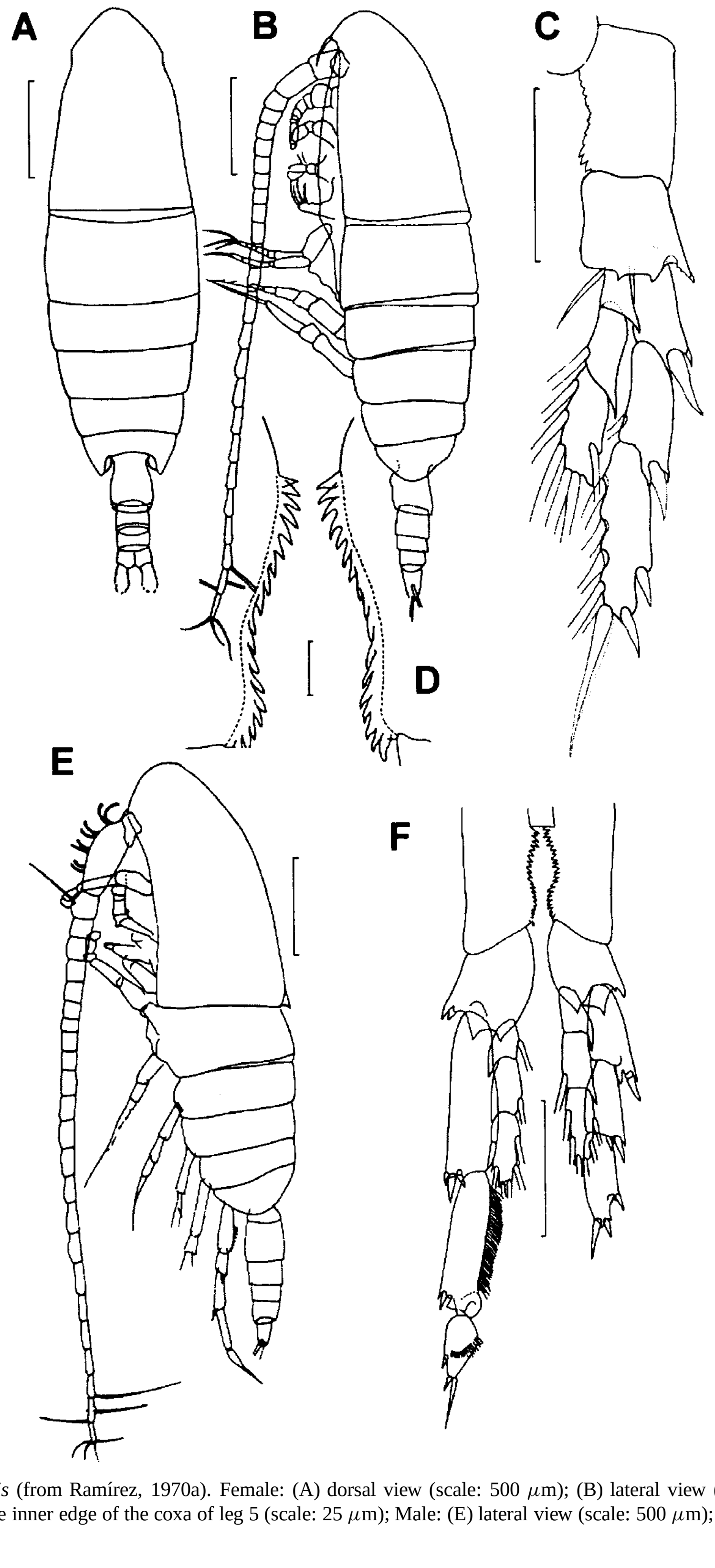

Figure 2. Calanus australis (from Ramírez, 1970a). Female: (A) dorsal view (scale: 500 μm); (B) lateral view (scale: 500 μm); (C) leg 5 (scale: 200 μm); (D) serrate inner edge of the coxa of leg 5 (scale: 25 μm); Male: (E) lateral view (scale: 500 μm); (F) leg 5 (scale: 200 μm).

the terminal seta of the exopod is slightly shorter than exopod segment 3.

Male. Total length = 3.07–3.57 mm, mean = 3.30±0.14, *n*= 15. Ratio of prosome length to maximum width= 2.57–3.13, mean 2.87±0.13, *n*=15. Ratio of prosome length to total length= 0.76–0.77, mean= 0.77±0.01, *n*=15. Slender body as in the female, front rounded in dorsal view. Posterior corners of the prosome rounded. Antennae stretching beyond the apex of the caudal rami by 3–3.5 segments, first and second segments fused. Exopod segments of left leg 5 thing and long ('thin type'), inner margin of the coxa serrated (15–19 teeth); proportion of breadth to length of exopod segments 1 and 2 are 1:3.7 and 1: 4.4, respectively. Right exopod leg 5 reaching 1/3 of the length of the left exopod segment 2.

Calanus simillimus *(Figure 3)*

Total length, female= 3.03–3.71 mm, male= 3.21–3.39 mm. In the female, the postero-lateral border of the last pedigerous somite is pointed, appearing in lateral view as a triangular, minute flap. Antenna with long and plumose setae in the 23rd and 24th joints; their length is equivalent to the sum of the 6 last segments. In leg 5, the serrate inner edge of the coxa is not lyre-like but convex, with 18–20 triangular teeth of nearly equal size, the distal group somewhat separated from the rest.

In the male, the antenna does not extend beyond the caudal rami. The right exopod of leg 5 does not reach the distal margin of the left exopod segment 1 and the left exopod extends beyond the caudal rami.

Neocalanus tonsus *(Figure 4)*

Records of adult females have been too few to allow drawings, and males have not been found at all. Copepodid stage V conforms to the description by Bradford et al. (1988). Remarkable characteristics are the presence of a recurved hook on the outer distal corner of exopod 1 of leg 2, and small distal spines on the posterior surface of the basis in legs 2–5. The inner edge of the coxa of leg 5 is naked. The antenna extends to the caudal rami.

Calanoides *cf.* carinatus *(Figure 5)*

Total length, female= 2.93–3.07 mm, male= 2.32–2.50 mm. In the female, the antenna does not extend beyond the caudal rami. The anterior head in lateral view is sharply keeled. The posterior corners of the prosome are rounded. Inner edge of the coxa of leg 5 without teeth. On the genital double somite, the spermathecae are elongated and perpendicular to the body axis. Both parts are connected by a curved, chitinous bar. The genital plate is small and nearly square-shaped.

In the male, the inner border of the coxa of leg 5 is not serrated; the endopod 1 and 2 of the right leg are naked and the left endopod is reduced to only one segment without setae or hairs; the distal margin of the right exopod segment 3 extends ca. 3/4 of the way along the left exopod segment 2; the terminal claw on the right exopod nearly reaches the distal border of the left exopod segment 3.

Calanoides patagoniensis *(Figures 6 and 7)*

Total length, female= 2.2 mm, male= 2.0 mm In the female, the body is elongated and slender with the anterior head laterally produced forming a carina. The distal borders of the last pedigerous somite are rounded, extending half the way along the genital double somite. The antenna does not extend beyond the caudal rami. Genital double somite is not barrel-like as typically found in *Calanus* spp, but elongated and longer than somite 2 and 3 combined, with a ventral indented swelling which is evident in lateral view; the genital pores are completely covered by a thin, flap-like structure; two symmetrical pointed structures, which may correspond to the lateral borders of the genital plate (*sensu* Frost & Fleminger, 1968), can be observed by transparency on both sides of the pores. The inner margin of the coxa of leg 5 is naked.

In the male, the body is elongated as in the female but with a less conspicuous cephalic extreme. Leg 5 is asymmetrical with both rami long and slender; the left leg is longer than the right one extending as far as the caudal rami. Left and right exopods end in a long spine-like setae (much longer in the right one); besides these latter, two small spines, one terminal and the other subterminal, are placed on the right side of the last segment of both exopods. In the last segment of the right exopod, a group of thick hairs is evident; right endopod is 3-segmented and the left one, remarkably atrophied, is reduced to only one segment.

Spatial and seasonal distribution

Calanus australis *(Figure 8)*

This species is widely distributed in waters off the inner and middle shelf along the coast of Argentina. In waters off southern Patagonia, it also extends over the coastal area. In this sector, it is the most abundant large copepod throughout all seasons, typically occur-

