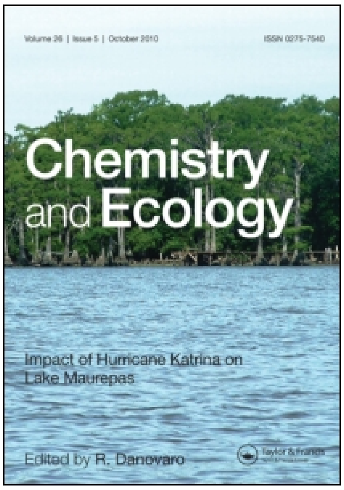

Chemistry and Ecology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713455114

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To cite this Article Harriague, Anabella Covazzi , Petrillo, Mario , Croce, Norberto Della , Panciroli, Hervè , Pusceddu, Antonio , Pelosi, Giulia , Danovaro, Roberto and Albertelli, Giancarlo(2008) 'Intertidal benthic communities of two Chilean coastal islands (Santa María and Mocha, Southeastern Pacific)', Chemistry and Ecology, 24: 1, 119 — 128

To link to this Article: DOI: 10.1080/02757540801965480
URL: http://dx.doi.org/10.1080/02757540801965480

Chemistry and Ecology
Vol. 24, No. S1, June 2008, 119–128

Intertidal benthic communities of two Chilean coastal islands (Santa María and Mocha, Southeastern Pacific)

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(*Received 15 July 2007; final version received 12 November 2007*)

Six macrotidal beaches located on two Chilean coastal islands (Santa María and Mocha, SE Pacific Ocean) were investigated in spring 2001 (29 October–3 November) to verify the role of the food supply (in terms of quantity and biochemical composition of the organic matter) on the abundance and diversity of the macro- and meiobenthic communities inhabiting the beaches. Samples of sediment were collected from the intertidal zone of the three beaches of each island investigated. The total organic matter content of the sediment did not differ between the islands, whereas the phytopigment and protein contents were significantly higher on Mocha (2.3 ± 0.9 and $75 \pm 21\,\mu g\ g^{-1}$, mean values of the three beaches ± SE, respectively) than on Santa María (0.5 ± 0.2 and $50 \pm 16\,\mu g\ g^{-1}$, mean values of the three beaches ± SE). The macro- and meiofaunal assemblages displayed the highest abundances on Mocha (821 ± 223 and 561 ± 194 ind. $10\,cm^{-2}$, respectively). The abundance of both assemblages was correlated with the quality of the food supply, and significant correlations were observed with the phytopigment content (Spearman-rank $R = 0.645$ $p < 0.01$ and $R = 0.934$ $p < 0.001$ for the macro- and meiofauna, respectively). The results of the present study suggest that food availability may play a key role in structuring benthic communities of the oceanic beaches of Chilean coastal islands. A single observation is not enough to fully understand the real mechanisms that shape the beach communities, however, the snapshot image we collected during this study suggests that the role of food availability in shaping benthic beach communities may be as important as that played by the hydrodynamic conditions.

Keywords: macrofauna; meiofauna; organic matter; beach; Chile; Pacific Ocean

1. Introduction

Oceanic macrotidal beaches exposed to continuous wave action have the most extreme hydrodynamic conditions of all beach communities, but, so far, investigations carried out synoptically on both the macro- and meiobenthic communities of these systems are relatively scant [1]. Intertidal benthic assemblages are subject to a wide array of environmental forcings, which include fluctuations in the major physical-chemical variables (e.g. humidity, temperature, sediment grain size), hydrodynamism, the availability of food resources and top-down control mechanisms operated by predators [2–6].

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ISSN 0275-7540 print/ISSN 1029-0370 online

DOI: 10.1080/02757540801965480
http://www.informaworld.com

Several global studies, using data from beaches around the world, have reported that physical factors such as sediment grain size, beach face slope and tides may have a role in controlling the abundance and community structure of macrobenthic intertidal assemblages. Abundance, biomass and species richness decrease when the reflectiveness of the beach (short surf zone, coarse sand and steep slope) increases [7,8].

