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# COMMUNITY ECOLOGY OF CHILEAN SANDY BEACHES

EDUARDO JARAMILLO  
*University of New Hampshire, Durham*

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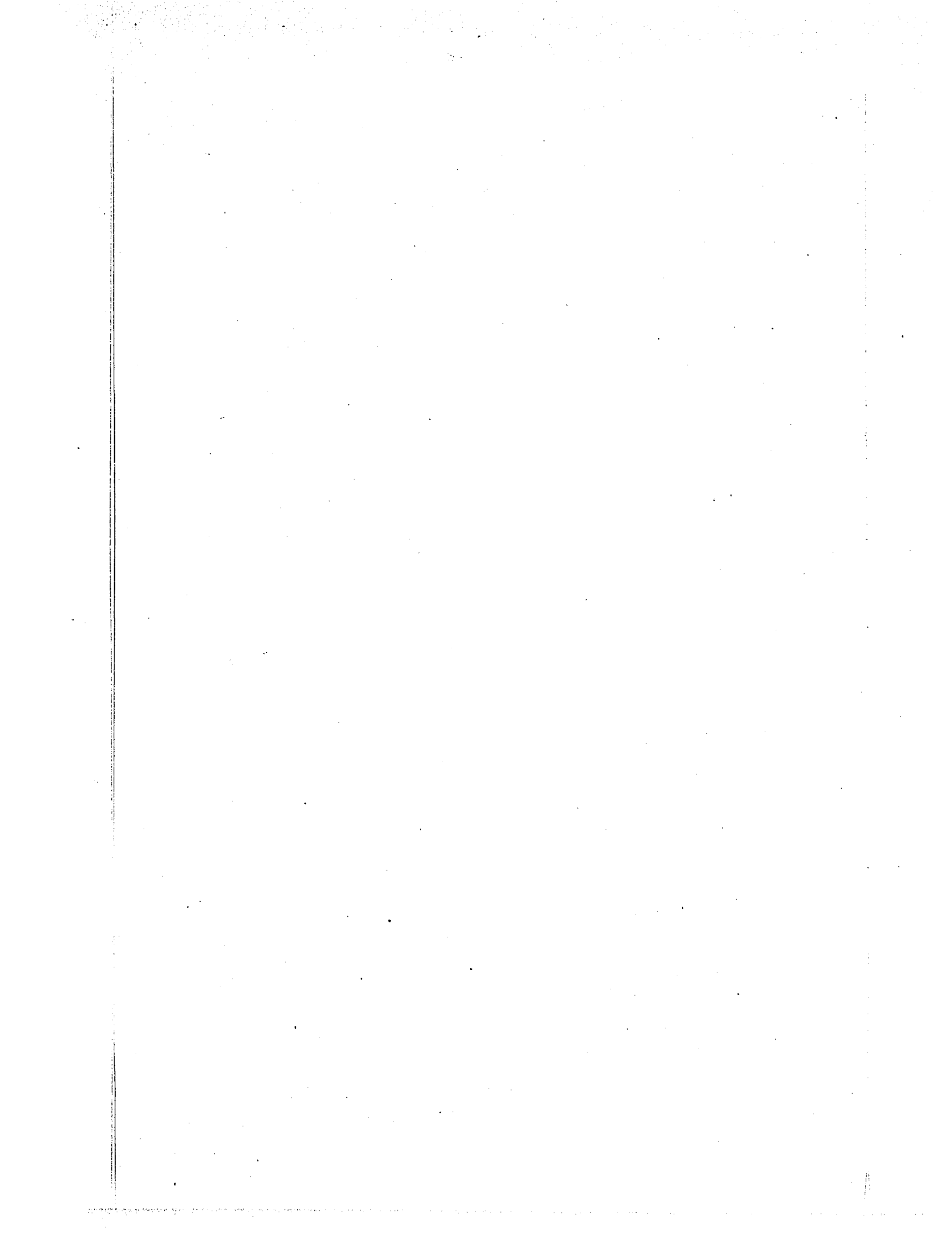
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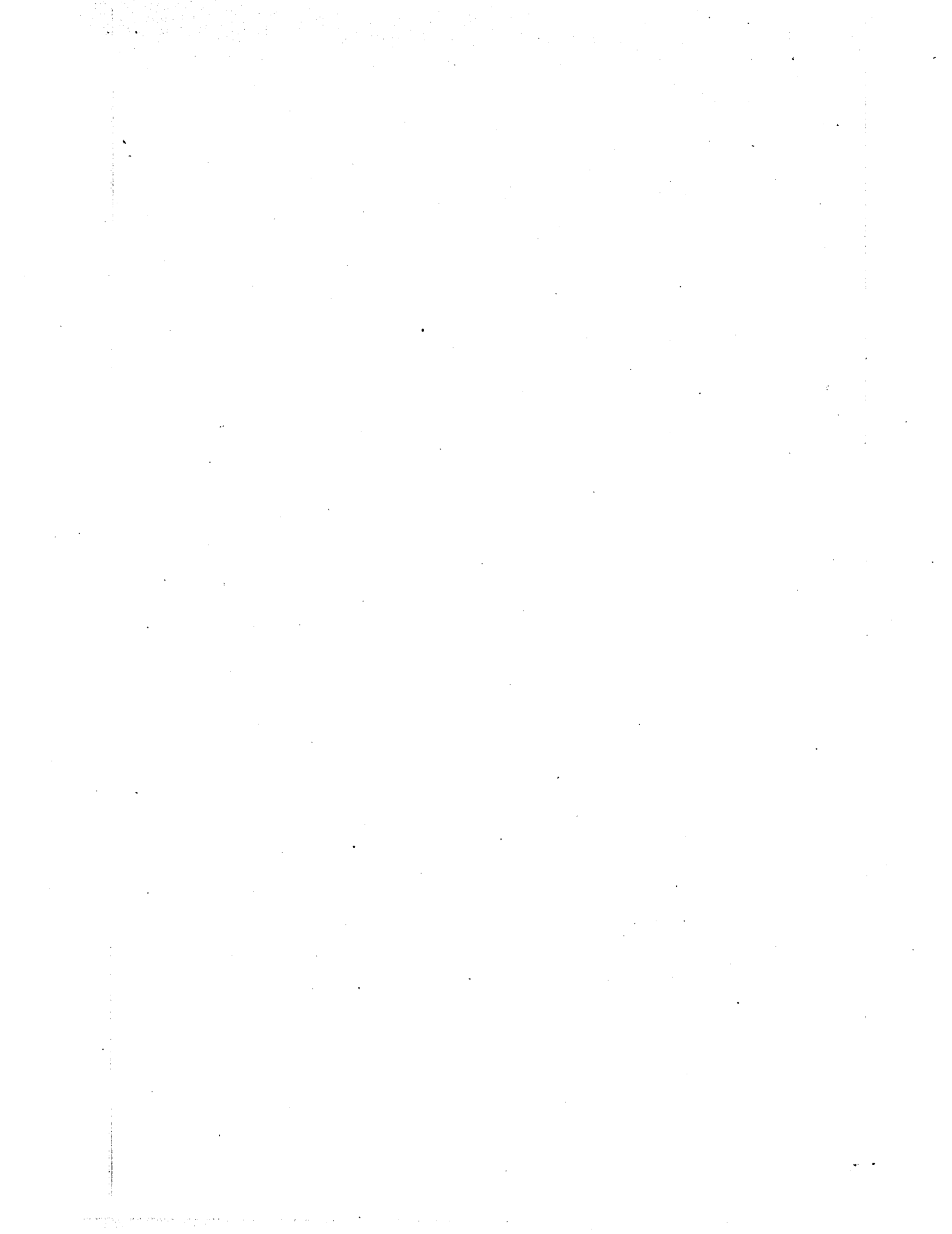
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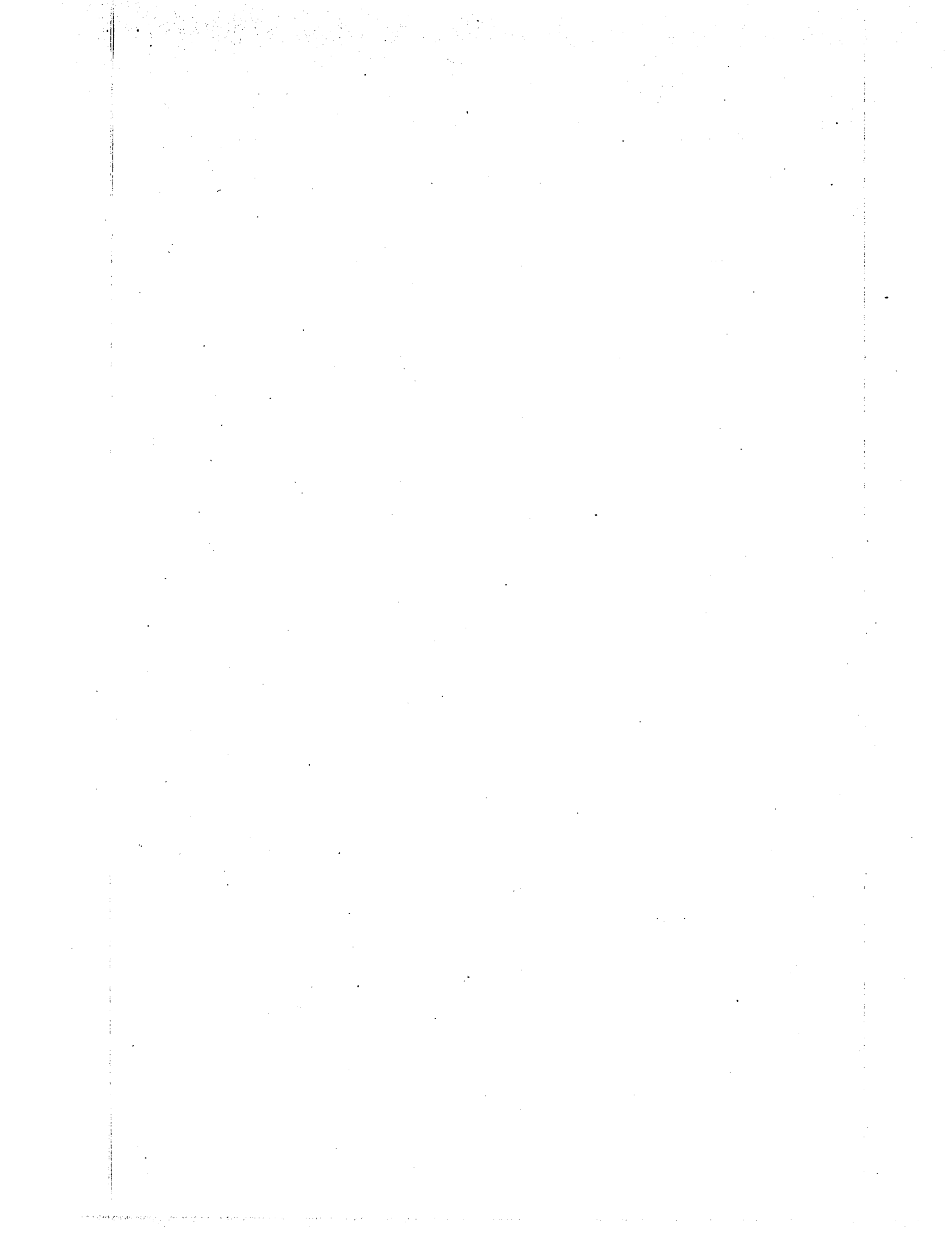


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**COMMUNITY ECOLOGY OF CHILEAN SANDY BEACHES**

**BY**

**EDUARDO JARAMILLO**

**Licenciado en Ciencias, Universidad Austral de Chile,  
Valdivia, Chile, 1976**

**DISSERTATION**

**Submitted to the University of New Hampshire  
in Partial Fulfillment of  
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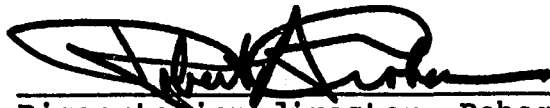
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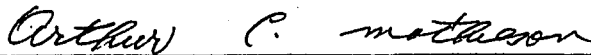
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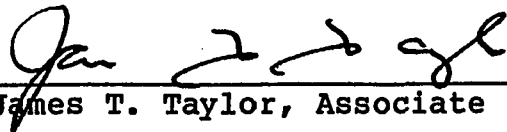
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Date

April 29, 1987

## DEDICATION

To the Universidad Austral de Chile which paved the road to the University of New Hampshire. To the University of New Hampshire which has paved the road to a better understanding of the soft bottom ecology of the south Chilean littoral.

## ACKNOWLEDGMENTS

My deepest gratitude to my advisor Dr. Robert A. Croker for his encouragement and disposition to accept my coming here to study under his guidance. To the members of my doctoral committee, Drs. Franz E. Anderson, Arthur C. Borrer, Arthur C. Mathieson and James T. Taylor for their help and criticism during the preparation of this dissertation. I also would like to thank Dr. James T. Taylor for his help in the statistical analyses. Special thanks to Dr. Franz E. Anderson; his advice, comments and disposition to use his laboratory did allow me to study the community structure of the macroinfauna in an intertidal mudflat of New Hampshire; a problem quite different from that studied here, but directly related to my general interest in soft bottom ecology.

To Universidad Austral de Chile, University of New Hampshire and Fulbright Commission for the financial support during my studies at this University. To Dr. Clayton A. Penniman for his help, advice, and above all patience, during the multivariate analyses of this study. To Mrs. Janis Marshall, who typed this dissertation with gentillesse and very much patience.

Many thanks to my friends Flaco, Mario, Alejandro, Claudio and René for their friendship and help. All of them helped with the field samplings, and Alejandro and René carried out some of the peracarids coexistence experiments while I was here. I owe special thanks to Flaco and Alejandro; the preparation of this dissertation could have been seriously affected, without their constant help by sending me more data sources than I originally brought from Chile in 1983. I am very much indebted to Mario because he introduced me to the sedimentological analyses.

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And last, but not least, my thanks to my parents who always knew that the wisest affection they could give to their sons was encouragement for advanced education.

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## ABSTRACT

### COMMUNITY ECOLOGY OF CHILEAN SANDY BEACHES

by

EDUARDO JARAMILLO

University of New Hampshire, May, 1987

Monthly abundances and life history traits of peracarid species (Orchestoidea and Excirolana), and the anomurid crab Emerita analoga were studied during May, 1978 to April, 1980 in an exposed sandy beach of southern Chile (Mehuín Beach, Bahía de Maiquillahue). Beach characteristics differed significantly during these years; i.e. more sand erosion and coarser sand occurred during the first year. The lowest abundances of the total macroinfauna ( $46-111 \text{ ind m}^{-2}$ ) occurred during winter 1978, while the highest abundances ( $896-1251 \text{ ind m}^{-2}$ ) occurred during winter 1979. The low abundances were a result of severe erosion of the habitat rather than just a coarsening of sand, a conclusion supported by grain-size preference experiments, and macroinfaunal data from adjacent beaches with coarser sand. Differences in beach physical characteristics did not affect the life history traits of



peracarids; in contrast, the same physical characteristics may indeed have affected the population structure of E. analoga.

Long-term studies (1978-1985) of seasonal abundances at Mehuín Beach, showed a downshore migration of peracarids during the warmer months. Multiple regression analyses were performed with the monthly data of species abundances and sediment characteristics during 1978 to 1980. The analyses showed that fluctuations of the upper beach O. tuberculata and E. braziliensis were primarily explained by the variability in sand desiccation related factors, while fluctuations of the middle beach E. hirsuticauda were explained by mean grain size variability.

Three distinct macroinfaunal zonation patterns were distinguished along the beaches of Bahía de Maiquillahue, and adjacent estuarine outlet areas. Differences in sediment texture, wave disturbance and water salinity are believed to be primarily responsible for these patterns. All these data, in addition to those from intra and interspecific coexistence experiments, suggest that the abundances and intertidal distribution of the peracarids O. tuberculata, E. braziliensis and E. hirsuticauda are regulated primarily by the spatial and temporal variability of substrate characteristics. This also holds true for E. analoga, although shorebird predation may be an additional factor regulating its population structure.

## I. INTRODUCTION

The morphology of exposed sandy beach habitats results from interactions between sediments and nearshore processes, such as waves and longshore currents, in what has been called beach morphodynamics (e.g. Short, 1979). The constantly changing harsh physical environment of exposed sandy beaches has typically been emphasized as a major structuring force for infaunal communities of these habitats (see e.g. review by McLachlan, 1983).

Investigations of sandy beach macroinfauna increased during the last 20 years with noteworthy studies on the east coast of North America (Croker, 1967a, 1977, Croker et al. 1975, Dexter, 1969, Knott et al. 1983, Leber, 1982, Sameoto, 1969a), the west coast of Europe (Eleftheriou and Nicholson, 1975, Fincham, 1971, Jones, 1970a, Salvat, 1967, Seed and Lowry, 1973), the tropical and subtropical coasts of the Americas (Dexter, 1972, 1974, 1976, 1979, Rodriguez, 1959, Shelton and Robertson, 1981), the Indian Coast (Ansell et al. 1972a, McIntyre, 1968, McLusky et al. 1975, Trevallion et al. 1970), Australia and New Zealand (Dexter, 1983, Fincham, 1974, 1977, Wood, 1968), and South Africa (Bally, 1983, Brown, 1973, McLachlan et al. 1981). Most of these studies stressed the significance of physical factors such as wave exposure and grain size in determining observed patterns of abundance and distribution of

macroinfauna. In addition, these studies supplied new information about intertidal zonation of macroinfauna on different beaches of the world, and provided the opportunity for examining the applicability of the classical sandy beach zonation schemes proposed by Dahl (1952), Pichon (1967) and Trevallion et al. (1970). Although these regional studies are valuable contributions, most are constrained by three basic factors: 1) a lack of long-term monitoring of macroinfaunal population fluctuations and beach morphodynamics; 2) a lack of quantitative correlations between and among macroinfaunal fluctuations and physical factors suggested to be significant in causing those fluctuations, and 3) a lack of coincidental field and laboratory studies with a view toward explaining the observed natural patterns.

In contrast to the relatively rich history of ecological work in other areas, studies of Chilean sandy beaches are limited, and primarily the result of short-term surveys (Bertrán, 1984, Castilla, 1983, Castilla et al. 1977, Jaramillo, 1978, Sanchez et al. 1982). Nevertheless, some general conclusions can be drawn from them. First, the numerically dominant organisms along the Chilean littoral are crustaceans (i.e. Peracarida, Anomura and Brachyura), although bivalves (Mesodesma donacium (Lamarck)) and polychaetes (e.g. Nephtys impressa Baird) are also found, mostly at the lowest intertidal levels. Second, peracarid species typically dominate upper and middle beach

levels. Third, the number of peracarid species increases from northern to southern latitudes. Fourth, the species of this crustacean assemblage show a distinctive zonation pattern across the intertidal zone.

The crustaceans that inhabit the intertidal zone in sandy beaches of southern Chile are represented by the talitrid amphipod Orchestoidea tuberculata Nicolet, the cirolanid isopods, Excirolana braziliensis Richardson, E. hirsuticauda Menzies, and E. monodi Carvacho, and the anomurid crab Emerita analoga (Stimpson). In this study, I analyzed the role of physical and biological processes in structuring the crustacean assemblage of sandy beaches of southern Chile, particularly that of Mehuín Beach, a high energy sandy beach. Thus, the objectives of this study were:

- 1) To determine spatial and temporal variability of the physical characteristics of sediments and species abundances.

- 2) To determine to what extent temporal changes in species abundances and intertidal macroinfaunal distribution are related to beach morphodynamics and/or other physical factors.

- 3) To explore whether biological interactions are important in population fluctuations and intertidal distributions of macroinfauna.

## II. MATERIAL AND METHODS

### Study Sites

The beaches analyzed in this study were located in or near Bahía de Maiquillahue (Fig. 1) and selected to illustrate varying degrees of exposure. The most protected sites were located in the outlet areas of Río Queule (site 7) and Río Lingue (site 8); they were protected from breaking waves by subtidal sand bars located nearby. Due to its location (facing the mainland), site 6, Isla de Maiquillahue, had a moderate exposure, while all the other sites were fully exposed to breaking waves of the Pacific Ocean. Sites 1-4 were at Mehuín ( $39^{\circ} 26'S$ ,  $73^{\circ} 13'W$ ); site 2 was the primary site and hereafter referred to as Mehuín Beach. Sites 3 and 4 were part of a long strand approximately 2000 m in length. Site 1 was a small pocket beach, nearly 20 m in length; the other sites had lengths varying between 100-200 m.

Sites 1-3 were backed by a cliff (7-12 m above beach level), supporting a coastal public road. Sites 4 and 8 were limited posteriorly by dunes that rise 2-3 m in some places, while the rest (sites 5, 6 and 7) were backed by natural cliffs of mainly metamorphic rocks ("piedra laja" formation; Illies, 1970).

### The Adjacent Waters

Data concerning general characteristics of the waters adjacent to Mehuín Beach were gathered by personnel from the Marine Biology Station of Universidad Austral de Chile at Mehuín. Surf water samples were collected weekly between 1982-1985 for salinity determinations. The values were calculated through conductivity values obtained from a conductivity meter (Lectro Mhometer by Lab-Line) as well as from a list of formulas quoted by Bennett (1976). Values reported here are overall monthly means for the period 1982-85, and are presented together with rainfall data. The latter are overall means of monthly averages (based on daily measurements: 0900, 1400, and 1800) for the period 1978-85 and gathered from the Meteorological Station of Universidad Austral de Chile at Mehuín (22 m above sea level). Since 1978, surf water and air temperatures have been measured daily (0900, 1400, and 1800) with mercury thermometers accurate to 0.1 C. The values presented here are overall means of monthly averages for the period 1978-85.