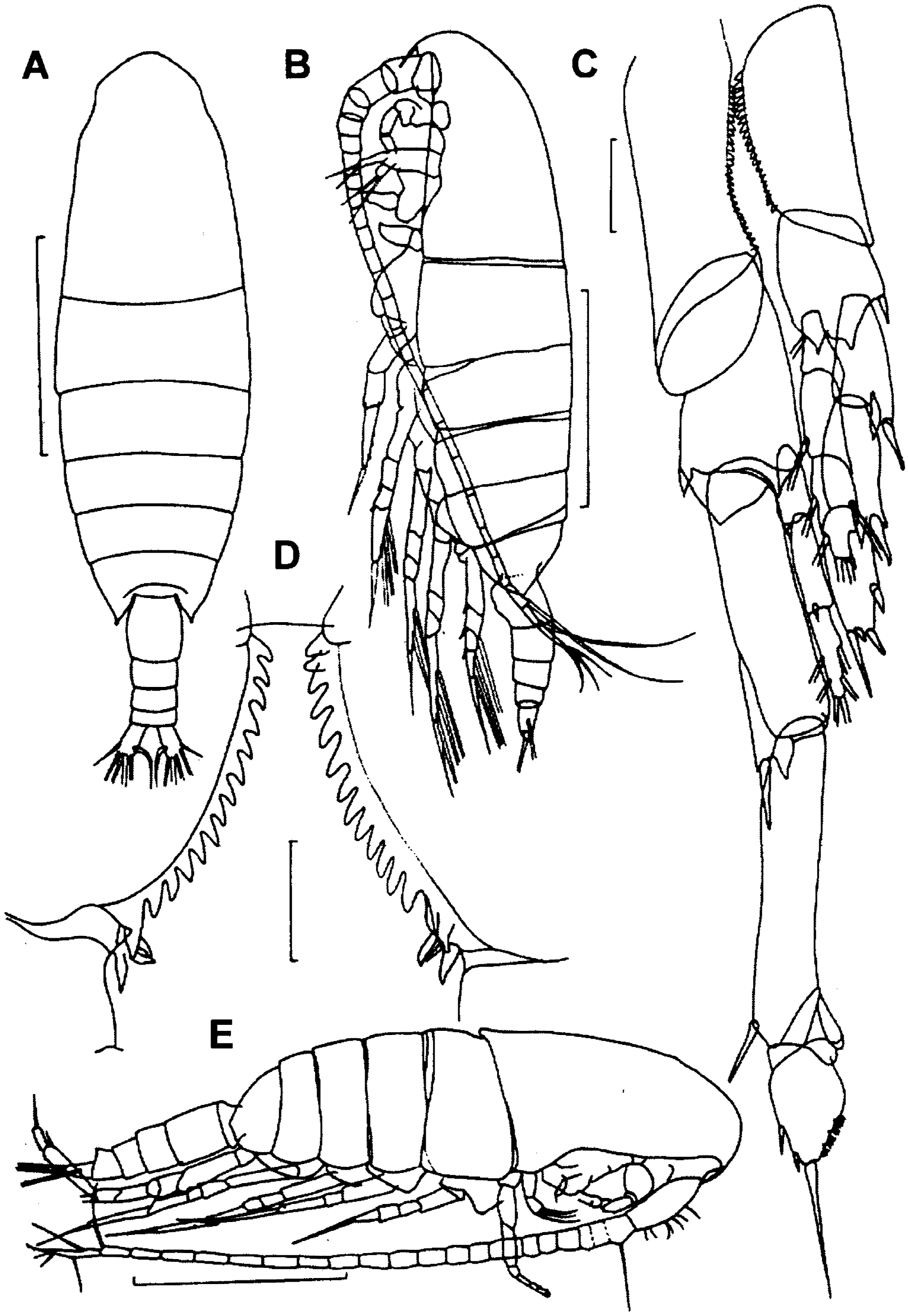

Figure 3. Calanus simillimus (from Ramírez, 1970a as *Calanus propinquus*). Female: (A) dorsal view (scale:1000 μm); (B) lateral view (scale: 1000 μm); (C) leg 5 (scale: 100 μm); (D) serrate inner edge of the coxa of leg 5 (scale: 500 μm); Male: (E) lateral view (scale: 1000 μm).

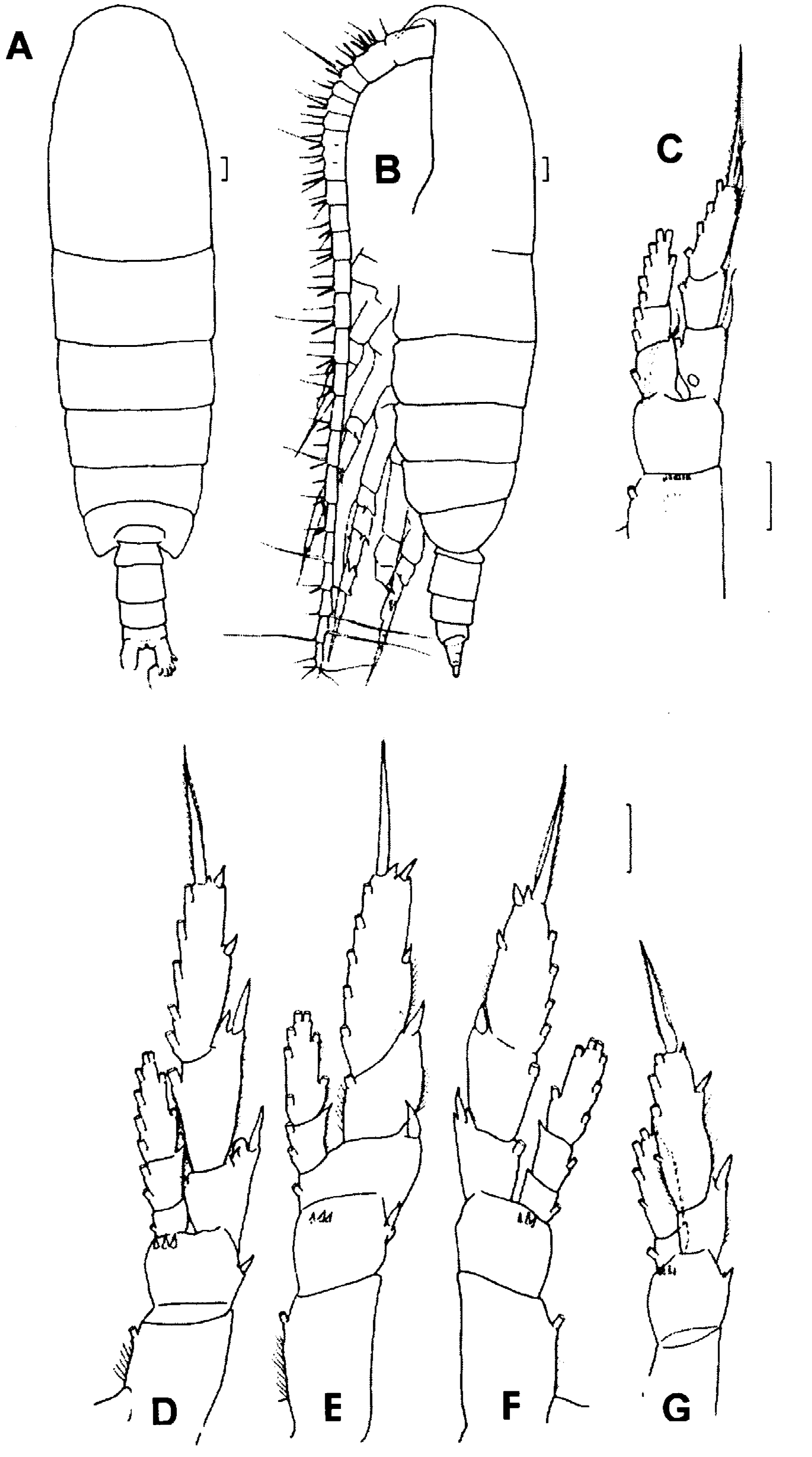

Figure 4. Neocalanus tonsus (from Bradford et al., 1988). Copepodid V: (A) dorsal; (B) lateral view; (C) leg 1; (D) leg 2; (E) leg 3 (deformed leg as endopod 1 and exopod 1 are fused); (F) leg 4; (G) leg 5. Scale: 100 μm.

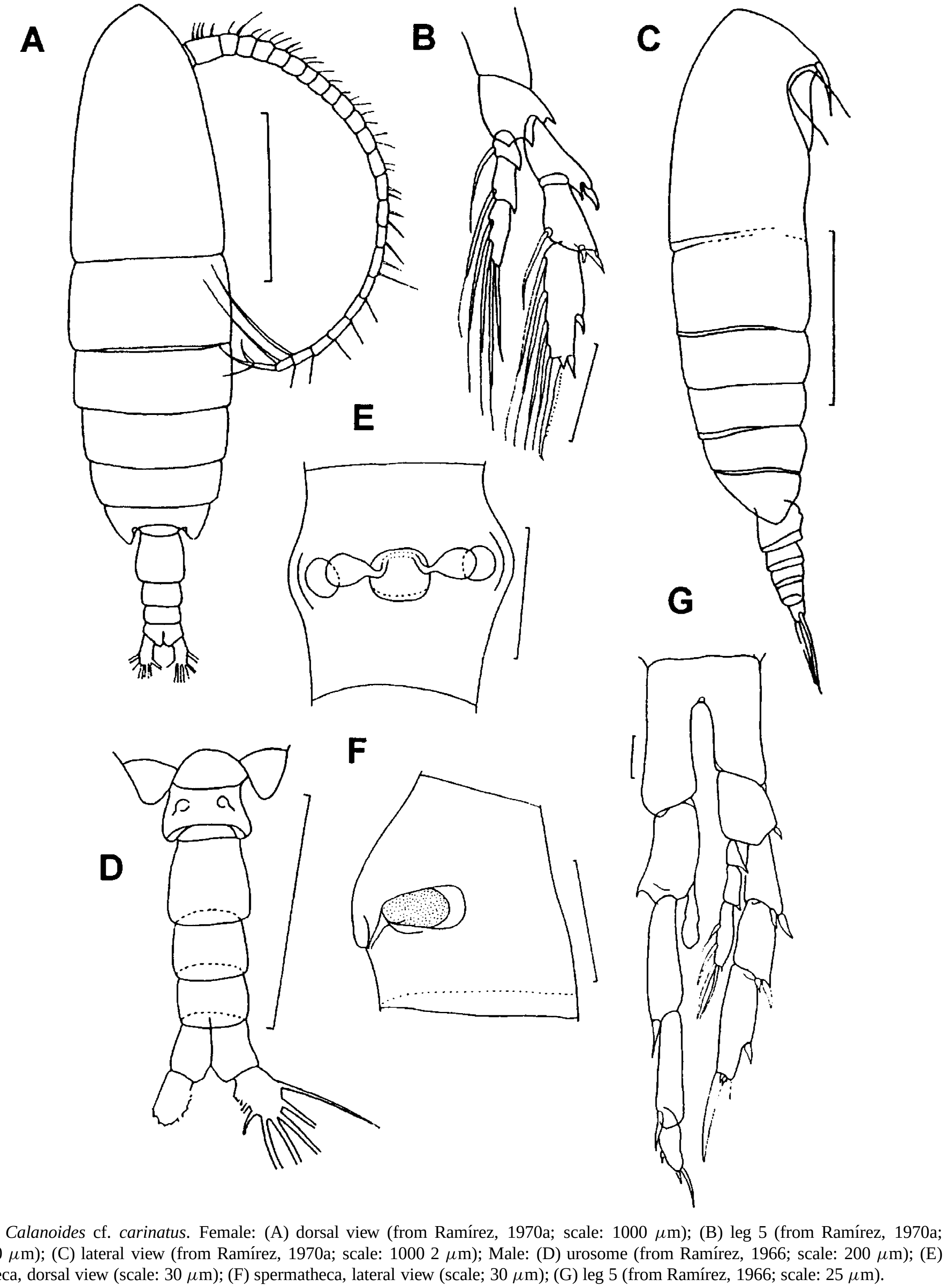

Figure 5. Calanoides cf. *carinatus*. Female: (A) dorsal view (from Ramírez, 1970a; scale: 1000 μm); (B) leg 5 (from Ramírez, 1970a; scale: 200 μm); (C) lateral view (from Ramírez, 1970a; scale: 1000 2 μm); Male: (D) urosome (from Ramírez, 1966; scale: 200 μm); (E) spermatheca, dorsal view (scale: 30 μm); (F) spermatheca, lateral view (scale; 30 μm); (G) leg 5 (from Ramírez, 1966; scale: 25 μm).

