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The distribution of littoral caprellids (Crustacea: Amphipoda: Caprellidea) along the Pacific coast of continental Chile

La distribución de caprélidos litorales (Crustacea: Amphipoda: Caprellidea) en la costa del Pacífico de Chile continental

MARTIN THIEL[1]* , JOSÉ M. GUERRA-GARCÍA[2], DOMINGO A. LANCELLOTTI[1] & NELSON VÁSQUEZ[1]

[1]Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile;
e-mail: thiel@ucn.cl
[2] Laboratorio de Biología Marina, Departamento de Fisiología y Biología Animal, Facultad de Biología, Universidad de Sevilla, Apartado 1095, E-41080, Sevilla, España
(*corresponding author)

ABSTRACT

Many littoral caprellid species have a very ample distribution, some having been reported from all over the world. The cosmopolitan distribution of many littoral caprellid species might be facilitated by the fact that they are often associated with fouling communities on floating objects, which have a high potential of far-range dispersal. This dispersal potential may also have implications for the distribution of caprellids on local and regional scales. Herein we examined the distribution of littoral caprellid species on two spatial scales, local (tens of kilometers) and regional (hundreds of kilometers) along the Pacific coast of continental Chile. On the local scale, we studied the caprellid fauna in different habitats (intertidal boulders, subtidal algal and seagrass beds, fouling community on buoys and ropes); on the regional scale we focused only on caprellids associated with the fouling community on buoys and ropes. We found a total of six caprellid species, some of which were very abundant both on the local as well as on the regional scale. On the local scale we found a difference between the three studied habitat types with respect to the assemblage of caprellid species, some of which were found in more than one habitat. The highest species richness and abundance of caprellids was found in the fouling community associated with anchored buoys and ropes. On the regional scale we found very high numbers of caprellids in the fouling community of the northern region (n of 30° S), and decreasing abundances and species richness in the central region (30–37° S). No caprellids were found in the southern region of the study area (37–42° S). This pattern coincides with the global distribution of littoral caprellid species, which are most abundant and diverse at low latitudes but occur in low abundances and low diversity at high latitudes. Detached buoys that were found a few km off the coast harbored similar caprellid assemblages (including ovigerous females) as anchored buoys, suggesting that buoys and other floating substrata (litter, macroalgae) may facilitate dispersal of caprellids (and other epibiota) along the Pacific coast of Chile. Since artificial and natural floating substrata are also abundant at high latitudes it is inferred that the low diversity of littoral caprellids at high latitudes is not due to lack of dispersal vectors, but rather of other factors.

Key words: Crustacea, Amphipoda, Caprellidea, Chile, biogeography.

RESUMEN

Muchas especies de caprélidos del litoral presentan una amplia distribución, algunas han sido citadas a lo largo de todo el mundo. La distribución cosmopolita de muchas especies de caprélidos podría deberse al hecho de que se asocian frecuentemente a las comunidades "fouling" en objetos flotantes, que presentan una capacidad importante de dispersión a largas distancias. Esta capacidad de dispersión puede tener implicaciones en la distribución de caprélidos a escala local y regional. En este estudio, nosotros examinamos la distribución de las especies de caprélidos litorales en dos escalas espaciales, local (decenas de kilómetros) y regional (cientos de kilómetros), a lo largo de la costa Pacífico de Chile continental. A escala local se estudió la fauna de caprélidos en distintos hábitats (bolones intermareales, praderas de algas y fanerógamas marinas, comunidades "fouling" de boyas y cuerdas); a escala regional el estudio se centró solamente en los caprélidos asociados a boyas y cuerdas. Se encontraron un total de seis especies de caprélidos, algunos de los cuales fueron muy abundantes a escala local y regional. A escala local, existió una diferencia entre los tres tipos de hábitat con respecto a la fauna de caprélidos, algunos de los cuales estuvieron presentes en más de un hábitat. Los valores más altos de riqueza específica y abundancia se encontraron en la comunidad "fouling" asociada a boyas y cuerdas ancladas. A escala regional, los caprélidos fueron más abundantes y diversos en las comunidades "fouling" de la región norte (n de 30º S), mientras que la abundancia y riqueza de especies disminuyeron en la región central (30-37º S). No se encontraron caprélidos en la región sur del área de estudio (37-42º S). Este patrón coincide con la distribución global de especies de caprélidos litorales, mostrando los valores más altos de abundancia y riqueza de especies en las bajas latitudes y los valores más bajos en las altas latitudes. Boyas desprendidas desde sus amarras y encontradas a varios km de la costa albergaron asociaciones de caprélidos (incluyendo hembras ovígeras) similares a las de las boyas fijadas, sugiriendo que las boyas y otros sustratos flotantes pueden facilitar la dispersión de caprélidos (y otra epifauna) a lo largo de la costa Pacífico de Chile. Teniendo en cuenta que los sustratos flotantes naturales y artificiales son también abundantes en altas latitudes se infiere que la baja diversidad de caprélidos litorales en altas latitudes no se debe a la falta de vectores dispersantes sino a otros factores.

Palabras clave: Crustacea, Amphipoda, Caprellidea, Chile, biogeografía.

INTRODUCTION

Caprellid amphipods are common members of many littoral habitats, and they are particularly abundant in epibiotic fouling communities. They are very common and diverse on erect bryozoans and hydrozoans and on plant substrata such as macroalgae and seagrasses (McCain 1968). They feed on suspended materials, prey on other organisms, or graze on epibiotic fauna and flora (Caine 1974). Locally, caprellids are important prey for many coastal fish species (Caine 1987, 1989, 1991), and they may be important members of littoral communities.

Many caprellid species have a wide distribution and there are many examples of species that are considered to be cosmopolitans (Takeuchi & Sawamoto 1998). With their general morphology, caprellids are well adapted to cling to substrata such as algae and hydroids (Takeuchi & Hirano 1995). Using their last pereiopods they can firmly hold onto branches of algae, bryozoans and hydrozoans. The pleopods, which are used for swimming in other amphipod crustaceans, are reduced in caprellids. Therefore, although caprellids can swim (Caine 1979), they probably are not very efficient swimmers. This, as well as the lack of a planktonic larval stage, suggests that cosmopolitan caprellid species may be distributed passively by clinging to floating materials rather than by active swimming. Floating materials such as macroalgae are easily distributed between distant locations (Ingólfsson 1995, Hobday 2000a) and caprellids and other amphipods are commonly found on this type of substrata (Hobday 2000b). Many caprellid species are also very unselective with respect to their substratum and they colonize a wide variety of different substrata. For example the species *C. equilibra* has been found on algae, seagrasses, bryozoans, bivalves, sponges and other substrata (Krapp-Schickel 1993). This low selectivity for a wide variety of substrata that have high floating potential suggests that these species might have a wide distribution, particularly in regions where ocean currents transport suspended or floating materials (algae, bryozoans, wood or buoys and other anthropogenic material) over large distances.

