

Relationships Between Community Structure of the Intertidal Macroinfauna and Sandy Beach Characteristics Along the Chilean Coast

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With 11 figures and 4 tables

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Abstract. Eight sandy beaches were seasonally sampled along the coast of Chile, from ca. 21 to 42° S (about 3000 km) to study the relationship between community structure of the intertidal macroinfauna and beach characteristics. Sediment samples (0.1 m², 30 cm deep) were collected (July – September 1998 and December 1998 – January 1999) with plastic cylinders at 15 equally spaced levels along three replicated transects extending from above the drift line to the swash zone. The sediment was sieved through a 1 mm mesh and the organisms collected stored in 5 % formalin. To define beach types, Dean's parameter (Ω) was calculated from wave heights and periods, and fall velocity of sand particles from the swash zone. Crustaceans (mainly peracarids) were the most diverse group with 14 species, followed by polychaetes with 5 species. The talitrid amphipod *Orchestoidea tuberculata*, the cirrolanid isopods *Excirrolana braziliensis* and *E. hirsuticauda* and the anomuran decapod *Emerita analoga* were the most widely distributed and common species. Regression analyses between species richness, abundance and biomass of the whole macroinfauna versus sediment characteristics, beach face slopes and morphodynamic beach states showed no significant relationships. Thus, macroinfaunal community characteristics did not increase linearly from lower intermediate to higher intermediate or dissipative beach states as had been found before in Chile or in other coasts. A comparative analysis with data from sandy beaches of other world regions showed that the number of species inhabiting Chilean sandy beaches was generally lower, whereas total population abundances were generally higher compared with values reported elsewhere.

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Problem

It has been argued that the interaction among particle size and wave characteristics (the so-called "beach morphodynamics") has a significant influence on the community structure of the sandy beach macroinfauna (see review by McLachlan & Jaramillo, 1995). It has been also argued that the interaction of those physical factors could affect macroinfaunal attributes at a population level (Jaramillo & McLachlan, 1993; Dugan & Hubbard, 1996; Gómez & Defeo, 1999; Defeo *et al.*, 2000).

Exposed sandy beaches are the most representative coastal habitat, extending almost continuously along the Chilean coast between about 18° and 42° S. Jaramillo & McLachlan (1993) found that species richness, abundance and biomass of the macroinfauna increase from reflective to dissipative conditions along a *ca.* 100-km-long stretch of coast located at a latitude close to 39° S in southern Chile. Further south, Jaramillo *et al.* (2000) found similar relationships at the north-east coast of Isla de Chiloe (*ca.* 41° S). However, the population abundances of those macroinfauna were higher than the values predicted by a worldwide model of species richness, abundance and biomass of macroinfauna as a function of beach morphodynamic types (McLachlan *et al.*, 1996). This suggests that other factors, apart from beach morphodynamics, may also affect macroinfaunal community structure. The conclusions of those studies, however, came from snapshot samplings carried out in different years; this may preclude some of the conclusions due to variability in population abundances related to seasonal dynamics of erosion and accretion of sands on sandy beaches of southern Chile (Jaramillo, 1987). In the present study we therefore analyzed the seasonal relationships between community structure and beach types at eight sites distributed from the northern coast of Chile (18–20° S) to that of southern Chile (40–42° S). This covered a range of coasts – long enough to cover a wide spatial and environmental variability – that allowed us to formulate a more general conclusion about macroinfauna/beach type relationships than that previously reported from spatially or temporally restricted studies in Chile (Jaramillo & McLachlan, 1993; Jaramillo *et al.*, 1998, 2000) or elsewhere (McLachlan, 1990; McLachlan *et al.*, 1993, 1996, 1998).

Material and Methods

Figure 1 shows the approximate location of the sandy beaches studied along the coast of Chile. The beaches of El Aguila (20°50' S, 70°10' W) and Hornitos (22°54' S, 70°17' W) are located in northern Chile, Apollillado (29°10' S, 71°29' W) in north central Chile, Las Cruces (33°30' S, 71°37' W), Matanzas (33°58' S, 71°53' W) and Cobquecura (36°08' S, 72°48' W) in central Chile, and La Misión (39°44' S, 73°23' W) and Mar Brava (41°48' S, 74°01' W) in southern Chile.

Samplings were carried out during August – September 1998 (winter sampling hereafter) and December 1998 – January 1999 (summer sampling hereafter). Water temperature was measured at the surf zone with a mercury thermometer (precision ± 0.1 °C). Water samples collected during low tide were used to measure water salinity in the laboratory.

Sediment samples (0.1 m², 30 cm deep) were collected with plastic cylinders at 15 equally spaced levels along three replicated transects (separated by 1 m) extending from above the drift line to the swash zone; *i. e.* the uppermost station was located above the drift line, the second on the drift line and the last at the lowest limit of the swash zone (indicated by bore collapse). The sediment was sieved through a 1 mm mesh and the organisms collected were stored in 5% formalin until sorting. Abundance and biomass (ash free dry mass) values per running meter of beach were obtained by linear interpolation between sampling stations, after obtaining mean abundances per m² at each sampling station.

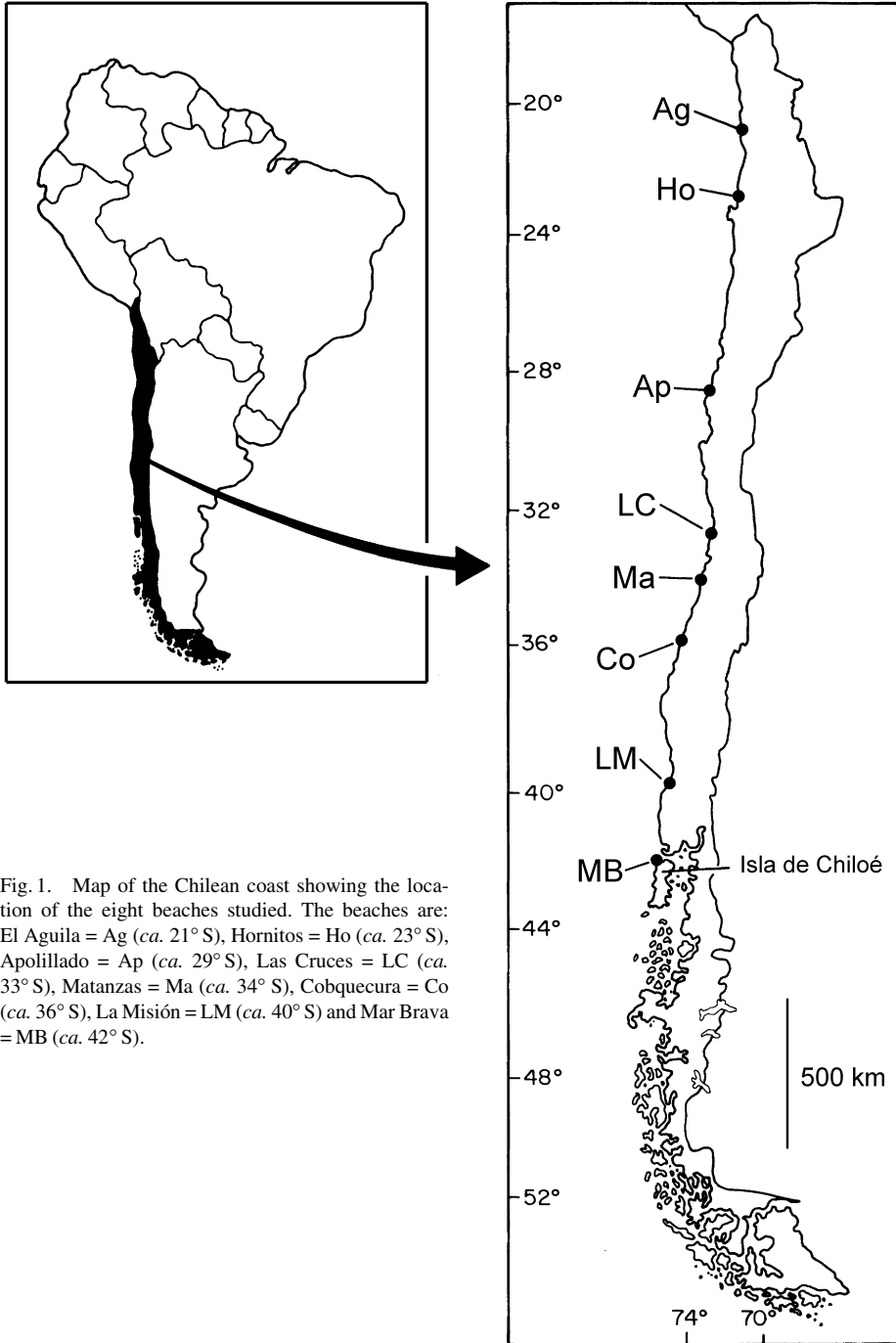


Fig. 1. Map of the Chilean coast showing the location of the eight beaches studied. The beaches are: El Aguila = Ag (ca. 21° S), Hornitos = Ho (ca. 23° S), Apollillado = Ap (ca. 29° S), Las Cruces = LC (ca. 33° S), Matanzas = Ma (ca. 34° S), Cobquecura = Co (ca. 36° S), La Misión = LM (ca. 40° S) and Mar Brava = MB (ca. 42° S).