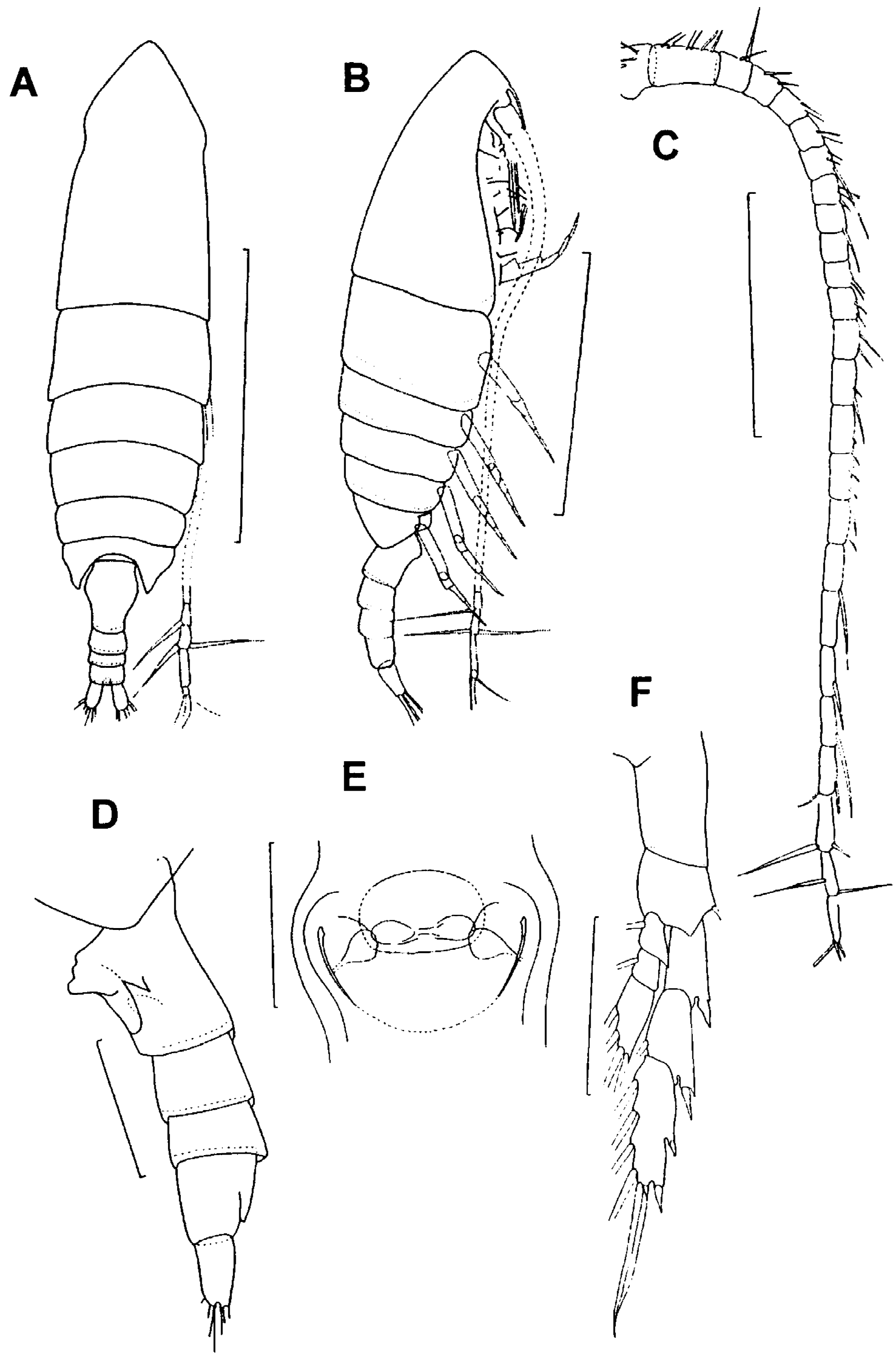

Figure 6. Calanoides patagoniensis. Female: (A) dorsal view (scale: 1000 μm); (B) lateral view (scale: 1000 μm); (C) antenna (scale: 500 μm); (D) urosome (scale: 200 μm); (E) spermatheca (scale: 100 μm); (F) leg 5 (scale: 200 μm).

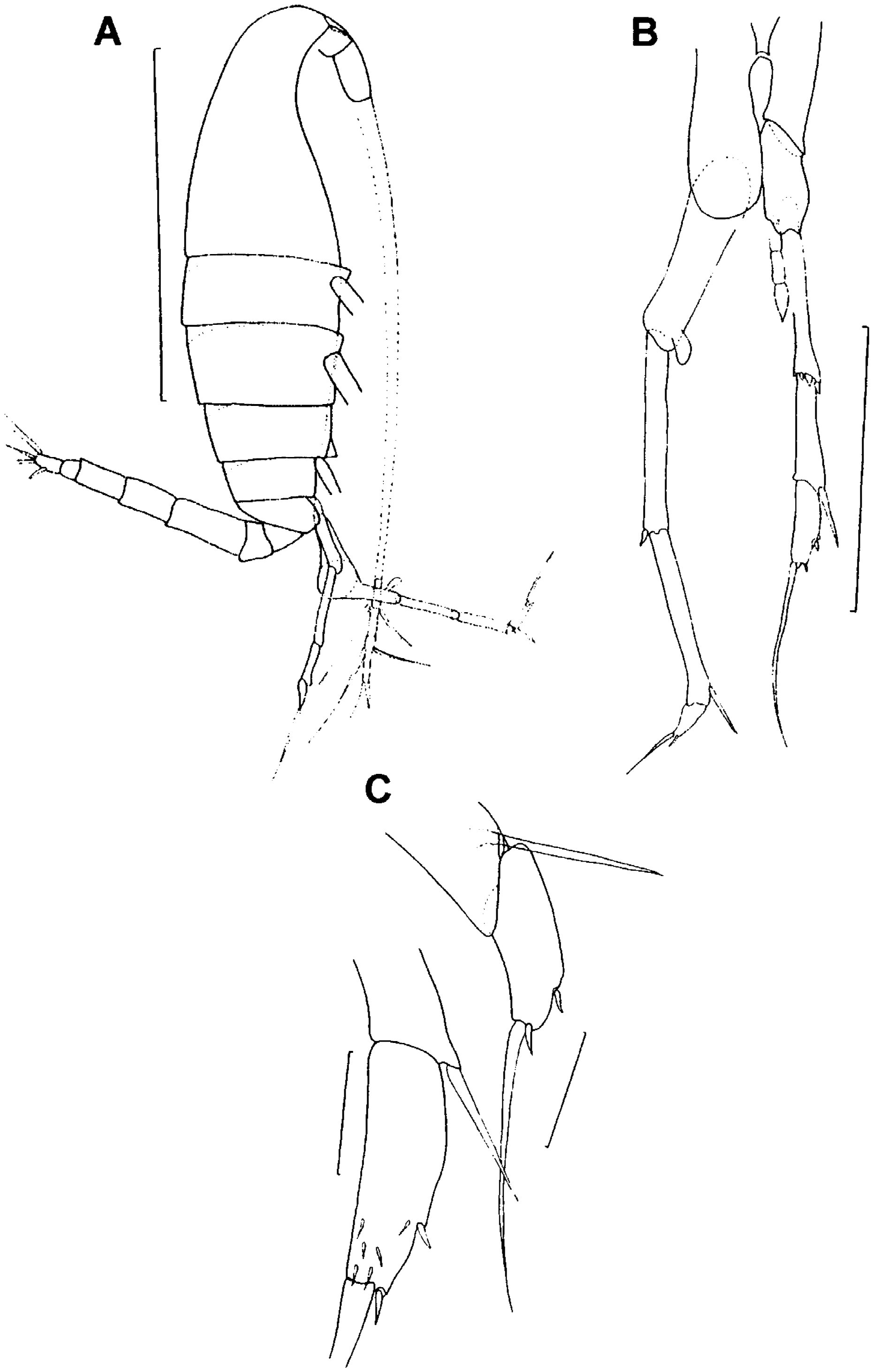

Figure 7. Calanoides patagoniensis. Male: (A) lateral view (scale: 1000 μm); (B) leg 5 (scale: 400 μm); (C) detail of last segments of right and left leg 5 (scale: 50 μm).