Although the abundance and species richness of caprellids in many areas of the world's oceans is still poorly known, Laubitz (1970) pointed out that surface water temperature is an important factor determining the distribution of littoral caprellids along the American coast of the North Pacific. Similar as for other taxa (e.g., corals – Fraser & Currie 1996; molluscans – Roy et al. 1998, 2000), species richness of caprellids decreases gradually towards northern latitudes (Laubitz 1970). Water temperature may affect the distribution of caprellids along the American coast of the South Pacific in a similar way as in the North Pacific since the oceanic regime and in particular the latitudinal variation in water temperatures show similarities between these two regions. It can therefore be expected that diversity of littoral caprellids along the Pacific coast of Chile also decreases towards high latitudes. Nevertheless, on a more local scale, and in particular in bay systems, water circulation leads to intense local mixing (Sobarzo 2002), and the distribution pattern of caprellid amphipods therefore can be expected to be relatively uniform within local bay systems.

In the present study, we examined the composition of the caprellid fauna both on a local and regional scale. The local distribution was examined within a system of bays, i.e., over a scale of tens of km, while the regional distribution of caprellids was examined along a latitudinal gradient at sites separated by hundreds of km. The principal objective of this study was to reveal the species richness of littoral caprellids and their distribution pattern along the Pacific coast of continental Chile. We incorporate data on the caprellid assemblage from detached buoys found a few km offshore since this information contributes to a better understanding of both the local and regional distribution of caprellids.

MATERIAL AND METHODS

The local distribution pattern of littoral caprellids was examined in the bay system of Coquimbo, northern-central Chile (Fig. 1). In November/ December 2000, semi-quantitative samples were taken in three different habitats, intertidal boulders, subtidal algal and seagrass beds and fouling communities from buoys and ropes. Preliminary surveys had revealed that caprellid amphipods

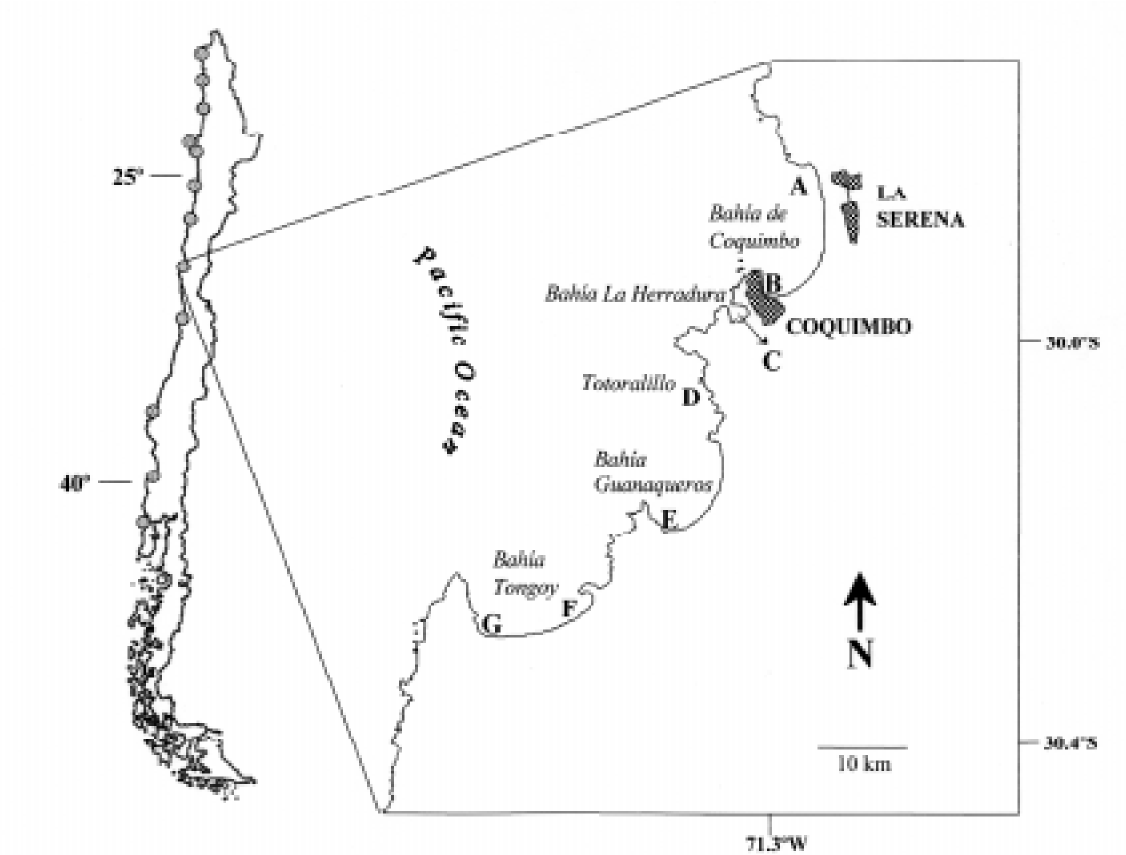

Fig. 1: Bay system investigated in the present study. Samples were taken from buoys, seagrass and algal beds, and boulders on exposed rocky shores along stations A-G; the three different substrata were not present at all sampling stations. Dots along the Pacific coast of continental Chile indicate sampling sites for regional study.

Sistema de bahías investigado en el presente estudio. Las muestras fueron recolectadas en boyas, praderas y bolones a lo largo de las estaciones A-G. Los tres substratos considerados no siempre estuvieron presentes en todos los puntos de muestreo. Los círculos a lo largo de la costa Pacífico de Chile continental indican los sitios de muestreo del estudio regional.

were more common in these than in other littoral habitats (Guerra-García & Thiel 2001). At each of the seven sampling sites we attempted to sample all three habitats keeping the minimum distance between different habitats < 1,500 m; at some sites not all habitats were represented. Sessile fauna together with any adhering amphipods was scraped from boulders located in the low intertidal zone. We focused on areas that were colonized by hydrozoans *Obelia dichotoma*, which we scraped from the underside of several boulders until completing a volume of 10-20 mL. In the subtidal beds of *Gracilaria chilensis* and *Heterozostera tasmanica* we collected the principal plant species together with other occasional algae (*Callophyllis variegata*, *Chondracanthus chamissoi*, *Sarcodiotheca gaudichaudii*, *Sphaerococcus coronopifolius* and *Halopteris* sp.). Plants were taken from the bottom by a semi-autonomous diver and placed in a sampling jar until completing a volume of approximately 1,000 mL. From buoys and ropes associated with aquaculture or harbor structures, we collected the most common epibiota (metazoans such as *Pyura chilensis*, *Bugula neritina* and *B. flabellata*, *Tubularia crocea*, cirripeds from the family Balanidae; and macroalgae such as *Ulva lactuca*, *Polysiphonia paniculata* and *P. mollis*, *Chondracanthus chamissoi*, *Lessonia trabeculata*, often covered with bryozoans of the genus *Membranipora*) together with the adhering amphipods. Samples were either taken by a semi-autonomous diver who separated the fouling organisms from the buoys and ropes and placed them in a sampling jar at the water surface. Alternatively, buoys and ropes were pulled into a boat where fouling organisms were separated and immediately placed in the jar. Fouling organisms were gathered from different buoys and ropes until completing a volume of 500 mL.