Surface (about 5 mm) samples were collected from the middle transect for grain size analyses with a settling tube (Emery, 1938). That sample's mean grain size was calculated according to the moments computational method (Seward-Thompson & Hails, 1973). An index of sediment diversity was calculated with the Shannon-Wiener diversity index (Brower & Zar, 1977) as used by Etter & Grassle (1992) and Dugan & Hubbard (1996). Wave height was estimated by measuring the height of breaking waves with graduated poles against the horizon. The wave period (measured with a stop watch) was the time interval between breakers. From estimated mean wave height, wave period and sand fall velocity (Gibbs *et al.*, 1971) of particles from the swash zone, Dean's (Ω) dimensionless parameter was calculated: $\Omega = \text{wave height (cm)} / [\text{sand fall velocity (cm} \cdot \text{s}^{-1}) \times \text{wave period (s)}]$ (Short & Wright, 1983). The morphology (*i. e.* beach face slope at the site of the transect) at each beach was determined by Emery's profiling technique (Emery, 1961).

ANOVA was used to analyze inter-season variability in physical and biological characteristics at each beach; the same analyses and an *a posteriori* test (Tukey's Honest-Significant-Difference or HSD) were used to carry out inter-beach comparisons at each sampling period (Sokal & Rohlf, 1995).

Results

1. Water characteristics at the surf zone

Table 1 shows that no abrupt changes in surf zone water temperatures were found along the long stretch of coast studied (*ca.* 3000 km). The values of this variable decrease gradually from El Aguila to Mar Brava with differences of 5 and 4.3 °C (winter and summer, respectively) between the most extreme locations. Lower geographic and temporal variability was observed in water salinity (Table 1).

2. Beach characteristics

The beaches studied covered a wide range of areal extension (Table 2). Thus, beaches as long as 5.5 to 6.5 km (Hornitos, Cobquecura and Mar Brava) and as short as 0.3 to 1.5 km (La Misión and Apolillado) were sampled. During the winter sampling, the widest intertidal zones were at the beaches of El Aguila (112 m) and Mar Brava (133 m), while the narrowest intertidal was at Cobquecura (42 m). Mar Brava also presented the widest intertidal during the summer sampling (119 m), with Las Cruces, Cobquecura

Table 1. Temperature and salinity of surf waters at the studied beaches. Salinity values are means ($n = 3$) with standard deviations in parentheses. Letter codes for beaches as in Fig. 1.

beach	temperature [°C]		salinity	
	winter 98	summer 98–99	winter 98	summer 98–99
Ag	17.0	18.8	33.3 (0.3)	34.5 (0.1)
Ho	17.0	18.3	34.2 (0.1)	34.3 (0.1)
Ap	13.5	18.0	33.9 (0.1)	34.2 (0.1)
LC	14.0	17.5	33.8 (0.1)	33.6 (0.1)
Ma	13.0	15.5	34.0 (0.2)	34.3 (0.0)
Co	12.0	15.5	32.4 (0.3)	34.2 (0.1)
LM	12.0	15.0	32.6 (0.1)	33.5 (0.1)
MB	12.0	14.5	32.7 (0.2)	33.1 (0.1)

Table 2. Physical characteristics of the studied beaches. Letter codes for beaches as in Fig. 1.

beach	approximate length [km]	season	intertidal width [m]	1/slope
Ag	4.0	winter	112	35
		summer	63	34
Ho	6.0	winter	70	25
		summer	70	24
Ap	1.5	winter	70	22
		summer	56	19
LC	3.5	winter	98	29
		summer	42	14
Ma	2.5	winter	98	22
		summer	84	26
Co	5.5	winter	42	10
		summer	49	10
LM	0.3	winter	84	24
		summer	35	10
MB	6.5	winter	133	38
		summer	119	35

and La Misión having the narrowest intertidal zones (42, 49 and 35 m, respectively). El Aguila and Mar Brava were the flattest beaches (beach face slopes between 1/34 and 1/38), while Cobquecura was the steepest site (beach face slope = 1/10). With the exception of Las Cruces and La Misión, beach slopes varied little between seasons (Table 2).

El Aguila, Hornitos and Mar Brava had the finest sediments (Fig. 2). The average of mean grain sizes estimated for the whole intertidal of those beaches corresponded to fine sands (125–250 μm ; Folk, 1980). Matanzas and Cobquecura had the coarsest sands; that of the former corresponded to medium sands (250–500 μm), whereas that of the latter (averages a bit higher than 500 μm) corresponded to coarse sands (Folk, 1980). The steepest beaches had the coarsest sediments and *vice versa*; these variables were significantly and positively correlated (beach face slope = $0.066 + 43.882 \times$ mean grain size, $r = 0.71$, $P < 0.5$, $df = 14$).

Significant seasonal differences in mean grain size were found at Las Cruces and Mar Brava (coarser sands during summer), as well as at La Misión (coarser sands during winter) (Fig. 2). Sediment diversity was higher (*i. e.* more heterogeneous sands) at Apollillado, Las Cruces, Matanzas and Cobquecura ($H' = 0.75\text{--}0.85$) and lower (*i. e.* more homogeneous sands) at El Aguila, La Misión and Mar Brava ($H' \leq 0.70$) (Fig. 2). Sediment diversity of Matanzas differed significantly between seasons, with higher values during summer (Fig. 2).

During the winter sampling, waves were highest at El Aguila, Cobquecura and Mar Brava (means > 3 m) and lowest at Hornitos and Apollillado (Fig. 2). During summer, the highest waves were recorded at Matanzas, Cobquecura and Mar Brava (means 2.5–2.9 m) and the lowest at La Misión and Hornitos (Fig. 2). With the exception of Horn-