### Mehuín Beach

Long-term dynamics of erosion and accretion of sand were followed at Mehuín Beach between 1978 and 1985. Temporal changes in sand levels were recorded at three reference points (Fig. 2). The highest was a post located

on the upper beach, approximately 2 m from the cliff, while the other two were rocks located at the middle beach, and on the lower beach.

Two sets of sand level data are presented here. The first covers the temporal fluctuations of sand levels during January, 1978 to December, 1985 (Fig. 5); here, the data are presented as monthly averages based upon fortnightly measurements. The second set, covers the period from May, 1978 to April, 1980 (Fig. 8). In this set, the lines showing sand level variability in the upper and middle beach are based upon fortnightly measurements (heights were not averaged), while those of the lower beach are based on daily measurements.

Sand level variability was analyzed in relation to the direction and frequency of longshore drift currents observed daily (0900) between 1978 and 1985. The direction and frequency of longshore drift currents were analyzed in relation to monthly averages of wind direction, derived from daily measurements (0900, 1400, and 1800) and gathered from the Meteorological Station at Mehuín.

The morphology of the beach was determined by the Emery's (1961) profiling technique. Each month between May, 1978 and April, 1980, the beach profile was surveyed in 5 m sections along a transect between the post on the upper beach and the low tide level. The slope of each profile was measured by the expression  $\frac{a}{L} \times 100$ , where  $a$  is

the difference in height between the highest and lowest point (low tide line) and L is the distance between these two points.

Duplicate sediment samples were collected at each station 5 m apart on the transects between May, 1978 and April, 1980. Samples were collected by inserting a 3.5 cm diameter metal core to a depth of 15 cm. One sample was used for textural analyses, the other was wrapped in aluminum foil and used for water content determinations. Samples for textural analyses were de-salted (tap water washing), dried (72 h at 110 C), quartered until a weight close to 150-200 g was obtained, and then sieved for 30 minutes with a Ro-Tap machine. Screens with the following openings in phi ( $\phi$ ) were used: ( $\phi = -\log$  of particle diameter in mm; Folk, 1980): 0, 1.00, 1.50, 2.00, 2.25, 2.50, 2.75, 3.00, 3.50, 4.00 and pan. Textural characteristics were calculated with a moments computational method (McBride, 1971), and using a program written by Pino (1982) for a Hewlett-Packard 41 CV. With this method, all grain sizes affect the final results, giving a clearer picture versus a graphic method, which is based only on selected percentages of the total particle distribution (Folk, 1980).

The following were calculated:

$$\text{Mean grain size, } \bar{x}\phi = \frac{\sum fm}{n}$$

$$\text{Sorting, } \sigma\phi = \sqrt{\frac{\sum f(m-\bar{x}\phi)^2}{100}}$$



where  $f$  = weight percent (frequency) in each grain size class.

$m$  = mid point of each grain size class in phi values.

$n$  = total number in sample which is 100 when  $f$  is in percent.

Water content of sand samples was estimated as the loss in weight of wet sediments after drying (110 °C for 96 h). Sediment temperatures were monitored at each station with a mercury thermometer accurate to 0.1 °C. Temperatures were read at the surface (approximately 3 mm depth), and at a depth of 15 cm; the values reported here are the averages of these two readings. The penetrability of the sediment was measured by dropping a 150 g metal rod down a 1 m tube. The depth to which the rod penetrated into the sediment was measured 10 times at each station, and the average calculated.

Variability of the physical characteristics of the beach, i.e. mean grain size, sorting, temperature, water content, and penetrability, were analyzed by principal component analysis. The component axes were rotated in order to obtain a clearer delineation of variables associated with each component. The rotational method used was the varimax approach, whose criterion centers on simplifying the columns of the correlation matrix; thus, the maximum possible simplification is reached if there are only ones and zeros in a single column (Hair et al. 1979). The computer program for this analysis was obtained from

the package BMDP (program 4M; University of California Press); a DECSYSTEM-2020 at the Universidad Austral de Chile was utilized.

### The Macroinfauna

Monthly population data were obtained from May, 1978 to April, 1980. A metal frame was used to collect five 0.1<sup>2</sup> m replicates of sand, 15 cm deep, from stations located at 10 meter intervals on intertidal transects. The highest station (station 1) was located 2 m seaward of the post on the upper beach; the lowest one was close to the low water line of spring low tides. The number of stations varied between 3 and 7, depending upon the width of the intertidal zone during each sampling day; however, most of the samplings had 5 stations. Sediment collected at each station was washed through a 0.5 mm sieve; animals were removed and preserved in 10% formalin.

Specimens were measured to the nearest 0.1 mm for life history analyses. For isopods, body length was the distance from rostrum tip to telson tip. With O. tuberculata this length was the distance from the rostrum tip to telson base, while in E. analoga the body length was considered as cephalothorax length. Animals were then sorted into 2 mm (E. braziliensis and E. hirsuticauda) or 4 mm size classes (O. tuberculata and E. analoga) for frequency determinations of populations. Juveniles and ovigerous females were distinguished to analyze

reproductive activity. Fecundity estimates were made for O. tuberculata, E. braziliensis and E. hirsuticauda. Due to the possibility that some of the life stages contained in the marsupium may be lost during sampling, sieving and sorting, fecundity estimates were made following the criterion used by Donn and Croker (1986). Ovigerous females were grouped into 0.5 mm (E. braziliensis and E. hirsuticauda) and 1.0 mm size classes (O. tuberculata), and the maximum number of life stages in each size class was counted.

Size differences among the marsupial life stages of the peracarid species were studied using the ovigerous females collected between May, 1978 and April, 1980. Size differences among the post-marsupium (juveniles) and adult stages were analyzed through seasonal samples collected between September, 1980 and September, 1981. In the isopods, the males were differentiated by the paired penes on the sternum of the 7th thoracic segment and the male appendices on the 2nd pleopod (Jaramillo, 1982), while in O. tuberculata, presence of penes, length of the second antennae, and size of second gnathopod were used (Jaramillo et al., 1980). The females of the isopods were recognized by the presence of oostegites, life stages in the marsupium, and by the absence of penes and male appendices. The criterion of Dexter (1977) was followed here, i.e. the minimum size of females was determined by the minimum size of males and animals smaller than the smallest male (in the

samples) were assigned to juveniles. The females of O. tuberculata were recognized by the presence of oostegites, life stages in the marsupium, absence of penes, length of the second antennae and size of the second gnathopod. As in the isopods, the same criterion was followed to find the smallest size of females and size of juveniles.

The depth distribution of the macroinfauna within the sand was seasonally analyzed between September, 1980 and September, 1981. A metallic core (20 cm diameter) was used to collect five  $0.03 \text{ m}^2$  replicates of sand 15 cm deep at stations located at five meter intervals over a transect extending from station 1 to the spring low tide level. Sand cores were sliced into 2.5 cm sections to a depth of 12.5 cm. Sediment sections were then separately washed through a 0.5 mm sieve and animals preserved in 10% formalin. A  $5 \text{ cm}^2$  core was collected from each 2.5 cm slice of a randomly chosen core at each station. These samples were used for water content measurements and granulometric analyses (mean grain size and sorting). Sand temperatures were monitored at 0, 2.5, 5.0, 7.5, 10.0 and 12.5 cm depths at each station with a mercury thermometer accurate to  $0.1 \text{ C}^\circ$ .

Two  $0.03 \text{ m}^2$  replicates of sand, 15 cm deep, were collected between July, 1983 and November, 1985 at the upper, middle, and lower beach. These levels corresponded to stations 1, 3 and 5 of the monthly transects performed between May, 1978 and April, 1980. Sediments collected in

this way were washed through a 0.5 mm sieve, with the animals preserved in 10% formalin. These data were used to investigate long-term population fluctuations and were analyzed together with the monthly (May, 1978 to April, 1980) and seasonal data (September, 1980 to September, 1981). All abundance estimates are expressed in numbers per m<sup>2</sup>.

The intertidal distribution and abundance of the macroinfauna were studied in different sites of Bahía de Maiquillahue and protected sites of the outlet areas of Río Queule and Río Lingue (Fig. 1) during the summer of 1983. The objective was to analyze zonation and macroinfaunal abundance in relation to wave exposure and grain size. Macroinfauna was sampled at a series of stations along transects, extending from spring low tide level to the back border of each beach (defined as foredunes, cliffs or wrack lines). At each station, two 0.03 m<sup>2</sup> replicates of sand, 15 cm deep were collected. The sediment was washed through a 0.5 mm sieve, and animals preserved in 10% formalin. One sediment core (3.5 cm diameter, 15 cm deep) was collected at each station for granulometric analyses (mean grain size and sorting). Analyses were performed as described earlier for the Mehuín Beach sands, but adding screens with coarser openings due to the presence of gravel in the Isla de Maiquillahue and Matías sediments. Beach profiles were surveyed at regular intervals along a transect between the back border of each beach and the low tide level.

Species-sediment and Inter-species Relationships  
in the Field

Simple and multiple regression analyses were used to study the relationships between the abundances of individual species, physical characteristics of the sediment, and abundances of coexisting species. Two approaches were followed in the multiple regression analyses. Approach A tested the relationships between mean abundances of individual species (dependent variables), and physical characteristics (independent variables) of the stations where species were collected. Approach B tested the relationships among that mean abundances, and physical characteristics and mean abundances of coexisting species (independent variables). The variance and means of the species abundances were highly correlated; therefore, the abundance data were transformed by  $\log_{10}(n + 1)$ . The forward selection technique was used in the multiple regression analyses. In this procedure, each variable is considered for inclusion in the regression model prior to developing the equation (Hair et al., 1979). The significance of the regression coefficients were tested by F-tests. Then, the F-statistics calculated for each independent variable were compared with a specified probability level of 0.05. The computer program for these analyses was obtained from the package SAS (program Stepwise Procedure, SAS Institute Inc.) and utilized on a VAX computer system at the University of New Hampshire.

### Laboratory Experiments

Salinity tolerance and grain-size preference experiments were designed to throw light on the zonation patterns and community structure in exposed beaches of Bahía de Maiquillahue and at protected sites of the outlet areas of Río Queule and Río Lingue. Experiments were conducted under dark conditions and with animals previously kept in the laboratory for two days.

Experimental salinities were obtained by diluting natural sea water with distilled water. Conductivity meter calculations as described above were used. Salinities used were 28, 20, 15, 10 and 5 o/oo. The control salinity was 28 o/oo, similar to the salinity in the water adjacent to Mehuín Beach during the experiments (22-29 December, 1981). With each salinity, four replicated plastic containers holding seven (*O. tuberculata*), six (*E. braziliensis* and *E. hirsuticauda*) or five (*E. analoga*) animals in approximately 1000 ml of water were observed over a one week period. Containers were individually aerated and placed on a sea water table with a water temperature of 12<sup>o</sup> C.

Four types of grain-size preference experiments were conducted. First, *O. tuberculata*, *E. braziliensis*, *E. hirsuticauda* and *E. analoga* were given a choice of four different sizes of sand previously prepared (de-salted, dried and sieved); very fine (3-4  $\phi$  or 62.5-125 microns), fine (2-3  $\phi$  or 125-250 microns), medium (1-2  $\phi$  or 250-500 microns) and coarse sand (0-1  $\phi$  or 500-1000 microns). The

size ranges represented the natural size ranges of sand found in exposed beaches of Bahía de Maiquillahue and near the outlets of Río Queule and Río Lingue. A portion of each sand grain size was placed in one of four compartments of replicated wooden boxes. Boxes used for E. braziliensis and E. hirsuticauda were 14 x 14 cm and held a 1.5 cm sand layer; those for O. tuberculata and E. analoga were 20 x 20 cm and had a 2.5 cm sand layer. Second, O. tuberculata, E. braziliensis, E. hirsuticauda and E. analoga were given the choice of two different sand sizes previously prepared. The size ranges (fine and medium) were represented at Mehuín Beach during May, 1978 to April, 1980. A portion of each size was placed in one of two compartments of replicated boxes of the same sizes as those used in the first set of experiments. Third, O. tuberculata, E. braziliensis and E. hirsuticauda were given the choice of two natural untreated sands; one half of the appropriate wooden boxes contained sand from the upper beach, the other half had sand from the middle beach. This experiment was designed to determine whether quality of sediments might be associated with the different abundance patterns of these species in the upper and middle beach. Fourth, E. braziliensis and E. hirsuticauda were given the choice of sands from two different beaches. One half of the boxes contained sediment from Isla de Maiquillahue, the other half contained sand from Matías. The purpose of this experiment was to investigate the absence of E.



braziliensis and E. hirsuticauda in the calcareous sands of Isla de Maiquillahue. Sediments from Matías were used, because, among all the beaches studied, the size ranges occurring here were the most similar to those of Isla de Maiquillahue. Sea water was then carefully added, reaching a depth of 0.5 cm. Boxes were placed on a sea water table held at 12 C. After 24 hours, metallic dividers were inserted into the boxes to isolate the sand-size categories and the included animals.

Sand desiccation tolerance experiments were designed to investigate the intertidal distribution and seasonal downshore migration of the macroinfauna during the warmest months. Experiments were conducted in a chamber with circulating air and with animals previously kept under laboratory conditions for at least two days. Relative humidity in this chamber varied between 32 and 39%, being controlled by two small fans and three pans of silica-gel. Pans were placed in the bottom of the chamber which was perforated with holes of approximately 2 cm diameter. Two electrical heaters maintained air temperature varying between 30-32 C and a sand temperature close to 30 C. Fifteen animals of both O. tuberculata and E. hirsuticauda, and 10 of E. braziliensis and E. analoga were placed in plastic containers (12 cm diameter, 7 cm height) with approximately 4 cm of presieved sand. Sand was prepared with an initial water content of 20%, similar to that found in wet natural sands close to the low tide line (the weight

of the animals was disregarded in this calculation). Three containers (two in E. braziliensis) were removed at 3-hour intervals for a period of 24 hours. Sand temperature, water content loss (determined by weight differences) and percent mortality were measured every three hours. Control animals, which were maintained in a similar way, but outside the experimental chamber (20% water content held constant), had minimal mortality.

Finally, experiments were performed to study intra and interspecific coexistence in and among O. tuberculata, E. braziliensis and E. hirsuticauda. After two days of laboratory conditioning, the animals were placed in plastic containers (12 cm diameter) and held on a sea water table with a temperature of 12<sup>o</sup> C. The walls of each container had nylon mesh windows to allow a constant flow of water. Three abundances were used in the intraspecific experiment: 10, 20 and 30 animals. Abundances were approximately two, four and seven times higher than the highest abundances found in the field during the period May, 1978 to April, 1980. Twenty animals were used in the interspecific experiments as shown in Table 1. The containers used in the intraspecific experiments had 3 cm of presieved sand. Most interspecific tests also had 3 cm, but some contained 6 cm of sand to provide a wider use of the resource space for the animals. Mortality of animals was checked daily for 15 days. All intraspecific and most interspecific

experiments were conducted under dark conditions; however, two series of interspecific comparisons (with 3 and 6 cm sand) were run under controlled lighting (12h/day).

Results of the grain size preference, desiccation tolerance, and coexistence experiments were analyzed by ANOVA on percentage data after angular transformation. Prior to ANOVA, Bartlett's test (Sokal and Rohlf, 1969) was performed to test for homogeneity of variances. If analyses of variance indicated significant differences among means, all means were compared using the a posteriori Student-Newman-Keuls (SNK) procedure (Ott, 1984).

### III. RESULTS

#### Physiography

Bahía de Maiquillahue is located in the northern area of the cold temperate region of the Chilean coast, between 40° and 53° S (e.g. Dahl, 1960; Knox, 1960). The region has also been called "the rainy zone of Chile" (Martin, 1923). Data from the Meteorological Station of Mehuín show that the highest mean monthly rainfall occurred between May and August, while the lowest values occurred in summer months (December-March) (Fig. 3a). Salinity of surf waters is affected by rain. During 1982-85, the mean surf salinity ranged from 25.6 o/oo to 32.4 o/oo. Typically higher values occurred during summer and early autumn (January-April), followed by a sharp decline during late autumn and winter months (May-July) when the rainfall was highest (Fig. 3a). During these months, salinities as low as 22 o/oo were measured. Mean surf and air temperature followed a similar trend during 1978-85 (Fig. 3b). Mean surf values ranged from a summer high of 14.2 C to a winter low of 11.2 C; mean summer and winter air temperature were 15.7° and 9.2 C, respectively.

Hydrographic conditions along the Bahía de Maiquillahue are characterized by semidiurnal tides with tidal ranges close to 1.5 m. Exposed fully to the Pacific Ocean, Mehuín Beach is subjected to waves of 0.3 to 1.3 m

(E. Jaramillo, unpublished data). Oblique waves approach the shoreline, producing littoral currents resulting in a longshore drift with a pronounced seasonal pattern. For the period 1978-85, the highest frequencies of the south flowing longshore drift were observed during summer (January-March) and spring months (October-December), while the north flowing longshore drift dominated during late autumn and winter (May-August) (Fig. 4a). The direction of the longshore drifts was largely controlled by wind direction, which, in turn, is seasonally variable (Oyarzún, 1977). Southwest winds are the most frequent during spring and summer months (September-March). During most of the autumn and winter (April-August), northwest winds are the most frequent. During the later period, northwest winds approach their highest frequencies, and they are the main source of winter storms that erode the sandy beaches of this area. During May, north winds are dominant, increasing from a mean of 10.3% in April to 28.4% in May (Fig. 4b). At the same time, north flowing longshore drift increased from 61% in April to 92% in May (cf. Fig. 4a and 4b). Frequency of north flowing longshore drift and north wind were highly correlated ( $r:0.954$ ), and the value of  $R^2$  (coefficient of determination) indicates that 91% of the variability in the longshore drift was accounted for by variability of north wind frequencies.

## Mehuín Beach

Long-term Dynamic. Monthly data gathered from 1978 to 1985 from the upper, middle and lower levels of Mehuín Beach, show that sand levels followed a seasonal pattern (Fig. 5). During summer and autumn (December-April), the beach was in an accretion period, gaining more sand versus the rest of the year. From winter through early spring (May to October) the beach experienced erosion. Then, the beach entered a recovery period lasting until the following March and April, when it was at maximum accretion (Fig. 5). This trend was slightly different in 1985 when the middle and lower beach continued to be eroded through the spring months. Annual differences between maximum accretion and erosion values were noted for the three levels of the beach (Table 2). During 1978-85, the middle and lower beach levels showed a similar difference; however, the greatest yearly differences occurred at the middle beach level (i.e. 1981: 169.0 cm and 1983: 166.7 cm).

Seasonal dynamics of accretion and erosion of sand can be related to seasonal patterns of longshore drifts, especially for the middle and lower levels of the beach (Fig. 5). Considering the entire period from 1978-1985, correlation coefficients between the frequency of the north flowing longshore drift and sand levels were significant ( $p < 0.05$ ) for the middle ( $r: 0.328, n = 84$ ) and lower beach levels ( $r: 0.345, n = 96$ ), but not for the upper beach ( $r: 0.151, n = 96$ ). However, the values of  $R^2$  for those

significant correlations were quite low (0.108 and 0.119, respectively), implying that a low percentage of the variability of sand levels was accounted for by variability in the frequency of north flowing longshore drift. In general, sand accretion periods coincided with the lowest frequencies of north flowing longshore drift, while erosion periods coincided with the highest frequencies of this current. In addition, the beginning of erosion periods were coincident with an increase of north flowing longshore drift between April and May (Fig. 5). These relationships are better seen in Fig. 6, which summarizes patterns of longshore drift and sand levels during 1978-1985.

Beach Morphology, Slope and Grain Size. Variations in beach morphology during 1978-1980 are illustrated by topographic profiles (Fig. 7). In general, winter and spring profiles were steeper and concave skyward, while summer and autumn profiles were less steep and convex.

The 1978-1979 and 1979-1980 periods differed in several aspects. The main erosion period during 1978 (May-August) was shorter and more intense than 1979 (June-October). During June-July, 1978, the beach was 1.5-1.7 times narrower than during similar months in 1979; in other words, more sand was eroded during 1978. The situation is clearly seen in Fig. 8, which shows that sand levels of the upper, middle and lower beach were lower during winter 1978, versus winter 1979.

From October onward sand was typically added to the beach, but with a few exceptions; e.g. during the spring and summer of 1978-79 some areas of the profiles showed erosion, while others showed accretion (November to December, 1978 and February to March, 1979; Fig. 7). During months of accretion, the beach reached its maximum width, especially in the summer of 1979 (up to 68 m) (Fig. 7). Figure 8 also shows this situation; the sand level of the upper, middle and lower levels of the beach were higher during summer 1979, when the beach was widest (Fig. 7 and 8).

Temporal variability in the beach face slope and mean grain size is shown in Fig. 9a. Steepest profiles occurred during winter 1978, when the coarsest grains and the most intense erosion occurred. On the other hand, the flattest profiles occurred during accretion periods when sand grains were finer. Beach face slope and mean grain size were significantly and negatively correlated, with 30.1%<sup>2</sup> ( $R : 0.301$ ) of the variability in beach face slope being accounted for by the variability in mean grain size (Fig. 9b).

#### Texture and Physical Characteristics of the Sediments.

Textural characteristics, temperature, water content and penetrability of the sand at three selected levels of the beach are shown in Table 3. Mean grain size of the sediments, sorting, and the ranges of these two variables, increased towards the lower beach. Water content also



increased seaward, while a general trend of increased temperature and penetrability was observed towards the upper beach. On the other hand, the ranges of the last three variables decreased seaward (Table 3).

Temporal variability of mean grain size and sorting are shown in Fig. 10. The figure also illustrates seasonal dynamics of accretion and erosion, by showing changes in the height of the post (located in the upper beach) above the sand surface, and consequently variability of intertidal height at each station (Fig. 10a).