The main results of the studies carried out on the ecology of beach meiofauna [3,5,9,10], indicate that meiofaunal abundance and biomass and the number of taxa increase exponentially with the increase in the degree of beach exposure (i.e. the exposure of the beach to wave action) at least up to certain threshold levels [11–13]). This relationship appears to be the opposite of that of the macrofauna, which typically displays decreasing biomass and diversity with increasing levels of hydrodynamic disturbance [14–16], which in turn is related to the degree of beach exposure. The discrepancy between the responses of the two benthic components to different hydrodynamic conditions suggests that macro- and meiofauna distributions in these environments are differentially influenced by physical processes associated with wave action [17]. These studies, however, did not take into account other factors – such as the availability of resources – possibly controlling the distribution of macro- and meiofauna in macrotidal beaches.

We investigated the abundance and taxa richness of macro- and meiobenthos on 6 beaches located on two coastal islands off the southern coast of Chile (Santa Maria and Mocha). In order to assess the relationships between the faunal abundance and community structure and the food resources available we also measured the principal components of the sedimentary organic matter and the phytopigment content of the sediment. The aim of this work was to ascertain the role of the food availability in structuring the macro- and meiofaunal beach communities.

2. Material and methods

2.1. *Study area and sampling*

Sediment sampling was carried out at six beaches located on two coastal islands (Santa María and Mocha) close to the Chilean coast (Southeastern Pacific; Figure 1) in spring 2001. Three beaches were investigated on each island: Dolores, Tres Cruces and Puerto Sur on Santa María and Las Docas, Fragata and Faro Viejo on Mocha. The principal environmental features of the beaches are reported in Table 1. All of the six beaches are macrotidal (maximum tidal elevation >1.5 m) and characterised by very fine sands and gentle slopes, with the exception of Fragata, which was characterised by gravely (shell-derived) sand and a steep slope.

All of the beaches on Santa Maria and Las Docas on Mocha were characterised by the presence of the crustacean decapod *Emerita analoga* (Stimpson, 1857). This decapod typically inhabits sandy beaches where it burrows just under the sediment surface, forming aggregated patches of several square metres in extent and with a great concentration of individuals. This crustacean lives on the west coast of America, apart from tropical zones with temperatures over 20 °C [18]. Their preferential habitat is the low-tide level of wave-exposed oceanic beaches, where the wash of wave and surf is extremely active. In southern-central Chile *E. analoga* is a common inhabitant of intermediate and dissipative sandy beaches [18,19].

For the analysis of the macrofauna (including *E. analoga*, where present) 5 replicate samples of sediment were collected with manual corers ($\Phi = 5.4$ cm) at three tidal levels: high, middle and low. The sediment was sieved using a 0.5 mm mesh net and preserved in a 10%-buffered formalin-seawater solution.

For the analysis of the meiofauna 3 replicate sediment samples were collected from the three tidal levels of the intertidal zone, using manual corers ($\Phi = 3.7$ cm) inserted into the sediment to a depth of 15 cm, and preserved in 4%-buffered formalin-seawater.

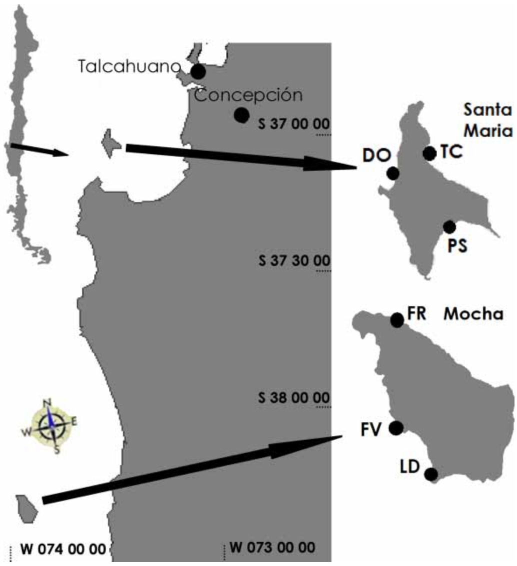

Figure 1. Study site. DO: Dolores beach, TC: Tres Cuevas beach, PS: Puerto Sur beach, LD: Las Docas beach, FR: Fragata beach and FV: Faro Viejo beach.

Table 1. Environmental characteristics (exposure, sediment texture and slope) of the six beaches investigated.