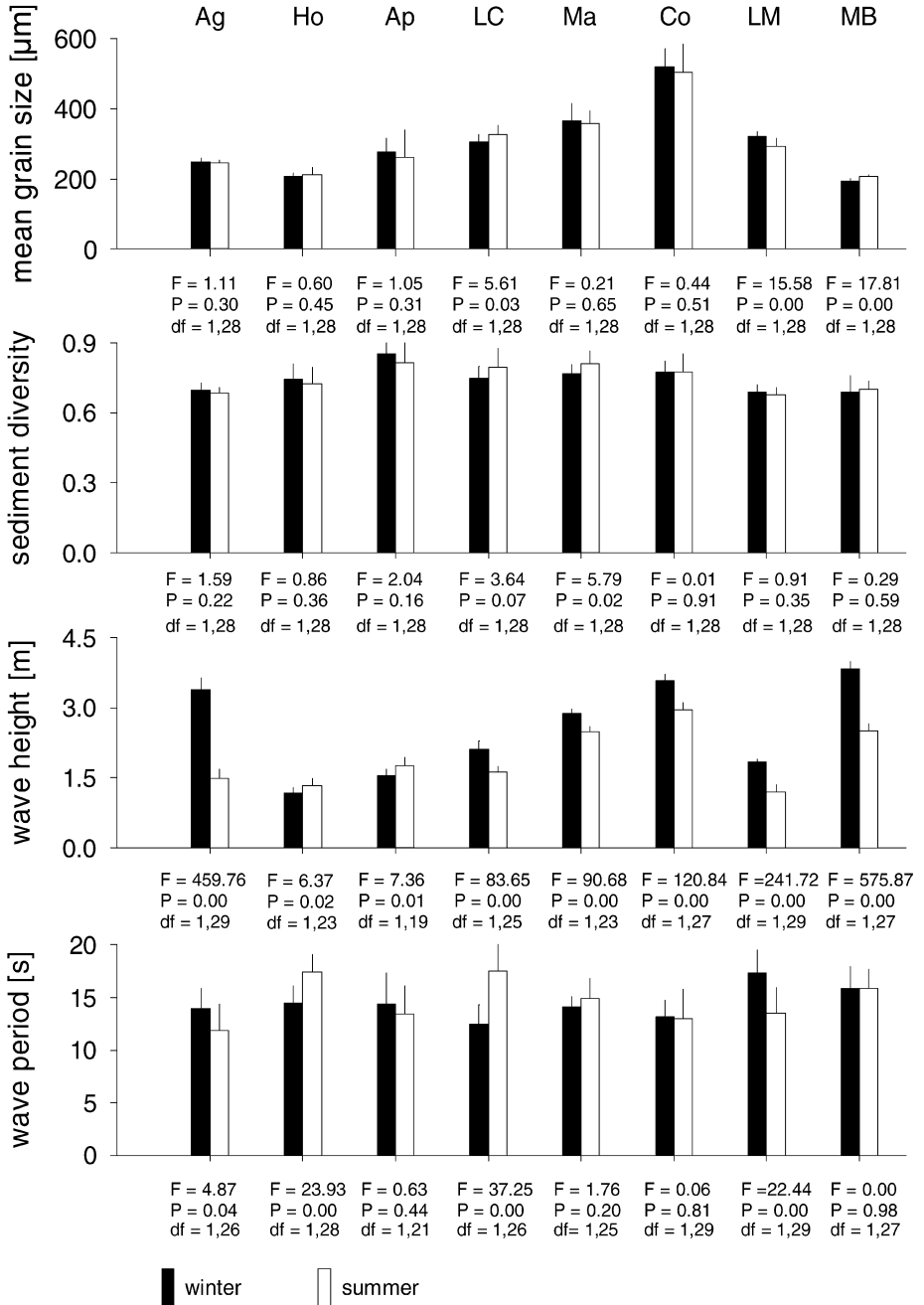


Fig. 2. Interseasonal comparisons of sediment and wave characteristics. The columns represent means (+ 1 SD). Values of F, P and df (degrees of freedom) resulted from ANOVA. Letter codes for beaches as in Fig. 1.

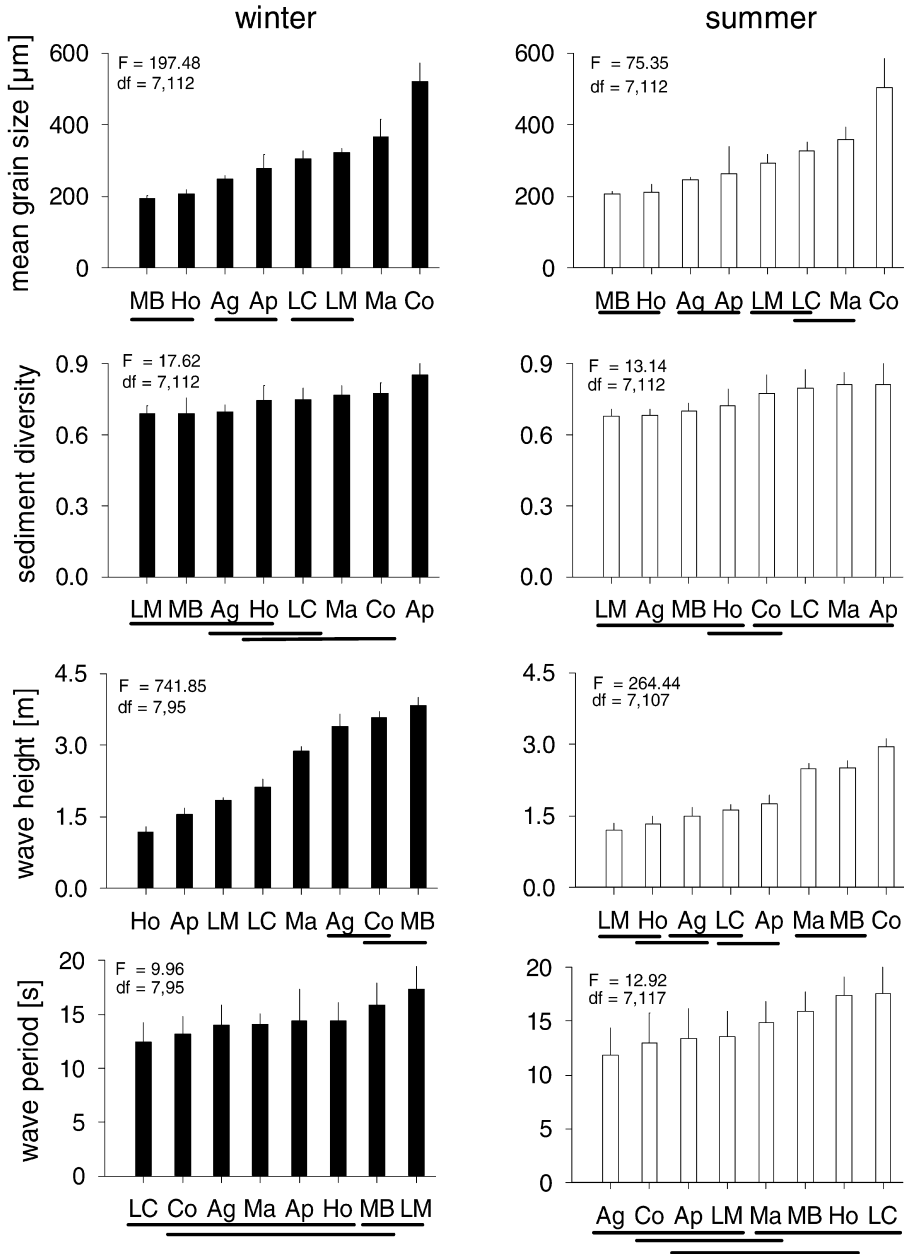


Fig. 3. Along-coast comparisons of sediment and wave characteristics. The columns represent means (+ 1 SD). Values of F and df resulted from ANOVA; all P values were significant at a probability level of 0.001. Lines link means not significantly different (results of Tukey's HSD *a posteriori* test). Letter codes for beaches as in Fig. 1.

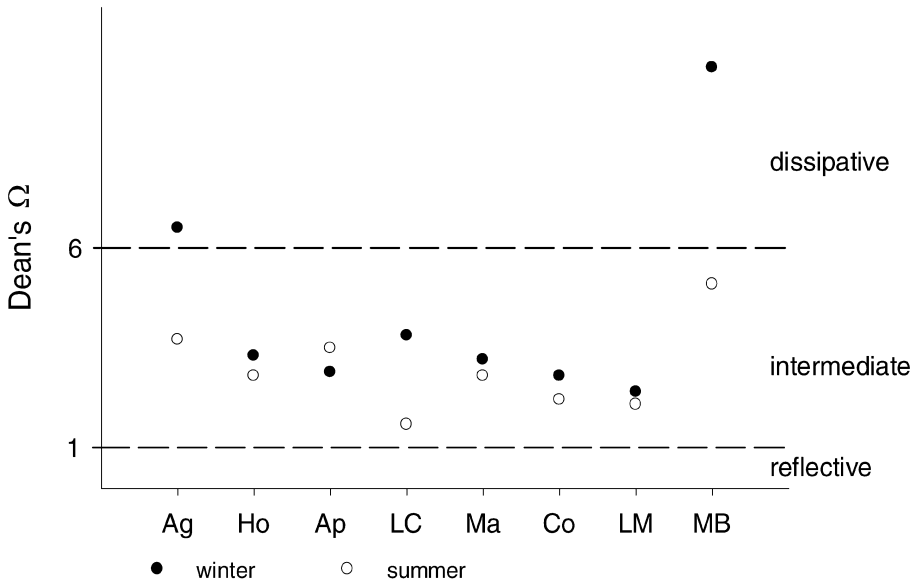


Fig. 4. Values of Dean's parameter (Ω) calculated for each beach during both sampling periods.

itos and Apollillado, waves were significantly higher at each site during the winter sampling (Fig. 2). Wave periods ranged from about 12 to 17.5 s; during the winter sampling the longest wave periods were found at La Misión and Mar Brava (16–17 s); during summer, waves at Hornitos and Las Cruces had the longest periods (around 17.5 s) (Fig. 2). Significant seasonal differences in wave periods were found at El Aguila, Hornitos, Las Cruces and La Misión (Fig. 2).

Figure 3 shows the along-shore variability in beach characteristics. Results of multiple comparison test (Tukey's HSD) tended to group beaches from different latitudes. Only during the winter sampling did almost all beaches differ significantly from each other, but only in wave height.

The values of Dean's parameter indicate that the beaches studied were mostly intermediate (cf. Short & Wright, 1983). During the winter, the beaches of El Aguila and especially that of Mar Brava were in a dissipative state ($\Omega > 6$), while all the others were low intermediates (Ω between 1 and 6) (Fig. 4). Dean's values also show quite a seasonal variability at El Aguila, Las Cruces and Mar Brava. Those three beaches had higher Dean's values during the winter sampling, when waves were higher (cf. Fig. 4 and 2).