Sediments of Mehuín Beach were mostly fine sands (2-3  $\phi$ ; Folk, 1980). Within this category, the finest sands (>2.3  $\phi$ ) occurred mainly on the high and middle beach during summer and autumn months of 1978-79 and 1979-80 (Fig. 10b). However, during 1979, these sizes were also found during winter months (June and July). Coarsest sands (<2.0  $\phi$ ) occurred during the intense erosion period of 1978 (July-August) (Fig. 10b). At this time, most of the intertidal zone was represented by sediments with sizes close to the lower range of medium sand (1-2  $\phi$ ; Folk, 1980). Grain sizes as a function of sand levels are shown for the upper, middle and lower beach in Fig. 11. Both variables were significantly ( $p < 0.05$ ) and negatively correlated. Values of  $R^2$  shown in Fig. 11, indicated that 25.6-42.3% of the variability in mean grain size was accounted for by variability in sand levels. The finest

sands occurred during the accretion periods (lower height values), while the coarsest grains were detected during erosion periods (higher height values).

During most of this study, the sands of Mehuín Beach were well sorted sediments (0.35-0.50  $\phi$ ; Folk, 1980). Within this category, the lowest values (more sorting) were primarily found during summer and autumn when the finest sediments occurred. On the other hand, the highest values (less sorting) were found for the coarsest sediments (cf. Fig. 10b and 10c). These relationships are shown in Fig. 12 where monthly averages of mean grain size and sorting are presented for 1978-80; both variables were significantly ( $p < 0.05$ ) and negatively correlated. The high  $R^2$  value (0.738), indicates that the variability of sorting values was highly accounted for by variability in mean grain size values.

Seasonal patterns of temperature, water content and penetrability of the sediments are shown in Fig. 13. Highest temperatures, 40-45<sup>o</sup> C, were detected at the highest stations and during summer months (December-February) 1978-79 and 1979-80 (Fig. 13a). Lowest temperatures were measured during June, 1979 when all stations registered 10.5<sup>o</sup> C. As expected, wider temperature ranges across the intertidal occurred during spring and summer.

Seasonal pattern of water content of the sediment was closely related to that of the temperature. Driest sediments (less than 6% of water content) were the hottest

ones and vice versa (cf. Fig. 13a and 13b). Water content and temperature were significantly ( $p < 0.05$ ) and negatively correlated; however, the value of  $R^2$  indicates that only 36.8% of the variability presented by the water content values was accounted for by variability in temperature (Fig. 14a). Similar to sediment temperature pattern, the widest differences in water content between the highest and lowest stations were detected during spring and summer; the mean difference was 16.6% (sd. 1.0%). On the other hand, the mean difference for the autumn and winter period was 10.6% (sd. 5.0%).

Penetrability and water content values showed a significant ( $p < 0.05$ ) and negative correlation with 71.6% of the variability of penetrability accounted for by variability in water content (Fig. 14b). Softest sediments primarily occurred at higher beach levels during spring and summer; i.e. when sediments were the driest (cf. Fig. 13b and 13c). During all seasons, the hardest sediments occurred in the middle, and particularly, lower beach levels, where water content values were highest.

Principal Component Analysis. Table 4 summarizes the results of the principal component analysis performed on the physical characteristics of 259 observations (stations) collected during May, 1978 to April, 1980 at Mehuín Beach. Both unrotated and rotated component loadings are shown.

The loadings and communalities for the first two components are presented in Table 4. In general, the

communality values calculated for each variable were high, indicating that a large amount of the variance in each variable was accounted for by two components.

Component I explained 58.8% of the total variance or trace in the unrotated component loadings pattern, while component II explained 24.4%. The first component had high and similar loadings (over 0.70) for all variables, except sorting, which was the variable with the highest loading in the second component (Table 4). Rotation of the first two axes produced an almost even percentage of trace for each component (CI: 38.8%, CII: 34.8%). After rotation, only water content and penetrability had high loadings in the first component, while mean grain size and sorting loaded highest in the second component. Therefore, during May, 1978 to April, 1980, variability in texture was as important as the variability in sand desiccation related factors in describing total variability of beach characteristics.

The distribution of station-points in the plane defined by the first two components is shown in Fig. 15. The distribution is shown in separate 3-month plots for clarity. The plots show differences between the two sampling years (May, 1978 to April, 1979 and June, 1979 to April, 1980). Samples from the June-November period of 1978 are located in the two upper quadrats of each plot, while those of the same period in 1979 are spread through the upper and lower quadrats. On the other hand, samples

of 1978 show more scatter along the vertical axis (Component II) in which mean grain size and sorting had the highest loadings (Table 4). As explained previously, during 1978, Mehuín Beach experienced a more intense erosion period resulting in higher variability of mean grain size and sorting. Fig. 15 also shows increasing scatter in the positions of stations from winter to spring and then to the summer of both sampling years, and along the horizontal axis. Water content and penetrability were the variables with highest loadings on this axis (Component I); this resulted from higher variability in water content and penetrability during the winter to spring and summer months.

#### The Macroinfauna

Population Abundance. Mean density of the total macroinfauna ranged from 46 ind m<sup>-2</sup> in July, 1978 to 1847 ind m<sup>-2</sup> in July, 1979, with 411 ind m<sup>-2</sup> being the overall mean during May, 1978 to April, 1980. The overall mean density during May, 1978 to April, 1979 was one half that observed during June, 1979 to April, 1980 (Fig. 16). The highest total abundances occurred during the late autumn and winter of 1979 (i.e. July, 1847 ind m<sup>-2</sup>) and were the result of high abundances of O. tuberculata, E. hirsuticauda and particularly E. analoga, a group of species that peaked during this period (Fig. 16). The abundance peak of O. tuberculata was suddenly reached, while that of E. hirsuticauda was preceded by a steady

increase during early summer, 1979. The July-August peak of E. analoga also represented a sudden increase, with abundances nearly 8 times higher than during June. After August, the population crashed to one of the lowest abundances observed during May, 1978 to April, 1980 (Fig. 16).

Life History. Analysis of the percentage frequencies of ovigerous females and juveniles of O. tuberculata, E. braziliensis and E. hirsuticauda showed ovigerous females generally peaking during spring and early summer, and juveniles during summer months (Fig. 17). Mean abundances of juveniles of O. tuberculata and E. braziliensis did not differ significantly ( $p > 0.05$ , t-test analyses) between the two recruitment seasons, while those of E. hirsuticauda showed higher abundances during 1978-1979. Ovigerous females of E. braziliensis had similar abundances at each reproductive season, while those of O. tuberculata and E. hirsuticauda were more abundant during the 1979-1980 reproductive period. It should be stressed that analyses involving ovigerous females may be misleading, since brood stages may have been lost during collecting and sorting. The situation probably explains why very low abundances of ovigerous females of O. tuberculata were detected during the reproductive season of 1978-1979, even when abundances of juveniles were similar between both recruitment seasons.

Obviously, the pulses of recruitment were not solely responsible for the abundance peaks of the peracarid

species shown earlier (Fig. 16). However, the increased abundance of E. hirsuticauda during February and March, 1980 (Fig. 16) seemed to have been, indeed, related to the abundance of juveniles observed during these months (Fig. 17). For E. analoga, the recruitment of juveniles during March and June-August, 1979 (Fig. 18), clearly produced the abundance peaks showed by the population during that year (Fig. 16). Figure 18 also shows that ovigerous females of E. analoga occurred during spring and summer months, while juveniles were detected almost every month sampled. However, the latter had their highest abundances during late autumn and winter, and they were significantly higher during the second year ( $p < 0.05$ , t-test analyses). In general, juvenile abundances of peracarid species were highest at the same stations where adults peaked (Fig. 19). For E. analoga, the low abundances of adults during the recruitment months override any analysis of this type.

Fig. 20 shows fecundity data for the peracarid species, based upon the maximum number of brood stages (eggs, embryos or juveniles) for size classes constructed with ovigerous females collected during May, 1978 to April, 1980. A typical linear relationship between mean body length was found for each species. Ovigerous females of E. braziliensis and E. hirsuticauda had similar sizes, but brood size for any particular female size was significantly larger (ANCOVA) in E. hirsuticauda versus E. braziliensis. Dimensions of brood stages of O. tuberculata, E.

braziliensis and E. hirsuticauda are given in Table 5. Eggs, embryos, and juveniles of O. tuberculata were larger than those of the isopods. For the isopods, the brood stages of E. braziliensis were larger than those of E. hirsuticauda.

Size-frequency distribution of O. tuberculata, E. braziliensis, E. hirsuticauda and E. analoga are summarized in Fig. 21. Due to the low abundances during some months, data were pooled to yield two-month composite histograms. The beginning of the reproductive period for O. tuberculata (November-December), resulted in a bimodal population dominated by juveniles, but with some adults present that reproduced throughout the summer and early autumn (Fig. 21). By late summer and autumn (February-April), size classes were almost evenly represented and growth of the smallest animals could be followed through the next reproductive period in 1979. No distinct bimodality was observed for E. braziliensis and E. hirsuticauda. In general, addition of the new recruits during summer either produced a flattening in the size distribution histogram of the pre-recruitment period (e.g. E. braziliensis during January-February 1979, 1980), or a change in the modal size class (e.g. E. hirsuticauda in January-February 1979). Contrary to the pattern observed for O. tuberculata, growth of new recruits of E. braziliensis and E. hirsuticauda was less obvious and the population structure of both isopods remained similar, especially during late autumn and winter,



1979 (June-September, Fig. 21). Recruitment periods for E. analoga produced a clear dominance of juveniles, whose growth could be followed after the autumn 1979 recruitment. Several recruitment pulses were observed during May, 1978 to April, 1979, obscuring obvious growth of juveniles (Fig. 21).

Analysis of seasonal variability in the mean body size of the peracarids shows that Q. tuberculata was the largest species of this group at Mehuín Beach (Table 6). Males were significantly larger than females ( $p < 0.05$ , t-test analyses) in Q. tuberculata; females of E. hirsuticauda were larger than males (with exception of September, 1980), and no significant differences of body size were found between males and females of E. braziliensis. Males of E. braziliensis were significantly larger than those of E. hirsuticauda, while females of both species did not differ in body sizes, with the exception of September, 1981, sample in which females of E. braziliensis were larger. In addition, juveniles of E. braziliensis were significantly larger than those of E. hirsuticauda during April, 1981. Body size ratios of males of E. braziliensis to males of E. hirsuticauda varied between 1.05-1.31 ( $\bar{x}$ : 1.18, s.d. 0.09), while those of females were between 0.97-1.08 ( $\bar{x}$ : 1.02, s.d. 0.04), and juveniles between 0.96-1.10 ( $\bar{x}$ : 1.03, s.d. 0.10) (Table 6). No important changes were observed in seasonal mean sizes of adult males or females (Table 6). Juveniles of Q. tuberculata were collected

during all months sampled. The increase in their percentage frequency from September to December, 1980 (as recruitment increased), resulted in a 28.3% decrease in juvenile mean length. From the February recruitment to the following spring (September, 1981) as recruitment decreased, mean length increased by 62.3%. Growth of new recruits of O. tuberculata, E. braziliensis and E. hirsuticauda is apparent with reference to their mean lengths during February and April, 1981 (Table 6). Orchestoidea tuberculata exhibited the fastest growth: from February to April the mean body size of juveniles increased by 42.9%. This growth rate was approximately 2.5 and 15 times higher than those of E. braziliensis (17.3%) and E. hirsuticauda (2.8%), respectively. During this seasonal study (September, 1980 to September, 1981), the sex ratios of females to males in O. tuberculata ranged from 0.5 to 2.4, with females outnumbering males in three of five samplings (overall mean ratio: 1.5). In E. braziliensis the ratios ranged from 0.8 to 4.2; females were more abundant than males in four of five samplings (overall mean ratio: 2.0). Females of E. hirsuticauda outnumbered males every month; sex ratios ranged from 1.3 to 3.6, with an overall mean of 2.0.

Intertidal Distribution. The intertidal zonation of the macroinfauna at Mehuín Beach based on the overall mean abundances during May, 1978 to April, 1980 is shown in Fig.

22. All peracarid species were collected throughout most of the tidal range (i.e. stations 1 to 6). However, they exhibited their highest abundances at different levels. Orchestoidea tuberculata and E. braziliensis were most abundant at station 1, the highest level sampled; E. hirsuticauda lower down at station 2, and E. monodi further down still at station 3. Emerita analoga primarily occupied the lower beach levels, with maximum abundances at station 4.

Although this general zonation pattern persisted through time, there were pronounced seasonal variations (Fig. 23). For example, during the late spring and summer of 1978-1979 (December-April), the zone of maximum abundance for O. tuberculata and E. braziliensis moved down, and in some months no animals were collected at station 1. During autumn, 1979, both species moved up and stayed there until the next December, when again they occurred with higher abundances at lower stations than those previously occupied during winter and early spring. Excirolana hirsuticauda showed a similar pattern to O. tuberculata and E. braziliensis, that is during warmer months, its highest abundances occurred at lower stations than during winter and early spring. During most of the year, E. analoga had its highest abundances at the lowest levels of its distribution. However, in June and July, 1979, it was more abundant at the middle levels of its distribution.

Some characteristics of Mehuín Beach where each species was collected are given in Table 7. Orchestoidea tuberculata and E. braziliensis mainly occupied the finest, warmest, driest and softest sands of the upper and slightly middle beach levels of Mehuín Beach. On the other hand, E. hirsuticauda, E. monodi and E. analoga were mainly collected from lower levels that had coarser, wetter and harder sands. The latter beach levels had narrower ranges of temperature, water content and penetrability than those where O. tuberculata and E. braziliensis dominated. Cross correlation coefficients between monthly mean abundances of macroinfauna, physical variables and monthly mean abundances of coexisting species are given in Table 8. Despite some significant correlation coefficients their respective coefficients of determination ( $R^2$ ) were quite low, ranging between 0.090 and 0.465. Thus, 9-47% of the variability in the dependent variable was accounted for by the variability in the independent variable. Monthly mean abundances of O. tuberculata and E. braziliensis were significantly correlated with water content (inverse relationship) and penetrability, while the mean abundances of E. hirsuticauda were significantly correlated with mean grain size. No significant correlations were found between monthly mean abundances of E. monodi and E. analoga and the physical variables, nor with the monthly mean abundances of coexisting species (Table 8). Variability in monthly mean abundances of O. tuberculata and E. braziliensis were

positively correlated to each other, and inversely correlated to E. hirsuticauda. Monthly mean abundances of E. hirsuticauda were inversely correlated with those of E. analoga.

Variability in monthly mean abundances of macroinfauna was analyzed using multiple regression analysis performed in two approaches (Table 9). Values of  $R^2$  in approach A indicated that 27, 18 and 13% of the variability in monthly mean abundances of O. tuberculata, E. braziliensis and E. hirsuticauda, respectively, were significantly accounted for by variability in some of the physical variables examined. Monthly mean abundances of O. tuberculata varied inversely with temperature and water content of sediments, while those of E. braziliensis and E. hirsuticauda were significantly accounted for by penetrability and mean grain size, respectively.

In approach B (Table 9), temperature and water content of sediments were the only variables significantly accounting for the variability in monthly mean abundances of O. tuberculata. The value of  $R^2$  obtained for E. braziliensis in the first approach (0.179 or 18%) increased to 0.465 (or 47%) in the second one, and due to variability in monthly mean abundances of its coexisting species, O. tuberculata. The later results can be explained by the fact that the determination coefficient between monthly mean abundances of E. braziliensis and O. tuberculata (0.465) was higher than that between monthly mean

abundances of E. braziliensis and penetrability of sediments (0.179). Therefore, the variance possible to be accounted for by variability in penetrability is already explained by the higher percentage being accounted for by temporal variability of O. tuberculata. Variability in monthly mean abundances of E. hirsuticauda was accounted for by 20% (a 7% increase over the first approach) through mean grain size and the inverse variability of monthly mean abundances of E. analoga. No variables were significant at the 0.05 probability level (neither in approach A or B) precluding their use in the multiple regression models for E. monodi and E. analoga.

Long-term Population Fluctuations. Long-term population fluctuations and downshore migration of the peracarid species at selected levels of Mehuín Beach are shown in Figure 24. The levels are those where the species are most abundant. In general, abundance peaks during 1978-1985 were similar in magnitude for O. tuberculata and E. hirsuticauda, while a decline appeared for E. braziliensis. Orchestoidea tuberculata and E. braziliensis--as already shown--had their highest abundances on the upper beach, while E. hirsuticauda occurred with high abundances, either at the middle or lower beach (also see Fig. 22).

During May, 1978 to April, 1980, O. tuberculata had its highest abundances (up to 450-500 ind m<sup>-2</sup>) during autumn months (May-June). From September, 1980 to

November, 1985 high abundances were reached, either during spring (i.e. 300 ind m<sup>-2</sup> in September, 1980 or 613 in November, 1983) or autumn (430 ind m<sup>-2</sup> in May, 1984) (Fig. 24). During late spring, summer and early autumn (December-April), O. tuberculata moved down to the middle beach, where its maximum abundances ranged between 108 ind m<sup>-2</sup> (April, 1980) and 194 ind m<sup>-2</sup> (March, 1984).

Excirolana braziliensis generally peaked in the spring (September-November) of the respective years, with values of up to 400-500 ind m<sup>-2</sup> on the upper beach (October, 1979 and November, 1978, respectively). From late spring to early autumn, this species peaked on the middle beach, reaching abundances of 170-270 ind m<sup>-2</sup> (February and January, 1979, respectively) (Fig. 24). With the exception of 1983, E. hirsuticauda reached its highest abundances during summer and early autumn months (January-May), particularly on the lower beach (Fig. 24). The highest abundance of this species occurred during April, 1979 (558 ind m<sup>-2</sup>, lower beach), November, 1983 (468 ind m<sup>-2</sup>, middle beach) and January, 1985 (403 ind m<sup>-2</sup>, lower beach).

Long-term fluctuations of E. analoga on the lower beach were very erratic (Fig. 25). During May, 1978 to April, 1980, the highest abundance (251 ind m<sup>-2</sup>) occurred in June, 1979. From September, 1980 to November, 1985 high abundances (over 80 ind m<sup>-2</sup>) occurred almost every month,

with the exception of late spring and summer (December-March), when E. analoga had the lowest abundances, or was not collected at this level of the beach (Fig. 25).

Sand Depth Distribution. Seasonal variability of physical characteristics and macroinfaunal abundances versus sand depth at Mehuín Beach, are shown in Figures 26-28. Coarsest sand grains (1.60-1.99  $\phi$ , medium sands; Folk, 1980) occurred during winter, 1980, primarily in deep sediment layers (below 7.5 cm) of the middle and lower intertidal zone (Fig. 26). At this time, the finest sands were restricted to the highest beach levels. During the following spring and summer, width of the intertidal zone and coverage of fine sand increased significantly. During autumn, 1981, the 2.30-2.60  $\phi$  sands extended further down, but only in the shallowest sediment layer (0-2.5 cm) (Fig. 26). With the exception of winter, 1980, most sands analyzed were well sorted (0.35-0.50  $\phi$ ; Folk, 1980). Some intertidal levels showed a depth stratification in mean grain size and sorting values (e.g. September, 1980), with finer and better sorted sands occurring in the shallowest sediment layers (Fig. 26).

Figure 27 shows the increased warming and drying of sediments from winter to summer. The greatest differences in vertical and intertidal variability of temperature occurred during spring and summer. For example, during December and February, differences of 12-20 C were detected between the shallowest and deepest sediment layers at



stations 1 and 2, while during September and April, differences of 3-9°C occurred. In addition, differences of 21-25°C were found between the highest and lowest stations (i.e. 1 and 12) during spring and summer, while during winter and autumn these differences decreased to 5-6°C. Stratification of water content was observed at the high and middle beach levels. Vertical differences at these levels were similar among seasons (3-9%); however, the lowest water content values occurred during spring and summer. With the exception of September, the range of variability across the intertidal was similar among seasons, with differences of 12-15% between the highest and lowest stations.

Several points emerge from the analysis of the sand depth distribution of the macroinfauna (Fig. 28). Foremost, all the species were collected from the shallowest to the deepest sand layers sampled, but their maximum abundances occurred at different depths, which generally varied seasonally. Among the isopods, E. braziliensis usually inhabited deeper layers than E. hirsuticauda, which in turn, generally had its highest mean abundances at the shallowest depths (0-5 cm). With the exception of April, 1981, the highest mean abundances of E. braziliensis were detected below 5 cm. Highest mean abundances of O. tuberculata occurred at 5-10 cm depth in December, 1980 and February, 1981, while during other months, its highest mean abundances occurred in shallower

sediments (0-5 cm). Finally, highest mean abundances of E. analoga were detected at the deepest sand layers. During December, 1980 and February, 1981, O. tuberculata, E. braziliensis and E. hirsuticauda moved to lower stations than during September, 1980. At the same time, O. tuberculata and E. braziliensis moved to deeper sediments. During these months the mean abundances of both species in the shallowest layers (0-5 cm) of the high and slightly middle beach levels were the lowest as compared with that observed at the same depths during September, 1980 and April and September, 1981. During February, no animals were collected at station 1, nor from some depths of station 2. During April, 1981, O. tuberculata, E. braziliensis and E. hirsuticauda began to move upward until September, 1981, when they occupied similar levels (stations) to those occupied during September, 1980. At the same time O. tuberculata and E. braziliensis again occupied shallower sediments.

Figure 28 also shows that even when vertical and horizontal macroinfaunal movement occurred seasonally at Mehuín Beach, the basic zonation pattern was generally maintained; O. tuberculata and E. braziliensis occurred on the upper intertidal, E. hirsuticauda on the middle, and E. analoga on the lower beach levels.