Island	Beach	Exposure features	Sediment texture	Slope
Santa María	Dolores	sheltered	fine sand	flat
	Tres Cuevas	exposed	fine sand	flat
	Puerto Sur	sheltered	fine sand	flat
Mocha	Las Docas	sheltered	fine sand	flat
	Fragata	exposed	gravel	steep
	Faro Viejo	slighty exposed	fine sand	flat

Additional triplicate sediment samples were collected using manual corers ($\Phi = 3.7$ cm) for the determination of the total organic matter (TOM), protein (PRT) and total phytopigment (TP) sedimentary content. The top 2 cm of each core was stored in Petri dishes at −20 °C until analysis.

2.2. *Quantity and quality of sedimentary organic matter*

The TOM content was determined gravimetrically after loss on ignition [20]. The chlorophyll-a and phaeopigment analyses were carried out according to Lorenzen and Jeffrey [21]. The pigments were extracted (12 h at 4 °C in the dark) from triplicate sediment samples (about 1 g each) using 3–5 ml of 90% acetone as extractant. The extracts were analysed fluorometrically to estimate the chlorophyll-a, and, after acidification with 200 μl 0.1 N HCl, to estimate the phaeopigments. The concentrations are reported as $\mu g\, g\, DW^{-1}$. The TP content was defined as the sum of the chlorophyll-a and phaeopigment contents.

The PRT sediment content was determined spectrophotometrically and the contents expressed as bovine serum albumin equivalents [22]. Blanks were obtained using pre-combusted sediments (450 °C for 4 h). All analyses were performed in 3 replicates of about 1 g of sediment for each sediment sample.

2.3. *Macro- and meiofaunal abundance and taxa richness*

For the analysis of the macrobenthos, the sediment samples were sorted under a stereomicroscope and the specimens identified at the species level whenever possible. Since the abundance of the macrofauna on all of the six beaches did not show a statistical difference between the three tidal levels investigated (data not shown), we used the mean values ± standard errors. The individuals of *E. analoga* were counted and separated by sex. The wet weight and the carapace length of each specimen were also determined.

The meiobenthos was extracted from the sediment using the decantation technique and sieved through 0.5 mm and 38 μm mesh sieves [23]. All the animals were counted and classified per taxon under a stereomicroscope after staining with Rose Bengal ($0.5\,g \cdot l^{-1}$).

2.4. *Statistical analyses*

To test for the relationships between all of the investigated variables, a Spearman-rank correlation analysis was performed. In addition, a two-way analysis of variance (ANOVA) was performed on the entire data set to assess differences between beaches and between islands. When significant differences were observed a Neumann-Kuels (N-K) test was also performed to quantify the observed differences.

The Shannon-Wiener diversity (H′, log base 2) of the macrofauna was calculated using the PRIMER 6β programme package (Plymouth Marine Laboratory).

The scaling of the meio- and macrofauna assemblages was carried out using Multidimensional Scaling (on fourth-root transformed abundance data), followed by a similarity percentage analysis (SIMPER) to assess the species contribution to the observed dissimilarity between beaches and between islands. In order to identify the main environmental factors controlling the distribution of the macro- and meiofaunal assemblages a Principal Component Analysis (PCA) was also performed on the normalised data of the total organic matter and the protein and total phytopigment contents using the PRIMER 6β programme package (Plymouth Marine Laboratory).

3. Results and discussion

3.1. *Quantity and quality of food resources*

The six beaches investigated were characterised by TOM contents lower than those reported for exposed beaches of the Ligurian Sea [3,5] and by only small differences in the quantity of food available. The TOM content of the sediments of the six beaches investigated was higher on Fragata (Mocha) and Tres Cuevas (Santa María) than on all other beaches (N-K Test, $p < 0.05$; Figure 2). Either the TP or PRT contents of the beaches were higher on Mocha (2.3 ± 0.9 and $75 \pm 21\,\mu g\,g^{-1}$, mean values of the three beaches ± SE, respectively) than on Santa María (0.5 ± 0.2 and $50 \pm 16\,\mu g\,g^{-1}$, mean values of the three beaches ± SE). These values were between those reported for exposed Ligurian beaches [5,24] and those reported for the exposed beaches of the northwestern coast of Spain [25].