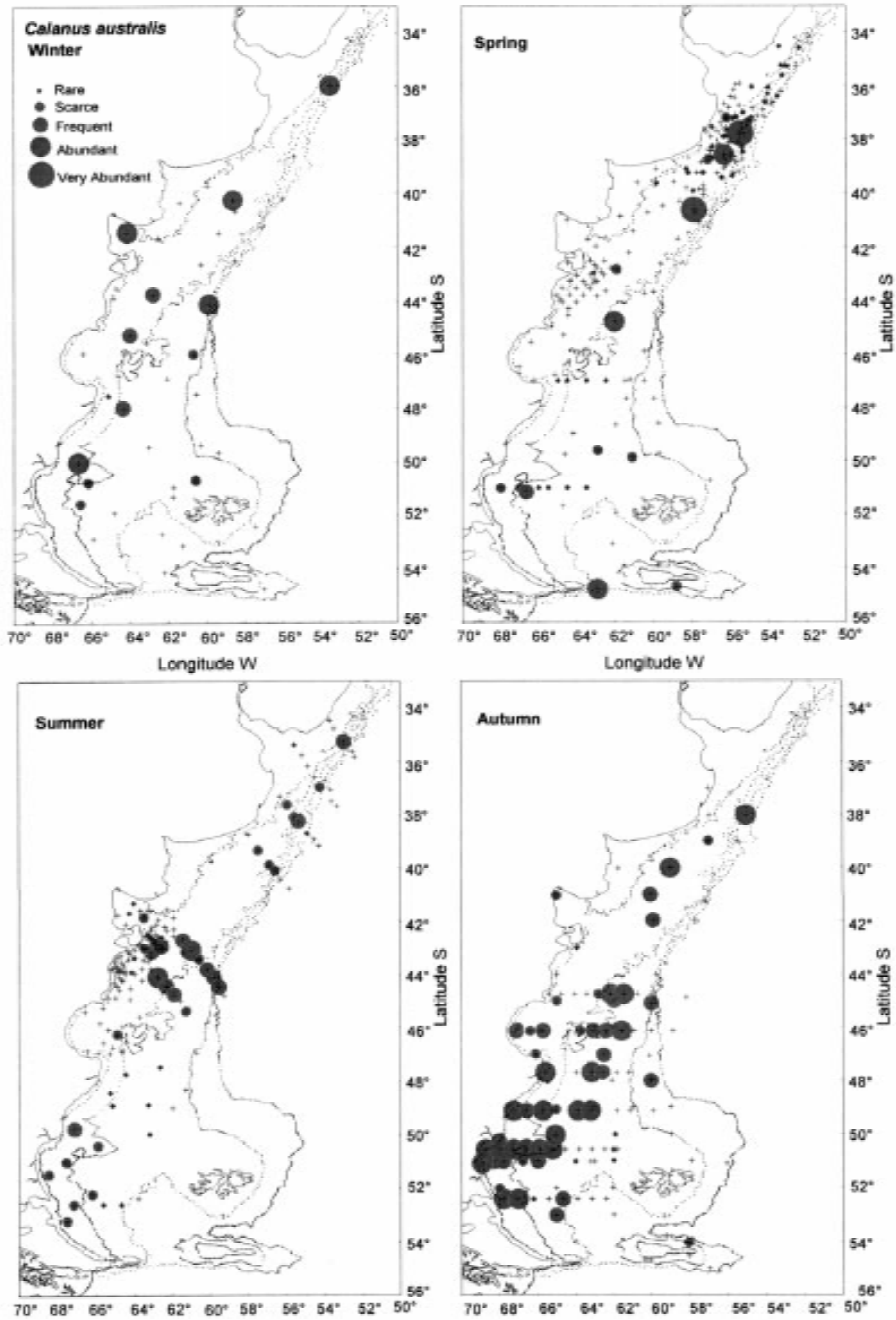

Figure 8. Calanus australis. Seasonal relative abundance and distribution of adults in waters off Argentina.

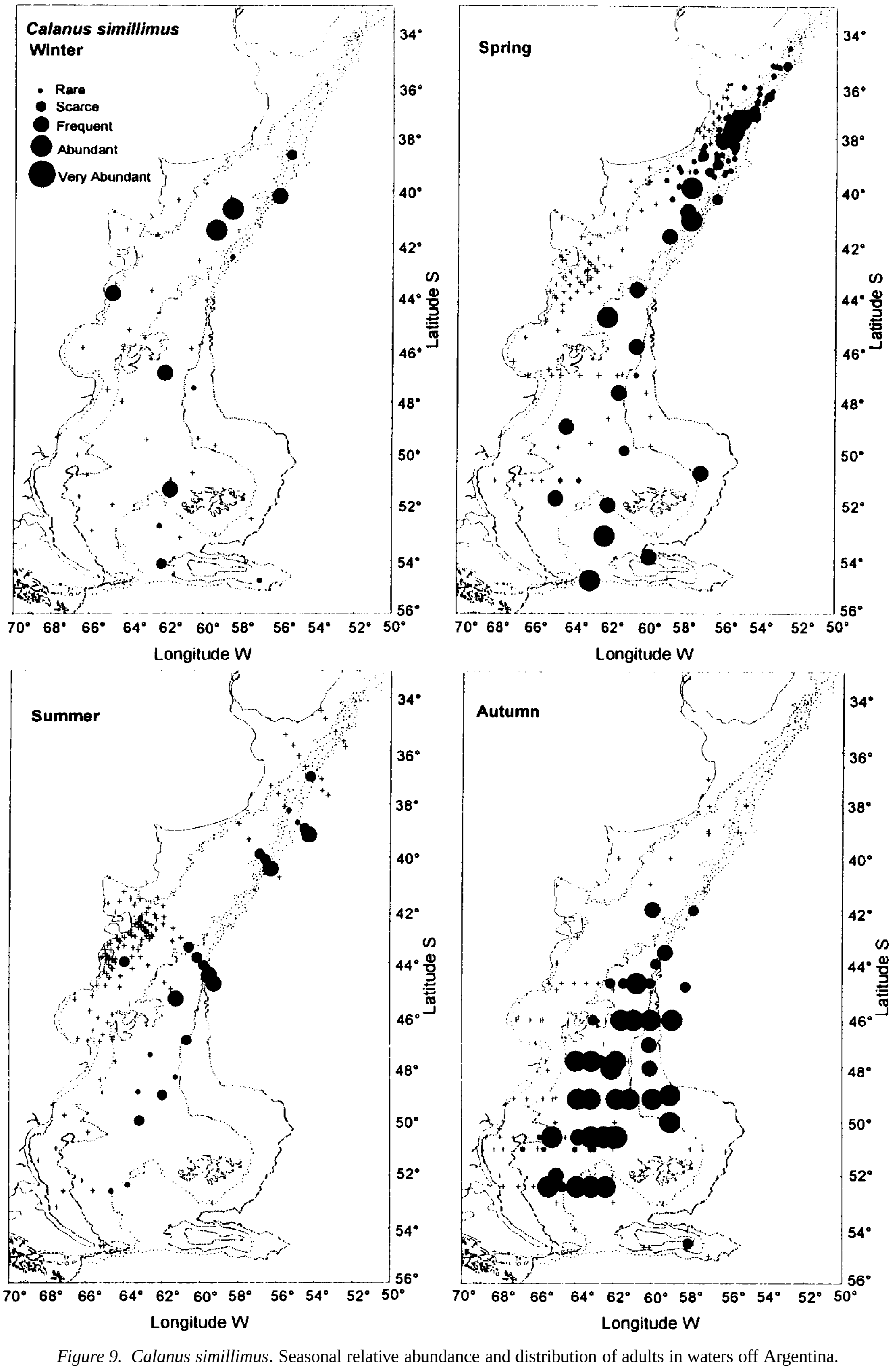

Figure 9. Calanus simillimus. Seasonal relative abundance and distribution of adults in waters off Argentina.

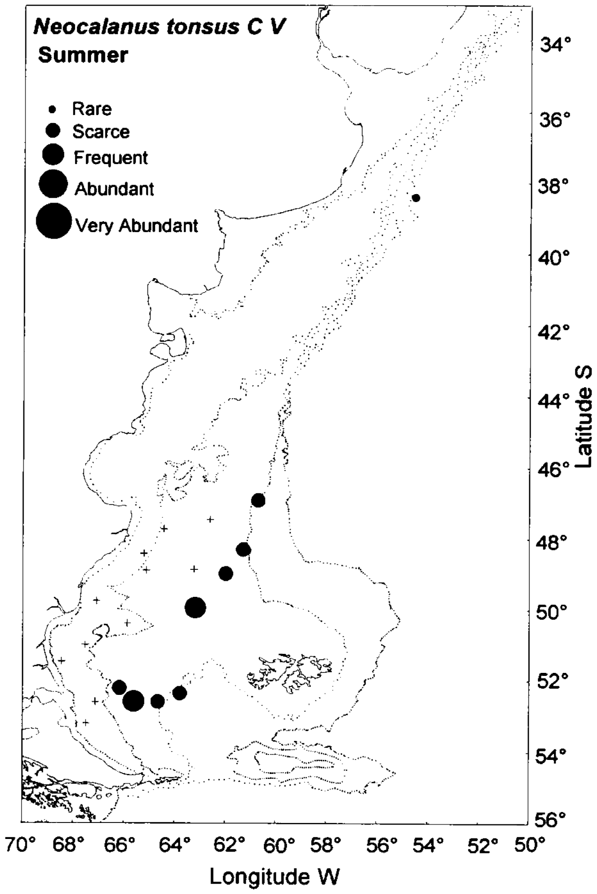

Figure 10. Neocalanus tonsus. Summer relative abundance and distribution of copepodid stage V in waters off Argentina.

ring at higher densities over the inner shelf at < 100 m depths. To the north of 46° S, its range of distribution partially overlaps that of *Calanoides* cf. *carinatus* (see below). Its abundance increases offshore up to middle shelf while *Calanoides* cf. *carinatus* decreases or even disappears. This is particularly evident in the area of Valdés Peninsula.

Calanus simillimus *(Figure 9)*

This species occurs primarily over the middle and outer Argentinian shelf from the 100 m isobath outwards. Its concentration increases towards the shelf-break, although on a few occasions it has also been recorded in coastal stations. Relatively higher abundances are recorded in waters near the shelf-break in spring and summer-early autumn.

Neocalanus tonsus *(Figure 10)*

Despite the fact that available information on abundance of *Neocalanus tonsus* is limited to copepodid V and only to summer–early autumn, our results show that this species is distributed in outer-shelf waters near the shelf-break. A few adult females found in autumn (OB-04/94 survey) and winter (OB-08/93 survey) allowed a confirmation of the identification of the species.

Calanoides *cf.* carinatus *(Figure 11)*

This species is distributed in inner and middle shelf waters, not occurring south of 46° S nor in waters > 200 m deep. The higher densities are found mostly in summer between 42°–45° S.

Calanoides patagoniensis *(Figure 12)*

Adult females of this species were recorded only on two occasions, both in coastal stations of southern Patagonia.

The same patterns described above were also found for the three most abundant species along a transect from the coast to the shelf-break at 38° S (Figure 13): both *Calanus australis* and *Calanoides* cf. *carinatus* typically occur in inner and middle shelf waters decreasing offshore, while *Calanus simillimus* is distributed in the outer shelf showing the opposite trend towards the shelf-break.