Cross correlation coefficients between the seasonal mean abundances of O. tuberculata, E. braziliensis and E. hirsuticauda, physical variables, and seasonal mean

abundances of coexisting species are given in Table 10. The respective coefficients of determination of those significant correlations ranged between 0.113 and 0.263 showing that a low percentage of variability in the dependent variable was accounted for by variability in the independent variable. Seasonal variability in sand depth distribution of the peracarid species was analyzed through multiple regression analyses (Table 11). No variable was significant at the 0.05 probability level, in order to be included in the multiple regression model for Q. tuberculata. When only physical characteristics were employed as independent variables (approach A), 19% of the variability in mean seasonal abundances of E. braziliensis was accounted for by variability in mean grain size and sediment temperature (inverse relationship). Similar percentage of variability in mean abundances of E. hirsuticauda was explained by the inverse variability of sediment water content. The addition of the mean abundances of coexisting species as independent variables (approach B) did not produce any change in the results obtained for E. braziliensis by the first approach (A, Table 11). On the other hand, approach B produced different results for E. hirsuticauda versus approach A; the value of  $R^2$  increased to 26.3% and no physical characteristics were significant in accounting for the variability in mean abundances of this species. Instead, the variability in mean abundances of E. hirsuticauda was

only accounted for by variability in mean abundances of E. braziliensis. Emerita analoga was not included in any regression analysis due to its low frequency in samples and samplings.

Local Distribution. Table 12 shows the physical characteristics of beaches sampled along Bahía de Maiquillahue and outlet areas of Río Queule and Río Lingue during the summer of 1983. The four sites at Mehuín (exposed) and those located at the outlet areas of Río Queule and Río Lingue (protected) are fine sand habitats (2-3  $\phi$ , Folk, 1980), with very well or well sorted sediments (under 0.35  $\phi$  and 0.35-0.50  $\phi$ , respectively; Folk, 1980). The exposed beach at Matías has fine and medium sands (1-3  $\phi$ ; Folk, 1980), while the semiexposed site at Isla de Maiquillahue is represented by coarse sands (0-1  $\phi$ ; Folk, 1980). The sorting values calculated for the sands of Matías and Isla de Maiquillahue are close to the ranges of moderately well sorted sediments (0.50-0.71  $\phi$ ; Folk, 1980), while all the others fit in the ranges of very well sorted or well sorted sediments. No significant correlation ( $p > 0.05$ ) was found between beach face slope and mean grain size ( $r = -0.14$ ), e.g. sites with similar values in slope (i.e., sites 1 and 6) had very different mean grain size values, and vice versa (Table 12).

Relationships between mean abundances of the species collected at those eight sites (Table 13) and mean grain

size and sorting values are shown in Fig. 29. Among the isopods, E. braziliensis and E. monodi were only collected at stations with fine sands, while E. hirsuticauda inhabited medium and fine sands. Orchestoidea tuberculata was collected from fine and coarse sand, while E. analoga inhabited sediments covering the range from fine to coarse sand (Fig. 29). Stations where E. braziliensis and E. monodi were collected had the narrowest range in sorting (from 0.25 to approximately 0.50  $\phi$ ), while those in which the other species were collected covered a wider range (Fig. 29). No significant correlations ( $p > 0.05$ ) between mean abundances and mean grain size and sorting were found for E. braziliensis, E. monodi and E. analoga. Mean abundances of O. tuberculata and E. hirsuticauda were significantly ( $p < 0.05$ ) and negatively correlated with mean grain size values and significantly and positively correlated with sorting. However, values of  $R^2$  were quite low (0.18-0.34).

Excirologana hirsuticauda and E. analoga reached the highest abundances along the beaches sampled at Bahía de Maiquillahue (Table 13). No isopods were collected from the coarse sands of Isla de Maiquillahue, while fine sands of the outlet areas of Río Queule and Río Lingue lacked E. analoga, a species present in the low beach levels of all the other beaches.

Intertidal distribution of the macroinfauna, along Bahía de Maiquillahue and the outlet areas of Río Queule

and Río Lingue can be described in terms of three zonation patterns (Fig. 30). The first pattern represents the distribution found at all the sites of Mehuín and Matías: E. braziliensis and O. tuberculata on the high beach levels, E. hirsuticauda and E. monodi on the middle beach levels and E. analoga on the low levels of each beach. The second pattern, is that found at the outlet areas of Río Queule and Río Lingue, and is characterized by the absence of E. analoga and the lower distribution of E. hirsuticauda and E. monodi. The third pattern characterizes the intertidal distribution of macroinfauna at Isla de Maiquillahue. At this beach, isopods are absent, and the middle beach levels lack any macroinfauna (Fig. 30).

#### Laboratory Experiments

Salinity Tolerances. No species experienced mortality at the control salinity (28 o/oo) after 1 week (Fig. 31). With the exception of the mortality shown by E. hirsuticauda at 5 o/oo, survival of the peracarids was near or higher than 90% at 5-15 o/oo. Emerita analoga exhibited the highest mortality at these salinities; i.e. all the animals died at the end of the first day in 5 o/oo and 10 o/oo (Fig. 31).

Grain-size Preferences. In the preference experiment with four prepared sands (Table 14), O. tuberculata did not show significant preferences in two experiments, while in two others it preferred medium and coarse sand. No

preferences were shown for E. braziliensis in one run, while in the other, it showed increased preference as grain size increased. Excirolana hirsuticauda had strong preference for coarse sand, while E. analoga showed no preference (Table 14).

Experiments with two sizes of prepared sand (Table 15) showed no preferences for O. tuberculata and E. analoga, while E. braziliensis and E. hirsuticauda preferred medium over fine sands. No significant preferences were found when sands from the upper and middle beach were offered to O. tuberculata, E. braziliensis and E. hirsuticauda (Table 16), or when sands from Isla de Maiquillahue and Matías were offered to the just mentioned two species of isopods (Table 17).

Sand Desiccation Tolerances. Species tolerances to sand desiccation are shown in Fig. 32. Water content in the sand dropped from 20% to 2.3% after 24 hours. Orchestoidea tuberculata, E. braziliensis and E. hirsuticauda showed significantly lower mortality than E. analoga (Table 18), whose mortality rate increased drastically after 3 hours, when water content fell to 16.5%. The mortality of E. analoga was 100% after 15 hours in sands of 7.2% water content (Fig. 32).

Mortality rates of O. tuberculata, E. braziliensis and E. hirsuticauda did not differ significantly from each other during the first 15 hours of the experiment. After 18 hours, the mortality rate of O. tuberculata was

significantly higher than that of both E. braziliensis and E. hirsuticauda (Table 18). Mortality of O. tuberculata was 100% after 21 hours with a water content in the sand of 3.8% (Fig. 32). At the end of the experiment mortality of E. braziliensis was complete, while 28.9% of the specimens of E. hirsuticauda were still alive (Table 18).

Species Coexistence Experiments. No significant differences were found in the mortality rate of O. tuberculata, E. braziliensis and E. hirsuticauda after 15 days in the intraspecific coexistence experiments (Table 19). As an overall mean, the mortality rate of O. tuberculata (35.4%) was approximately 7 and 5 times higher than those of E. braziliensis (5.3%) and E. hirsuticauda (6.5%) species which had similar mortality rates.

No consistent differences emerged from the interspecific coexistence experiments run with different depths of sand or different light conditions (Table 20 and 21). In half of the runs, the mortality rate of E. braziliensis and E. hirsuticauda was significantly higher when held with O. tuberculata, versus controls where each species was held alone (Table 20 and 21). In these runs, the overall mean mortality rate of E. braziliensis was almost 6 times higher than in the controls, while for E. hirsuticauda its overall mean mortality rate was approximately 8 times higher than the single species controls. There were no significant differences in



mortality rates of coexisting E. braziliensis and E. hirsuticauda over a period of 15 days versus control treatments (Table 20 and 21). Similar results were obtained for O. tuberculata when maintained with either E. braziliensis or E. hirsuticauda.

#### IV. DISCUSSION

##### Mehuín Beach

Recent studies in sand beach dynamics have resulted in the classification of these coastal habitats as distinct beach types. Dissipative and reflective beaches represent the extreme forms, between which several intermediate types occur (Short, 1979, Wright and Short, 1983, 1984, Wright et al., 1985). Mehuín Beach, fits the dissipative category quite well. Dissipative beaches have a wide multibarred surf zone; waves break 100-200 m seaward of the face of the beach, and consequently, dissipate most of their energy before reaching the beach. Other characteristics of these beaches are: rarity of significant longshore irregularities (e.g. beach cusps), flatter profiles that prevail in the presence of high steep waves, and usually fine grain sands. In contrast, reflective beaches (e.g. Matías and Isla de Maiquillahue, Fig. 1) are characterized by an almost virtual absence of surf zone. On reflective beaches, breakers surge and collapse close to the base of the beach face; consequently, much of the incident-wave energy is reflected from the beach face. They also have steeper profiles, coarser grains, and occur primarily as pocket beaches bordered at either end by rocky headlands, and take the form of an embayment (Short, 1979, Wright et al., 1979, 1985). Thus, this categorization is based upon

the relative contributions of nearshore processes (i.e. wave energy, longshore drifts), sediment size, and sediment abundance (Short and Hesp, 1982, Wright and Short, 1984).

The long-term study of the direction and frequency of the longshore drifts at Mehuín Beach, permitted me to analyze the relationship between sand dynamics, and the seasonality of these currents produced by the oblique wave approach to the shoreline (Putnam et al. 1945, Komar, 1976, 1983, Longuet-Higgins, 1970). However, these results should be considered preliminary as more work is needed.

When the entire 1978-1985 period was considered, it was found that the frequency of the north flowing longshore drift, was significantly correlated with sand level variability at the middle and lower beach, but coefficients of determinations were very low. This suggests that other factors (e.g. wave height, wave steepness, wave period, level of water table) may have been more important than longshore drift in producing the observed patterns. The same argument may be applied to the lack of correlation between longshore drift and sand level variability at the upper beach, where other physical processes (e.g. wind blowing) may be more important than nearshore water processes. Similar arguments were used by Pino (1982) to explain temporal variability of sand levels at the north and south ends of an exposed beach close to Mehuín Beach. He found that north flowing longshore drift was correlated

with variability in sand levels, but only at the south end, i.e. the end primarily affected by drift. Thus, the apparent importance of direction of wave approach to the shoreline dynamics of Mehuín Beach and adjacent beaches is not readily explained. Nevertheless, north flowing longshore drifts have usually been associated with storms and higher waves, while south flowing longshore drifts usually accompany moderate winds and lower waves (personal observation).

Seasonal patterns of sand dynamics at Mehuín Beach are similar to those commonly described for sandy beaches in temperate latitudes, where erosion occurs during winter storms, and sediment fill after summer swell (e.g. Davies, 1973, Fox and Davis, 1978, King, 1959, Komar, 1976). But, caution is suggested when the terminology winter and summer profiles is used in other geographic areas when the seasonal connotations may not be correct (Komar, 1976). In some areas, the so-called winter profiles are independent of season. For example, Jaramillo et al. (in press) reported the total erosion of sand at Rye Beach, New Hampshire, during the second quarter of 1977. Hayes and Boothroyd (1969) and Owens (1977) noted that cycles of erosion and accretion occur during any season in Massachusetts, and the east-facing barriers of Magdalen Islands (Gulf of St. Lawrence), respectively. These examples seem to be related to changes of wave energy, which may occur at any time. Consequently, changes in sand

levels may also occur at any time. By contrast, in other areas, such as the Pacific coast of the Americas, variability of wave energy follows a more predictable pattern. Consequently, beach dynamic is also more predictable (i.e. sand erosion during winter and sand accretion during summer) (King, 1959, Komar, 1976).

Several terms have been used to eliminate the seasonality implied in the terms winter and summer profiles, e.g. "storm" and "normal profile" (Johnson, 1949), "storm" and "post-storm profile" (Hayes and Boothroyd, 1969) and "storm" and "swell profiles" (Komar, 1976). The terms erosion and accretion profiles are used here, since the entire erosion and accretion periods covered more than one season, although the minimum and maximum sand levels usually occurred during winter and summer, respectively.

Periodic analyses of beach profiles at Mehuín Beach showed that during erosion periods, sand was moved off the beach, forming a rather concave profile, while during accretion periods, sand was moved onshore forming a convex profile. Considering the entire period between 1978-1985, differences between erosion and accretion levels were greatest at the middle and lower beach (nearly 142 cm as an overall mean). Reduced sand level variability at the upper

beach was probably due to the position of the post used to study sand variability; i.e. the wave energy dissipates farther up the surf zone.

The changes in sand levels conveyed a temporal variability in the size of the sediments; coarser grains usually occurred when the heights of the post and reference rocks were highest (more erosion), and vice versa (more accretion) (Fig. 11). The mean grain size data for the period May, 1978 to April, 1980 showed that the magnitude of variability was quite different from year to year. Coarsest grains occurred during winter, 1978, particularly at the lower intertidal. The pattern was different from that observed during winter, 1979 (June to August) when particles were finer, and mean grain sizes changed little during the entire year. Thus, the intensity of erosion has a critical magnitude to produce significant changes in the size of the sand particles, as during 1978, particularly at the middle and lower beach. Differences in intensity of erosion between winters of 1978 and 1979 may have been related to the effect of waves, tides, or a combination of these factors, plus longshore drift, since no apparent differences in the frequency of the north flowing longshore drift was observed between the two erosion seasons. Thus, even if the seasonality of the erosion-accretion cycle at Mehuín Beach was quite predictable from year to year, the magnitude of the variability was not. Consequently, the

values of textural characteristics of the sediments (e.g. mean grain size, sorting) and beach face slope may be quite unpredictable.

Beach sands have been considered to be one of the best sorted sediments (e.g. Folk, 1980, Inman, 1949). Sorting and grain size are usually correlated (e.g. Bascom, 1951, Folk and Ward, 1957, Griffiths, 1951, Inman, 1949, King, 1959), as they were at Mehuin Beach. The relationship is useful in the interpretation of dynamic beach processes (Folk, 1980, Krumbein, 1944). Most homogeneous (best sorted) particles at Mehuin Beach occurred during accretion periods, when finest sands were observed. On the other hand, most heterogeneous grains (or less sorted) occurred at the lower intertidal during winter and early spring, 1978. These were the coarsest sediments ever observed. The poorer sorting during this period probably arose from a mixture of two grain sizes in the samples, a result of intense erosion on the beach during winter and early spring, 1978.

In addition to waves and longshore currents, water content of sediments has also been shown to influence sand dynamics (Chappell et al. 1979, Duncan, 1964, Grant, 1948, Harrison, 1969, Sallenger and Richmond, 1984, Waddell, 1976). A water table near the surface accelerates erosion, due to minimal downward movement of water and increased erosive backwash. On the other hand, a deeper water table

(e.g. in drier sediments) facilitates deposition since downward movement of water increases and so, backwash velocities decrease (Duncan, 1964, Grant, 1948). Studies of Duncan (1964), Harrison (1969) and Waddell (1976) showed sequential movements of sand according to tidal variability of water table level. It is also possible that water level fluctuations of wider resolution (e.g. seasonal) affect sediment dynamics of exposed sandy beaches; e.g. an increased water content of the substrata should enhance backwash velocity, and consequently erosion. More sand was in fact moved off the intertidal zone at Mehuin Beach during months having wetter sands and vice versa; i.e. water content of the sediment and mean erosion were significantly correlated. Coefficient of determination indicates that variability in water content accounted for by 61.9% of variability in mean erosion, a higher percentage than that accounted for by variability in frequency of north flowing longshore drift during May, 1978 to April, 1980 ( $R^2$ : 0.156). The analyses show that no adequate understanding of sand dynamics can be achieved without combining a study of sand level variability with data concerning the temporal variability in water content, and the location of the water table.



### Temporal Fluctuations of the Macroinfauna

Species composition, abundance and zonation patterns of the sandy beach macroinfauna have been discussed in the literature in relation to: wave exposure and grain size (e.g. Bowman and Dolan, 1985, Colman and Segrove, 1955, Croker, 1977, Dexter, 1979, Fincham, 1974, Jones, 1970a, McLachlan et al. 1981, Sameoto, 1969c, Seed and Lowry, 1973), beach face slope (McLachlan et al. 1981, Perry, 1980), sediment temperature (Bertrań, 1985, Jones, 1970a, Vohra, 1971), water content of the sediments (Bally, 1983, Bertrań, 1985, Hager and Croker, 1979, Hayes, 1977, McLachlan, 1980, Salvat, 1964, Sameoto, 1969a, Wendt and McLachlan, 1985), and beach profile changes due to storms (Ansell et al. 1972a, Jaramillo et al. in press, McLusky et al. 1975). Nevertheless, quantitative correlations among those factors and macroinfaunal variability have rarely been performed, particularly on a single beach.

Contrary to what the field data from Mehuín Beach showed; coarser sands associated with lower macroinfaunal abundances, none of the species showed significant avoidance of the coarsest grains in the laboratory experiments. This indicates that differences in sand coarseness between the winters of 1978 and 1979 were not important for the observed differences in macroinfaunal abundances during these times. Other physical characteristics of the beach (i.e. temperature, water content and penetrability of the substrata) were not

implicated either, since their variability was similar during both winters. Instead, the low macroinfaunal abundances of the winter, 1978 were probably caused by a significant loss of habitat, simply followed by the appearance of coarser particles than those present before erosion. Field data from different beaches of Bahía de Maiquillahue during summer, 1983 support this explanation. Orchestoidea tuberculata, E. braziliensis, E. hirsuticauda and E. analoga were collected from beaches with coarser sediments than those of Mehuín Beach. Moreover, some of these species had higher abundances at these beaches, e.g. O. tuberculata at Isla de Maiquillahue, and E. hirsuticauda at Matías (Table 13). Therefore, the peracarids of Mehuín Beach may occur abundantly at beach levels having coarse sands similar to those observed during the erosion period of 1978 (1.60-2.00  $\phi$ ) or even coarser, e.g. E. hirsuticauda in sediments of Matías (1.76-1.86  $\phi$ ), and O. tuberculata in the upper beach levels of Isla de Maiquillahue (0.63-0.81  $\phi$ ). The key factor seems to be the distance of the particular beach levels from the wave breaking zone.

Invertebrates with planktonic larvae such as E. analoga, are subjected to spatial and temporal variability of physical and chemical factors, both in the substrata and in the water column. Significant variability of atmospheric and nearshore processes may occur from year to year affecting larval dispersal, which in turn affects the

intensity of settlement and subsequent population structure. Consequently, species without planktonic development, such as the peracarids found at Mehuín Beach, should exhibit more stable population structures than E. analoga. Life history characteristics of macroinfaunal species observed during May, 1978 to April, 1980 support this assertion.

The reproductive season of Q. tuberculata, E. braziliensis and E. hirsuticauda occurred during warmer months, which is similar to reports from other temperate areas (e.g. Bowers, 1964, Fish, 1970, Jones, 1970b, Sameoto, 1969b). The seasonality of the life cycle of these species was illustrated by the abrupt disappearance of ovigerous females when recruits peaked, a clear annual cycle. Although the beach characteristics and species abundances during the pre-reproductive winter seasons of 1978 and 1979 were quite different, the general characteristics in the life cycle of the peracarids remained similar during these time periods. No apparent differences in size structure were observed, and the percent occurrence and mean abundances of juveniles and ovigerous females were generally similar. Consequently, even though the abundances of the peracarids of Mehuín Beach were severely depressed during the winter of 1978, the reproductive capability of these species was not significantly affected. On the other hand, erosion events during the winter of 1978 and 1979 may have indeed affected

the population structure of E. analoga. Juveniles of this species were more abundant during late autumn-winter of each year, although mean abundances were nearly 24 times higher during the winter, 1979 (205 ind m<sup>-2</sup>), versus similar period in 1978 (9 ind m<sup>-2</sup>). The dispersal pattern of E. analoga is typically aggregated, and usually attributed to physical characteristics such as wave energy, tidal levels, grain size, beach face slope, and the presence of beach cusps (Barnes and Wenner, 1968, Bowman and Dolan, 1985, Cubit, 1968, Dillery, 1970, Perry, 1980). All of these characteristics would be significantly different during an intensive erosion period, and may have impacted patterns of juvenile distribution and abundance. In fact, hydrographic characteristics such as waves, winds, and littoral currents may have even acted earlier by affecting dispersion and availability of larval stages, in this way impacting on subsequent juvenile abundances of Emerita. Changes in beach characteristics and associated atmospheric variability have also been assumed to cause changes in the population structure of other species of Emerita, e.g. E. talpoida in North Carolina, USA (Diaz, 1980), and E. holthuisi in India (Ansell et al., 1972b).

Seasonal temperature variability is an important physical factor on temperate sandy beaches. When beaches are exposed to the air, heating, drainage, and wind action cause surface layers to dry, particularly at high tide levels (Brown, 1971, Jansson, 1967, Johnson, 1965, Pearse

et al., 1942, Pollock and Hummon, 1971, Salvat, 1967). Heat alone, or associated with desiccation stress, has been shown to determine the upper distributional limits of intertidal organisms (e.g. Connell, 1972, Dring, 1982, Newell, 1979, Stephenson, 1942). Croker (1967a), Hager and Croker (1979), and Preece (1971) have shown, for example, that sandy beach species with higher intertidal distributional limits have higher sand desiccation tolerances. The results of the sand desiccation experiments of this study provide some exceptions to this generalization.

Contrary to what was expected in view of the field distributional data, sand desiccation tolerance of the middle beach E. hirsuticauda was higher than for the upper beach O. tuberculata and E. braziliensis. The lowest values of water content in the experimental sands (2.3-6.1%) were well within the variability of the water content of beach levels inhabited by O. tuberculata and E. braziliensis. In contrast, experimental values were higher than those calculated for the beach levels occupied by E. hirsuticauda; even though, the mortalities of this species were quite low (i.e. below 18%). The results suggest that sand desiccation is not a significant barrier to the landward distribution of E. hirsuticauda.