The PCA analysis applied to the food resources data showed that the autotrophic components together (chlorophyll-a and phaeopigments) explained more than 70% of the difference in organic loads between the six different beaches (PC1). Another 22% (PC2) of the difference was explained by the protein content in the sediment (Figure 3).

The ANOVA applied to the TOM content did not reveal significant differences between the two islands, but rather highlighted significant differences between beaches on the same island. The total organic matter, chlorophyll-a and protein sediment contents of Santa María were significantly

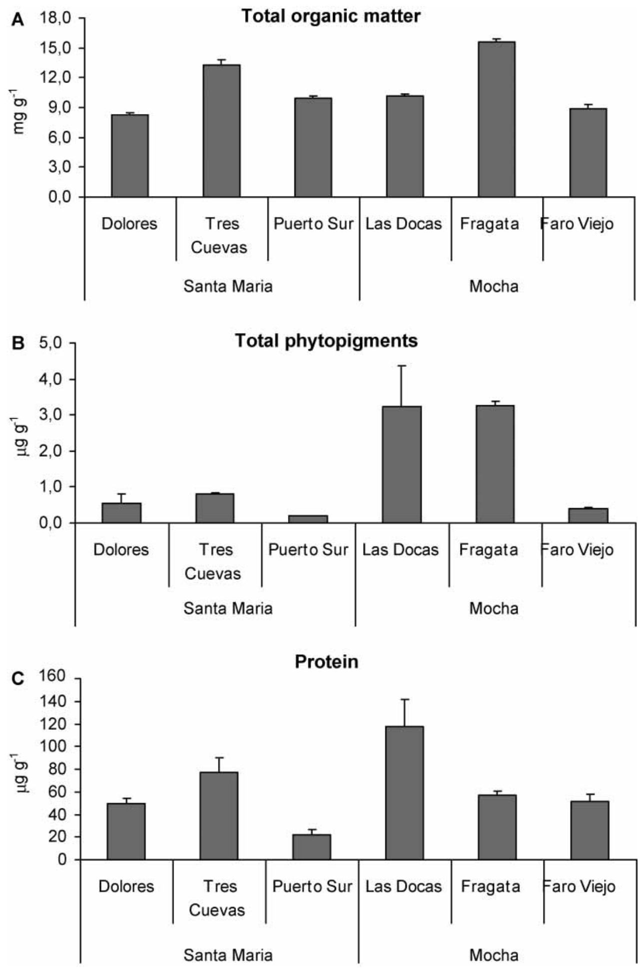

Figure 2. Organic matter content of the sediments of the six beaches of the Chilean coastal islands expressed as mean values plus standard error. (A) total organic matter content (mg g^{-1}); (B) total phytopigment content ($\mu g\ g^{-1}$); (C) protein content ($\mu g\ g^{-1}$).

higher on Tres Cuevas than on the other two beaches (N-K test, $p < 0.05$). The differences in the organic matter content between the three beaches of Santa María can be explained by the presence of huge inputs of organic material transported from the sea on Tres Cuevas. During this study, in fact, a strong nutrient upwelling event was observed in the coastal area facing Tres Cuevas and this was accompanied by the accumulation of huge swarms of krill, which attracted hundreds of seagulls.

The highest total organic matter content on Mocha was found on Fragata and the lowest on Faro Viejo (N-K test, $p < 0.05$). The phytopigment content was lower on Faro Viejo than on the other two beaches (N-K test, $p < 0.05$), whereas the highest protein content was observed on Las Docas (N-K test, $p < 0.05$). The three beaches investigated on Mocha, thus, displayed large differences in their total organic matter, protein and phytopigment contents, but these differences were apparently not coupled with the physico-chemical differences between the three beaches (the highest organic load was observed on the beach with the coarsest sediment). On the other hand, the values of the protein to TOM and chlorophyll-a to TOM ratios (Figure 4), used here as descriptors of food quality, on Las Docas, the most sheltered of the Mocha beaches, were significantly