The main objective of this survey was to determine the species richness of littoral caprellids in different habitats. In order to obtain representative estimates of species, we selected different sample volumes in each habitat (20 mL under boulders, 500 mL in buoys and ropes and 1,000 mL in algal beds) thereby taking structural differences among habitats into account. Preliminary sampling had indicated that under boulders caprellids cling to small hydroids or to the substratum directly, while on algae they roam over large areas of algal surface. A survey by Guerra-García & Thiel (2001) in the bay system of Coquimbo indicated that the selected sampling volumes are sufficient to obtain representative estimates of species richness in the habitats studied herein. Since this preliminary survey had revealed large differences in caprellid abundance, herein we used a semi-quantitative method in order to estimate caprellid abundances in the different habitats: present (1-10 individuals sample^{-1}), common (11-100 individuals sample^{-1}), abundant (101-1,000 individuals sample^{-1}) and superabundant (> 1,000 individuals sample^{-1}). We expressed the abundance of caprellids as individuals per sample and not as individuals per sample volume thereby taking into account the different habitat structure. The usefulness of a semi-quantitative scale in multivariate analysis has been demonstrated in ecological studies dealing with marine invertebrates (Maldonado & Uriz 1995, Carballo et al. 1996, Naranjo et al. 1996, Guerra-García 2001). Nevertheless, according to Clarke & Warwick (1994), when sampling artifacts render quantitative comparisons unfeasible, a reduction to simple presence or absence of each species is recommended. Following these suggestions, similarities of caprellid occurrence among different habitats on the local scale were examined by means of a classification analysis based on presence/absence data instead of the semi-quantitative data. The Jaccard similarity index (Jaccard 1908) and the UPGMA (unweighed pair-group average method) aggregation algorithm (Sneath & Sokal 1973) were used. The significance of the resulting clusters was established following the bootstrap methodology as in Lancellotti & Trucco (1993) (after Jaksic & Medel 1987). From the initial species*habitat matrix with presence/absence data, 1,000 stochastic reassignments were made, computing on each occasion similarity pseudo-values for each possible combination of habitats. All pseudo-values generated after 1,000 shuffles were plotted in a frequency histogram, establishing the significance, i.e., at a 0.05 or 0.10 α-level, at the 95th or 90th percentile, respectively. The similarity value to which the 95th percentile corresponded was considered the critical value. Thus, for any cluster, a similarity value above this critical value was considered higher than expected at random, and it was considered significant at the $\alpha = 0.05$ level.

For the study of the regional distribution of caprellids we focused on the species associated with the fouling community from buoys and ropes, since previous studies had revealed that this is a very important habitat for littoral caprellid species (Bynum 1978, Caine 1987). At 12 different sites between 18.4° and 41.9° S, spanning ~ 3,000 km along the Pacific coast of continental Chile (Fig. 1), samples were taken from buoys and ropes associated with aquaculture or harbor structures. For Coquimbo we considered the results from Bahía La Herradura (site C in Fig. 1). Sampling was done during austral summer 2001 in the same way as described above. Fouling organisms were separated from different buoys and ropes and placed into the sampling jar until completing a volume of 500 mL. In this way we obtained one cumulative sample for each of the 12 different sites. All samples were fixed with 5 % formalin and later washed over a mesh of 250 µm before sorting them in the laboratory. The Bray-Curtis distance index (Bray & Curtis 1957) and the UPGMA (unweighed pair-group average method) aggregation algorithm (Sneath & Sokal 1973) were used. The analysis was conducted using the semi-quantitative data, i.e., with an order of magnitude corresponding to a logarithmic transformation, which is typically used for this sort of analysis in order to standardize interspecific variability (Clarke & Warwick 1994). Before conducting the analysis we added the value of 1×10^{-5} to each element in the original matrix, which allowed to incorporate the localities with no caprellids (zero values) into the analysis – this procedure produced no changes in the general association pattern. The significance of the clusters resulting from this analysis was established following the same procedure as on the local scale but based on the species*site semi-quantitative data matrix.

During a two-day oceanographic cruise conducted during the austral fall 2002 in coastal waters off the Bay system of Coquimbo we collected six detached buoys together with their fouling community. Additionally, during several oceanographic cruises along the Chilean coast, which were conducted during austral summer 2002 (nine cruises between Arica, 18° S, and Isla Madre de Dios, 50° S, each cruise 10-30 Nm off the coast), we collected two detached buoys off the coast at approximately 27° S. On most occasions we sampled the entire buoy and after washing it over a mesh of 250 µm we scraped the fouling community from the buoys. Due to logistic reasons different volumes were sampled of the fouling community from these detached buoys. In all cases the semi-quantitative estimates represent minimum estimates of the total caprellid abundance on each buoy. Following preservation in the field, these samples were processed in the laboratory in the same way as described above. Detailed information about the detached buoys can be found in Appendix 1.

RESULTS

Local distribution of caprellids from different littoral habitats

A total of six caprellid species were collected in different littoral habitats along the bay system of Coquimbo. None of these species was found in all sampled habitats, but some species (*Caprella equilibra* Say, 1818, *C. scaura* Templeton, 1836, *Deutella venenosa* Mayer, 1890) occurred in two of the three studied habitats, while others (*Caprellina longicollis* (Nicolet, 1849), *Caprella verrucosa* Boeck, 1871, *Paracaprella pusilla* Mayer, 1890) were only found in one of these habitats (Table 1). The species *C. scaura* was one of the most widespread species, being common in almost all samples from buoys and present in all samples from algal and seagrass beds. Although the presence of *C. scaura* in algal and seagrass beds was constant along the bay system studied, its abundance was comparatively low, never exceeding 10 individuals per sample. The species *D. venenosa* was very abundant on buoys and did also occur under intertidal boulders. *Caprella verrucosa* also was very abundant on buoys but did not occur in any of the other two habitats. *Caprella equilibra* was present on some buoys, but also occurred under boulders together with *D. venenosa*, both species being associated with the hydroid *Obelia dichotoma*. The presence of *Paracaprella pusilla* was restricted to the boulders from sampling site C. *Caprellina longicollis*

TABLE 1

Abundance of caprellid species in the different habitats (1 - buoys, 2 - algal and seagrass beds, 3 - boulders) and the sampling sites (A-G) in the bay system of Coquimbo; (*) indicates the seagrass bed; sample volume for buoys is 500 mL, for algal and seagrass beds is 1,000 mL and for boulders approximately 20 mL. For further details see text

Abundancia de las especies de caprélidos en los distintos hábitats (1 – boyas, 2 – praderas, 3 - bolones) y estaciones muestreadas (A-G) a lo largo del sistema de bahías de Coquimbo; (*) indica la pradera de fanerógama. El volumen de muestreo para boyas fue 500 mL, para praderas 1.000 mL y para bolones aproximadamente 20 mL. Ver texto para más detalles

	Buoys						Algal and seagrass beds							Boulders				
	A1	B1	C1	E1	F1	G1	A2	B2	C2	D2	E2	F2	G2*	A3	C3	D3	E3	F3
Caprellina longicollis										Co		Pr	Co					
Caprella equilibra			Pr		Pr	Pr								Pr	Co	Pr		
Caprella scaura	Co	Co	Co	Pr	Co	Co	Pr	Pr	Pr	Pr	Pr	Pr	Pr					
Caprella verrucosa	Co	Pr	Ab	Pr	Ab	Ab												
Deutella venenosa	Co	Pr	Ab	Pr	Ab	Ab								Pr	Pr		Pr	Co
Paracaprella pusilla															Pr			

(A) Bahía de Coquimbo, north
(B) Bahía de Coquimbo, south
(C) Bahía de La Herradura
(D) Bahía de Totoralillo
(E) Bahía de Guanaqueros
(F) Bahía de Tongoy, north
(G) Bahía de Tongoy, south
(*) Seagrass bed (*Heterozostera tasmanica*)

Abundance per sample:
Pr - present (1-10 individuals)
Co - common (11-100 individuals)
Ab - abundant (101-1,000 individuals)

was, together with *C. scaura*, the only species recorded from the algal and seagrass beds.