During warmer months, the peracarid assemblage at Mehuín Beach undergoes a general downshore migration. Similar movements have been reported in other temperate

sandy beaches. Fish (1970) and Salvat (1966) found that during summer, the abundance of the isopod Eurydice pulchra decreased at its upper limit of distribution in sandy beaches of Wales and France, respectively. Jaramillo et al. (in press) reported that in Rye Beach, New Hampshire, amphipods (Acanthohaustorius milsi) and polychaetes (Scolelepis squamata and Paraonis fulgens) moved seaward during the summer. Likewise, in northern central Chile, Sanchez et al. (1982) found that the zone of maximum abundance of O. tuberculata and E. braziliensis moved downshore during summer. The same two species also moved down to the low intertidal during the warmer months on a protected beach (site 8 of this study, Fig. 1) at the outlet area of Río Lingue (Bertran, 1985).

Sand desiccation is a major factor correlated with the seasonal fluctuations in the intertidal distribution of O. tuberculata and E. braziliensis. During warmer months, both species were essentially absent from dry sediments of the upper beach, bringing to mind the low survival of both species in laboratory experiments with sand having desiccation values similar to those for the upper beach during these months. In addition, among the physical variables considered here, only sand desiccation related factors (i.e. water content and penetrability of the sands) significantly accounted for the temporal variability of O. tuberculata and E. braziliensis. The non-significance of

textural variability (sand grain size and sorting) in accounting for the population fluctuations of these species in the field was in agreement with the lack of significant response of these animals to textural differences in some experiments with prepared sands, and in that experiment with natural sands from the upper and middle beach.

The position of the wrack line may also be important in regulating the intertidal location of O. tuberculata, as it is for other talitrids; i.e. higher abundances are close to the drift line (Bowers, 1964, Griffiths and Stenton-Dozey, 1981, Koop and Griffiths, 1982). At Mehuín Beach, the wrack line is primarily composed of detritus from brown macroalgae such as Macrocystis pyrifera and Durvillaea antarctica, the main food sources for O. tuberculata (Duarte, 1974). During warmer months, the wrack line is generally located lower in the intertidal zone than in late autumn-early spring. During summer, sand levels are higher (beach accretion), therefore waves usually reach the uppermost beach levels only during spring tides. Thus, the downshore migration of O. tuberculata during warmer months, may well be a response to the combined effect of sand desiccation and the changing location of the wrack line.

The monthly mean abundances of O. tuberculata and E. braziliensis were lower in sediments with lower penetrability, suggesting that the seaward distributional limits of both species during summer migration are determined by hardness of sediments. Sand penetrability

may also be important in driving these species up during late autumn-early spring, when lower intertidal levels have harder sands. At that time, O. tuberculata and E. braziliensis become concentrated in the uppermost beach levels where sediments maintain a degree of penetrability suitable for burrowing.

Excirolana hirsuticauda also showed a downshore migration during the warmer months, a migration that was particularly distinctive during the seasonal study (September, 1980 to September, 1981). Sand desiccation related factors are probably not the primary factors involved here since E. hirsuticauda experienced low mortality in experimental sands that were even drier than those in which it naturally occurs. In addition, no sand desiccation related factors significantly accounted for variability in monthly mean abundances for this species. Instead, textural variability (i.e. mean grain size) was involved. Significant avoidance of the finest prepared sands shown by E. hirsuticauda in the laboratory, suggests that its downshore migration during warmer months, may result from avoidance of fine sands deposited during the accretion period of the beach, particularly at the upper and middle beach levels.

Since E. hirsuticauda reaches the hardest beach sediments during its downshore migration, and since no negative correlation was found between its monthly mean abundances and sand penetrability, it is concluded that



compactness of substrata does not determine the lower distributional limit of this species versus O. tuberculata and E. braziliensis. Instead, its limits may be related to wave disturbance. At exposed sandy beaches, the greatest wave shock occurs towards the breaking wave zone where sediments are churned into a suspension. This has been evaluated, among others, by Duncan (1964) who found that during rising tides, larger amounts of sands (up to 30 cm depth) are removed from areas close to the surf zone of a California beach. Perhaps, an increase in sediment disturbance during late autumn-early spring is connected with the upshore movement of the maximum abundance zones of E. hirsuticauda to higher beach levels. At that time, the upshore movement would not be affected by the sand size since grains are coarser than during the warmer months. This would also explain why E. hirsuticauda did not avoid the upper beach sands in the experiment with natural sediments collected during winter, 1983; i.e. at that time the upper beach sands were coarser than during the warmer months.

Several differences were found between the MRA performed with the monthly and seasonal population data of E. braziliensis and E. hirsuticauda. The main differences were found for the latter species (cf. Table 9 and 11). The low number of samplings in the seasonal study may have missed some higher variability in textural characteristics, accentuating differences in sand desiccation related

factors. Thus, these differences may have played a major role in accounting for seasonal variability of E. hirsuticauda in approach A. The chosen sampling frequency may also have missed differences between the mean abundances of E. braziliensis and E. hirsuticauda, thus yielding a positive correlation between the two species and in turn overriding the role of physical variables in approach B. It should also be stressed that the population data included many values from the overlap zone between the two species, where their abundance transformed values were quite similar.

#### Local Distribution of the Macroinfauna

Three different macroinfaunal zonation patterns were recognized in Bahía de Maiquillahue and outlet areas of Río Queule and Río Lingue. The typical zonation of sites 1-5 (including Mehuin Beach) differed from that found at Isla de Maiquillahue by the absence of cirolanid isopods. Apart from the obvious differences in grain size, the sands of Isla de Maiquillahue also differed from the other sites in grain shape. Sites 1-5 had subangular sediments (0.29-0.34), while Isla de Maiquillahue had subrounded grains (0.42) (after Powers, 1953).

Neither, E. braziliensis or E. hirsuticauda showed significant avoidance of sands from Isla de Maiquillahue in the preference experiments, results which were not expected because of the absence of cirolanids at this site. Two

explanations may be offered for this absence. Foremost, there are other physical factors or biological interactions involved. Secondly, coarseness and angularity of the sands of Isla de Maiquillahue may be important factors, not in themselves, but rather through some more subtle properties (e.g. porosity, permeability, fabric, compactation) that are altered when sediments are removed from the field. Thus, the absence of cirrolanids at Isla de Maiquillahue remains an unanswered question.

Zonation patterns at the exposed sites 1-5 also differed from those of the protected beaches of the outlet areas of Río Queule and Río Lingue. The low salinity tolerances of *E. analoga* in the laboratory experiments, suggest that its absence from the outlet estuarine areas is due to the lower salinities of these habitats (Bertrañ, 1985, Jaramillo, 1978, Jaramillo et al. 1985, Richter, 1985). In addition, the absence of a surf zone at these estuarine areas, may in turn indicate an absence of an adequate food source in suspension, precluding the establishment of this suspension-feeder at these sites.

The lower salinities of the waters adjacent to the outlet areas were first suspected as being responsible for the lower abundances of peracarids there, as compared with higher abundances at the exposed beaches of Bahía de Maiquillahue (Bertrañ, 1984, Jaramillo, 1978). However, this was not supported by laboratory salinity tolerance

experiments with O. tuberculata, E. braziliensis and E. hirsuticauda. The significant avoidance of the finest sands shown by E. hirsuticauda in the experiments with prepared sands (also O. tuberculata and E. braziliensis in some runs), suggests that the lower abundances of peracarids throughout the intertidal fine sand habitats of both estuaries is related to grain size of sediments. On the other hand, absence of wave shock, and differences in sediment disturbance and predation may be suggested as causing the wider intertidal distribution of cirolanid isopods at these outlet estuarine areas (i.e. occupying the lower beach levels) versus exposed sites 1-5. As discussed earlier, the greatest sediment disturbance in the exposed sandy beaches occurs towards the breaking wave zone. Therefore, the lower distribution of cirolanids at the outlet areas of Río Queule and Río Lingue may well be a response to the absence of that disturbance at these sites.

Concerning potential predators on the macroinfauna, the shorebird Calidris alba (Scolopacidae) feeds on the swash zone of the exposed beaches of Bahía de Maiquillahue. Its usual prey includes E. analoga and the cirolanid isopods (E. Jaramillo, unpublished data). Consequently, shorebird predation may play a role in setting the lower limit of distribution of cirolanids on these beaches. On the other hand, shorebirds are rarely seen at the estuarine outlet sites studied. It has been shown, that higher densities and smaller distance between prey (Excirolana

spp., E. analoga) increase the capture rate of C. alba in experimental conditions (Myers et al. 1980). So, the low abundances of cirolanids (and consequently, more spacing among individuals) and the absence of E. analoga in the protected sites of the outlet areas of Río Queule and Río Lingue would preclude more frequent predation by C. alba at these sites. In addition, more penetrable substrata also increases the rate of prey capture of C. alba under controlled conditions (Myers et al. 1980). The absence of a swash zone at the outlet sites may also convey important differences in sand penetrability; differences which in turn may affect the suitability of these sites as foraging areas for C. alba. But, even though shorebird predation may have some effect on the population abundances of cirolanids at the exposed sandy beaches of Bahía de Maiquillahue, their participation in materially affecting the observed zonation differences in the intertidal distribution of the peracarid species is ruled out for several reasons. Foremost, shorebirds are migratory species that use the coastal habitats of southern Chile, only during the winter migration from the northern hemisphere. Calidris alba appears in Bahía de Maiquillahue during spring and leaves during late summer-early autumn (Schlatter and Jaramillo, 1983). The presence of shorebirds does not appear to negatively impact the intertidal distribution of isopods, i.e. cirolanids generally have a lower distribution in the intertidal zone

during spring and summer than during other seasons of the year, and they are in the zone where shorebirds usually forage. Secondly, the abundances of C. alba on exposed beaches of Bahía de Maiquillahue are far less than on beaches in northern Chile (P. Myers, personal communication). On those northern exposed beaches, cirolanids show a zonation pattern similar to those on exposed beaches of Bahía de Maiquillahue further south (Castilla et al. 1977, Jaramillo, in press, Sanchez et al., 1982). Thus, there is, no evidence that higher abundances of shorebirds produce differences in zonation patterns of cirolanid species.

Shorebird predation may have a more important role for the population structure of E. analoga. Juveniles of E. analoga are preyed on by the shorebirds C. alba and Numenius phaeopus (Scolopacidae) (E. Jaramillo, unpublished data). Mean abundances of juveniles of Emerita during 1978-1980 showed a pattern of late summer or winter recruitment when shorebirds had either left Mehuín Beach or were present in very low numbers (Fig. 33, Jaramillo, unpublished data). Published evidence (Schlatter and Jaramillo, 1983) and personal observations document the departure time of shorebirds. Currently, the only data concerning recruitment periods of Emerita are those presented here. A potential relationship between shorebird predation and the abundance of Emerita juveniles could work in one of two ways: 1) low abundances of juveniles during

maximum abundance periods of C. alba and N. phaeopus (i.e. late spring-early summer) could be the result of shorebird predation, and 2) even though some juveniles are recruited during periods of maximum shorebird predation, most of them would arrive (from the plankton) close to the time or after C. alba and N. phaeopus leave the area. Therefore, the recruitment patterns of Emerita would be synchronized with the shorebird departure, minimizing loss of new recruits. Since ovigerous females of E. analoga were detected from middle spring (October-November), this would imply that incubation and the planktonic period are long enough to produce a recruitment peak during late summer-early winter. This would be true if the life history of E. analoga at Mehuín Beach is similar to that of Californian populations that take 18-32 days for incubation (Booolotian et al., 1959, Cox and Dudley, 1968). In fact, a pelagic period as long as four months was deduced from planktonic collections off the coast of San Diego (Johnson, 1939). Clearly, long-term study of recruitment of Emerita and shorebird predation would be required to test the earlier hypotheses.

#### Peracarid Interactions

The situation at Mehuín Beach illustrated by E. braziliensis and E. hirsuticauda with maximum abundances at the upper and middle beach, respectively, represents a common example of two closely related species partitioning available space. Both horizontal and vertical space

partitioning have been suggested as reducing, or avoiding potential competition between peracarids of oceanic sandy beaches (Jones, 1979, Croker, 1967a, Croker and Hatfield, 1980), and intertidal sand flats (Fenwick, 1984, Grant, 1981). For example, Croker and Hatfield (1980) reported that at Long Sands, Maine, the haustoriids Haustorius canadensis and Acanthohaustorius millsii illustrated horizontal segregation that was most marked for ovigerous females and juveniles. Furthermore, they reported that in the laboratory, adults of A. millsii experienced increased mortality and lower reproductive output when in combination with H. canadensis, as compared with single species controls. Similarly, Grant (1981) reported that at North Inlet, South Carolina, A. millsii and Pseudohaustorius carolinensis were vertically segregated in the upper oxidized layer, and the underlying reduced layer, respectively. When these two species were tested under laboratory conditions, it was shown that at high densities and in the absence of A. millsii, P. carolinensis expanded its niche to the oxidized layer. In contrast, when maintained at low densities, both species were able to co-exist in the oxidized layer (Grant, 1981).

The coexistence experiments between E. braziliensis and E. hirsuticauda did not provide adequate evidence for competition between these species. It is, of course, still possible that some sort of negative interaction might occur



over a longer time period, affecting other characteristics of their life history not studied here, e.g. reproductive output. Furthermore, it may also be true that partitioning of the intertidal by E. braziliensis and E. hirsuticauda is an evolutionary result of past competition (e.g. Diamond, 1986).

The results of the coexistence experiments were similar to those of Abramsky and Sellah (1982) and Schroder and Rosenzweig (1975) where in the absence of one species the other failed to show a response. Thus, it has been argued that competition may have operated in the past, but that lack of response in the present is due to genetically fixed habitat differences resulting from that interaction, process which has been called habitat selection (e.g. Abramsky and Sellah, 1982, Diamond, 1986, Rosenzweig, 1981). The responses detected by Croker and Hatfield (1980) and Grant (1981) might therefore represent some evidence of an ongoing competitive process, while the lack of response in the coexistence experiments with Excirolana spp. might indicate that competition had already run its course. One field test of this hypothesis would be a comparison of the intertidal distribution of both species at sympatric and allopatric locations. For example, E. braziliensis in allopatry (northern Chile, Jaramillo, in press) does not occupy the middle beach levels that are occupied by E. hirsuticauda at Mehuín Beach, or in other sympatric localities of southern Chile (Jaramillo, in

press). Conversely, a comparison of Mehuin Beach with the beach at Muicolpue (approximately 100 km to the south of Mehuín Beach), an allopatric locality for E. hirsuticauda (Jaramillo, in press), shows that this species does not expand its distribution to the uppermost beach levels at this site where E. braziliensis is absent. Yet, sandy beaches of northern and southern Chile are affected by very different environmental conditions (Jaramillo, in press). Consequently, there is no certainty that the only difference between the compared beaches is the absence of one of the species. All the available information then suggests that the habitat partition shown by E. braziliensis and E. hirsuticauda at Mehuín Beach is not the result of obvious competition at present. If so, it is reasonable to suspect that these interactions may have affected not only space partitioning, but also some characteristics of the life history of the species, and this in turn could have reinforced niche differences between E. braziliensis and E. hirsuticauda.

Differences in time of reproduction and body size ratios have been assumed to be important for decreasing potential competition in closely related sandy beach crustaceans (Croker, 1967a, 1967b, Dexter, 1967, Sameoto, 1969a). For example, Croker (1967a) found that in sandy beaches of Georgia the co-occurring and primarily upper intertidal haustoriids Neohaustorius schmitzi and Haustorius sp. had their reproductive peaks at slightly

different periods. He also found that reproducing N. schmitzi showed higher mortality in the laboratory when held together with the larger Haustorius sp. Croker concluded that staggering of reproductive periods along with vertical segregation would be advantageous for decreasing potential competition between the two species. Similarly, Sameoto (1969a) reported that in sandy beaches of Massachusetts, Haustorius canadensis had a slightly earlier reproduction than the co-occurring smaller Neohaustorius biarticulatus, augmenting the size difference between the species that the author believed important from the standpoint of the foods eaten and the reduction of potential competition. Common to the conclusions of Croker (1967a) and Sameoto (1969a) is the argument that body size is a criterion of niche differentiation in the amphipod species studied. Thus, based on the concept of a minimum size allowing coexistence between closely related species that consume the same food (Hutchinson, 1959), as haustoriids do (e.g. Croker, 1967a, 1967b), Croker (1967a) and Sameoto (1969b) calculated body size ratios between pairs of haustoriids in Georgia and Massachusetts, respectively. Croker (1967a) found that the overall mean ratio of body lengths for co-occurring species pairs was 1.42, close to the minimum body size ratio tentatively suggested by Hutchinson (1.3), and slightly higher than the overall mean for species pairs spatially segregated in the intertidal zone (1.27). Body size ratios reported by

Sameoto (1969a) varied between 1.50-2.20 depending upon the time of year. But it should be addressed that the generality of a minimum body size ratio among coexisting and closely related species has been strongly criticized (Simberloff, 1983, Simberloff and Boecklen, 1981).

The analyses of life history characteristics of E. braziliensis and E. hirsuticauda documented here showed that even though some differences were detected (e.g. brood sizes), most characteristics were very similar, e.g. ovigerous females and new recruits peaked at the same time period, and ratios of female/male were alike. The fact that body size ratios between the species are close to unity (overall mean: 1.09) suggests that juveniles and adults of E. braziliensis and E. hirsuticauda consume similar sizes of food, consisting primarily of organic material attached to sand grains (Jaramillo, personal observation), and again provides no grounds for assuming current competitive interactions between these species. The assertion supports earlier conclusions derived from the laboratory experiments and the intertidal zonation of the two species at sympatric and allopatric localities. Finally, if it is assumed that physical factors had a significant role in regulating population size in the past--as they do in the present--it can be concluded that density levels at which competition would occur were rarely reached. Therefore, the present segregation of E. braziliensis and E. hirsuticauda is more adequately

explained as a result of different adaptations to particular levels of the intertidal. For example, these isopods at first may have lived in allopatry under different environmental conditions. Later on, they became sympatric and occupied different areas of the intertidal at which each was better adapted (Connell, 1980).

Earlier I stated that neither an interaction with its congeneric, E. braziliensis, nor dryness in the upper beach, limits the upper distribution of E. hirsuticauda. The results of some of the coexistence experiments with O. tuberculata (i.e. higher mortality of E. hirsuticauda versus single species controls), suggest however, that this cirolanid might be limited in its landward distribution by the larger O. tuberculata. Nevertheless, the following points work against this idea. First, it is possible that the high mortalities of E. hirsuticauda when maintained with O. tuberculata in the laboratory do not represent a true picture of what really happens in the field. Talitrid amphipods are widely regarded as omnivorous (e.g. Behbehani and Croker, 1982, Bowers, 1964) with macroalgal debris stranded on beaches serving as their main food source (e.g. Behbehani and Croker, 1982, Duarte, 1974, Griffiths and Stenton-Dozey, 1981, Koop and Griffiths, 1982). The absence of its preferred food in the experimental containers may have induced O. tuberculata to prey on E. hirsuticauda to a greater extent than it does in nature.

In addition, the high abundances of animals in the containers (i.e. high frequency of interspecific encounters) may have reinforced intense predatory behavior, which is also assumed to be the cause of the high mortalities of O. tuberculata when maintained by itself. Second, although horizontal and vertical distribution of both species overlap during some months, their zones of maximum abundances do not. Thus, the frequency of interspecific encounters would be lower in the field. Another related point is that O. tuberculata shows high activity on the beach surface at time of low tides and primarily at night (Jaramillo et al., 1980). In contrast, E. hirsuticauda has its major activity during high tides, when it leaves the substratum to swim in the surf zone, as do other cirrolanids (Jones and Hobbins, 1985, Klapow, 1972). This difference in behavior would also decrease the frequency of interspecific encounters between the talitrid and E. hirsuticauda. It is concluded that the upper intertidal distribution of E. hirsuticauda is not regulated by biological interactions, but rather by physical factor variability as discussed earlier. Concerning the results of the interspecific experiments with E. braziliensis and O. tuberculata, arguments similar to those just presented for E. hirsuticauda may be put forward.

In summary, evidence to date shows that interspecific interactions do not play a significant role in the regulation of the abundance and intertidal distribution of

O. tuberculata, E. braziliensis and E. hirsuticauda at Mehuín Beach. Nor does it appear that we understand what the carrying capacity is for these peracarids, e.g. no significant differences were found in the mortality rate of the individual peracarid species even when abundances were increased up to 7 times the highest abundances observed in situ. Similar conclusions cannot be advanced for E. monodi, since no correlations were found between its abundances and the variability of coexisting species and that of any of the physical factors studied.

Finally, it is necessary to point out that the downshore migration of the peracarids of Mehuín Beach is contemporaneous with the human disturbance by vacationers during the December-March period of each year, particularly of the shallow sand layers on the upper beach. Human activities have been shown to affect the community structure of Chilean sandy beaches (Castilla, 1983, Castilla et al., 1977), but the specific effects on sand-burrowing invertebrates of people vacationing on sandy beaches have not been studied in Chile, or elsewhere. Two approaches may be taken to accomplish this. The first would be to close half the area of Mehuín Beach to human use and compare macroinfaunal responses there versus those on an adjacent control half. The second approach would require the choice of another beach, similar as possible to

Mehuín Beach, but where little or no human disturbance occurs. Fortunately, the coast of southern Chile may still provide the opportunity to carry out this experiment.



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Table 1. Number of animals used in the control and combination treatments of the interspecific coexistence experiments. The control treatments (single species) had 20 animals, while the pair comparisons had 10 animals from each species.