3. The macroinfauna

Table 3 shows the taxonomic composition of the intertidal macroinfauna along the studied beaches. Crustaceans (mainly peracarids) were the most diverse group, with 14 species, followed by polychaetes with five. The cirrolanid isopod *Excirrolana brazilien-*

Table 3. Sandy beach organisms collected at each of the beaches studied. IC: Insecta Coleoptera, CA: Crustacea Amphipoda, CI: Crustacea Isopoda, CAN: Crustacea Anomura, CB: Crustacea Brachyura, MB: Mollusca Bivalvia; AP: Annelida Polychaeta. Letter codes for beaches as in Fig. 1. w = winter sampling, s = summer sampling.

taxa	Ag		Ho		Ap		LC		Ma		Co		LM		MB	
	w	s	w	s	w	s	w	s	w	s	w	s	w	s	w	s
<i>Phalerisida maculata</i> Kulser IC			X		X	X	X		X	X			X			
<i>Orchestoidea tuberculata</i> Nicolet CA					X	X	X	X	X	X	X	X	X	X	X	X
<i>Bathyporeiapus magellanicus</i> Schellenberg CA						X	X	X					X			X
<i>Phoxocephalopsis mehuinensis</i> Varela CA									X							
<i>Huarpe</i> sp. CA															X	
<i>Hyale</i> sp. CA									X							
<i>Tylos spinulosus</i> Dana CI					X	X										
<i>Excirolana braziliensis</i> Richardson CI	X	X	X	X	X	X	X	X	X	X	X	X		X		X
<i>Excirolana hirsuticauda</i> Menzies CI				X	X	X	X	X	X	X		X	X	X	X	X
<i>Excirolana monodi</i> Carvacho CI									X				X	X		
<i>Macrochiridothea setifer</i> Menzies CI							X						X		X	X
<i>Chaetilia paucidens</i> Menzies CI							X									
<i>Emerita analoga</i> (Stimpson) CAN	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Lepidopa chilensis</i> Lenz CAN	X				X		X		X							
<i>Ocypode gaudichaudii</i> Milne Edwards CB	X	X	X	X												
<i>Mesodesma donacium</i> (Lamarck) MB						X	X								X	X
<i>Donax peruvianus</i> Deshayes MB			X	X												
<i>Nephtys impressa</i> Baird AP			X	X	X	X			X						X	X
<i>Euzonus heterocirrus</i> Rozbaczylo & Zamorano AP				X				X							X	X
<i>Leitoscoloplos</i> sp. AP			X									X			X	X
<i>Lumbrinereis</i> sp. AP			X													
Glyceridae indet. AP	X		X	X												
Nemertina indet.			X	X		X	X		X	X						X

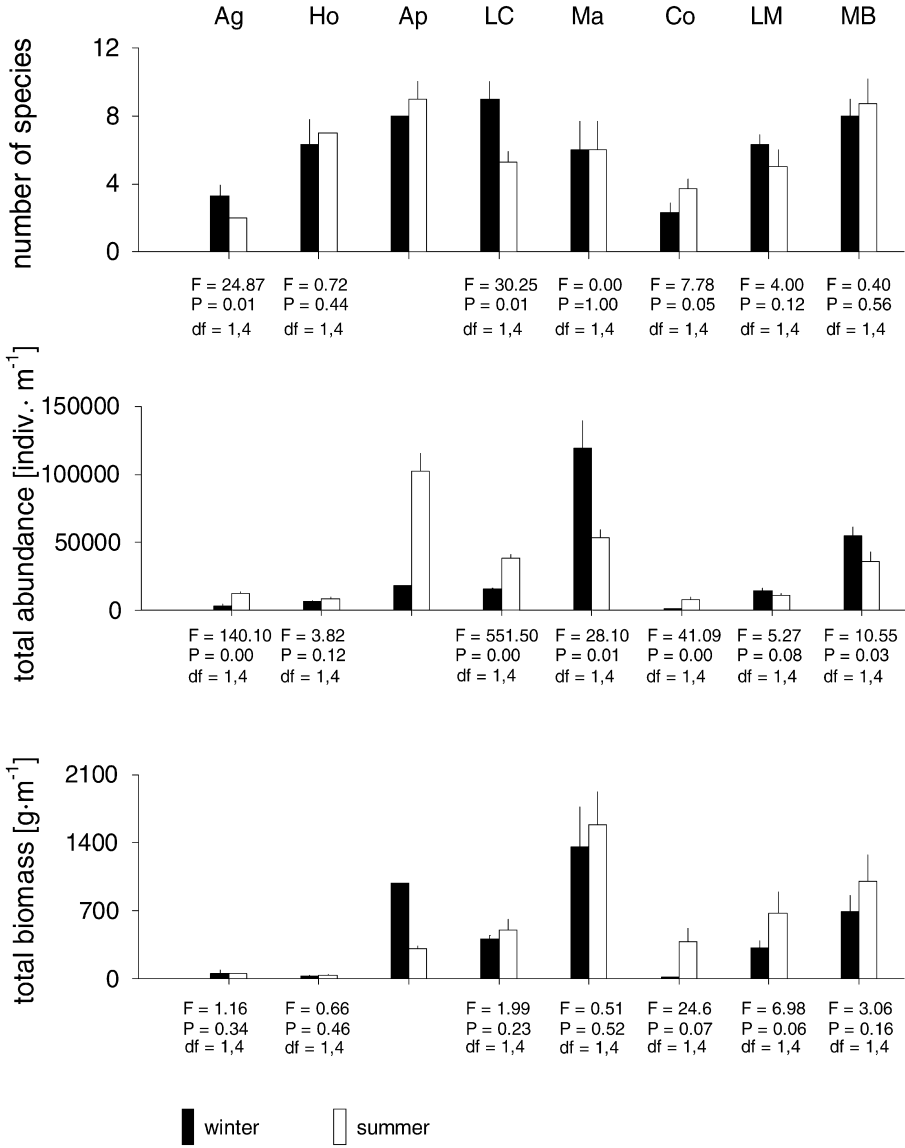


Fig. 5. Interseasonal comparisons of the number of species, abundance and biomass of the total macroinfauna. The columns represent means (+ 1 SD) with the exception of the winter sampling at Apollillado, when no replicates were collected (see Material and Methods). Values of F, P and df resulted from ANOVA. Letter codes for beaches as in Fig. 1.

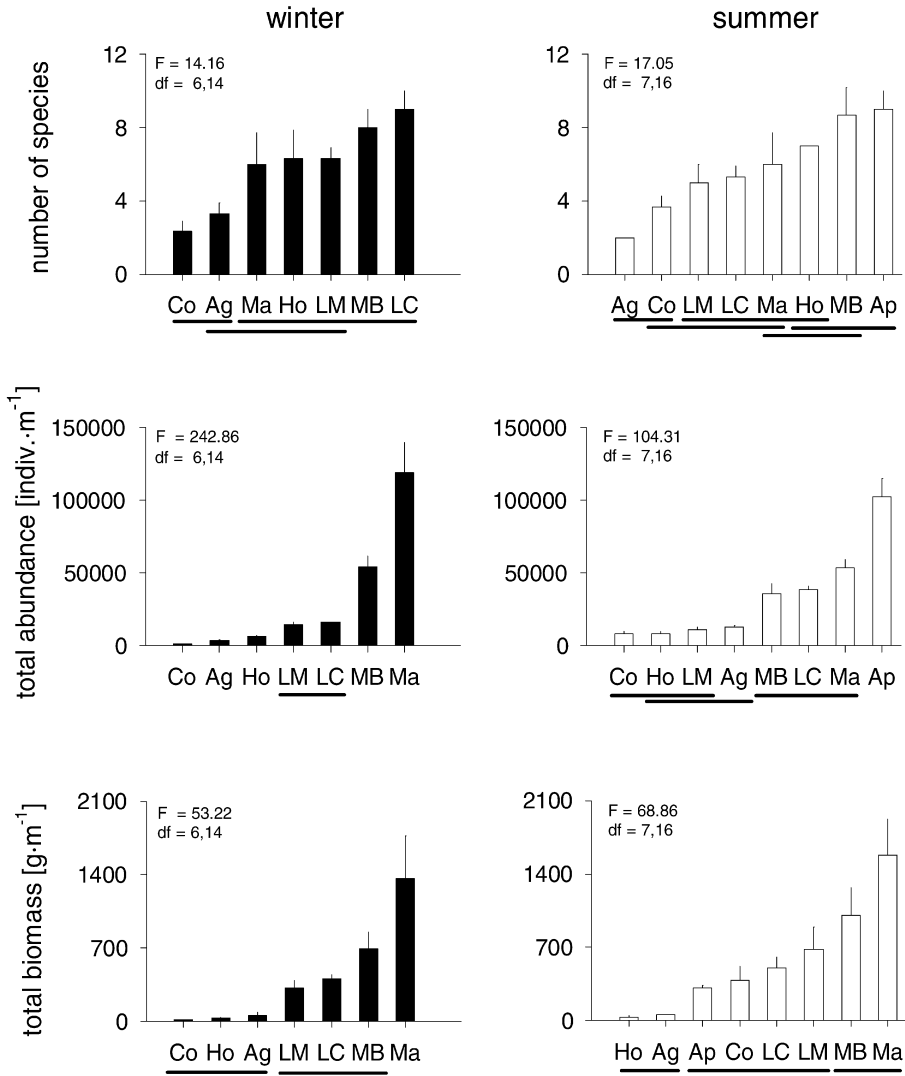


Fig. 6. Along-coast comparisons of number of species, abundance and biomass of the total macrofauna. The columns represent means (+ 1 SD). Values of F and df resulted from ANOVA; all P values were significant at a probability level of 0.001. Lines link means not significantly different (results of Tukey's HSD *a posteriori* test). Letter codes for beaches as in Fig. 1.