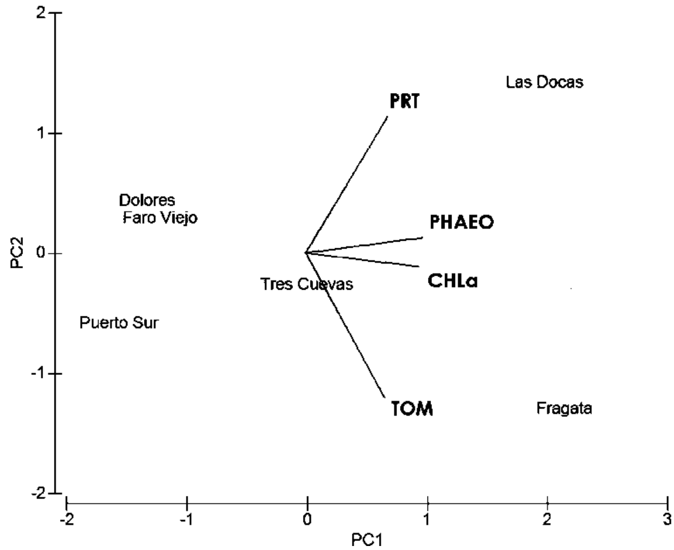

Figure 3. PCA analysis performed on the normalised data of the total organic matter content (TOM), chlorophyll-a content (CHL-a), phaeopigment content (PHAEO) and protein content (PRT).

higher than on all the other beaches. By decreasing the flushing action of tidal waves entering the beach with low energy, the sheltered conditions of Las Docas promoted the accumulation of labile organic compounds (i.e. proteins), suggesting that sheltered beaches might provide more available substrates for heterotrophic benthos – likely because of the reduced sediment reworking mediated by wave action.

3.2. *Macrofaunal and meiofaunal abundance and diversity*

The ANOVA revealed that the macrofaunal abundance on the Santa María beaches was significantly lower than that on Mocha ($p < 0.05$), and that the three beaches of each island did not display any significant differences (Figure 5). Whilst macrofauna abundance was not correlated with the total organic matter content, a significant relationship was found between the macrofaunal abundance and the phytopigment and protein contents (Spearman-rank R = 0.645 and 0.669, respectively; $p < 0.01$ for both). This result indicates that, on these beaches, the quality of organic matter rather than the absolute quantity was a major factor controlling macrobenthos abundance. Similar results were reported for exposed beaches in the Ligurian Sea [5,26].

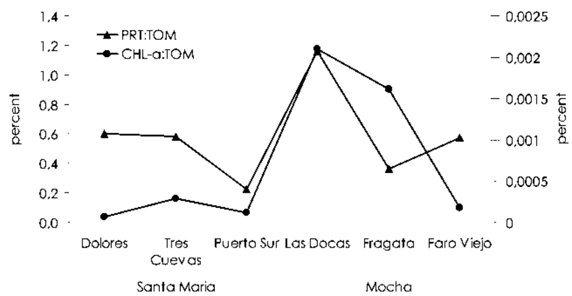

Figure 4. Percentage values of chlorophyll-a (CHL-a):total organic matter (TOM) and protein (PRT):total organic matter (TOM) ratios of the six beaches investigated.

As expected for a transitional system, macrofaunal diversity was extremely low at all of the beaches. The Santa María beaches, very similar to each other, displayed lower Shannon diversity (0.44 ± 0.06 on average of the three beaches $\pm$ SE) than the Mocha beaches (0.87 ± 0.21 on average for the three beaches $\pm$ SE). This pattern of macrobenthos diversity is consistent with the differences in the availability of labile organic compounds (e.g. TP and PRT) and indicates that even on oceanic beaches the availability of food, together with hydrodynamism, is a key factor controlling macrobenthos distribution, and, in particular, the number of taxa and the species diversity, which, indeed, were significantly correlated to the phytopigment content (Spearman-rank $R = 0.650$ $p < 0.01$ and 0.460 $p < 0.05$, respectively) [5,26,27].