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	<u>Q. tuberculata</u>	<u>E. braziliensis</u>	<u>E. hirsuticauda</u>
<u>Q. tuberculata</u>	20	10 + 10	10 + 10
<u>E. braziliensis</u>		20	10 + 10
<u>E. hirsuticauda</u>			20

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Table 2. Annual variability in the sand levels at the upper, middle and lower beach of Mehuín. Each value is the height (cm) between the top of the post (upper beach) or rocks (middle and lower beach) and the sand level. The negative values presented for the lower beach represent accretion periods in which the sand level surpassed the top of the rock (level 0).

	upper beach			middle beach			lower beach		
	1 a	2 e	3 d	a	e	d	a	e	d
1978	62.5	136.5	74.0	138.5	279.7	141.2	22.0	148.0	126.0
1979	95.3	124.5	29.2	116.0	268.0	152.0	-9.5	148.5	158.0
1980	89.0	147.5	58.5	168.0	304.5	136.5	26.5	165.0	138.5
1981	97.3	138.0	40.7	125.5	294.5	169.0	-11.0	160.0	171.0
1982	79.0	152.3	73.3	no data			12.0	156.7	144.7
1983	90.7	114.7	24.0	126.3	293.0	166.7	2.7	148.3	145.6
1984	80.0	106.7	26.7	145.0	254.7	109.7	16.5	125.3	108.8
1985	71.3	105.3	34.0	145.0	265.7	120.7	-19.0	139.3	158.3
		$\bar{x}$ : 45.1			$\bar{x}$ : 142.3			$\bar{x}$ : 143.9	
		sd: 20.7			sd: 22.2			sd: 19.7	

- 1  
maximum accretion value for the year  
2  
maximum erosion value for the year  
3  
difference between <sup>1</sup> and <sup>2</sup>

Table 3. Mean and ranges of sand characteristics at three selected levels of Mehuín Beach; May, 1978 to April, 1980.

variables	upper beach		middle beach		lower beach	
	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
mean grain size (x $\phi$ )	2.31	2.06 - 2.52	2.25	1.93 - 2.48	2.15	1.70 - 2.44
sorting ( $\phi$ )	0.42	0.34 - 0.58	0.44	0.31 - 0.52	0.44	0.32 - 0.79
temperature ( C )	26.33	10.50 - 45.00	20.54	10.50 - 31.20	17.77	10.50 - 25.50
water content (%)	6.28	0.98 - 14.93	16.51	4.66 - 21.73	19.35	16.00 - 21.85
penetrability (cm)	6.07	4.13 - 9.00	3.73	2.66 - 7.15	3.54	2.60 - 4.53



Table 4. Summary of principal component analysis of sand characteristics at Mehuín Beach; May, 1978 to April, 1980.

variables	Unrotated component loadings <sup>1</sup>		Communality <sup>2</sup>	Rotated component loadings		
	CI	CII		CI	CII	Communality
mean grain size	0.76	-0.50	0.83	0.29	-0.88	0.85
sorting	-0.61	0.71	0.87	0.01	0.92	0.85
temperature	0.81	0.04	0.66	0.36	-0.28	0.21
water content	-0.84	-0.46	0.92	-0.91	0.16	0.86
penetrability	0.79	0.51	0.88	0.95	-0.11	0.91
eigenvalue <sup>3</sup>	2.94 + 1.22 = 4.16 <sup>4</sup>			1.94 + 1.74 = 3.68		
% of trace <sup>5</sup>	58.80 + 24.40 = 83.20 <sup>6</sup>			38.80 + 34.80 = 73.60		

<sup>1</sup> correlations between the variables and the components.

<sup>2</sup> row sum of squared component loadings; it represents the amount of variance in a variable that is accounted for by the two components taken together.

<sup>3</sup> column sum of squared component loadings; it indicates the relative importance of each component in accounting for by the variance associated with the set of variables.

<sup>4</sup> sum of the two eigenvalues; it represents the total amount of variance extracted by the component solution.

<sup>5</sup> obtained by dividing each eigenvalue for the number of variables. The trace indicates the total amount of variance the component solution is based upon and is equal to the number of variables based in the assumption that the variance in each variable is equal to one (Hair et al. 1979).

<sup>6</sup> cumulative % of trace (variance) accounted for by the two components.

Table 5. Dimensions of the brood life stages of the peracarid species at Mehuín Beach. The values are means (mm)  $\pm$  1 standard error of pooled eggs, embryos and juveniles collected during May, 1978 to April, 1980.

life stages	<u><i>O. tuberculata</i></u>	<u><i>E. braziliensis</i></u>	<u><i>E. hirsuticauda</i></u>
diameter of eggs	1.76 $\pm$ 0.02 (87)*	0.90 $\pm$ 0.01 (78)	0.66 $\pm$ 0.01 (123)
length of embryos	2.26 $\pm$ 0.03 (31)	1.75 $\pm$ 0.02 (131)	1.42 $\pm$ 0.02 (142)
length of juveniles	3.72 $\pm$ 0.01 (79)	2.24 $\pm$ 0.02 (160)	1.83 $\pm$ 0.01 (137)

\*sample size

Table 6. Seasonal mean lengths and percentage juveniles of the peracarid species at Mehuín Beach. The values are expressed in mm  $\pm$  1 standard error.

life stages	September 80	December	February 81	April	September
<b>Males</b>					
<u>O. tuberculata</u>	13.82 $\pm$ 0.67 (17)*	15.20 $\pm$ 0.80 (5)	15.38 $\pm$ 1.32 (8)	15.92 $\pm$ 0.94 (13)	15.83 $\pm$ 1.17 (6)
<u>E. braziliensis</u>	7.43 $\pm$ 0.36 (12)	8.01 $\pm$ 0.16 (29)	7.66 $\pm$ 0.42 (5)	6.79 $\pm$ 0.25 (11)	7.58 $\pm$ 0.19 (17)
<u>E. hirsuticauda</u>	6.40 $\pm$ 0.27 (6)	6.13 $\pm$ 0.05 (4)	6.35 $\pm$ 0.11 (12)	6.45 $\pm$ 0.09 (26)	6.58 $\pm$ 0.23 (8)
<b>Females</b>					
<u>O. tuberculata</u>	12.63 $\pm$ 0.44 (30)	12.83 $\pm$ 0.98 (12)	11.00 $\pm$ 0.38 (8)	12.14 $\pm$ 0.98 (7)	10.90 $\pm$ 0.93 (10)
<u>E. braziliensis</u>	7.25 $\pm$ 0.32 (10)	7.88 $\pm$ 0.24 (34)	7.55 $\pm$ 0.26 (8)	7.23 $\pm$ 0.16 (46)	7.86 $\pm$ 0.19 (30)
<u>E. hirsuticauda</u>	7.00 $\pm$ 0.28 (8)	8.10 $\pm$ 0.38 (10)	7.34 $\pm$ 0.25 (11)	7.26 $\pm$ 0.11 (54)	7.31 $\pm$ 0.21 (29)
<b>Gravid females</b>					
<u>E. braziliensis</u>	--	10.86 $\pm$ 0.63 (8)	--	--	--
<u>E. hirsuticauda</u>	--	--	7.89 $\pm$ 0.22 (8)	--	--
<b>Juveniles</b>					
<u>O. tuberculata</u>	6.39 $\pm$ 0.23 (18)	4.58 $\pm$ 0.21 (59)	3.85 $\pm$ 0.30 (23)	5.50 $\pm$ 0.26 (26)	6.25 $\pm$ 0.25 (12)
<u>E. braziliensis</u>	--	--	3.12 $\pm$ 0.16 (12)	3.66 $\pm$ 0.07 (20)	--
<u>E. hirsuticauda</u>	--	3.20 $\pm$ 0.15 (7)	3.25 $\pm$ 0.07 (38)	3.34 $\pm$ 0.07 (36)	3.38 $\pm$ 0.09 (23)
<b>Juveniles, %</b>					
<u>O. tuberculata</u>	27.69	77.63	58.97	56.52	42.86
<u>E. braziliensis</u>	--	--	41.38	11.36	--
<u>E. hirsuticauda</u>	--	25.00	21.11	21.69	19.83

\*sample size

Table 7. Mean and ranges of some characteristics of Mehuín Beach where *O. tuberculata*, *E. braziliensis*, *E. hirsuticauda*, *E. monodi*, and *E. analoga* were collected, May, 1978 to April, 1980.

	<i>O. tuberculata</i>	<i>E. braziliensis</i>	<i>E. hirsuticauda</i>	<i>E. monodi</i>	<i>E. analoga</i>
mean grain size	2.33( 2.06 - 2.54)	2.31( 1.77 - 2.54)	2.23( 1.86 - 2.54)	2.19( 1.77 - 2.46)	2.16( 1.75 - 2.40)
sorting	0.38( 0.27 - 0.58)	0.39( 0.27 - 0.58)	0.40( 0.27 - 0.55)	0.41( 0.32 - 0.55)	0.42( 0.33 - 0.65)
temperature	27.02(10.50 - 41.50)	24.09(10.50 - 45.00)	20.00(10.50 - 34.50)	19.49(11.00 - 30.50)	15.46(10.50 - 25.00)
water content	9.77( 0.98 - 19.49)	11.97( 2.03 - 20.67)	16.86( 3.59 - 20.73)	17.86(11.21 - 20.73)	19.07(10.70 - 23.71)
penetrability	5.43( 2.80 - 9.00)	4.98( 2.56 - 9.00)	3.71( 2.36 - 8.55)	3.48( 2.51 - 4.57)	3.51( 2.36 - 4.60)

Table 8. Correlation coefficients between the mean abundances of *O. tuberculata*, *E. braziliensis*, *E. hirsuticauda*, *E. monodi*, *E. analoga* and physical variables and mean abundances of coexisting species at Mehuín Beach; May, 1978 to April, 1980. The number of observations were: *O. tuberculata* 52, *E. braziliensis* 71, *E. hirsuticauda* 73, *E. monodi* 48 and *E. analoga* 44. Underlined coefficients are significant at the 0.05 probability level.

	<u><i>O. tuberculata</i></u>	<u><i>E. braziliensis</i></u>	<u><i>E. hirsuticauda</i></u>	<u><i>E. monodi</i></u>	<u><i>E. analoga</i></u>
mean grain size	0.102	0.193	<u>0.361</u>	0.227	0.073
sorting	0.226	-0.109	-0.212	-0.030	-0.120
temperature	-0.160	0.187	0.097	0.084	-0.148
water content	<u>-0.394</u>	<u>-0.395</u>	-0.164	0.223	0.098
penetrability	<u>0.337</u>	<u>0.423</u>	0.073	-0.093	-0.221
<u><i>O. tuberculata</i></u>		<u>0.682</u>	0.078	-0.107	
<u><i>E. braziliensis</i></u>	<u>0.339</u>		0.130	-0.066	
<u><i>E. hirsuticauda</i></u>	<u>-0.375</u>	<u>-0.403</u>		0.207	-0.284
<u><i>E. monodi</i></u>			0.092		
<u><i>E. analoga</i></u>			<u>-0.300</u>	-0.0003	

Table 9. Summary of multiple regression analyses with monthly samples collected at Mehuín Beach during May, 1978 to April, 1980. The values given in this table (other than probability values, intercept and multiple coefficient of determination) are the partial regression coefficients or values of each variable in the multiple regression equation.

variables	<u>Q. tuberculata</u>	<u>E. braziliensis</u>	<u>E. hirsuticauda</u>
approach A			
mean grain size	NE***	NE	1.769 (0.002)
sorting	NE	NE	NE
temperature	-0.023 (0.004)**	NE	NE
water content	-0.051 (0.009)	NE	NE
penetrability	NE	0.156 (0.0002)	NE
intercept	2.647	0.689	-2.363
<sup>2</sup>			
R *	0.268	0.179	0.130
approach B			
mean grain size	NE	NE	1.659 (0.002)
sorting	NE	NE	NE
temperature	-0.023 (0.004)	NE	NE
water content	-0.051 (0.009)	NE	NE
penetrability	NE	NE	NE
<u>Q. tuberculata</u>	NC****	0.491 (0.0001)	NE
<u>E. braziliensis</u>	NE	NC	NE
<u>E. hirsuticauda</u>	NE	NE	NC
<u>E. monodi</u>	NC	NC	NE
<u>E. analoga</u>	NC	NC	-0.291 (0.010)
intercept	2.647	0.989	-2.027
<sup>2</sup>			
R	0.268	0.465	0.204

<sup>2</sup>  
 \*R : coefficient of determination  
 \*\* : p>F  
 \*\*\*NE : variable not entered into the model (F-statistic lower than 0.05 probability level)  
 \*\*\*\*NC : do not correspond

Table 10. Correlation coefficients between the mean abundances of Q. tuberculata, E. braziliensis and E. hirsuticauda and physical variables and mean abundances of coexisting species at Mehuín Beach, September, 1980 to April, 1981. The number of observations were Q. tuberculata 73, E. braziliensis 61 and E. hirsuticauda 39. Underlined coefficients are significant at the 0.05 probability level.

	<u>Q. tuberculata</u>	<u>E. braziliensis</u>	<u>E. hirsuticauda</u>
mean grain size	0.133	0.245	<u>0.344</u>
sorting	0.153	0.049	-0.037
temperature	-0.114	<u>-0.336</u>	0.038
water content	-0.028	-0.049	<u>-0.434</u>
<u>Q. tuberculata</u>		-0.013	-0.132
<u>E. braziliensis</u>	-0.006		<u>0.513</u>
<u>E. hirsuticauda</u>	-0.130	-0.204	

Table 11. Summary of multiple regression analyses with seasonal samples collected at Mehuín Beach during September, 1980 to April, 1981. The values given in this table (other than probability values, intercept and multiple coefficient of determination) are the partial regression coefficients or values of each variable in the multiple regression equation.

variables	<i>E. braziliensis</i>	<i>E. hirsuticauda</i>
approach A		
mean grain size	0.817(0.022)**	NE
sorting	NE***	NE
temperature	-0.024(0.008)	NE
water content	NE	-0.091(0.006)
intercept	0.020	3.049
<sup>2</sup> R *	0.190	0.188
approach B		
mean grain size	0.817(0.022)	NE
sorting	NE	NE
temperature	-0.024(0.008)	NE
water content	NE	NE
<u><i>O. tuberculata</i></u>	NE	NE
<u><i>E. braziliensis</i></u>	NC****	0.579(0.0008)
<u><i>E. hirsuticauda</i></u>	NE	NC
intercept	0.020	1.400
<sup>2</sup> R	0.190	0.263

<sup>2</sup>  
\*R : coefficient of determination  
\*\* : p>F  
\*\*\*NE : variable not entered into the model (F-statistic lower than 0.05 probability level)  
\*\*\*\*NC : do not correspond



Table 12. Transect width in meters, slope in % and mean grain size and sorting in  $\phi$  at beaches sampled in Bahía de Maiquillahue and outlet areas of Río Queule and Río Lingue; February-March, 1983.

site	location	width	slope	mean grain size		sorting	
				$\bar{x}$	range	$\bar{x}$	range
1	Mehuín	25	6.8	2.41	2.33-2.45	0.33	0.30-0.37
2	Mehuín	60	3.0	2.46	2.36-2.55	0.33	0.31-0.38
3	Mehuín	50	3.1	2.28	2.15-2.39	0.35	0.32-0.38
4	Mehuín	50	2.5	2.39	2.21-2.56	0.33	0.30-0.39
5	Matias	25	9.3	2.21	1.76-2.52	0.69	0.50-0.88
6	Isla de Maiquillahue	25	8.8	0.60	0.18-0.81	0.68	0.58-0.74
7	Queule	25	6.2	2.47	2.38-2.56	0.29	0.26-0.34
8	Lingue	15	13.3	2.67	2.50-2.82	0.33	0.31-0.37

Table 13. Mean densities per m<sup>2</sup> of the macroinfaunal species collected at beaches located in Bahía de Maiquillahue and outlet areas of Río Queule and Río Lingue; February-March, 1983.

site	location	<u>Q. tuberculata</u>	<u>E. braziliensis</u>	<u>E. hirsuticauda</u>	<u>E. monodi</u>	<u>E. analoga</u>
1	Mehuín	16.70	16.70	62.53	16.70	283.30
2	Mehuín	44.43	58.30	208.35	0.00	166.65
3	Mehuín	83.30	33.35	525.00	0.00	94.47
4	Mehuín	33.30	38.90	137.48	41.70	33.30
5	Matias	66.70	83.30	866.67	0.00	33.35
6	Isla de Maiquillahue	200.00	0.00	0.00	0.00	50.00
7	Queule	41.65	33.30	96.66	50.03	0.00
8	Lingue	166.70	25.00	50.00	50.00	0.00

Table 14. Percentage of individuals, 24 hours after release in four sizes of sand: very fine (3-4  $\phi$  or 62.5-125 microns), fine (2-3  $\phi$  or 125-250 microns), medium (1-2  $\phi$  or 250-500 microns) and coarse (0-1  $\phi$  or 500-1000 microns). The numbers are means (n:4) with standard errors in brackets.

species	date		1	2	3	4	ANOVA-SNK (p<0.05)
			very fine	fine	medium	coarse	
<u>O. tuberculata</u>	November	19,81	6.3(3.1)	12.8(5.2)	68.1(8.9)	12.8(4.8)	1-3,2-3,3-4
	December	2,81	12.6(5.2)	19.0(4.2)	41.8(9.2)	26.7(7.3)	NS*
	January	29,82	28.8(11.6)	18.8(5.2)	22.5(10.1)	30.0(8.7)	NS
	January	30,82	16.3(4.3)	18.8(4.3)	21.3(5.2)	43.8(6.3)	1-4,2-4,3-4
<u>E. braziliensis</u>	January	12,82	21.3(9.7)	17.5(2.5)	27.5(3.2)	33.8(5.5)	NS
	January	20,82	5.0(2.0)	16.4(5.5)	26.3(2.4)	52.0(7.6)	1-2,1-3,1-4,2-4,3-4
<u>E. hirsuticauda</u>	November	20,81	8.8(5.2)	10.1(5.4)	16.3(4.2)	64.9(8.8)	1-4,2-4,3-4
	December	2,81	0.0	13.8(3.1)	31.3(5.2)	55.0(7.4)	2-3,2-4,3-4
	December	3,81	2.7(1.5)	4.0(1.3)	20.9(3.8)	72.6(5.6)	1-3,1-4,2-3,2-4,3-4
<u>E. analoga</u>	December	3,81	15.0(8.7)	15.0(8.7)	40.0(7.1)	30.0(9.1)	NS
	December	4,81	22.5(4.8)	25.0(12.6)	37.5(9.5)	15.0(2.9)	NS

\*NS: not significant, p>0.05

Table 15. Percentage of individuals, 24 hours after release in two sizes of sand: fine (2-3  $\phi$  or 125-250 microns) and medium (1-2  $\phi$  or 250-500 microns). The numbers are means with standard errors in brackets.

species	date	n*	fine	medium	ANOVA
<u>O. tuberculata</u>	May 17,83	8	36.1(11.7)	63.9(11.7)	NS**
	May 20,83	8	50.0(11.8)	50.0(11.8)	NS
<u>E. braziliensis</u>	June 24,83	10	41.4(5.5)	58.6(5.5)	p<0.05
	June 25,83	10	40.6(5.5)	59.4(5.5)	p<0.05
<u>E. hirsuticauda</u>	May 3,83	8	31.0(4.6)	69.0(4.6)	p<0.05
	May 25,83	10	37.0(8.2)	63.0(8.2)	p<0.05
<u>E. analoga</u>	May 23,83	6	49.0(7.1)	51.0(7.1)	NS
	May 24,83	6	40.4(6.3)	59.6(6.3)	NS

\*n: number of replicates

\*\*NS: not significant, p>0.05

Table 16. Percentage of individuals, 24 hours after release in sands collected at the upper and middle beach of Mehuín; June 23, 1983. The numbers are means (n:5) with standard errors in brackets.

species	upper beach sand*	middle beach sand**	ANOVA
<u>O. tuberculata</u>	51.0 (8.4)	49.0 (8.4)	NS***
<u>E. braziliensis</u>	46.5 (7.4)	53.5 (7.4)	NS
<u>E. hirsuticauda</u>	46.3 (6.7)	53.7 (6.7)	NS

\* $\bar{x}$   $\sigma$ : 2.15,  $\sigma$   $\sigma$ : 0.55

\*\* $\bar{x}$   $\sigma$ : 1.96,  $\sigma$   $\sigma$ : 0.56

\*\*\*NS: not significant,  $p > 0.05$

Table 17. Percentage of individuals, 24 hours after release in two kinds of sand; calcareous (native of Isla de Maiquillahue) and volcanic (native of the beach of Matias). The numbers are means with standard errors in brackets.

species	n*	calcareous sand**	volcanic sand***	ANOVA
<i>E. braziliensis</i>	5	46.0(3.1)	54.0(3.1)	NS****
<i>E. hirsuticauda</i>	10	52.8(2.1)	47.2(2.1)	NS

\*n: number of replicates

\*\* $\bar{x}$   $\phi$ : 0.60,  $\sigma$   $\phi$ : 0.68, roundness: 0.42

\*\*\* $\bar{x}$   $\phi$ : 2.21,  $\sigma$   $\phi$ : 0.69, roundness: 0.34

\*\*\*\*NS: not significant,  $p > 0.05$

Table 18. Percentage mortality of peracarids and *E. analoga* in the sand desiccation tolerance experiments. The numbers are means (n: 2 in *E. braziliensis* and 3 in *O. tuberculata*, *E. hirsuticauda* and *E. analoga*) with standard errors in brackets.