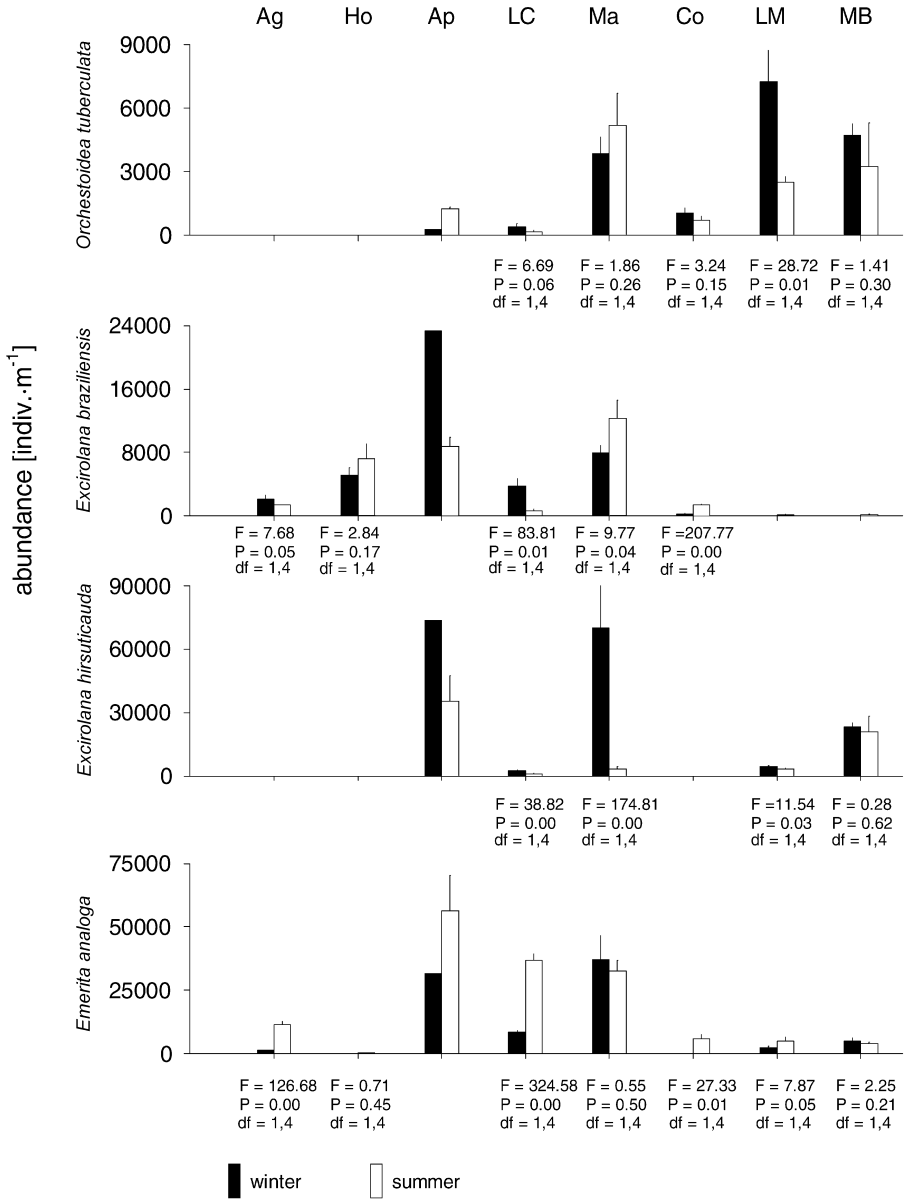


Fig. 7. Interseasonal comparisons of the abundance of the most common macroinfaunal species along the Chilean coast. The columns represent means (+ 1 SD) with the exception of the winter sampling at Apollillado, when no replicates were collected (see Material and Methods). No comparisons were carried out for *E. braziliensis* at La Misión (LM) and Mar Brava (MB) since this isopod was not collected at those beaches during the winter sampling. Values of F, P and df resulted from ANOVA. Letter codes for beaches as in Fig. 1.

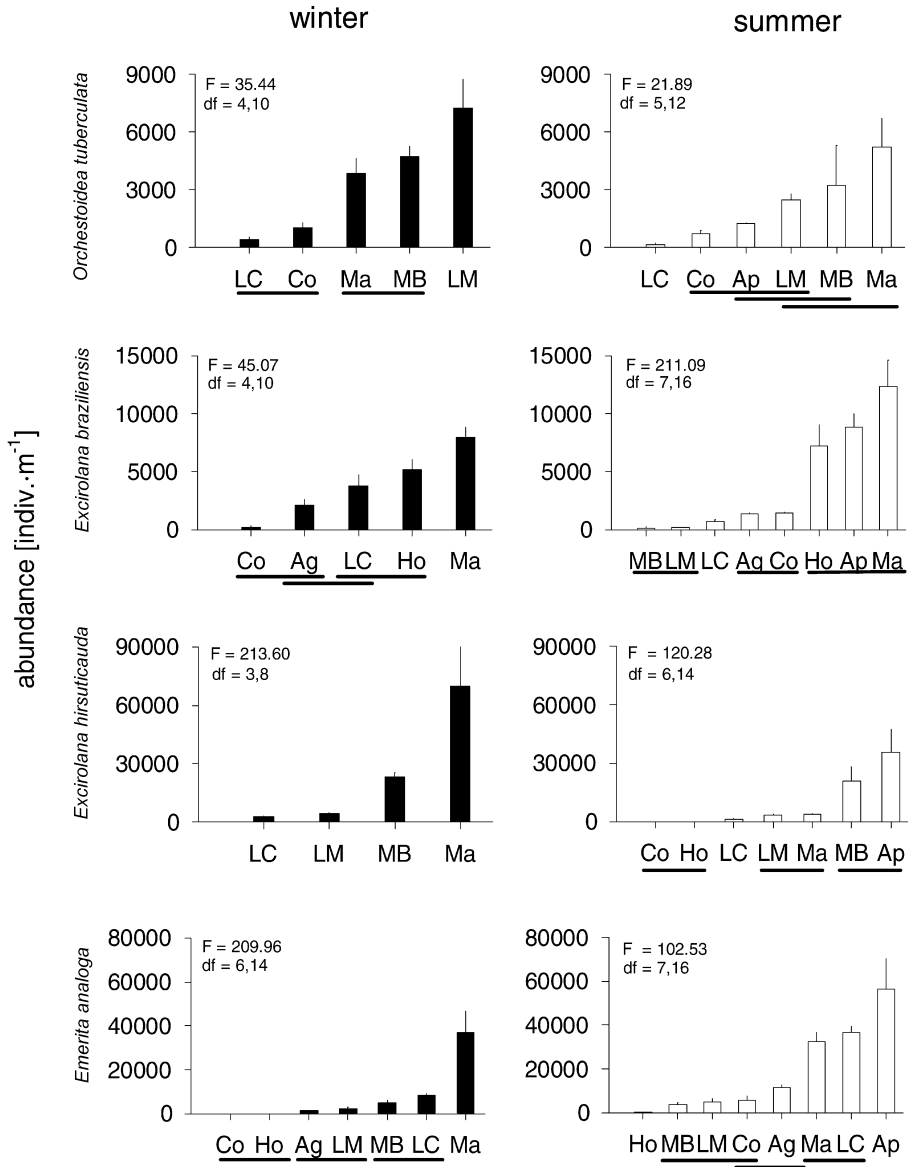


Fig. 8. Along-coast comparisons of the abundance of the most common macrofaunal species. The columns represent means (+ 1 SD). Values of F and df resulted from ANOVA; all P values were significant at a probability level of 0.001. Lines link means not significantly different (results of Tukey's HSD *a posteriori* test). Letter codes for beaches as in Fig. 1.