The epifouling community from buoys and ropes was the habitat with the highest species richness and abundance of littoral caprellids. The caprellid fauna differed among the studied habitats, but on a local scale (tens of km) little variation was found within habitats, with the exception of boulders (Fig. 2). The samples from buoys and algal/seagrass beds were grouped in two separate groups, both connecting two subgroups. While the group connecting caprellid fauna from buoys was significant ($P < 0.05$), those from the algal/seagrass beds formed distinct subgroups at $0.10 > P > 0.05$. In contrast, samples from boulders formed no distinct group suggesting a comparatively heterogeneous habitat, possibly exposed to frequent extinction/colonization events.

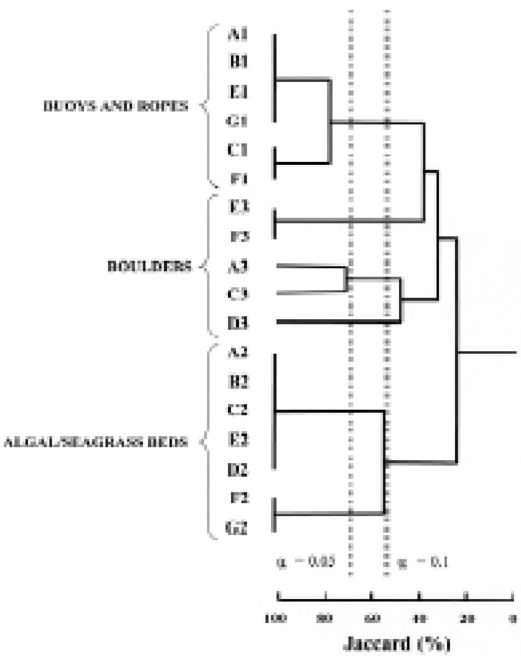

Fig. 2: Cluster analysis showing the relationships among samples on the local scale. Similarities based on presence/absence of caprellid species on different substrata (buoys: 1, algal/seagrass beds: 2; boulders: 3) and sampling stations (A-G). Dashed lines indicate significant levels: Groups of habitats 1 (buoys) and 2 (algal/seagrass beds) significant at $0.10 > P > 0.05$.

Análisis de conglomerados mostrando las relaciones entre substratos en una escala local. Las similitudes están basadas sobre la presencia/ausencia de caprélidos en los diferentes substratos (boyas: 1, praderas: 2; bolones: 3) y estaciones de muestreo (A-G). Las líneas sombreadas indican niveles de significancia: los grupos de hábitats 1 (boyas) y 2 (praderas) fueron significativos a una probabilidad 0,10 > P > 0,05.

Regional distribution of caprellids associated with anchored buoys

Four caprellid species were found on the anchored buoys along the Chilean coast (Fig. 3). Similar as in the bay system of Coquimbo, *Caprella verrucosa* and *C. scaura* were the most abundant species on buoys, being widely distributed in the northern region of the Chilean coast. *Caprella equilibra* was only present in a few localities and the species *Deutella venenosa* only occurred in Coquimbo. Both, abundance and species richness of caprellids on the buoys and ropes decreased from north to south, and no caprellids were found in the southern region (at 39.8° and 41.9° S) (Fig. 3). The classification analysis showed three distinct clusters, one in the northern region characterized by relatively high species richness and abundances, where two subgroups are connected with $P < 0.10$, one in the central region with higher heterogeneity, where species richness and abundance decreased, and one in the south where no littoral caprellids were found in the fouling community associated with buoys (Fig. 4).

Some intraspecific morphological variation has been found for *Caprella scaura* and *C. verrucosa* at some sites. The striking head spine, typical of *C. scaura* reported throughout the world, was very reduced in the specimens collected from Isla Sta. Maria (23.4° S). Nevertheless, examination of antennae, gnathopods, mouthparts and abdomen of these specimens confirmed that they belonged to *C. scaura*. In the specimens of *Caprella verrucosa* from Caleta Tumbes (36.6° S), the southernmost station where caprellids were found, the tubercles on the dorsal pereonites were absent. Taking in consideration the features of antennae, these specimens were assigned to *C. verrucosa*. These observations, however, confirm the great need for future taxonomic studies in the complex of species similar to *C. verrucosa* (see also Guerra-García & Thiel 2001). Regardless of the morphological variations in some of the specimens found herein, a strong decrease in abundance and species richness of littoral caprellid towards higher latitudes was found (Fig. 3).

Caprellids associated with detached (= pelagic) buoys

On the six detached buoys that were collected while floating in coastal waters off the Bay system of Coquimbo, a total of four different caprellid species was found (Table 2). The most common caprellid species were *Caprella scaura* and *C.*