	1	2	3	4	
hours after start	<i>O. tuberculata</i>	<i>E. braziliensis</i>	<i>E. hirsuticauda</i>	<i>E. analoga</i>	ANOVA-SNK (p<0.05)
3	6.7(3.9)	0.0	0.0	16.7(9.0)	NS*
6	11.1(6.0)	5.0(5.1)	2.2(2.3)	72.6(17.8)	1-4,2-4,3-4
9	13.3(3.9)	5.0(5.1)	6.7(6.8)	86.7(6.8)	1-4,2-4,3-4
12	46.7(20.4)	15.0(5.1)	6.7(6.8)	93.3(6.8)	1-4,2-4,3-4
15	68.9(12.6)	35.0(5.1)	15.5(9.9)	100.0(0.0)**	NS
18	93.3(3.9)	35.0(5.1)	11.1(6.0)	--	1-2,1-3
21	100.0(0.0)**	60.0(20.2)	48.9(9.1)	--	NS
24	--	100.0(0.0)**	71.1(17.7)	--	

\*NS: not significant, p>0.05

\*\*values not used, S<sup>2</sup> = 0

Table 19. Percentage mortality of peracarids in the intraspecific coexistence experiments. The numbers are means (n:4) with standard errors in brackets and refer to the mortality after 15 days (April 23-May 8, 1985).

species	abundances			ANOVA
	10	20	30	
<i>O. tuberculata</i>	50.0(10.0)	28.8(5.2)	27.5(3.7)	NS*
<i>E. braziliensis</i>	0.0	7.5(3.2)	8.4(2.9)	NS
<i>E. hirsuticauda</i>	7.5(2.5)	6.3(3.1)	5.8(2.5)	NS

\*NS: not significant,  $p > 0.05$



Table 20. Percentage mortality of peracarids in the interspecific coexistence experiments, 24 hours light. The numbers are means (n: 4) with standard errors in brackets and refer to the mortality found after 15 days.

sand depth	dates	control			ANOVA-SNK
		a) <u><i>O. tuberculata</i></u>	b) + <u><i>E. braziliensis</i></u>	c) + <u><i>E. hirsuticauda</i></u>	
3 cm	Nov. 29-Dec. 14,82	13.8( 3.8)	7.5( 4.8)	32.5(20.2)	NS*
	Jan. 4-Jan. 19,83	35.0( 3.5)	12.5( 2.5)	25.0(11.9)	NS
	May 2-May 16,83	20.0(12.1)	0.0	37.5(17.5)	NS
	Oct. 4-Oct. 19,84	20.0( 5.9)	36.7(20.7)	50.0(10.2)	NS
	Jan. 30-Feb. 14,85	28.8( 5.2)	37.5( 6.3)	27.5(11.1)	NS
6 cm	Oct. 4-Oct. 19,84	43.3( 9.0)	36.7(14.8)	73.3( 3.4)	NS
		a) <u><i>E. braziliensis</i></u>	b) + <u><i>E. hirsuticauda</i></u>	c) + <u><i>O. tuberculata</i></u>	
3 cm	Nov. 29-Dec. 14,82	10.0( 3.5)	12.5( 4.8)	67.5( 4.8)	a-c**,b-c**
	Jan. 4-Jan. 19,83	8.8( 1.3)	15.0( 6.5)	22.5( 8.5)	NS
	May 2-May 16,83	6.3( 3.1)	2.5( 2.5)	75.0( 8.7)	a-c,b-c
	Oct. 4-Oct. 19,84	20.0( 5.9)	13.3( 3.4)	30.0( 5.9)	NS
	Jan. 30-Feb. 14,85	7.5( 3.2)	22.5( 4.8)	15.0( 5.0)	NS
6 cm	Oct. 4-Oct. 19,84	16.7( 6.8)	20.0( 5.9)	20.0(10.2)	NS
		a) <u><i>E. hirsuticauda</i></u>	b) + <u><i>E. braziliensis</i></u>	c) + <u><i>O. tuberculata</i></u>	
3 cm	Nov. 29-Dec. 14,82	5.0( 2.0)	2.5( 2.5)	57.5( 8.5)	a-c,b-c
	Jan. 4-Jan. 19,83	3.8( 1.3)	5.0( 2.9)	20.0( 4.1)	a-c,b-c
	May 2-May 16,83	7.5( 3.)	17.5( 8.5)	67.5( 8.5)	a-c,b-c
	Oct. 4-Oct. 19,84	6.7( 3.4)	0.0	23.3( 6.8)	NS
	Jan. 30-Feb. 14,85	6.3( 3.1)	2.5( 2.5)	12.5( 7.5)	NS
6 cm	Oct. 4-Oct. 19,84	0.0	10.0( 5.9)	13.3( 9.0)	NS

\*NS: not significant,  $p > 0.05$

\*\* :  $p < 0.05$

Table 21. Percentage mortality of peracarids in the interspecific coexistence experiments, 12 hours light. The numbers are means (n:3) with standard errors in brackets and refer to the mortality found after 15 days (Nov. 28-Dec. 13, 1984).

sand depth	control			ANOVA-SNK
	a) <u><i>O. tuberculata</i></u>	b) + <u><i>E. braziliensis</i></u>	c) + <u><i>E. hirsuticauda</i></u>	
3 cm	23.3(13.6)	23.3( 9.0)	13.3( 9.0)	NS*
6 cm	10.0( 0.0)	16.7( 9.0)	16.7( 3.4)	NS
	a) <u><i>E. braziliensis</i></u>	b) + <u><i>E. hirsuticauda</i></u>	c) + <u><i>O. tuberculata</i></u>	
3 cm	13.3( 3.4)	13.3( 3.4)	50.0( 5.9)	a-c**,b-c**
6 cm	20.0(10.2)	26.7(12.2)	80.0( 5.9)	a-c,b-c
	a) <u><i>E. hirsuticauda</i></u>	b) + <u><i>E. braziliensis</i></u>	c) + <u><i>O. tuberculata</i></u>	
3 cm	10.0(10.2)	3.3( 3.4)	30.0( 5.9)	NS
6 cm	6.7( 3.4)	6.7( 6.8)	46.7( 3.4)	a-c,b-c

\*NS: not significant,  $p > 0.05$

\*\* :  $p < 0.05$

Fig. 1. Map of the Chilean coast showing the location of Bahía de Maiquillahue and the beaches analyzed in this study; 1: Mehuín, transect 1; 2: Mehuín, transect 2; 3: Mehuín, transect 3; 4: Mehuín, transect 4; 5: Matías; 6: Isla de Maiquillahue; 7: Queule, and 8: Lingue.

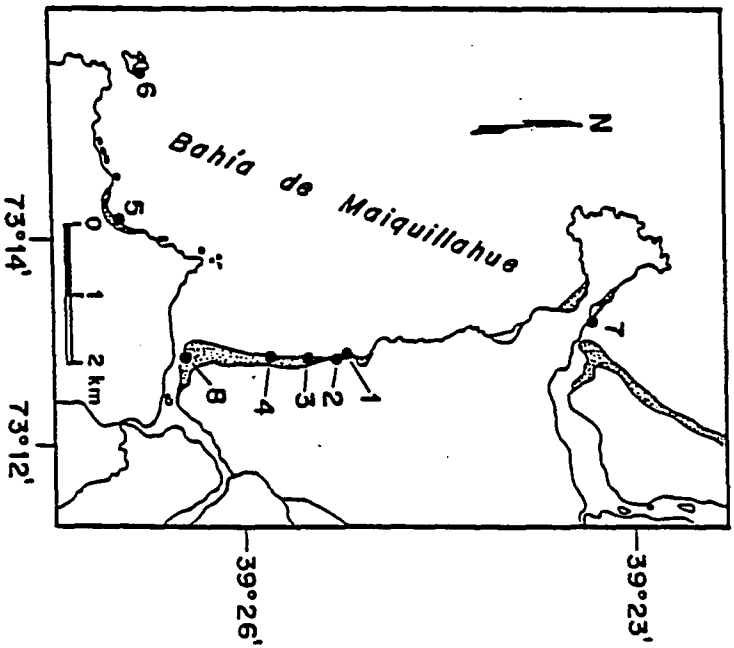
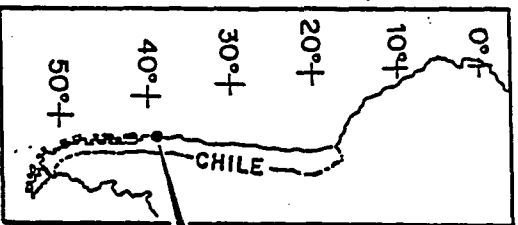


Fig. 1

**Fig. 2. Scheme showing the position and height above the sand of the post and rocks used in the analyses of the sand level fluctuations at the upper, middle and lower beach. The upper half of this scheme shows an accretion profile, while the lower represents an erosion profile.**

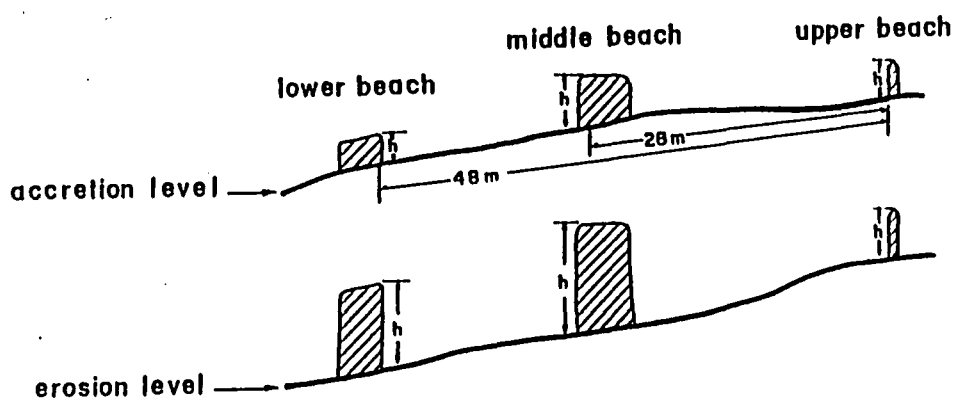


Fig. 2

Fig. 3. Seasonal variability in a) mean total rainfall and mean water salinity, and b) mean air and water temperature.

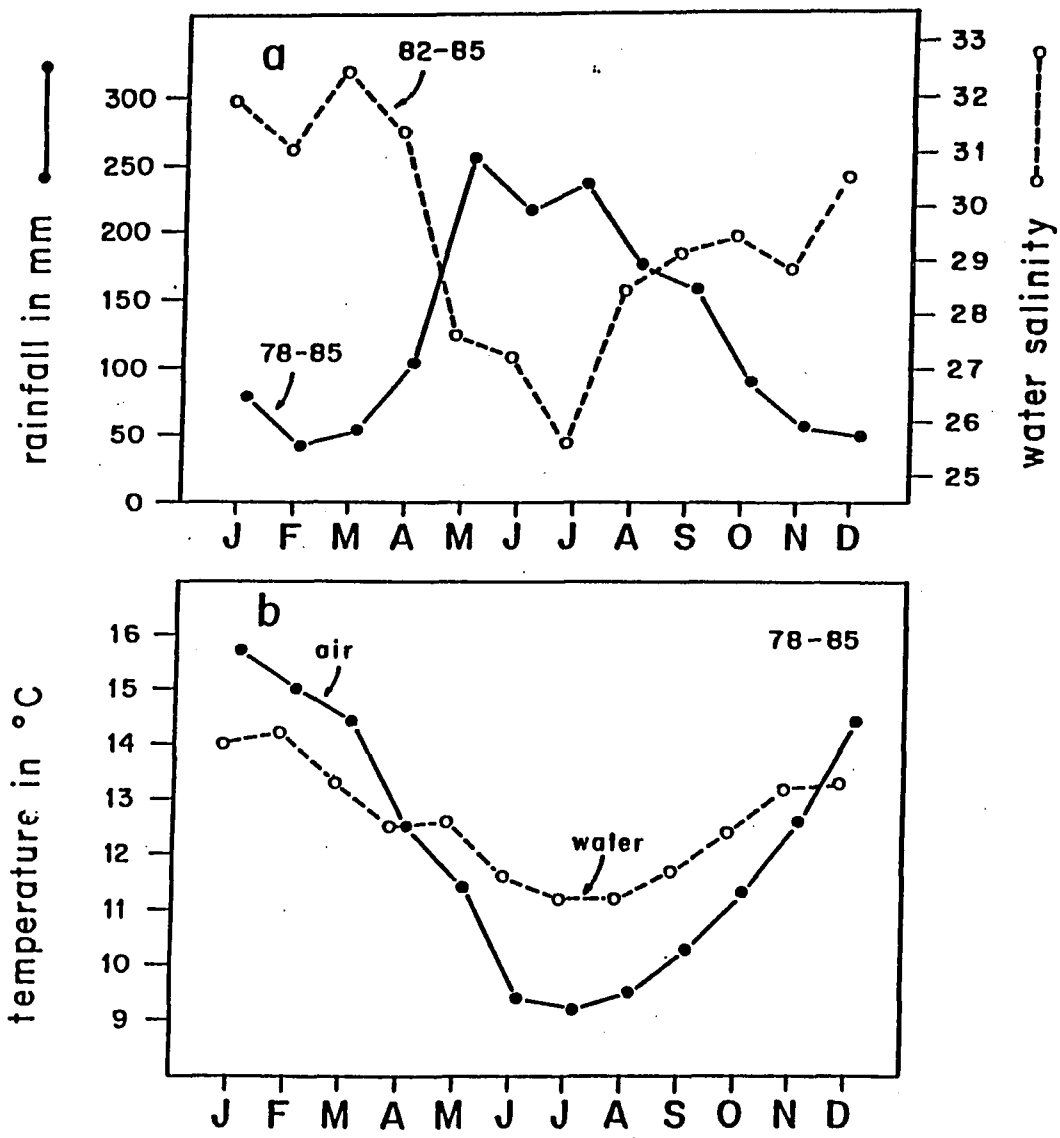


Fig. 3



Fig. 4. Seasonal variability in a) the frequency of the longshore drift, and b) north wind at Mehuín.

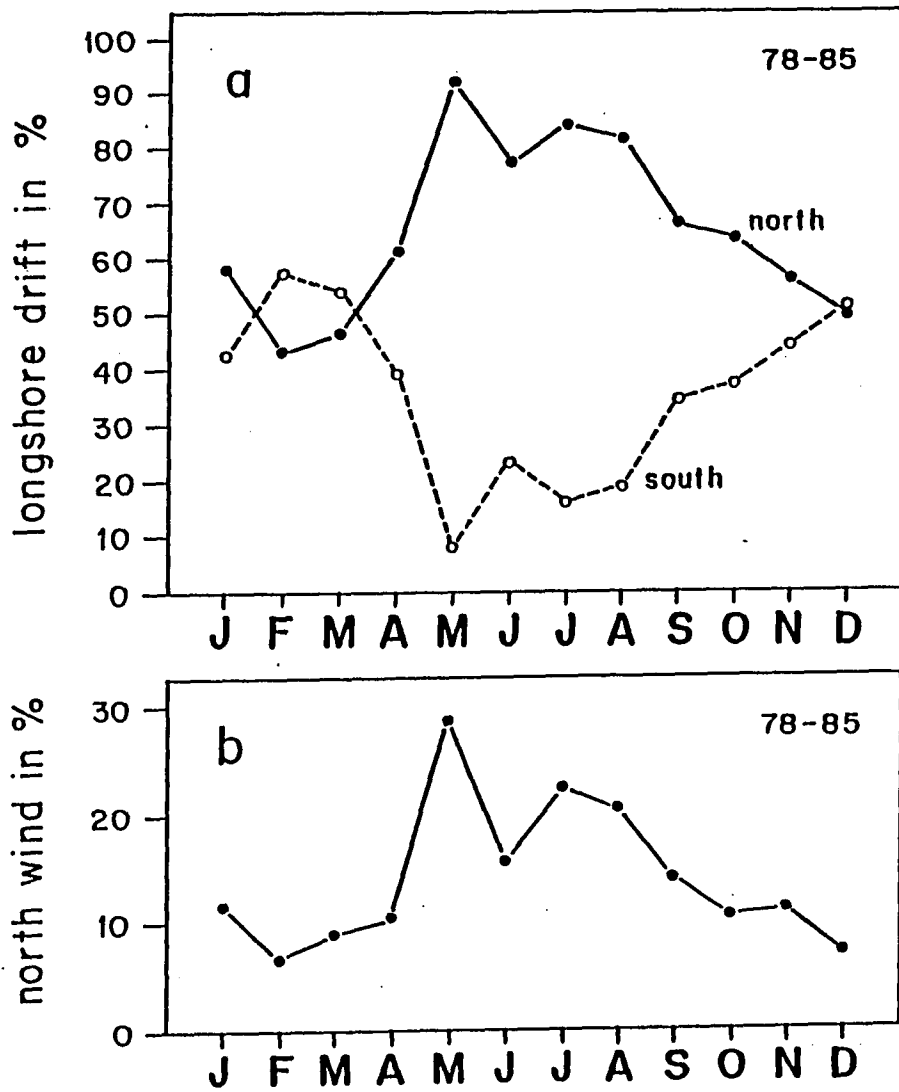


Fig. 4

Fig. 5. Long-term variability in the frequency of the north longshore drift and the sand levels at the upper, middle and lower beach of Mehuín.

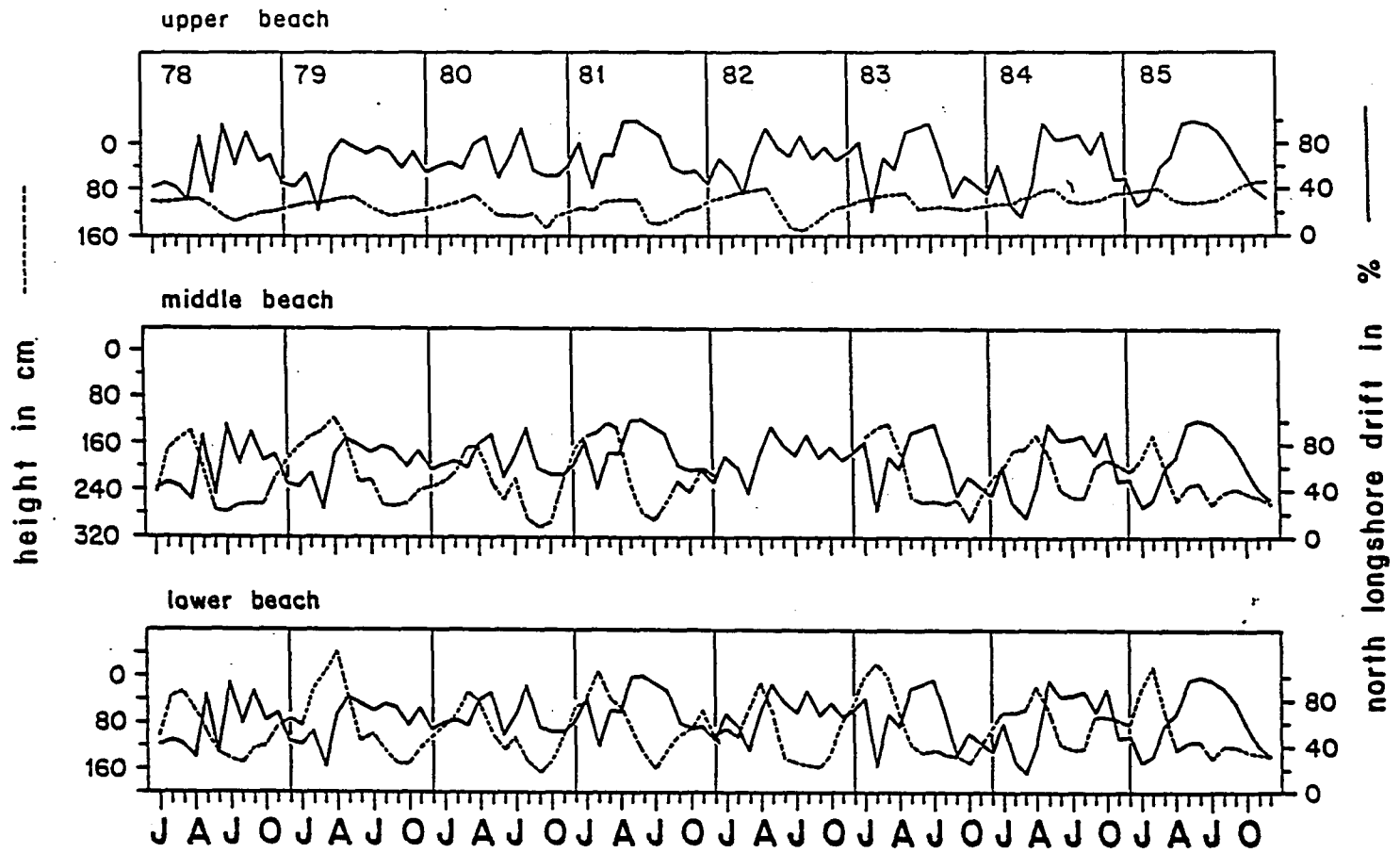


Fig. 5

Fig. 6. Summary of seasonal variability in the frequency of the north longshore drift and the sand levels at the upper, middle and lower beach of Mehuín showing mean values for the period 1978-85. The height 0 represents the top of the post and the rocks used for the temporal analysis of sand level fluctuations. During some accretion periods, the sand levels covered over the top of the reference rock located on the lower beach (i.e. 1979, 81, 83, 85).