In summary, the species *Calanus australis*, *Calanus simillimus* and *Neocalanus tonsus* appear to be related to the overall drift northwards of subantarctic waters. Although the three species co-occur within the southern region, they occupy different areas offshore–inshore. *Calanus australis* dominates inshore of the 100 m contour where it has been found even in the most coastal of stations. Conversely, *Calanus simillimus* predominates offshore from mid-shelf waters to the continental slope, a region predominantly influenced by the Malvinas Current. Even though the information on *Neocalanus tonsus* is scarce, the trend to occur primarily in the outer shelf sector seems to be stronger than in the two other species. *Calanoides* cf. *carinatus* is present year round from 35° S to about 46° S and has not been recorded at higher latitudes. Among the members of Calanidae in the region, this species appears to be the least related to the subantarctic water mass, establishing in the coastal area centres of high relative abundance. In the northern region of the Argentine Sea, the continental shelf narrows northwards and the

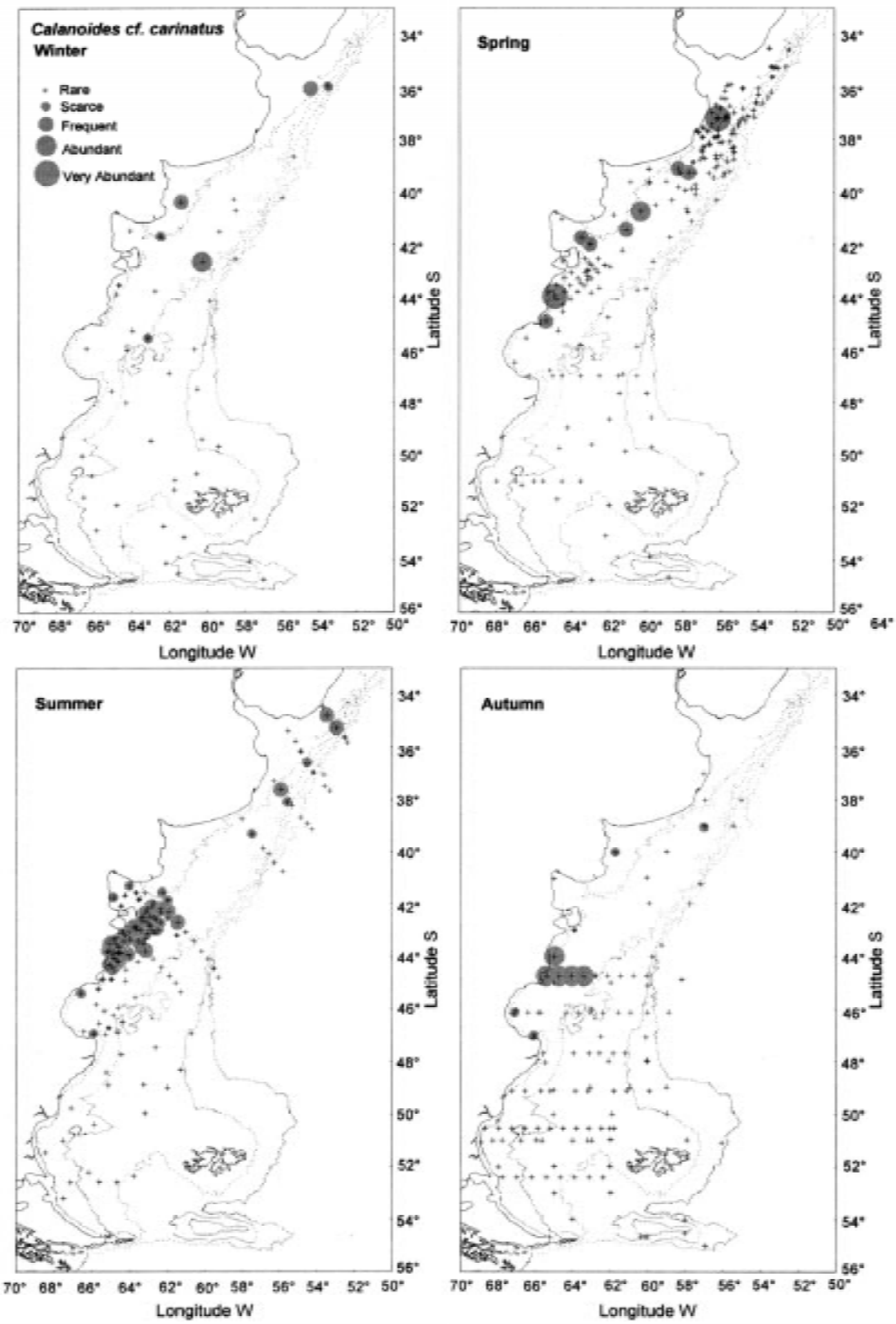

Figure 11. Calanoides cf. *carinatus*. Seasonal relative abundance and distribution of adults in waters off Argentina.

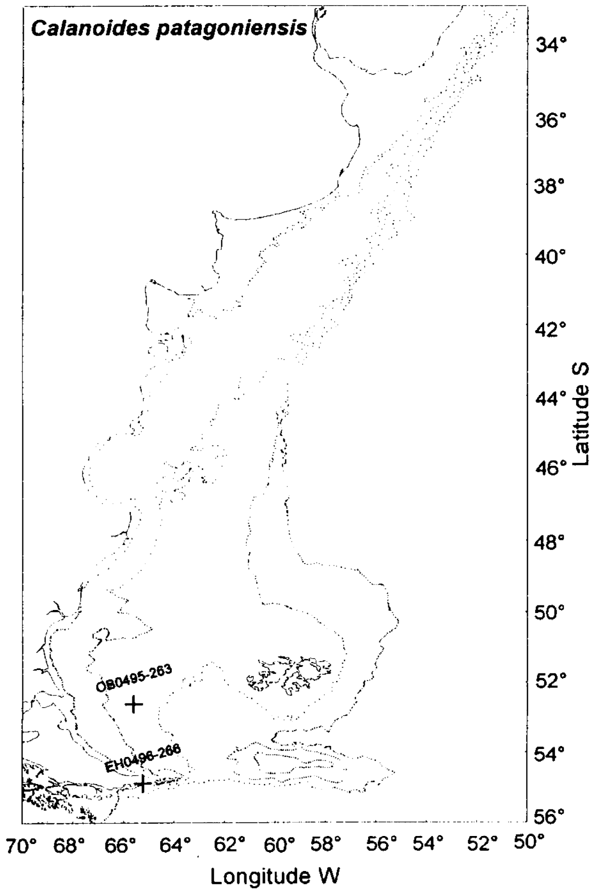

Figure 12. Calanoides patagoniensis. Location of the few available records of adults of the species for waters off Argentina. References are given to cruise and station number.

hydrographic picture becomes very complex mainly due to the encroachment of the Malvinas Current over the outer shelf combined with the huge runoff from La Plata River. Nevertheless, *Calanoides* cf. *carinatus* appears to maintain the same pattern of distribution found in the southern region.

Discussion

Calanus australis has been often erroneously identified as *Calanus finmarchicus* and *Calanus helgolandicus,* especially before the taxonomy of Southern Hemisphere was clarified by Brodsky (1959). Brodsky (1961) described *Calanus chilensis* and *Calanus australis,* both strictly restricted to the Southern Hemisphere. Whereas the former is confined to the Pacific Ocean, *Calanus australis* occurs in the Pacific and Atlantic as the varieties *pacificus* and *atlanticus,* respectively. The only available records for *Calanus australis* var. *atlanticus* correspond to waters off Argentina (Brodsky, 1961; Ramírez, 1970a) and Magallanes Strait (Mazzochi & Ianora, 1991; Mazzochi et al., 1995). Brodsky's (1961) diagnosis of the varieties, however, are rather ambiguous as they are based on very small morphological differences among animals coming from different geographical localities. In any case, our specimens conform to descriptions for the species given by Brodsky (1961) and Bradford-Grieve (1994). According to Brodsky (1961), the southern species are closely related to *Calanus helgolandicus* and *Calanus pacificus,* which are species typical of temperate latitudes of the Northern Hemisphere. At present *Calanus australis* is included in the lineage *helgolandicus* of the genus *Calanus* (after Bucklin et al., 1995). Hence, early references to *Calanus finmarchicus* for the SW Atlantic (Farran, 1929; Wilson, 1950) may most likely correspond to *Calanus australis.* This species has been mentioned among the group of temperate-cold neritic species occurring primarily in coastal and middle shelf waters off the Argentinian Patagonia (Ramírez & Björnberg, 1981). Saito & Kubota (1995) found the species also distributed further offshore beyond the continental slope. In the SE Pacific, it has been recorded in waters off Chile between 18° and 52° S (Brodsky, 1961; Vidal, 1968; Björnberg, 1973; Arcos, 1976). In the SW Pacific, it has been found in New Zealand and southeastern Australian waters (Bradford-Grieve, 1994). In the Atlantic and Indian sectors of South Africa, *Calanus australis* seems to have a vicarious species in *Calanus agulhensis,* recently created by De Decker et al. (1991). It has to be pointed out that morphological differences between both species are extremely subtle and refer mainly to minor characteristics of female and male legs 5 (De Decker et al., 1991). Even though animals off Argentina seem to be morphologically closer to *Calanus australis,* a genetic comparison would be needed to unambiguously clarify their identity. Furthermore, molecular analysis should extend to *Calanus australis* var. *pacificus* off Chilean waters and *Calanus chilensis* in order to establish if *Calanus australis* actually maintains a circumglobal distribution.