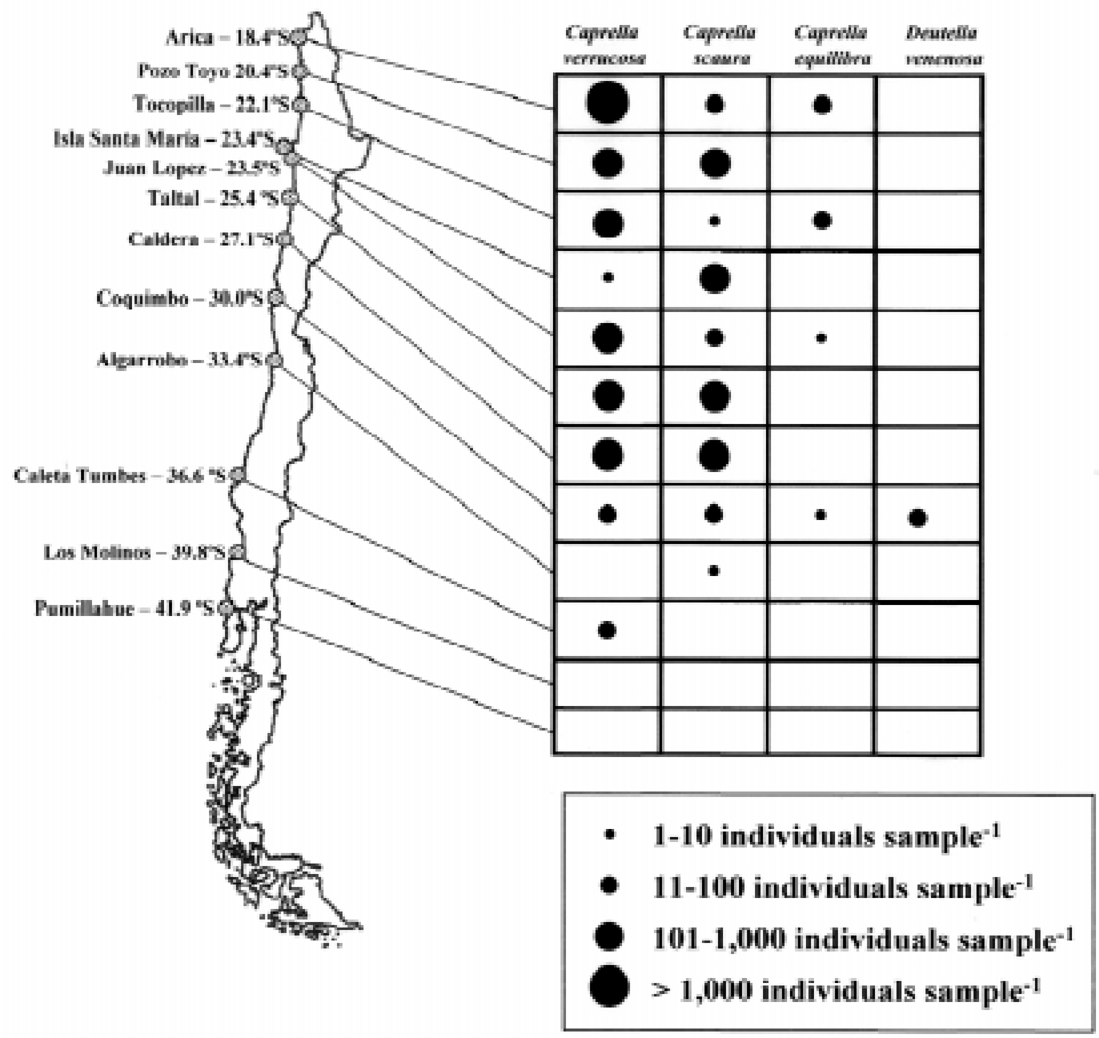

Fig. 3: Abundance and distribution of the caprellid species associated with the fouling community of buoys and ropes along the Pacific coast of continental Chile. At each site, epifaunal organisms from different buoys and ropes were gathered until completing a volume of 500 mL.

Abundancia y distribución de los caprélidos asociados a la comunidad epifita de boyas y cuerdas a lo largo de la costa Pacífico de Chile continental. En cada localidad, se recolectaron organismos epífitos de diferentes boyas y cuerdas hasta completar un volumen de 500 mL.

equilibra, which were each found on four of the six buoys. The other two caprellid species, *C. verrucosa* and *Deutella venenosa*, were each found on two buoys. Abundances of individual caprellid species frequently exceeded 100s of individuals per buoy (Table 2). On all buoys, we also found ovigerous females.

During the nine research cruises between Arica and Isla Madre de Dios we found two detached buoys floating in coastal waters off Caldera. Each of these two buoys harbored three caprellid species (*C. equilibra*, *C. scaura* and *C. verrucosa*) (Table 2). Abundances of *C. equilibra* was highest on the buoys itself, while *C. scaura* dominated on the rope still attached to one of these two buoys. Of all three caprellid species and on each of the two buoys, ovigerous females were found.

DISCUSSION

The results of the present study demonstrated that the caprellid fauna along the Pacific coast of continental Chile is comparatively poor. Despite a relatively large sampling effort on the local and regional scale only six species of littoral caprellids were found. Regardless of the low species number, distinct geographic patterns were found. In

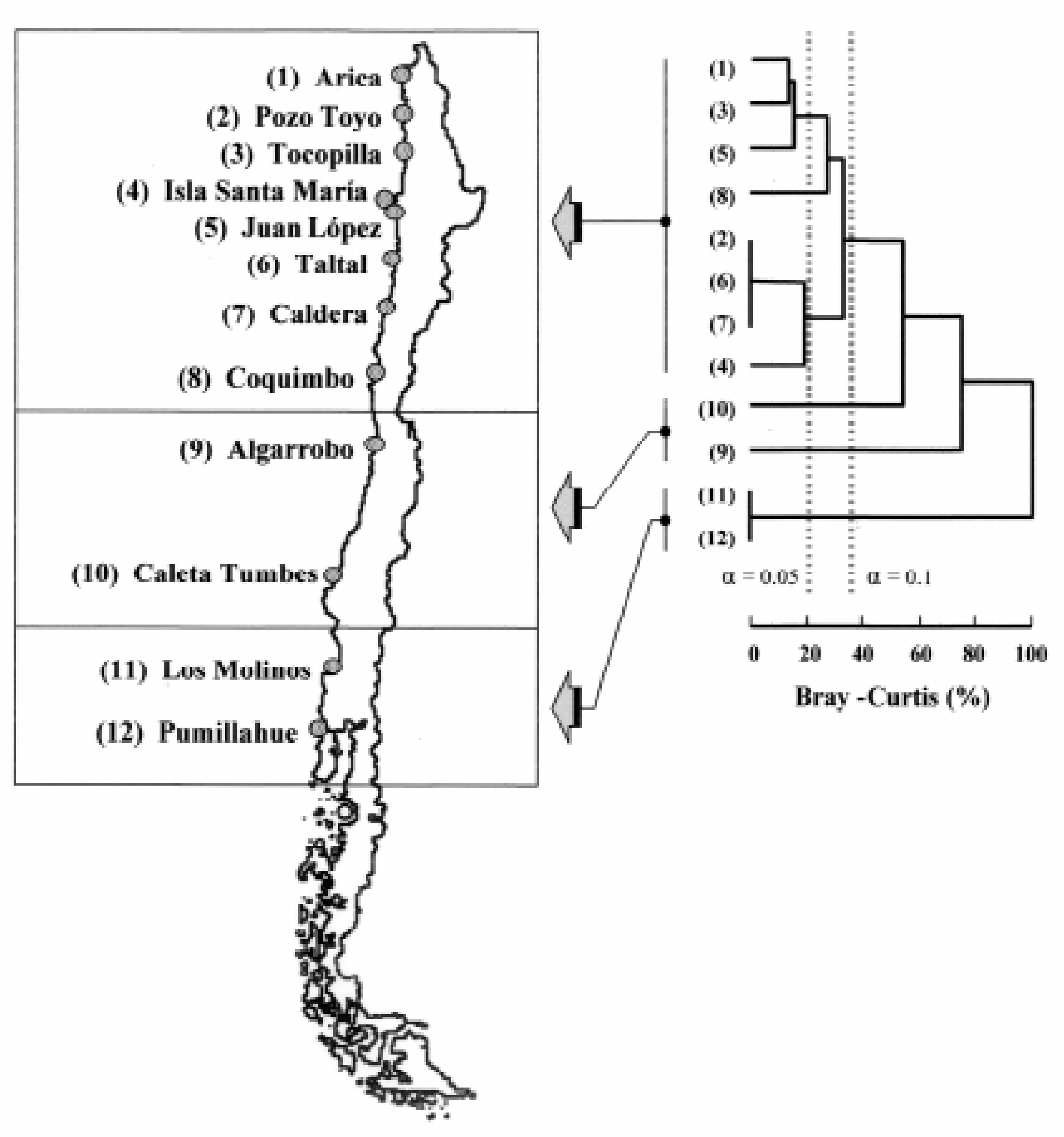

Fig. 4: Cluster analysis showing the relationships among sampling sites along the Pacific coast of continental Chile (regional scale). Distance was based on semi-quantitative values of caprellid abundance. Dashed lines indicate significant levels: group of sampling sites from the northern region significant at 0.10 > P > 0.05.