The Multidimensional scaling (Figure 6) highlighted the presence of strong dissimilarities in the macrofauna community structures between the beaches of the same Island (SIMPER: on average 67% dissimilarity between the beaches on Santa María, and 89% dissimilarity between the beaches on Mocha). Wide differences were also revealed between the two islands (SIMPER: 96%). The SIMPER analysis also revealed that the major contributor (22%) to the differences between the islands was the presence of the decapod *Emerita analoga*, whose abundance was significantly higher on Santa María (6–299 specimens) than on Mocha (132 specimens, all on Las Docas). *E. analoga* is a suspension feeder decapod that catches suspended particles transported by tidal waves and, in this way, intercepts the particulate organic matter that would otherwise enter the beach sediments from the sea [28]. Osorio et al. [29] reported that (resuspended) diatoms may represent a major fraction of the diet of this decapod. This hypothesis is corroborated by the fact that the lowest organic matter loads in the sediment were observed on those beaches hosting this decapod and, particularly, on those beaches where the mean size of the sampled individuals was the highest (i.e. on Dolores, Santa María Island; Figure 7).

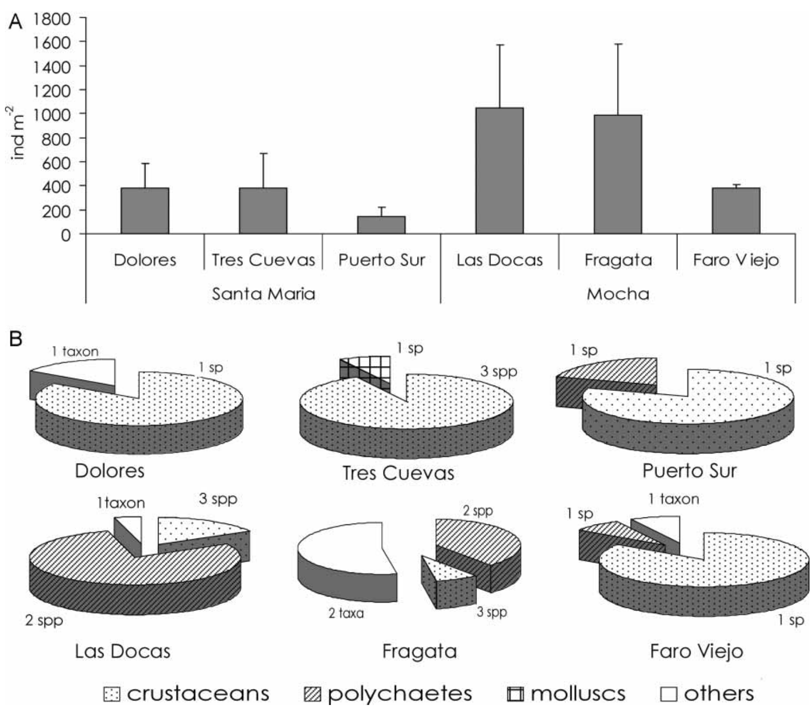

Figure 5. (A) Average macrofaunal densities plus standard error, (B) macrofaunal community composition of the beaches of Santa María and Mocha Islands.

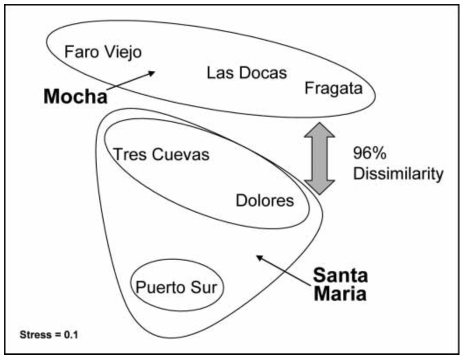

Figure 6. MDS analysis performed on the fourth-root transformed data of the macrobenthos density.

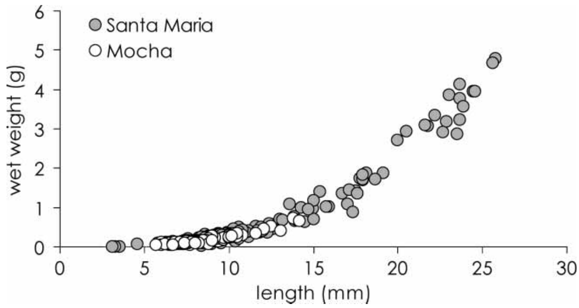

Figure 7. Scatter plots of the relationships between the wet weight (g) and length (mm) of the specimens of *Emerita analoga* of the beaches of Santa María and Mocha Islands.