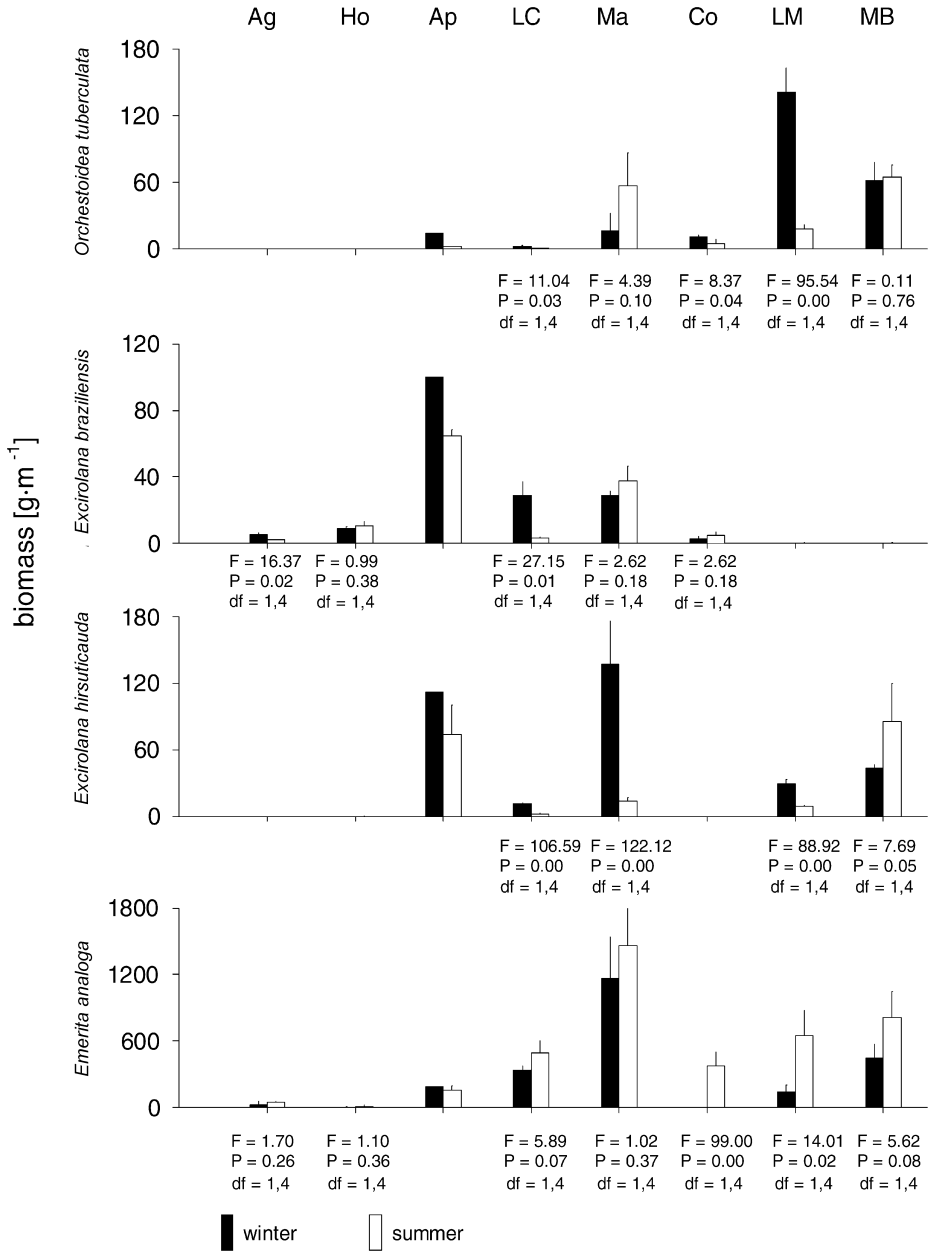


Fig. 9. Interseasonal comparisons of the biomass of the most common macroinfaunal species along the Chilean coast. The columns represent means (+ 1 SD) with the exception of the winter sampling at Apollillado, when no replicates were collected (see Material and Methods). No comparisons were carried out for *E. braziliensis* at La Misión (LM) and Mar Brava (MB) since this isopod was not collected at those beaches during the winter sampling. Values of F, P and df resulted from ANOVA. Letter codes for beaches as in Fig. 1.

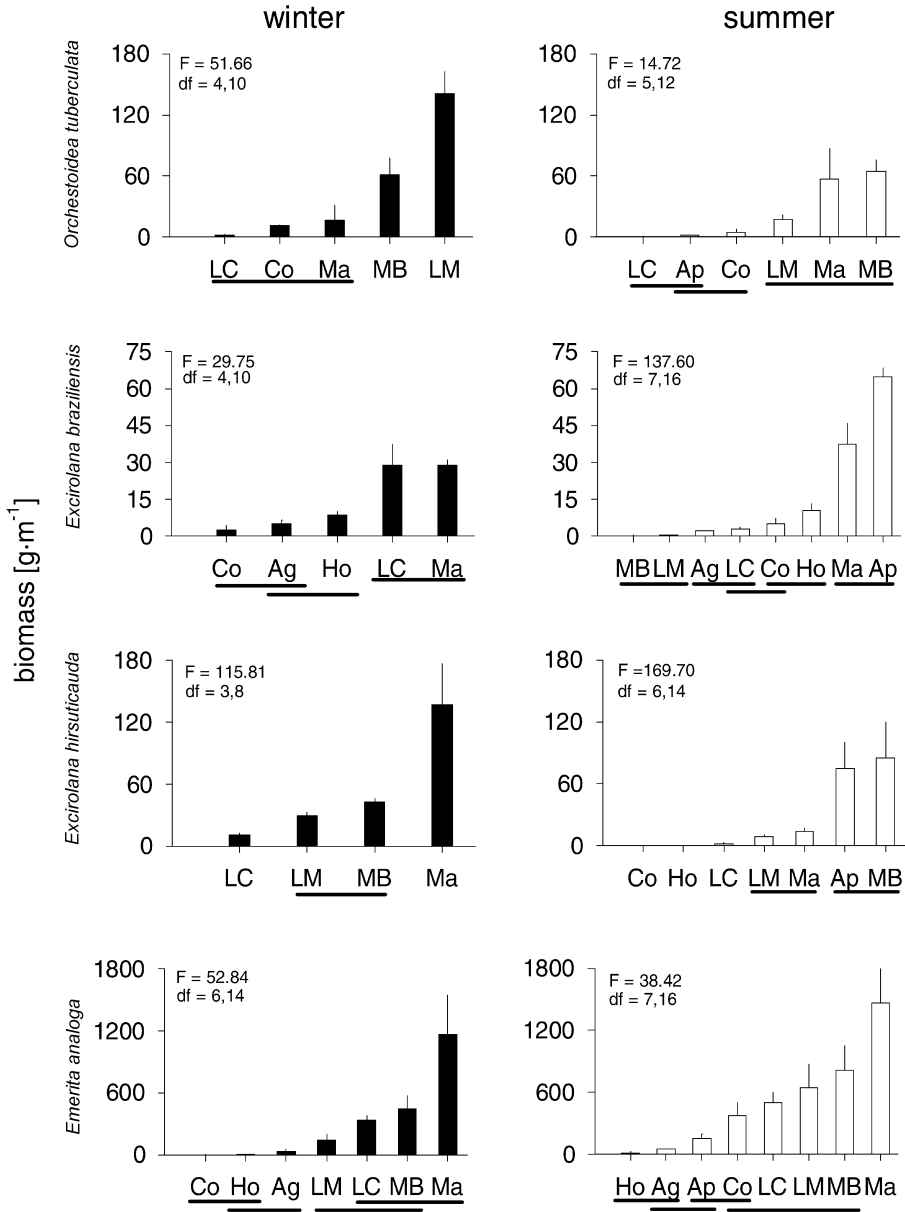


Fig. 10. Along-coast comparisons of the biomass of the most common macroinfaunal species. The columns represent means (+ 1 SD). Values of F and df resulted from ANOVA; all P values were significant at a probability level of 0.001. Lines link means not significantly different (results of Tukey's HSD *a posteriori* test). Letter codes for beaches as in Fig. 1.

sis Richardson and the anomuran decapod *Emerita analoga* (Stimpson) were the most widely distributed species (*i. e.* both of them occurred at virtually all samplings).