Análisis de conglomerados mostrando las relaciones entre las localidades de muestreo a lo largo de la costa del Pacífico de Chile continental (escala regional). Las distancias están basadas en los valores semi-cuantitativos de la abundancia de caprélidos. Las líneas sombreadas indican niveles de significancia: el grupo de estaciones de muestreo de la región norte fue significativo a una probabilidad 0,10 > P > 0,05.

the following we will compare the distribution patterns of littoral caprellids on different geographic scales, and we discuss the factors influencing these patterns.

Local distribution of caprellid species in the bay system of Coquimbo

Within the bay system examined herein, most caprellid species were found in two types of habitat. Those habitats were very different (e.g., foul-

TABLE 2

Abundance of caprellid species on detached buoys off the Pacific coast of Chile: present (1-10 individuals); common (11-100 individuals); abundant (101-1,000 individuals); superabundant (>1,000 individuals). All abundance estimates represent minimum values; (Cq) Coquimbo; (Ca) Caldera. For details about buoys see Appendix 1

Abundancia de las especies de caprélidos en boyas desprendidas y encontradas frente a la costa Pacífico de Chile: presente (1-10 individuos); común (11-100 individuos); abundante (101-1.000 individuos); superabundante (>1.000 individuos). Todas las estimaciones de abundancia representan valores mínimos; (Cq) Coquimbo; (Ca) Caldera. Para más detalles ver Anexo 1

				Coquimbo					Caldera	
	Cq1	Cq2-b	Cq2-r	Cq3	Cq4	Cq5	Cq6	Ca1	Ca2-b	Ca2-r
Sample type	Buoy	Buoy	Rope	Buoy	Buoy	Buoy	Buoy	Buoy	Buoy	Rope
Latitude	29º49'23"	29º47'06"		29º58'38"	30º03'56"	30º13'00"	29º37'59"	27º01'23"	27º05'45"	
Longitude	71º26'39"	71º27'44"		71º24'59"	71º40'55"	71º42'35"	71º31'33"	70º56'55"	71º00'15"	
Distance from shore (km)	12.5	11.8		1.9	19.7	7.7	20	6.8	6.5	
Caprellina longicollis										
Caprella equilibra	Co	Co				Pr	Pr	Co	Ab	Ab
Caprella scaura		Ab	Co	Ab	Su		Ab	Pr	Pr	Su
Caprella verrucosa		Ab	Su				Ab	Pr	Co	Co
Deutella venenosa		Ab			Co					
Paracaprella pusilla										

Abundance per sample:
Pr - present (1-10 individuals)
Co - common (11-100 individuals)
Ab - abundant (101-1,000 individuals)
Su - superabundant (> 1,000 individuals)

ing community on buoys and ropes versus algal and seagrass beds) suggesting that the caprellid species found in the bay system of Coquimbo are relatively unselective with respect to their substratum, which appears to be generally true for littoral caprellid species. For example, *Caprella scaura* has been reported from bryozoans, sponges, seaweeds and seagrasses (Lim & Alexander 1986, Takeuchi & Hino 1997, Serejo 1998). *Caprella equilibra* has been collected from seaweeds, bryozoans, sponges and ascidians (Krapp-Schickel 1993). Aoki & Kikuchi (1990) found *C. verrucosa* on very different substrata, and *Caprellina longicollis* has been collected from algae, bryozoans and ascidians along the coast of New Zealand, where it is the most abundant species (McCain 1969). Mayer (1890) reported that *C. verrucosa* and *D. venenosa* were often found on various substrata belonging to the fouling community along the coast of Coquimbo. In general, at the local scale, the environmental habitat conditions (such as hydrodynamics, sedimentation rate, turbidity, substratum stability) seem to be more important in determining the distribution of littoral caprellids than substratum characteristics (Takeuchi et al. 1987, 1990, Guerra-García & García-Gómez 2001). Recently, Guerra-García & García-Gómez (2001) found that the species composition of the Caprellidea from one particular substratum (the seaweed *Cystoseira usneoides*) along the coast of Ceuta (North Africa) changed considerably according to environmental factors such as local hydrodynamics. This suggests that environmental conditions are usually more important in determining the distribution of littoral caprellids than substratum characteristics. The importance of hydrodynamic conditions for the distribution of littoral caprellids is not surprising since many species feed directly on organisms or materials captured from the water column (Takeuchi & Hirano 1995).

Hydrodynamic conditions may also have implications for caprellid dispersal within bay systems. Most bays along the continental coast of Chile are characterized by strong circulation and efficient mixing of surface waters (Sobarzo 2002). This contributes to efficient exchange and a relatively uniform distribution pattern of benthic species within such bays or bay systems (Castilla et al. 2002). Apparently buoys, anchored in the bays along the Chilean coast, are frequently detached together with their caprellid fauna and subsequently moved by predominant currents within bay systems. This process may contribute to frequent dispersal and thereby to the relatively uniform distribution pattern of littoral caprellid species within the bay system of Coquimbo.

Regional distribution of caprellids along the Pacific coast of continental Chile

The regional sampling revealed a latitudinal gradient with littoral caprellids being abundant in the northern region of Chile, but virtually absent from buoys and ropes at the southern sites (39.8° and 41.9° S) examined herein. The latitudinal change in the distribution of littoral caprellids takes place in the central region of the continental coast of Chile, where important faunal changes have been identified for a variety of taxa and functional groups (e.g., Lancellotti & Vásquez 2000, Ojeda et al. 2000, Camus 2001, Rivadeneira et al. 2002, Thiel 2002). Most of these authors agree that northern species disappear between 30° and 37° S, being gradually displaced by southern species, some of which may reach as far north as 25° S. This overlap of southern and northern species in the central region of Chile in some groups results in highest regional species richness in this region (e.g., Rivadeneira et al. 2002). This trend may be reenforced by the presence of other species that only occur in the central region (Thiel 2002). Along the continental coast of Chile, in some taxa the overall species richness decreases towards higher latitudes (e.g., in littoral fishes - Ojeda et al. 2000), while it increases in others (e.g., bryozoans – Moyano 1991). Herein we observed the total disappearance of littoral caprellids from anchored buoys south of 37° S, without replacement by southern species. Similar observations have also been made for some taxa in other regions of the world (corals - Fraser & Currie 1996; prosobranch gastropods, bivalves - Roy et al. 1998, 2000). In these studies the observed decrease in species richness or diversity towards higher latitudes was best correlated with decreasing sea surface temperature, but the ultimate factors (productivity, predation, competition, disturbance) are not well known.