Calanus simillimus has previously been referred to as *Calanus propinquus* in most of the local literature. Earlier misidentification may be attributed to the fact that both species, beyond their differing sizes, are morphologically very similar. Main diagnostic characters

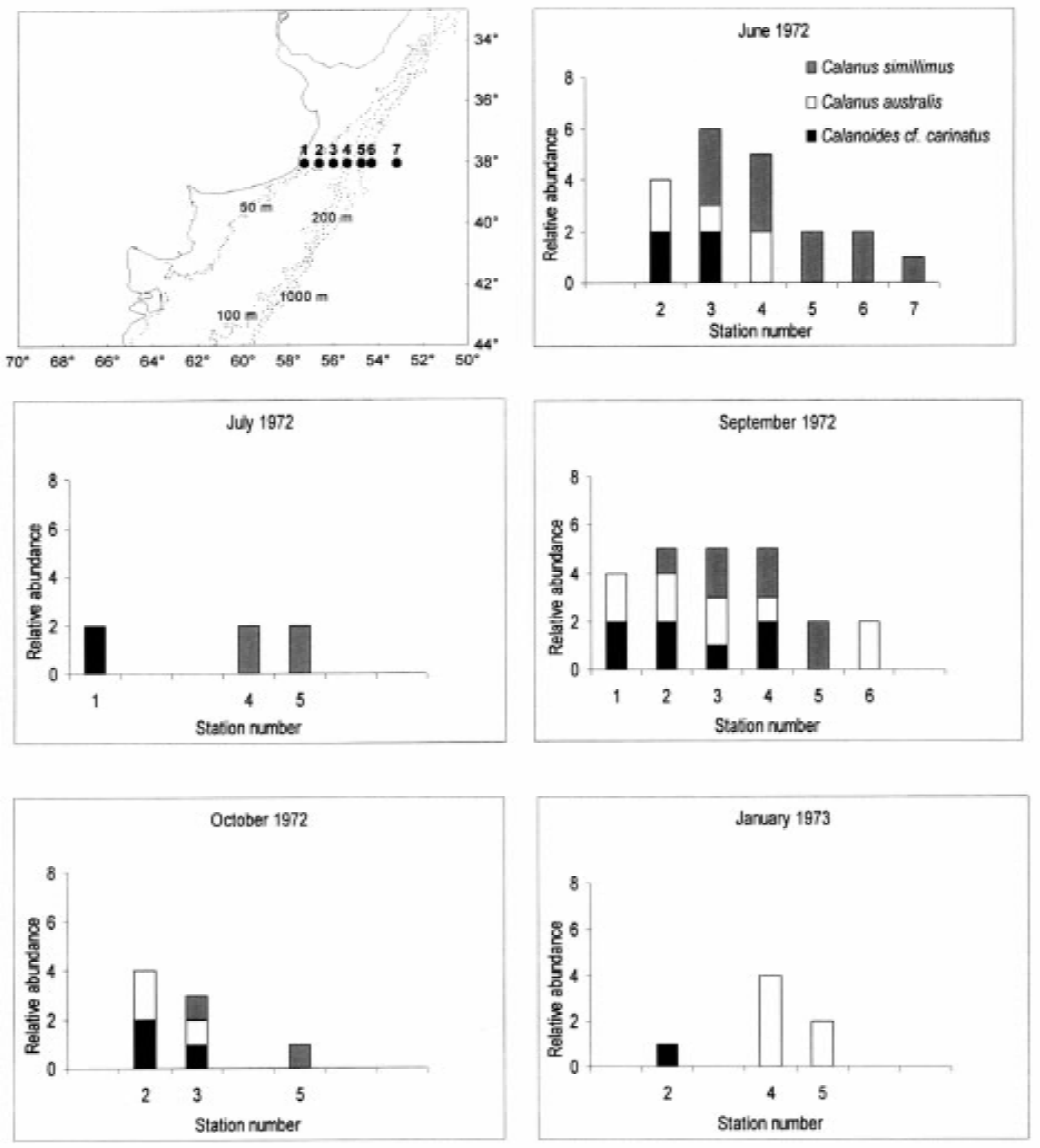

Figure 13. Seasonal relative abundance of *Calanoides* cf. *carinatus, Calanus australis* and *Calanus simillimus* along a transect from the coast to the shelf-break located at 38° S.

refer to the length of the setae on the antenna and the shape and size of the inner teeth of the coxa of the fifth leg in the female, and to the structure of the fifth leg in the male. Animals off Argentina were first classified, although with some reservations, as *Calanus propinquus* (Ramírez, 1970a) after the detailed description by Vervoort (1951) which is, nevertheless, misleading as regards the structure of the fifth leg in the male. In *Calanus simillimus* the "right 5th foot is not greatly modified, reaching slightly beyond the distal margin of the left 1st exopodal joint" (p. 24) while in *Calanus propinquus* the "right 5th exopod is slightly longer than the 1st left exopodal joint" (p.38). In females, the antenna are often damaged, and some doubt may arise concerning the nature of the coxal teeth of the fifth leg since the distal group of teeth can look larger because they are somewhat apart from the rest. A new examination of our specimens through this work showed that they correspond unequivocally to *Calanus simillimus* according to the more accurate recent descriptions by Bradford-Grieve (1994) and Mazzochi et al. (1995). This species is commonly distributed in subantarctic oceanic areas; it can be also found near the Antarctic Convergence (Vervoort, 1951; De Decker, 1984; Atkinson, 1991; Bradford-Grieve, 1994). Correspondingly, its occurrence off Argentina appears to be related to subantarctic waters of the mid and outer shelf. Saito & Kubota (1995) mention this species as a major component among the copepods of the SW Atlantic between 35° and 45° S, associated with the cold water of the Malvinas Current. It is also the most common *Calanus* species recorded in the Pacific sector of the Magallanes Strait (Mazzochi & Ianora, 1991; Mazzocchi et al., 1995).

Neocalanus tonsus (Brady, 1883) was originally described as *Calanus tonsus* from female specimens collected during the 'Challenger' expedition to the Southern Atlantic. Given the other *Calanus* species known at that time for the austral region, i.e. *C. finmarchicus* and *Calanus propinquus*, Brady (1883) created the species on the basis of the erroneously perceived absence of setae in the first antenna, except the terminal joints, the absence of teeth on the coxa of the fifth leg and the bulbous shape of the genital double somite in dorsal view. The species was finally assigned to the genus *Neocalanus* Sars, 1925 after the revision of *Calanidae* by Bradford & Jillet (1974), mainly because of the presence of a recurved spine on the outer distal border of the first exopod segment of the second leg. Major characters to recognise *Neocalanus tonsus* from the other local *Calanidae* species, in particular from *Calanus australis* and *Calanus simillimus*, are the presence of a posterior surface group of spinules on the inner distal part of the basis in legs 2–5, its large size, the lack of the postero-lateral sharpening of the fifth thoracic somite and the fifth leg with the inner border of the coxa naked in both sexes. This copepod has not often been recorded in waters off Argentina. This is likely due to the fact that the species is normally present in shelf surface waters elsewhere only as copepodid V in spring and summer, as it performs ontogenetic vertical migration to deep water depth to overwinter (Jillet, 1968; Ohman *et al*, 1989). Consequently, it has not been reported in previous local studies which were based on checklists of adults exclusively, or where all Calanidae immatures were pooled together, which has been normally the case. Only Saito & Kubota (1995) previously recorded *Neocalanus tonsus* in the Argentine Sea, occupying waters of the middle and outer shelf as we also found. They consider this species along with *C alanus simillimus* as typical components of the Malvinas Current. Voronina (1975, reported by Bradford-Grieve & Jillet, 1998) also found *Neocalanus tonsus* along the continental slope between *ca.* 20° and 60° S in November–December. The species has been recorded in the SE Pacific along the Chilean coast (Björnberg, 1973; Marin & Antezana, 1985), but there appears to be no population continuity to Argentinian waters through the Magallanes Strait. The species has not been recorded in the eastern, Atlantic influenced, side of Magallanes. Björnberg (1973), and Mazzochi & Ianora (1991) and Mazzochi et al. (1995) found it only on the western side of the Strait. Arcos (1976) did not mention its occurrence among the copepods of the Chilean sector of Magallanes. *Neocalanus tonsus* is distributed entirely in the Southern Hemisphere. It occurs in the Indian, Pacific and Atlantic Oceans at latitudes ranging from 30° to 55° S, i.e. between the Polar and Subtropical Fronts. It is abundant over the edges of the continental shelf and slope, decreasing towards both neritic and oceanic waters (Jillet, 1968; Bradford-Grieve, 1994; Richardson & Verheye, 1998; Bradford-Grieve & Jillet, 1998). Although the species was previously considered to have a subantarctic distribution, it has been suggested recently that *Neocalanus tonsus* is a transition species (*sensu* Bradford-Grieve & Jillet, 1998). In the SE Atlantic, it appears to be related to the Benguela System, occurring in deep waters off Africa as well as in shelf and coastal cold waters during spring and summer (De Decker, 1984; Ohman, 1987; Richardson & Verheye, 1998). The occurrence of stage V copepodids as we exclusively found in surface waters in summer and early autumn (March–April) in the austral area has to be related to a life cycle involving seasonal ontogenetic vertical migration. In southern New Zealand, for instance, *Neocalanus tonsus* breeds in winter in deep layers followed by the ascent of juveniles that may reproduce again in spring–summer in shelf waters. By mid-summer, the descent of lipid-rich copepodids V takes place and thus the population returns to deep waters (Ohman, 1987). The occurrence of surface populations of only copepodids (mainly C V) has been mentioned frequently (Marin & Antezana, 1985; Mazzochi & Ianora, 1991).