During the winter sampling, the highest number of species occurred at the intermediate beaches of Apolillado (mean = 8), Las Cruces (mean = 9) and Mar Brava (mean = 8). Similarly, during the summer the highest species richness was found at Apolillado (mean = 9) and Mar Brava (mean = 9) (Fig. 5). The number of species collected at El Aguila and Las Cruces were significantly higher during winter, while the species richness at Cobquecura was significantly higher during summer (Fig. 5). Apolillado, Matanzas and Mar Brava had the highest macroinfaunal abundances (with values as high as 102 000 – 119 000 indiv. · m⁻¹). Significant seasonal differences were found at five sites: El Aguila, Las Cruces and Cobquecura with higher abundances during summer, and Matanzas and Mar Brava the other way around (Fig. 5). The highest biomass of the total macroinfauna occurred at Apolillado, Matanzas and Mar Brava (up to 1300–1580 g · m⁻¹); no significant seasonal differences were found at any beach (Fig. 5).

Intersite comparisons show no clear-cut differences among beaches in species richness (Fig. 6). The abundance of the total macroinfauna was significantly higher at Matanzas (intermediate) and Mar Brava (dissipative) versus the other ones during the winter sampling. On the other hand, during the summer the total abundance of the macroinfauna was significantly higher at the intermediate beach of Apolillado (Fig. 6). Biomass tended to be higher at Mar Brava and Matanzas during both samplings (Fig. 6).

During both samplings, *Orchestoidea tuberculata* Nicolet, *Excirrolana braziliensis*, *Excirrolana hirsuticauda* Menzies and *Emerita analoga* had the highest abundances at most beaches, but in Mar Brava the polychaete *Euzonus heterocirrus* Rozbaczylo & Zamorano also occurred in high abundances. At most beaches where it was present, *O. tuberculata* had greater abundances during the winter; however, significant differences were found only at La Misión (Fig. 7). *E. braziliensis* showed quite a variable trend: in some beaches the abundances were significantly higher during summer, in other sites during winter (Fig. 7). *E. hirsuticauda* abundances were higher during the winter period at most beaches, while those of *E. analoga* were usually higher during summer (Fig. 7). Intersite comparisons show that during the winter period these four species had higher abundances at intermediate beaches: *O. tuberculata* at La Misión, *E. braziliensis*, *E. hirsuticauda* and *E. analoga* at Matanzas (Fig. 8). This was similar to the findings during the summer samplings for *E. braziliensis* and *E. analoga*, *i. e.* higher abundances at intermediate sites.

The highest biomass of *O. tuberculata* was found at La Misión during winter (Fig. 9). *E. braziliensis* had the highest biomass at Apolillado during winter, while the biomass of *E. hirsuticauda* peaked at this beach and Matanzas (Fig. 9). *E. analoga* also had the highest biomass at the latter beach during both sampling periods. In general, *O. tuberculata* and the isopods had significantly higher biomass in winter, *E. analoga* in summer (Fig. 9). Intersite comparisons of biomass show that during the winter the biomass of *O. tuberculata* and the isopods was significantly higher at intermediate beaches (La Misión, Las Cruces, Matanzas); a similar but not significant trend was observed for *E. analoga*. That trend was different during the summer because the amphipod and *E. hirsuticauda* had similar biomass at intermediate and dissipative sites, while *E. braziliensis* and *E. analoga* peaked significantly at intermediate sites (Fig. 10).

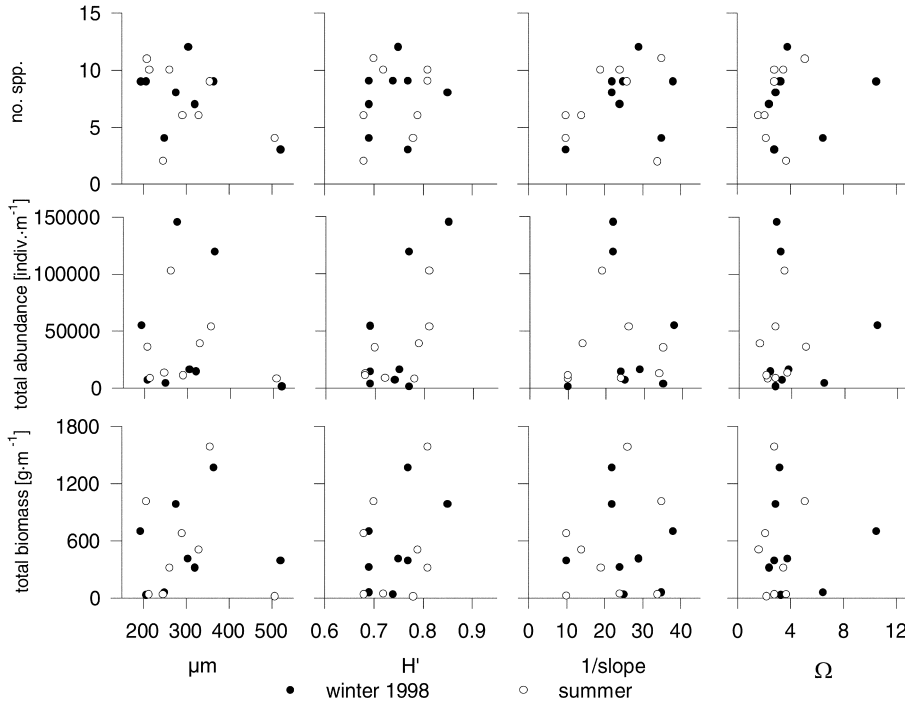


Fig. 11. Relationships between species richness, abundance and biomass of the total macroinfauna versus mean grain size (μm), sediment diversity (H'), beach face slope ($1/\text{slope}$) and beach type (defined by $\Omega = \text{Dean's parameter}$) for the winter and summer sampling.

4. Community structure of the macroinfauna versus beach characteristics

Figure 11 shows quite a dispersion of values of species richness, abundance and biomass of the macroinfauna in relation to beach characteristics. Thus, no significant relationships ($P > 0.05$) were found when species richness, abundance and biomass of the whole macroinfauna were regressed against mean grain size of sands, sediment diversity, beach face slope and Dean's parameter, either during the winter or summer samplings.

Discussion

The sandy beaches analyzed in this study included sites with different morphodynamic characteristics, *i. e.* from the dissipative beach stages at El Aguila and Mar Brava during winter 1998, to the low intermediate stages found at most of the other beaches and sampling days. Comparative analyses of physical variability during both seasons showed that sediment characteristics varied significantly in some beaches. Also, wave heights showed quite a seasonal variability; in most cases higher waves occurred during winter,

which resulted in high variability in morphodynamic beach stages as defined by Dean's parameter.

Regression analyses among species richness, abundance and biomass of the whole macroinfauna versus sediment characteristics, beach face slopes and morphodynamic beach states showed no significant relationships. Thus, macroinfaunal community characteristics did not increase linearly from lower intermediate to higher intermediate or dissipative beach stages as shown in other coasts (McLachlan *et al.*, 1993, 1996, 1998). Sampling sites with intermediate values of Dean's parameter (low intermediate beach states) usually had the highest abundance and biomass values. Consequently, the abundances of the total macroinfauna were higher than the worldwide trend predicted by McLachlan *et al.* (1993, 1996). The earlier assertion allows us to suggest that morphodynamic beach stage is not always a straight predictor of the community structure of the sandy beach macroinfauna. This is similar to the conclusions of Jaramillo *et al.* (2000) for sandy beaches of Isla de Chiloé (southern Chile) and that of Dugan & Hubbard (1996), who found that the abundances of just one species (*Emerita analoga*) in sandy beaches of California was higher than the worldwide trend in population abundances predicted by McLachlan *et al.* (1993).

Table 4 shows the species richness and total abundance of the macroinfauna at beaches located in other world regions and sampled in a similar way to that studied here. The macroinfauna of exposed sandy beaches of Chile is generally less diverse than that of the west coast of the USA, South Africa, Australia and Oman. On the other hand, population abundances of the Chilean sandy beach macroinfauna were generally higher than those of the compared coasts (Table 4). The high abundance of the Chilean macroinfauna was, in most cases, the result of the high abundances of the anomuran crab *Emerita analoga*. Along the Chilean coast, the abundance of this species is usually higher than 50 % at every type of beach (Jaramillo & Lastra, 2001), a finding similar to that reported by Dugan *et al.* (2000) for sandy beaches of California.