Global distribution of littoral caprellid species

In general, the number of caprellid species found along the coast of Chile on the local and regional scale is very low when compared with other areas at similar latitudes. In Japan, Takeuchi et al. (1987) found 16 caprellid species in a bed of *Sargassum* spp. that had a maximal extension of only 100 m x 80 m. Aoki & Kikuchi (1990), also in Japan, found nine caprellid species in just one bed of *Sargassum patens* 400 m long and 100 m wide. Takeuchi & Hino (1997) cite 10 caprellid species associated with seagrass beds in the Bay of Otsuchi in Japan, and in Brazil, Serejo (1998) found five caprellid species associated with only one species of sponge, *Dysidea fragilis*. In Bahía de Algeciras, southern Spain, Sánchez-Moyano & García-Gómez (1998) cite nine caprellid species associated with a single algal species, *Halopteris scoparia*. Guerra-García & Takeuchi (2002) found 19 caprellid species in the littoral zone of Ceuta (a 10 km long stretch of coastline) in northern Africa. Most of these reports are from areas with temperate water conditions. In contrast to the relatively high values of species richness reported from other areas, in a seagrass bed of *Heterozostera tasmanica* in Bahía de Tongoy, Chile, González (1990) found only two caprellid species, and in a study by Alcayaga (1990) on the fauna associated with a bivalve culture in the same bay, only one caprellid species was reported. Presently, the reasons for the low species richness of littoral caprellids along the Pacific coast of continental Chile are not well known. Caprellid amphipods have also been reported from further south than 37° S, for example from the Magellan Strait (Schellenberg 1935), but little is known about their abundance in this region with predominantly cold waters. Thus, caprellid amphipods can be found all along the Pacific coast of Chile, but abundance and species richness of littoral species associated with the fouling community on buoys is highest in the northern region.

Although the biogeographical distribution of caprellid species on a global scale is not well known so far, Laubitz (1970) studied the caprellids from intertidal and shallow waters along the North Pacific from the zoogeographical point of view. She found that the major limiting factor in the distribution of the caprellid species was water temperature; most of the species occurred almost exclusively in the 10-15 °C temperature range (from Alexander Archipelago to the Strait of Georgia) and only a few species were found in the subantarctic range 5-10 °C. This pattern is similar to that revealed for the Southeast Pacific in the present study. The abundance and species richness of littoral caprellids decreases towards high latitudes with cold surface waters. Along the Chilean coast we found the highest abundances at 18° S, i.e., closer to the Equator than in the North

Pacific. In the eastern North Pacific, caprellid abundance starts declining only at ~ 50° N, while in our study of littoral caprellids from the eastern South Pacific already at 37° S no caprellids were found. For example, Laubitz (1970) reported that *Caprella equilibra* and *C. verrucosa* had not been recorded north of the Queen Charlotte Islands (~ 49° N), but on the continental coast of the eastern South Pacific these species did not occur further south than 37° S. The differences between the eastern North Pacific and the South Pacific could be due to the strong effect of the cold Humboldt Current moving northwards along the Chilean coast.

Similar as in the eastern Pacific, the distribution of littoral caprellids in the south-western Pacific appears to underscore the importance of oceanographic currents and water temperature. Tasmania is situated approximately at the same latitude as Southern Chile, but the number of littoral species is relatively high (approximately 20 species - Guiler 1954, J. Guerra-García & I. Takeuchi unpublished results), comparable with other areas of Australia (J. Guerra-García, unpublished results). This high species richness in Tasmania and the deviation from the general pattern (see Fig. 5) probably is affected by the warm East Australian Current, moving southwards along the coast of Eastern Australia extending its influence up to Tasmania. For New Zealand, which at least at its southern island is very similar to the coast of Southern Chile with respect to the oceano-

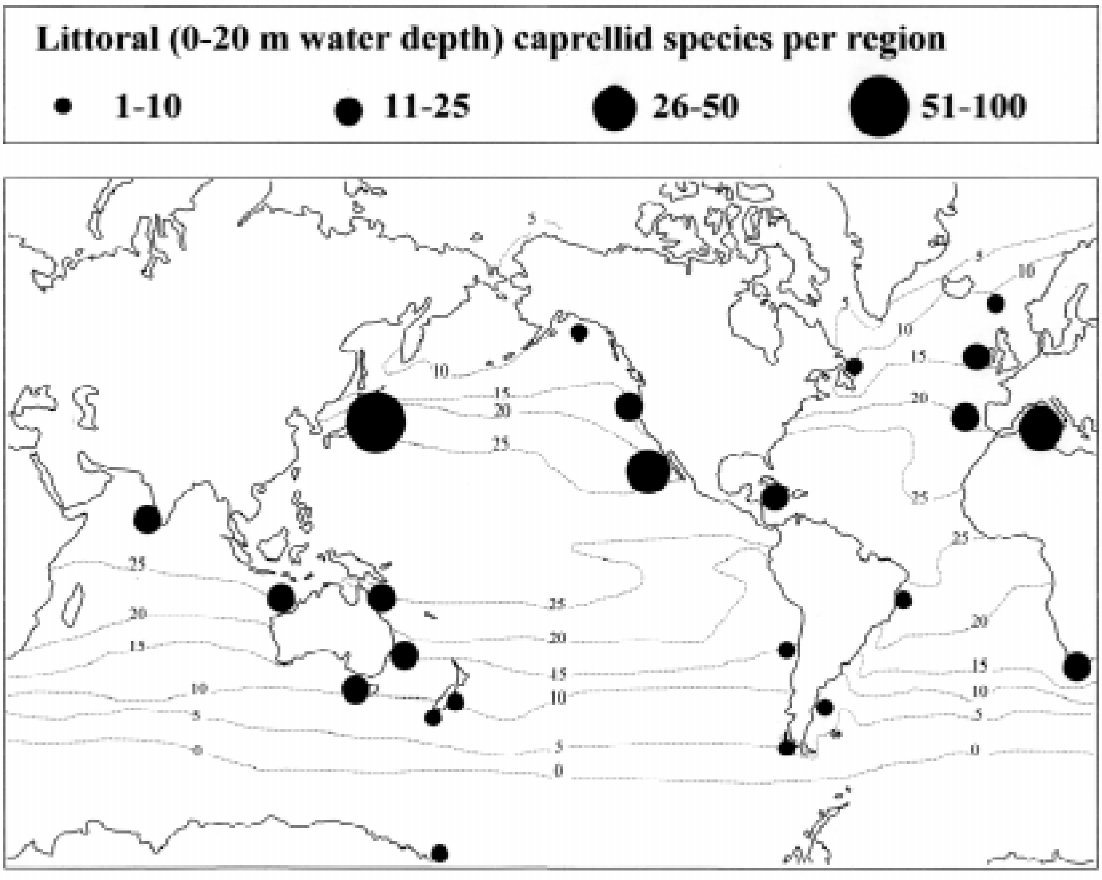

Fig. 5: World map with isolines of sea surface temperature (ºC) and approximate number of littoral caprellid species reported from different regions. Data are taken from Schellenberg (1935), McCain (1968, 1969), McCain & Steinberg (1970), Laubitz (1970, 1972), McCain & Gray (1971), Griffiths (1976), Sivaprakasam (1977), Marques & Bellan-Santini (1985), Swaldon (1990), Wakabara et al. (1991), Watling (1996), Larsen (1998), Serejo (1998), Takeuchi (1999), Guerra-García & Takeuchi (2002, unpublished results).