Calanoides carinatus was created by Krøyer (1848) and redescribed by Giesbrecht (1892) as belonging to the genus *Calanus* and was later transferred to *Calanoides* Brady, 1883. The genus can be immediately identified by the pointed anterior head. *Calanoides carinatus, Calanoides macrocarinatus, Calanoides patagoniensis* and *Calanoides acutus*, potential inhabitants of South American Waters, can be distinguished from one another by the shape of the genital double somite and seminal receptacles in the female, and by the form of the fifth leg in the male. *Calanoides acutus* is the largest species and has been found in waters off Argentina only by Saito & Kubota (1995) where it was exclusively beyond the continental slope. In comparison with *Calanoides macrocarinatus* Brodsky, 1972, the general body shape of the female *Calanoides* cf. *carinatus* off Argentina is similar to the New Zealand specimens described by Bradford-Grieve (1994) which in turn conforms to Brodsky's original description. However, Argentinian females are smaller, and the position and shape of the spermathecae fit those of *Calanoides carinatus* according to Brodsky (1972). For males, the overall structure of leg 5 of our specimens also resembles that of *Calanoides macrocarinatus*, but the left endopod is reduced to one naked segment, conforming to the description of *Calanoides carinatus*. Nevertheless, the proportional lengths of both rami differ from Giesbrecht's original drawings (as *Calanus brevicornis*, Plate 8, Figure 28) having a more asymmetrical appearance (right leg slightly shorter than the left one). Therefore, we choose to refer to the Argentinian specimens as *Calanoides* cf. *carinatus*. Figure 11 suggests that *Calanoides* cf. *carinatus* occurs typically in inner and middle shelf waters, although low numbers are found further offshore in the northern-most area of the Argentine Sea. A significant finding was the absence of the species to the south of *ca.* 46° S, while to the north *Calanoides carinatus* has been quoted as occurring off Uruguay (Goberna, 1986) and Brazil up to Cabo Frío (Neto & Paiva, 1966; Campaner & Honda, 1987; Valentin et al., 1987). This latitudinal distribution in the SW Atlantic corresponds roughly to that along the African coast from Liberia to South Africa (Bainbridge, 1960; Vervoort, 1963; Binet & Dessier, 1971; Mensah, 1974; Petit & Courties, 1976; Binet, 1979; De Decker, 1984; Timonin et al., 1992; Verheye et al., 1992). *Calanoides carinatus* is largely distributed in tropical and subtropical areas of the Atlantic and Indo-Pacific where it is commonly related to upwelling events (Verheye et al, 1992). In the SW Atlantic, it has been mentioned as a characteristic species of the upwelling waters off Cabo Frío, Brazil (Valentin et al., 1987). Yet, there appears to be some confusion amongst species similar to *Calanoides carinatus* and hence several species may be going by the name *carinatus*. Therefore, the species may not be as widespread as is currently thought (Bradford, 1988). In Argentina, *Calanoides* cf. *carinatus* adults are particularly abundant in spring and summer in waters to the south of Valdés Peninsula down to *ca.* 45° S (Figure 11). In this area, strong tidal mixing over the shelf in those seasons results in a convergent front that can have a similar effect to upwelling and hence enhanced production (Bakun & Parrish, 1991). This frontal system starts disappearing in autumn and is gone by winter, in coincidence with the occurrence of the lowest concentrations of *Calanoides* cf. *carinatus* adults. Further north, its relatively high densities may be associated with the occurrence of a coastal front (Carreto et al., 1995) that follows the development and breakdown of the seasonal thermocline typical of temperate seas. Therefore, we suggest that the life cycle of *Calanoides* cf. *carinatus* in Argentinian waters involves strategies that are most likely related to local upwelling events. There is no evidence from our data to either rule out or support ontogenetic vertical migration and diapause at depth during low food periods (e.g. winter, non-upwelling season), a strategy reported for *Calanoides carinatus* in several other localities (e.g. Petit & Courties, 1976).

Calanoides patagoniensis has a sharply pointed cephalon that is also present in *Calanoides carinatus* and *Calanoides acutus*. However, it can be distinguished by the presence in the genital double somite of the female of a conspicuous anteroventral swelling with a distinctive indentation. In males, endopodal segments of both rami of the fifth leg are atrophied, unlike in the other two species in which atrophy occurs in only one side. *Calanoides patagoniensis* is a subantarctic species. In the Pacific Ocean, it has been recorded in waters off Chile from 30° S (Björnberg, 1973) to the Magallanes Strait (Mazzochi & Ianora, 1991; Mazzochi et al., 1995). The species has been frequently found in Chilean fjords (Marin & Antezana, 1985) as well as in neritic waters (Björnberg, 1973; Arcos, 1974) where it is a major component of zooplankton. This is the first record of *Calanoides patagoniensis* in the SW Atlantic. Its presence in the southern Argentinian shelf region is probably related to the influence of waters flowing from the Pacific through the Magallanes Strait.

We have reported on the broad distribution patterns of species of Calanidae occurring in the Argentine Sea and their possible relationship to main hydrographic features. As recommended by Bradford-Grieve & Jillet (1998), next the focus should be on gathering information relating their life histories to the physical environment at the different scales that processes of change take place.

Acknowledgements

We are grateful to N. Fernández Aráoz, B. Santos and M. D. Viñas for kindly providing rough data of published and unpublished information. Comments by J. Bradford-Grieve greatly improved an earlier version of this manuscript. Thanks are given to two anonymous reviewers for their critical comments. We thank A. Prieto for his help with drawings. This is contribution N° 1113 of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina.

References

Arcos, D. F., 1974. Los copépodos calanoideos colectados en la región magallánica por la Expedición HERO 72-4b. Bol. Soc. Biol. de Concepción 47: 215–225.

Arcos, D. F., 1976. Los copépodos calanoideos de la región magallánica. Expedición HERO 72-4. Rev. Com. Perm. Pacífico Sur 5: 85–100.

Atkinson, A., 1991. Life cycles *of Calanoides acutus, Calanus simillimus* and *Rhincalanus gigas* (Copepoda: Calanoida) within the Scotia Sea. Mar. Biol. 109: 79–91.

Bakun, S. & R. H. Parrish, 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita)* of the southwestern Atlantic. ICES J. mar. Sci. 48: 343–361.

Bainbridge, V., 1960. Occurrence of *Calanoides carinatus* (Krøyer) in the plankton of the Gulf of Guinea. Nature 188: 932–933.

Bianchi, A., C. F. Massonneau & R. Olivera, 1982. Análisis estadístico de las características T-S del sector austral de la plataforma continental argentina. Acta Oceanogr. Arg. 3: 93–118.

Binet, D., 1979. Le zooplancton du plateau continental ivoirien. Essai de synthèse écologique. Oceanol. Acta 2: 397–410.

Binet, D. & A. Dessier, 1971. Premières données sur les copépodes pélagiques de la région congolaise.1. Liste des espèces et notes ecologiques. Cah. O.R.S.T.O.M., sér. Océanogr. 9: 411–457.

Björnberg, T. K. S., 1973. The planktonic copepods of the Marchile I expedition and the 'Eltanin' cruises 3–6 taken in the Pacific. Bol. Zool. e Biol. Mar., N.S. 30: 245–394.

Björnberg, T. K. S., 1981. Copepoda. In: Boltovskoy, D. (ed.), Atlas del Zooplancton del Atlántico Sudoccidental y Métodos de Trabajo con el Zooplancton Marino. Publicación especial INIDEP (Inst. Nac. Inv. y Des. Pesq.), Mar del Plata, Argentina: 587–679.

Bradford, J. M. & J. B. Jillett, 1974. A revision of generic definitions in the Calanidae (Copepoda, Calanoida). Crustaceana 21: 5–16.

Bradford, J. M., 1988. Review of the taxonomy of the Calanidae (Copepoda) and the limits to the genus *Calanus*. Hydrobiologia 167/168 (Dev. Hydrobiol. 47): 73–81.

Bradford, J. M. & J. B. Jillett, 1998. Ecological constraints on horizontal patterns – with special reference to the copepod *Neocalanus tonus* (Brady, 1883). In Pierrot-Bults A.C. & S. van der Spoel (eds.), Pelagic Biogeography ICoPB II, Proc. 2^{nd} Int. Conf., IOC Workshop Report 142: 65–77.

Bradford-Grieve, J. M., E. L. Markhaseva, C. E. F. Rocha & B. Abiahy. 1999. Copepoda. In: Boltovskoy, D. (ed.). South Atlantic Zooplankton. Backhuys Publishers, Leiden, The Netherlands. Vol. 2: 869–1098.

Brady, G. S., 1883. Report on the Copepoda obtained by H. M. S. 'Challenger' during the years 1873-1876. Rep. Scient. Results Voy. Challenger, Zool. 8: 1–142.

Brodsky, K. A., 1959. On the phylogenetic relationship of certain species of *Calanus* (Copepoda) from the northern and southern hemispheres. Zool. J. Acad. Sci. URSS 38: 1537–1553.

Brodsky, K. A., 1961. Comparison of *Calanus* species (Copepoda) from the southern and northern hemispheres. New Zeal. Ocean. Inst. Contr. 95: 1–22.

Brodsky, K. A., 1972. Phylogeny of the family Calanidae (Copepoda) on the basis of a comparative morphological analysis of its characters. Issled. Fauny Morej 12: 1–127. (English translation, Israel Program for Science Translations 1975).

Bucklin, A., B. W. Frost & T. D. Kocher, 1995. Molecular systematics of six *Calanus* and three *Metridia* species (Calanoida: Copepoda). Mar. Biol. 121: 655–664.

Campaner, A. F. & S. Honda, 1987. Distribution and co-occurrence of *Calanoides carinatus* and larvae of *Sardinella brasiliensis and Engraulis anchoita* over the southern Brazilian continental shelf. Bolm. Inst. oceanogr., S. Paulo 35: 7–16.

Carreto, J. I., F. C. Ramírez, B. H. Roa & C. A. Verona, 1972. Plancton y condiciones ecológicas en las aguas de la plataforma bonaerense frente a Mar del Plata. II. Campañas 'Transección II'. Doc. Téc. Prel. Proy. Des. Pesq., Mar del Plata, Argentina 30: 1–23.

Carreto, J. I., V. A Lutz, M. O. Carignan, A. D. Cucchi Coleone, & S. G. Demarco, 1995. Hidrography and chlorophyll a in a transect from the coast to the shelf-break in the Argentinean Sea. Cont. Shelf Res. 15: 315–336.

De Decker, A. H. B., 1984. Near-surface copepod distribution in the south-western Indian and south-eastern Atlantic Ocean. Ann. s. afr. Mus. 93: 303–370.

De Decker, A. H. B., B. Z. Kaczmaruk & G. Marska, 1991. A new species of *Calanus* (Copepoda, Calanoida) from South African waters. Ann. s. afr. Mus. 101: 27–44.

Farran, G. P., 1929. Crustacea, Pt 10 Copepoda. British Antarctic ("Terra Nova") Expedition, 1910. Nat. Hist. Rep., Zool. 8: 203–306.