The abundance and the number of taxa of meiofauna had patterns very similar to those exhibited by the macrofauna (Figure 8). In fact, while the differences between beaches on the same Island were relatively limited, the differences between the two islands followed the availability and quality of the food resources, with abundance and taxa richness values significantly higher on Mocha Island than on Santa María (ANOVA, $p < 0.05$ for both variables). Similarly to that of the macrofauna, the meiofauna abundance was significantly correlated to the phytopigment content (Spearman-rank $R = 0.934$ $p < 0.001$). The importance of the food availability in structuring meiofaunal assemblage was previously observed on the exposed beaches of the Mediterranean and Baltic Seas [5,30]. The similar patterns displayed by the macro- and meiofauna suggest that the biotic relationships between these two benthic compartments (namely competition and/or predation) had only a minor role in controlling their community structures. Most likely, the very limited food availability led to the concurrent development of poor communities of both macro- and meiobenthos and kept the competition levels between the two communities below their respective carrying capacities. Previous studies, indeed, reported that on oligotrophic beaches (i.e. characterised by limiting food availability) the competition between macro- and meiofauna for food resources is more evident than in more eutrophic systems [5].

Overall, only four meiofaunal taxa were present on all of the investigated beaches (Nematoda, Copepoda, Polychaeta and Gastrotricha), but the community structures were completely different between the islands. In fact, while the meiofaunal communities of the beaches of Santa María were dominated by copepods (on average $47 \pm 14\%$ for the three beaches $\pm$ SE), those on Mocha were dominated by nematodes (on average $41 \pm 27\%$ for the three beaches $\pm$ SE). In addition, the meiofaunal community on Fragata (Mocha) displayed a completely different taxa composition,

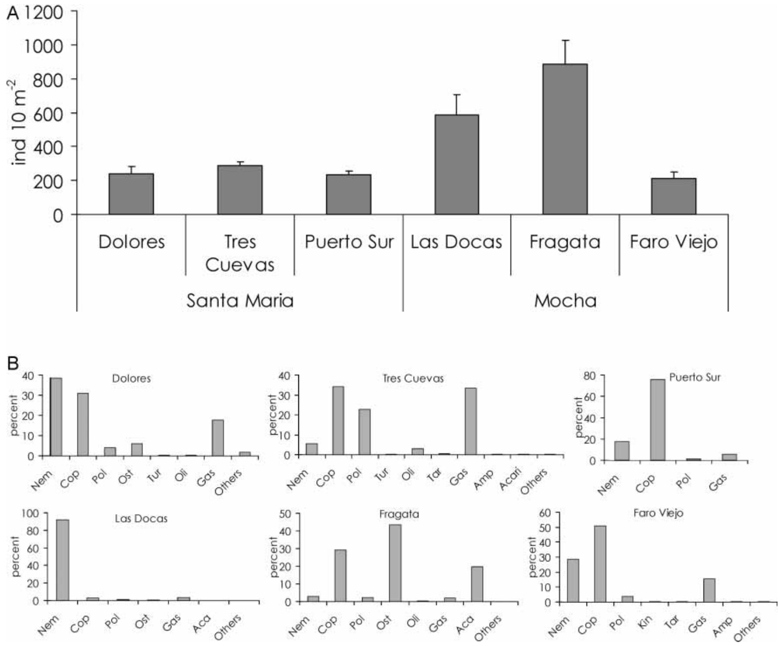

Figure 8. (A) Average meiofaunal densities plus standard error, (B) meiofaunal community composition of the beaches of Santa María and Mocha islands.

being characterised by the dominance of Ostracoda (42%), followed by Copepoda (29%) and Acaria (20%).

Overall, our results indicate that food availability may play a key role in structuring the benthic communities of the oceanic beaches of the southern coast of Chile. Even if a single observation is not enough to fully understand the real mechanisms that shape the beaches communities, the snapshot image we obtained during this study suggests that the role of food availability may be as important in shaping benthic beach communities as that played by hydrodynamic conditions.

Acknowledgements

We are grateful to the Centro EULA in Concepciòn for its help in the organisation of the expedition to Santa María and Mocha Islands and to S. Bava, F.M. Perrone, S. Fraschetti and A. Terlizzi for sampling.

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