Mapamundi de las isolíneas de temperatura superficial del agua (ºC) y número aproximado de especies de caprélidos litorales citados en diferentes regiones. Los datos están tomados de Schellenberg (1935), McCain (1968, 1969), McCain & Steinberg (1970), Laubitz (1970, 1972), McCain & Gray (1971), Griffiths (1976), Sivaprakasam (1977), Marques & Bellan-Santini (1985), Swaldon (1990), Wakabara et al. (1991), Watling (1996), Larsen (1998), Serejo (1998), Takeuchi (1999), Guerra-García & Takeuchi (2002, resultados no-publicados).

graphic conditions, only three species of littoral caprellids have been reported (McCain 1969).

The decrease of caprellid abundance and diversity towards colder waters as observed in the eastern Pacific Ocean can also be observed in other regions of the world (Fig. 5). Even though Laubitz (1972) and Larsen (1998) reported the presence of more than 25 species in cold waters around the Arctic Atlantic, most of them inhabit the deep sea and only a few species are littoral. Similarly for Antarctica, where the period of isolation of the fauna has favored the process of speciation (Clarke & Crame 1993), the number of littoral species is also low, even though 20 species have been reported from the Antarctic deep sea (McCain & Gray 1971). In summary, the latitudinal pattern observed along the Pacific coasts appears to reflect global trends with decreasing species richness towards higher latitudes.

Dispersal of caprellid crustaceans and biogeographical implications

Passive dispersal via rafting and floating are supposed to be the main migration mechanisms for small crustaceans with direct development (Highsmith 1985, Locke & Corey 1989). The occurrence of most caprellids encountered in this study on substrata with high dispersal potential (macroalgae, fouling community associated with buoys and other floating materials) may also explain their relatively uniform distribution on the local scale. At most sites from the northern region of the study area, the three most common caprellid species occurred frequently on anchored buoys. Upon being detached, these substrata may be easily distributed over distances on the local (tens of km) and regional (hundreds of km) scale. Jara & Jaramillo (1979), reporting on a detached buoy captured a few km off the coast near Maiquillahue, Chile (39.4° S), discuss the possibility that such objects may be transported over large distances within the West Wind Drift. Floating objects may during their journey carry with them many associated species, such as for example caprellids (Ingólfsson 1995, Hobday 2000a, 2000b). This idea is supported by the finding of all four caprellid species, which usually inhabit the fouling community on anchored buoys, rafting on detached buoys several km offshore. Rafting has also been suggested by Aoki & Asakura (1995), who discussed that the caprellid fauna on the Ogasawara Islands may have colonized this oceanic island from source populations of the Japanese Islands or the Asian mainland. Some caprellid species seem to be specially prone to passive rafting as appears to be the case of *Caprella andreae*, which adapted to ecologically isolated habitats such as drifting objects, possibly evolving from a benthic species, related to *C. acutifrons* (Aoki & Kikuchi 1995). In a study of the planktonic distribution of caprellid amphipods in the western North Pacific, Takeuchi & Sawamoto (1998) found that *C. equilibra* was the dominant species in the plankton samples, suggesting that this species has a greater tolerance for longer periods of planktonic dispersal than other caprellids; it is not known, though, whether the specimens collected in these plankton samples were associated with floating substrata, such as macroalgae. *Caprella equilibra*, as well as *C. scaura*, is often associated with artificial constructions such as aquaculture nets and floating docks (Takeuchi & Sawamoto 1998, this study), both substrata with a high rafting potential. Rafting substrata also occur abundantly at high latitudes (Barnes 2002, Smith 2002), and thus the geographic distribution pattern of littoral caprellid species does not appear to be limited by lack of dispersal substrata, although oceanographic currents might impose restrictions on dispersal frequency and direction of littoral caprellids. However, the occurrence of some individuals (but not the large numbers found in the northern region) of *C. scaura* and of *C. verrucosa* at 33.4° and at 36.6° S suggests that dispersal (if important) might not be the only factor limiting the geographic distribution of littoral caprellids along the coast of Chile. Rather other factors (productivity, predation, competition, disturbance) that are mediated by sea surface temperature may be responsible for the observed disappearance of littoral caprellids towards higher latitudes, such as has been proposed for other taxa (Fraser & Currie 1996, Roy et al. 1998, 2000, Rivadeneira et al. 2002).

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APPENDIX 1

Detailed information about detached buoys found off the Pacific coast of Chile: (Cq) Coquimbo; (Ca) Caldera; sampling volumes differed due to logistic reasons (e.g., length of rope still attached to buoys)

Información detallada de boyas desprendidas encontradas al frente de la costa Pacífico de Chile: (Cq) Coquimbo; (Ca) Caldera; volumenes de muestreo difieren por razones logísticas (e.g., largo de la cuerda aun fichado a las boyas)

				Coquimbo					Caldera	
	Cq1	Cq2-b	Cq2-r	Cq3	Cq4	Cq5	Cq6	Ca1	Ca2-b	Ca2-r
Sample type	Buoy	Buoy	Rope (7m)	Buoy	Buoy	Buoy	Buoy	Buoy	Buoy	Rope (12m)
Volume (1000 cm^3)	11	21.5		11	11	11	11	11	21.5	
Surface area (100 cm^3)	23.8	37.4		23.8	23.8	23.8	23.8	23.8	37.4	
Latitude	29º49’23”	29º47’06”		29º58’38”	30º03’56”	30º13’00”	29º37’59”	27º01’23”	27º05’45”	..
Longitude	71º26’39”	71º27’44”		71º24’59”	71º40’55”	71º42’35”	71º31’33”	70º56’55”	71º00’15”	..
Distance from shore (km)	12.5	11.8		1.9	19.7	7.7	20	6.8	6.5	
Sampling date	11 June 2002	11 June 2002		12 June 2002	12 June 2002	12 June 2002	24 June 2002	9 February 2002	9 February 2002	..
Sampling volume (l)	0.5	0.5		1.0	1.0	0.5	0.5	0.1	0.5	1.3
Buoy entirely/partially scraped	Entire	Partial	Entire	Entire	Entire	Entire	Entire	Entire	Partial	Partial
Other epibiota	*Ulva* sp.	*Bryozoa* spp.	*Ulva* spp., *Bryozoa* spp.,	*Bryozoa* spp.,	*Bryozoa* spp.	*Bryozoa* spp.	*Ulva* spp. *Bryozoa* spp *Ascidia* spp.	*Hydrozoa* spp.	*Hydrozoa* spp. *Ulva* spp., *Bugula neritina*, *Ascidia* spp.	*Hydrozoa* spp. *Ulva* spp., *Bugula neritina*, *Ascidia* spp. Pyura chilensis