Fernández Aráoz, N. C., 1994. Estudios sobre la biomasa de Copepoda (Crustacea), con especial énfasis en Calanoida, del Atlántico Sudoccidental. Parte I, Tesis Doctoral Universidad Nacional de Mar del Plata, Argentina, 91 pp.

Fernández Aráoz, N. C., G..M. Pérez Seijas, M.D. Viñas & R. Reta, 1991. Asociaciones zooplanctónicas de la Zona Común de Pesca Argentino-Uruguaya en relación con parámetros ambientales. Primavera 1986. Frente Marítimo 8 Sec. A: 85–99.

Fernández Aráoz, N. C., B. A. Santos & F.C. Ramírez, 1994. Análisis ecológico de los copépodos planctónicos, de una campaña de primavera, en la Zona Común de Pesca. Frente Marítimo 15 Sec. A: 133–140.

Frost, B. & A. Fleminger, 1968. A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters. Bull. Scripps Inst. Oceanogr. 12: 1–235.

Giesbrecht, W., 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel. Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresabschnitte 19: 831 pp, 54 pls.

Goberna, E., 1986. Copépodos planctónicos del sector uruguayo de la la Zona Común de Pesca Argentino-Uruguaya. Publ. Co. Téc. Mix. Fr. Mar. 1: 581–597.

Guerrero, R. A. & A. R. Piola, 1997. Masas de agua en la plataforma continental. In: Boschi E.E. (ed.), El Mar Argentino y sus recursos pesqueros. Tomo 1. Antecedentes históricos de las exploraciones en el mar y las características ambientales. INIDEP, Mar del Plata, Argentina: 107–118.

Guerrero. R. A., E. M. Acha, M. B. Framiñan & C. A. Lasta, 1997. Physical oceanography of the Río de la Plata estuary, Argentina. Cont. Shelf Res. 17: 727–742.

Heath, M., J. O. Backhaus, K. Richardson, E. McKenzie, D. Slagstad, D. Beare, J. Dunn, J. Fraser, A. Gallego, D. Hainbucher, S. Hay, S. Jonasdottir, H. Madden, J. Mardaljevic & A. Schacht, 1997. Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. Fish. Ocenogr. 8 (Suppl. 1): 163–176.

Jillett, J. B., 1968. *Calanus tonsus* (Copepoda, Calanoida) in southern New Zealand waters with notes on the male. Aust. J. mar. Freshwat. Res. 19: 19–30.

Marin, V. & T. Antezana, 1985. Species composition and relative abundance of copepods in Chilean fjords. J. Plankton Res. 7: 961–966.

Mazzochi, M. G. & A. Ianora. 1991. A faunistic study of the copepod assemblages in the strait of Magellan. Boll. Oceanol. Teor. Appl. 9: 163–177.

Mazzochi, M. G., G. Zagani, A. Ianora, L. Guglielmo, N. Crescenti & J. Hure. 1995. Copepods. In: L. Guglielmo & A. Ianora (eds.), Atlas of Marine Zooplankton, Straits of Magellan. Springer Verlag: 1–279.

Mensah, M. A., 1974. The occurrence of the marine copepod *Calanoides carinatus* (Krøyer) in Ghanaian waters. Ghana J. Sci. 14: 147–166.

Negri, R. M., R. Akselman & R. H. Benavídes, 1992. Floración excepcional de un dinoflagelado en aguas de la plataforma de Argentina y Uruguay. Frente Marítimo Sec. A: 71–82.

Ohman, M. D., 1987. Energy sources for recruitment of the subantarctic copepod *Neocalanus tonsus*. Limnol. Oceanogr. 32: 1317–1330.

Ohman, M. D., J. M. Bradford & J. B. Jillet, 1989. Seasonal growth and lipid storage of the circumglobal, subantarctic copepod *Neocalanus tonsus* (Brady). Deep Sea Res. 36: 1309–1326.

Petit, D. & C. Courties, 1976. *Calanoides carinatus* (Copépode Pélagique) sur le plateau continental congolais. Cah. O.R.S.T.O.M., sér. Océanogr. 14: 177–199.

Piola, A. R. & A. L. Rivas, 1997. Corrientes de la plataforma continental. In: Boschi, E. E. (ed.), El Mar Argentino y sus recursos pesqueros. Tomo 1. Antecedentes históricos de las exploraciones en el mar y las características ambientales. INIDEP, Mar del Plata, Argentina: 119–132.

Provost, C. V. Garcon & L. Medina Falcon, 1995. Hydrographic conditions in the surface layers over the slope-open ocean transition area near the Brazil-Malvinas Confluence during summer 1990. Cont. Shelf. Res. 16: 215–235.

Ramírez, F. C., 1970a. Copépodos planctónicos del sector bonaerense del Atlántico Sudoccidental. Proy. Des. Pesq. Ser. Inf. Téc., Mar del Plata, Argentina 10: 1–116.

Ramírez, F. C., 1970b. Copépodos planctónicos del sector patagónico. Resultados de la Campaña 'Pesquería XI'. Physis 79: 473–476.

Ramírez, F. C., 1971. Copépodos planctónicos de los sectores bonaerense y norpatagónico. Resultados de la Campaña 'Pesquería III'. Rev. Mus. La Plata, n.s. Zool. 11: 73–94.

Ramírez, F. C., 1977. Planktonic indicators of Argentine shelf and adjacent areas. In: . Proc. Symp.Warm Water Zoopl., Goa, 1976, National Institute of Oceanography, Spec. Publ.: 65–68.

Ramírez, F. C., 1981. Zooplancton y producción secundaria. Parte I. Distribución y variación estacional de los copépodos. In: Angelescu, V. (ed.), Campañas de investigación pesquera realizadas en el Mar Argentino por los B/I 'Shinkai Maru' y 'Walther Herwig' y B/P 'Marburg', años 1978 y 1979. Resultados de la Parte Argentina. Ser. Contr. Inst. Nac. Invest. Des. Pesq., Mar del Plata, Argentina 383: 202–212.

Ramírez, F. & T. Björnberg, 1981. Distribución horizontal, por masas de agua, de los copépodos más frecuentes y abundantes (indicadores hidrológicos) en el Atlántico Sudoccidental. In: Boltovskoy D. (ed.), Atlas del Zooplancton del Atlántico Sudoccidental y Métodos de Trabajo con el Zooplancton Marino. Publicación especial INIDEP (Inst. Nac. Inv. y Des. Pesq.), Mar del Plata, Argentina: 595 pp.

Ramírez, F. C. & B. A. Santos, 1991. Variación estacional de las asociaciones de copépodos en una transecta de la plataforma argentina. Bolm. Inst. oceanogr., S. Paulo 39: 71–86.

Ramírez, F. C. & B. A. Santos, 1994. Análisis del zooplancton de la plataforma bonaerense en relación con algunas variables ambientales: Campañas 'Transección' de 1987. Frente Marítimo 15 Sec. A: 141–156.

Ramírez, F. C., B. H. Roa, C. A. verona & J. I. Carreto, 1973. Plancton y condiciones ecológicas en las aguas de la plataforma bonaerense frente a Mar del Plata. III. Campañas 'Transección III'. Doc. Téc. Prel. Proy. Des. Pesq., Mar del Plata, Argentina 33: 1–27.

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

Roa, B. H., C. A. Verona, J. I. Carreto & F. C. Ramírez, 1974. Plancton y condiciones ecológicas en las aguas de la plataforma bonaerense frente a Mar del Plata. IV. Campañas 'Transección

IV'. Doc. Téc. Prel. Proy. Des. Pesq., Mar del Plata, Argentina 40: 1–38.

Runge, J., 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 (Dev. Hydrobiol. 47): 61–71.

Saito N. & T. Kubota, 1995. Species composition of copepods related to surface water masses in squid fishing grounds off Argentina. Proc. NIPR Symp. Polar Biol. 8: 139–153.

Santos, B. A. & F. C. Ramírez, 1995. Distribución y abundancia de copépodos en el sistema frontal de Península Valdés, durante florecimientos fitoplanctónicos. Thalassas 11: 133–142.

Timonin, A. G., E. G. Arashkevich, A. V. Drits & T. N. Semenova, 1992. Zooplankton dynamics in the northern Benguela ecosystem, with special reference to the copepod *Calanoides carinatus* s. afr. J. mar. Sci. 12: 545–560.

Valentin, J. L., W. M. Monteiro-Ribas, M. A. Mureb & E. Pessotti, 1987. Sur quelques zooplanctontes abondants dans l'upwelling de cabo Frío (Brésil). J. Plankton Res. 9: 1195–1216.

Verheye, H. M., L. Hutchings, J. A. Hugget & S. Painting, 1992. Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. S. afr. J. mar. Sci. 12: 561–584.

Verona, C. A., J. I. Carreto, F. C. Ramírez & B. H. Roa, 1972. Plancton y condiciones ecológicas en las aguas de la plataforma bonaerense frente a Mar del Plata. I. Campañas 'Transección I'. Doc. Téc. Prel. Proy. Des. Pesq., Mar del Plata, Argentina 24: 1–35.

Vervoort, W., 1951. Plankton Copepods from the Atlantic sector of the Antarctic. Verh. K. ned. Akad. Wet., Afd. Natuuk (2) 47: 1–156.

Vervoort, W., 1963. Pelagic Copepoda. Part I. Copepoda Calanoida of the families Calanidae up to and including Euchaetidae. Atlantidae Rep. 7: 77–194.

Vidal, J., 1968. Copépodos calanoideos epipelágicos de la expedición Marchile II. Gayana Zool. 15: 1–99.

Viñas, M. D., F. C. Ramírez, B. A. Santos & G. M. Pérez Seijas, 1992. Zooplancton distribuído en el área de desove y de crianza norpatagónica de la merluza (*Merluccius hubbsi*). Frente Marítimo 11 Sec. A: 105–113.

Voronina, N. M., 1975. On the ecology and biogeography of plankton of Southern Ocean. Trudy Instituta Okeanologii 103: 60–87, (in Russian).

Wilson, C. B., 1950. Copepods gathered by the U.S. fisheries steamer 'Albatross' from 1887 to 1909, chiefly in the Pacific Ocean. U.S. Nat. Mus. Bull. 100: 141–441.