Table 4. Range in the number of species and abundance of the total macroinfauna at sandy beaches of Chile, USA, South Africa, Australia and Oman.

	species	indiv · m ⁻¹
this study	3–9	1280–119 053
coast of Oregon, USA (McLachlan, 1990)	16–21	49 940–288 998
mainland coast of California, USA * (Dugan <i>et al.</i> , 2000)	37	88 500
coast of South Africa (McLachlan, 1990)	1–13	3–6569
tropical coast of Australia (McLachlan <i>et al.</i> , 1996)	15–30	8693–32 857
temperate coast of Australia (McLachlan <i>et al.</i> , 1996)	12	4752–5875
coast of Oman (McLachlan <i>et al.</i> , 1998)	20–25	3216–73 326

* = only maximum values are reported since no ranges were given by Dugan *et al.* (2000).

Note that intermediate beaches (Apolillado and Matanzas) with the highest macroinfaunal abundance and biomass are at or close to coastal regions with persistent upwelling (cf. Fonseca & Farías, 1987). The high values here primarily reflected the high abundances and biomass of the anomuran crab *Emerita analoga*. Thus, it could be argued that proximity to such persistent upwelling areas results in higher primary production and, consequently, also in higher secondary production of suspension feeders such as *E. analoga*. If this is true, it is puzzling why beaches located right at the persistent upwelling area of northern Chile (El Aguila and Hornitos) did not have high macroinfaunal abundance and biomass. Perhaps there is some covariation between proximity to persistent upwelling areas and morphodynamic beach states.

The analyses of species richness at the studied beaches showed no consistent pattern of seasonal variability: while the species number in some beaches decreased from winter to summer, in other beaches the opposite occurred. Seasonal changes in species richness were not followed by seasonal changes in macroinfaunal abundances or biomasses. This implies that those changes in number of taxa were primarily related to species that were not common or abundant. Indeed, at most beaches, the same species dominated in abundance and biomass during the winter and summer samplings. Similar patterns of species persistence over seasons have been shown before for sandy beaches of the Chilean coast (Jaramillo *et al.*, 1996, 1998), eastern USA (Crocker *et al.*, 1975), Uruguay (Brazeiro & Defeo, 1996), India (Ansell *et al.*, 1972) and South Africa (de Ruycck *et al.*, 1992).

Summary

This study shows that the community structure of the intertidal macroinfauna of Chilean sandy beaches located along a latitudinal gradient of about 3000 km does not change linearly with changes in beach morphodynamics. Highest abundances and biomass of the macroinfauna were found at intermediate beaches located near areas of persistent upwelling, suggesting that, apart from beach morphodynamics, bottom-up effects (upwelling waters enhancing primary productivity) are also important in the community structure of the sandy beach macroinfauna. Nonetheless, this is not always the case (*i. e.* El Aguila and Hornitos), contrasting with that conclusion. More detailed studies of the spatial variability of the sandy beach macroinfauna along the Chilean coast should convey a deeper insight into the factors determining community structure of that macroinfauna.

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References

- Ansell, A. D., D. S. McLusky, A. Stirling & A. Trevallion, 1972: The ecology of two sandy beaches in South West India. I. Seasonal changes in physical and chemical factors and in the macroinfauna. *Mar. Biol.*, **17**: 38–62.
- Brazeiro, A. & O. Defeo, 1996: Macroinfauna zonation in microtidal sandy beaches: is it possible to identify patterns in such variable environments? *Estuarine Coastal Shelf Sci.*, **21**: 587–599.
- Brower, J. E. & J. H. Zar, 1977: Field and laboratory methods for general ecology. Wm. C. Brown Company Publishers, Dubuque, Iowa (USA); 194 pp.
- Crocker, R. A., R. P. Hager & K. J. Scott, 1975: Macroinfauna of northern New England marine sand. II. Amphipod dominated intertidal communities. *Can. J. Zool.*, **53**: 42–51.
- Defeo, O., J. Gómez & D. Lercari, 2000: Testing the swash exclusion hypothesis in sandy beach populations: the mole crab *Emerita brasiliensis* in Uruguay. *Mar. Ecol. Prog. Ser.*, **212**: 159–170.
- Dugan, J. E. & D. M. Hubbard, 1996: Local variation in populations of the sand crab *Emerita analoga* on sandy beaches in southern California. *Rev. Chil. Hist. Nat.*, **69**: 579–588.
- Dugan, J. E., D. M. Hubbard, J. M. Engle, D. L. Martin, D. M. Richards, G. E. Davies, K. D. Lafferty & R. F. Ambrose, 2000: Macrofauna communities of exposed sandy beaches on the Southern California mainland and Channel Islands. Fifth California Islands Symposium, OCS Study, MMS 99–0038: 339–346.
- Emery, K. O., 1938: Rapid method of mechanical analysis of sands. *J. Sedim. Petrol.*, **8**: 105–111.
- Emery, K. O., 1961: A simple method of measuring beach profiles. *Limnol. Oceanogr.*, **6**: 90–93.
- Etter, R. J. & J. F. Grassle, 1992: Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature*, **360**: 576–578.
- Folk, R., 1980: Petrology of sedimentary rocks. Hemphill Publishing Co., Texas, USA; 182 pp.
- Fonseca, T. & M. Farías, 1987: Estudio del proceso de surgencia en la costa chilena, utilizando percepción remota. *Invest. Pesq. (Chile)*, **34**: 33–46.
- Gibbs, R. J., M. D. Mathews & D. A. Link, 1971: The relationship between sphere size and settling velocity. *J. Sedim. Petrol.*, **41**: 7–18.
- Gómez, J. & O. Defeo, 1999: Life history of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda) in sandy beaches with contrasting morphodynamics. *Mar. Ecol. Prog. Ser.*, **182**: 209–220.
- Jaramillo, E., 1987: Community ecology of Chilean sandy beaches. Ph.D. Thesis, University of New Hampshire, Durham, NH, USA; 216 pp.
- Jaramillo, E., F. Carrasco, P. Quijón, M. Pino & H. Contreras, 1998: Distribución y estructura comunitaria de la macroinfauna bentónica en la costa del norte de Chile. *Rev. Chil. Hist. Nat.*, **71**: 459–478.
- Jaramillo, E., C. Duarte & H. Contreras, 2000: Sandy beach macroinfauna from the coast of Ancud, Isla de Chiloé, southern Chile. *Rev. Chil. Hist. Nat.*, **73**: 771–786.
- Jaramillo, E. & M. Lastra, 2001: Suspension feeders on sandy beaches. In: K. Reise (Ed.), *Ecological comparisons of Sedimentary Shores*. Springer-Verlag, Heidelberg, *Ecological Studies* 151: 61–72.
- Jaramillo, E. & A. McLachlan, 1993: Community and population responses of the macroinfauna to physical factors over a range of exposed sandy beaches in south-central Chile. *Estuarine Coastal Shelf Sci.*, **37**: 615–624.
- Jaramillo, E., R. Stead, P. Quijón, H. Contreras & M. González, 1996: Temporal variability of the sand beach macroinfauna in south-central Chile. *Rev. Chil. Hist. Nat.*, **69**: 641–653.
- McLachlan, A., 1990: Dissipative beaches and macrofauna communities on exposed intertidal sands. *J. Coastal Res.* **6**: 57–71.
- McLachlan, A., M. Fisher, H. Al-Habsi, S. Al-Shukairi & A. Al-Habsi, 1998: Ecology of sandy beaches in Oman. *J. Coastal Conserv.*, **4**: 181–190.
- McLachlan, A. & E. Jaramillo, 1995: Zonation on sandy beaches. *Oceanogr. Mar. Biol. Annu. Rev.*, **33**: 305–335.
- McLachlan, A., E. Jaramillo, T. E. Donn & F. Wessels, 1993: Sandy beach macroinfauna communities and their control by the physical environment: a geographical comparison. *J. Coastal Res. (Special Issue)*, **15**: 27–38.
- McLachlan, A., A. de Ruyck & N. Hacking, 1996: Community structure on sandy beaches: patterns of richness and zonation in relation to tide range and latitude. *Rev. Chil. Hist. Nat.*, **69**: 451–467.
- Ruyck, A. de, T. E. Donn & A. McLachlan, 1992: Distribution of three cirrolanid isopods (Flabellifera: Cirrolanidae) on a South African sandy beach. *Cah. Biol. Mar.*, **33**: 147–168.
- Seward-Thompson, B. & J. Hails, 1973: An appraisal on the computation of statistical parameters in grain size analysis. *Sedimentology*, **11**: 83–98.
- Short, A. D. & L. D. Wright, 1983: Physical variability of sandy beaches. In: A. McLachlan & Th. Erasmus (Eds.), *Sandy beaches as ecosystems*. W. Junk, The Hague: 133–144.
- Sokal, R. R. & F. J. Rohlf, 1995: *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman, New York; 877 pp.