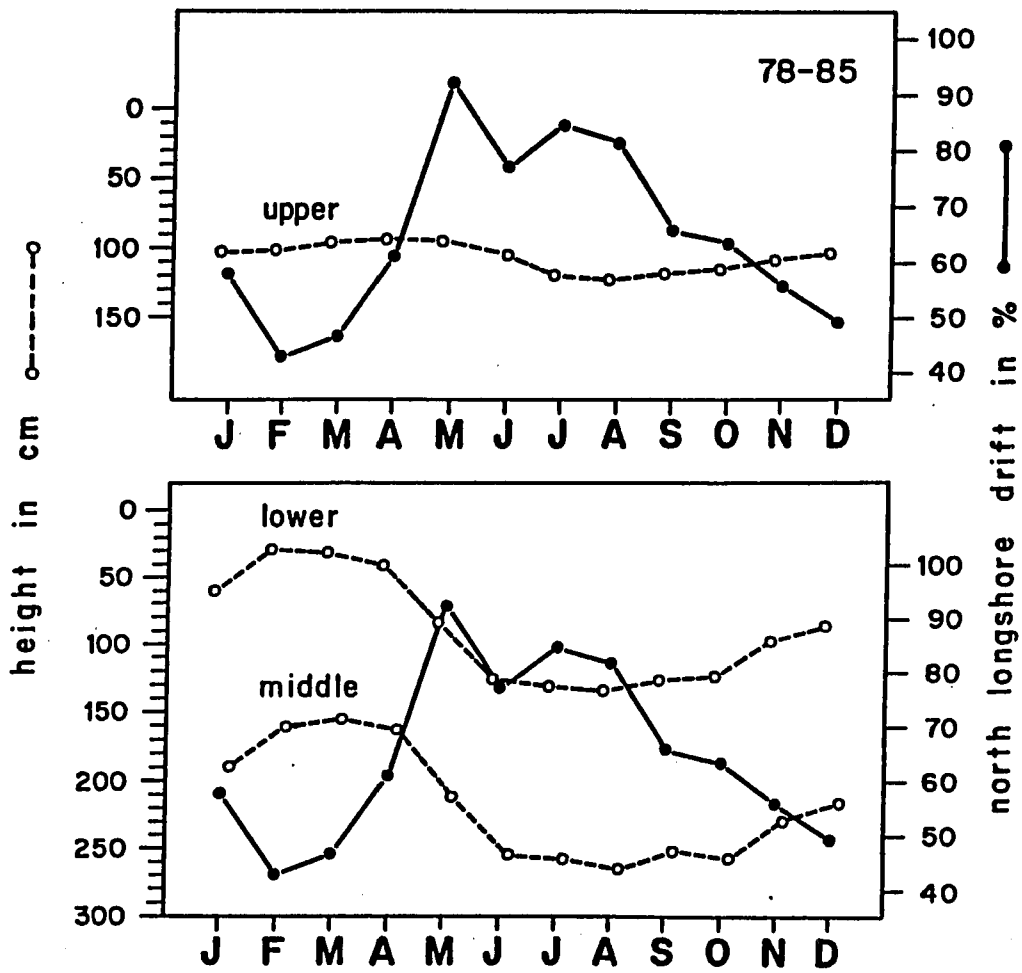


Fig. 6

**Fig. 7. Seasonal changes in the topographic profiles at Mehuín Beach during May, 1978 to April, 1980.**

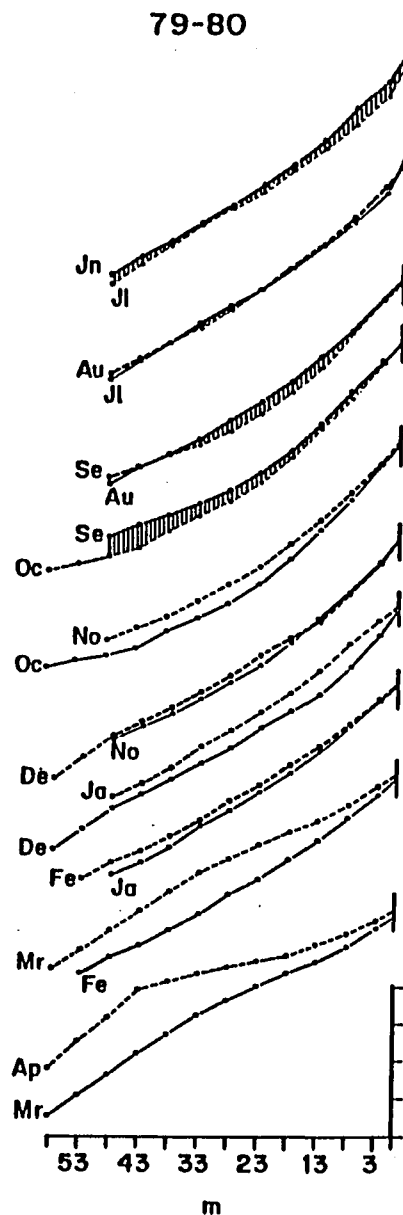
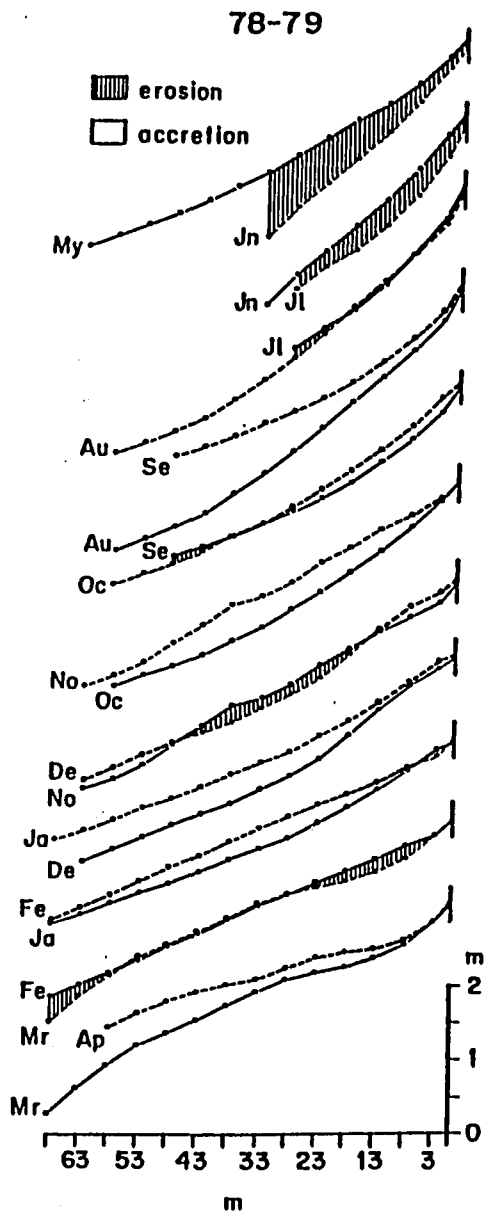


Fig. 7



Fig. 8. Temporal variability of the sand levels at the upper, middle and lower beach of Mehuín during May, 1978 to April, 1980. The lines representing the sand levels of the upper and middle beach are based on data collected fortnightly, while those of the lower beach are based on daily measurements.

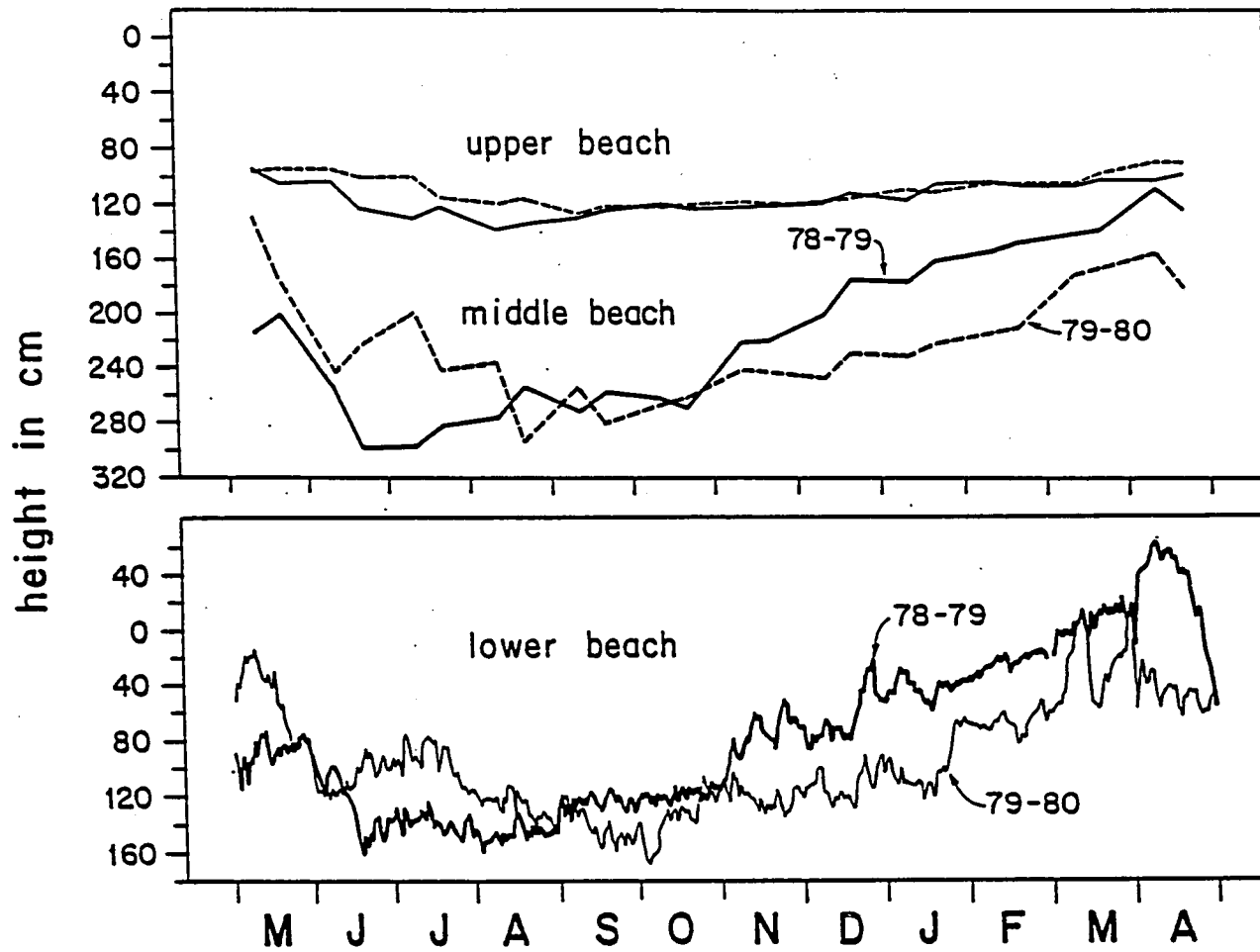


Fig. 8

Fig. 9. Temporal variability in the beach face slope and mean grain size values at Mehuín Beach during May, 1978 to April, 1980. The monthly grain size values are the means of the sizes (mean grain size in  $\phi$ ) calculated for each station. The relationship beach face slope and mean grain size is shown in the lower half of this figure.

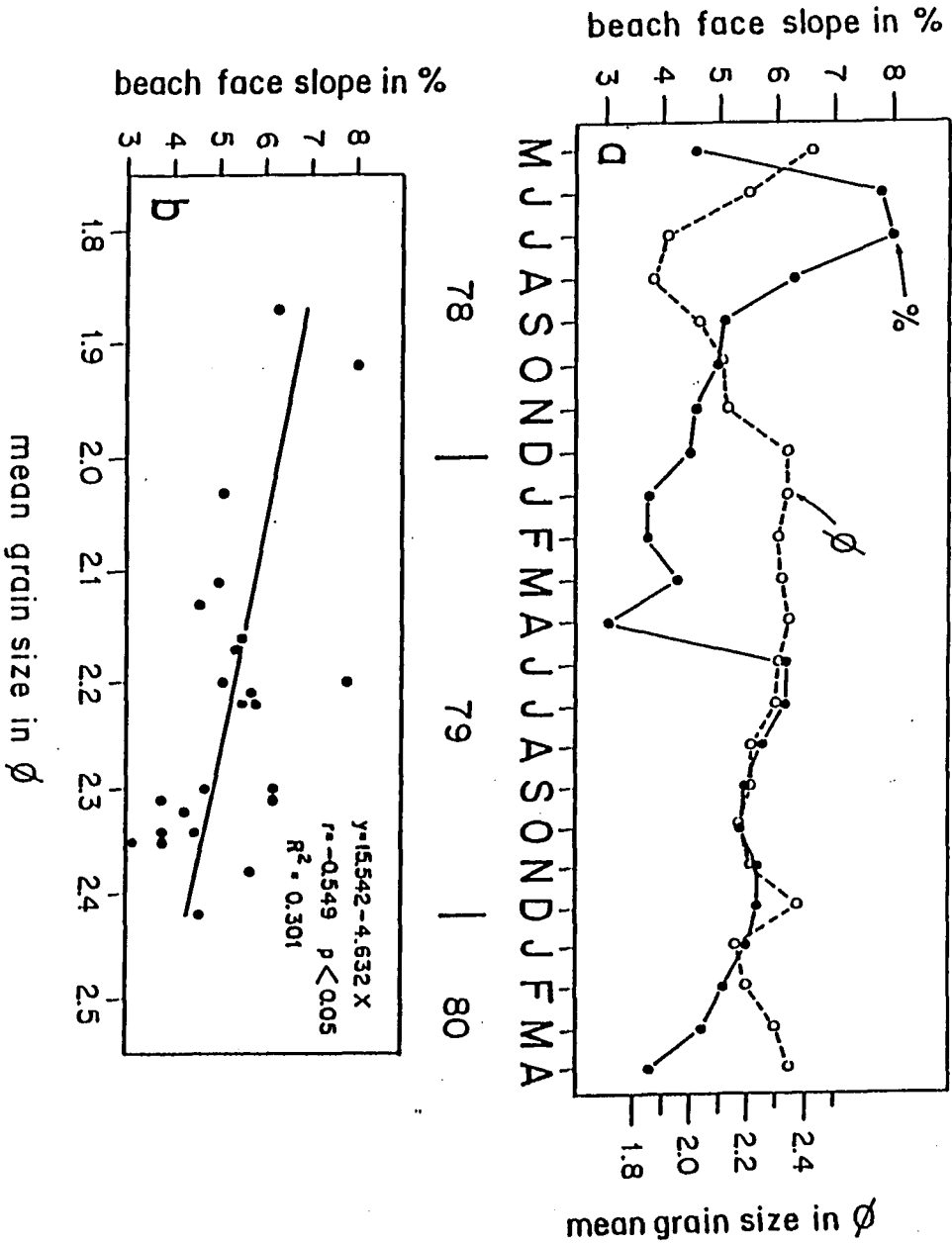


Fig. 9

Fig. 10. Temporal variability in a) the station levels, b) mean grain size, and c) sorting of the sediments at Mehuín Beach, during May, 1978 to April, 1980. The levels of the stations (height below 0) correspond to their heights in relation to the top (height 0) of the post located on the upper beach.

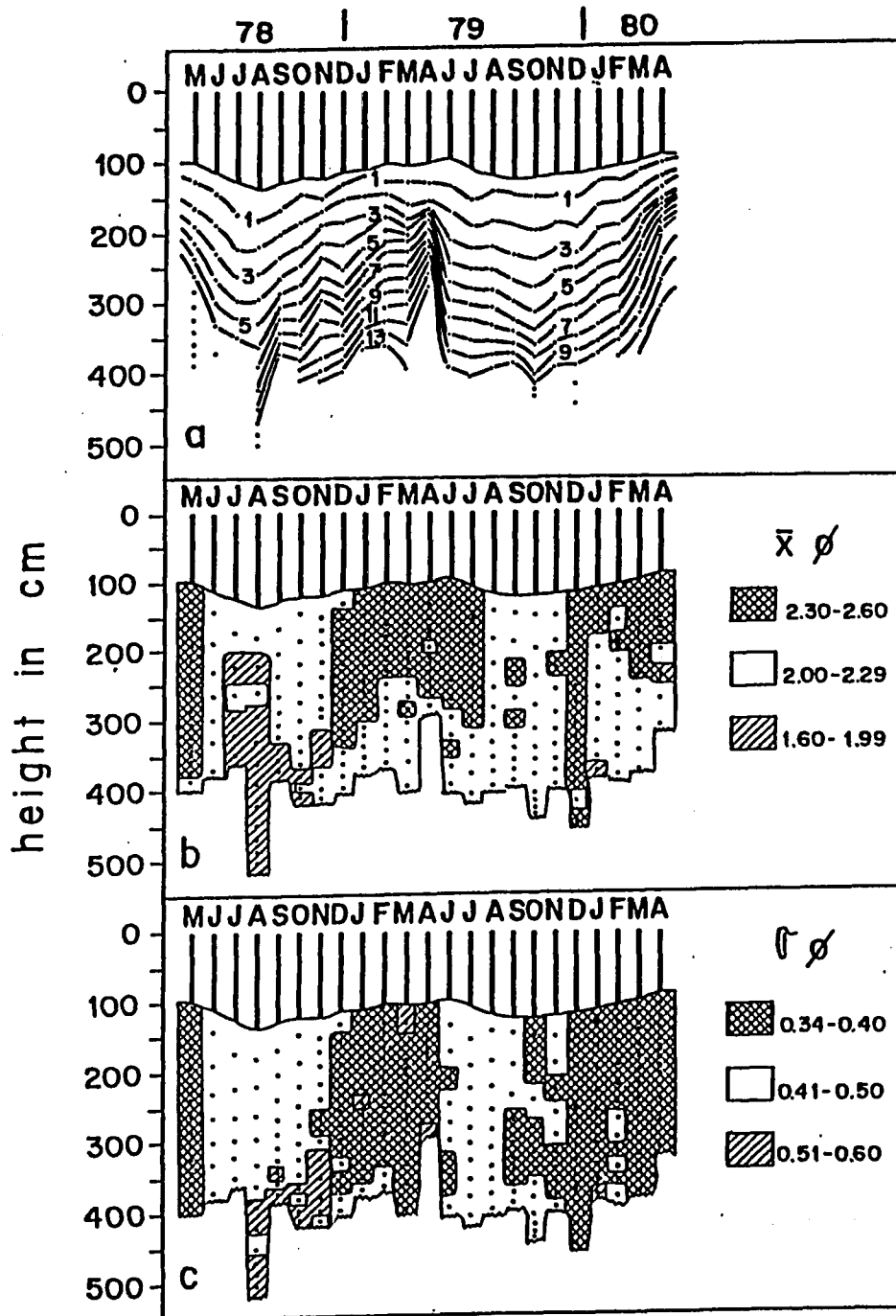


Fig. 10

Fig. 11. Relationships between the monthly averages of mean grain size and sand levels at the upper, middle and lower beach of Mehuín during May, 1978 to April, 1980. The height 0 represents the top of the post and the rocks used for the temporal analysis of sand level fluctuations. At the lower beach, two height values are negative; they represent periods in which the sand level covered over the top of the reference rock.

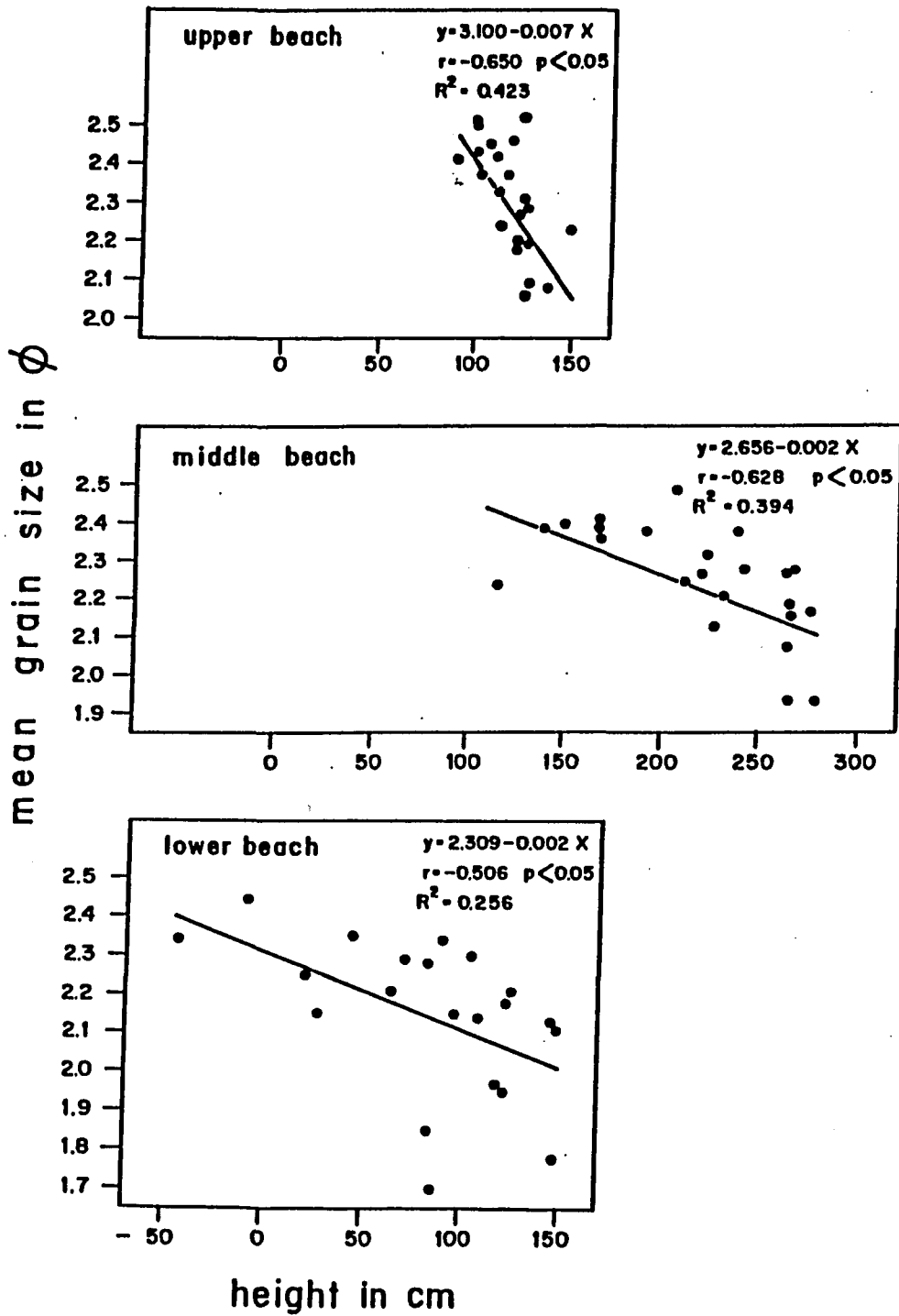


Fig. 11



Fig. 12. Relationships between the monthly means of sorting and mean grain size of the sediments of Mehuín Beach during May, 1978 to April, 1980.

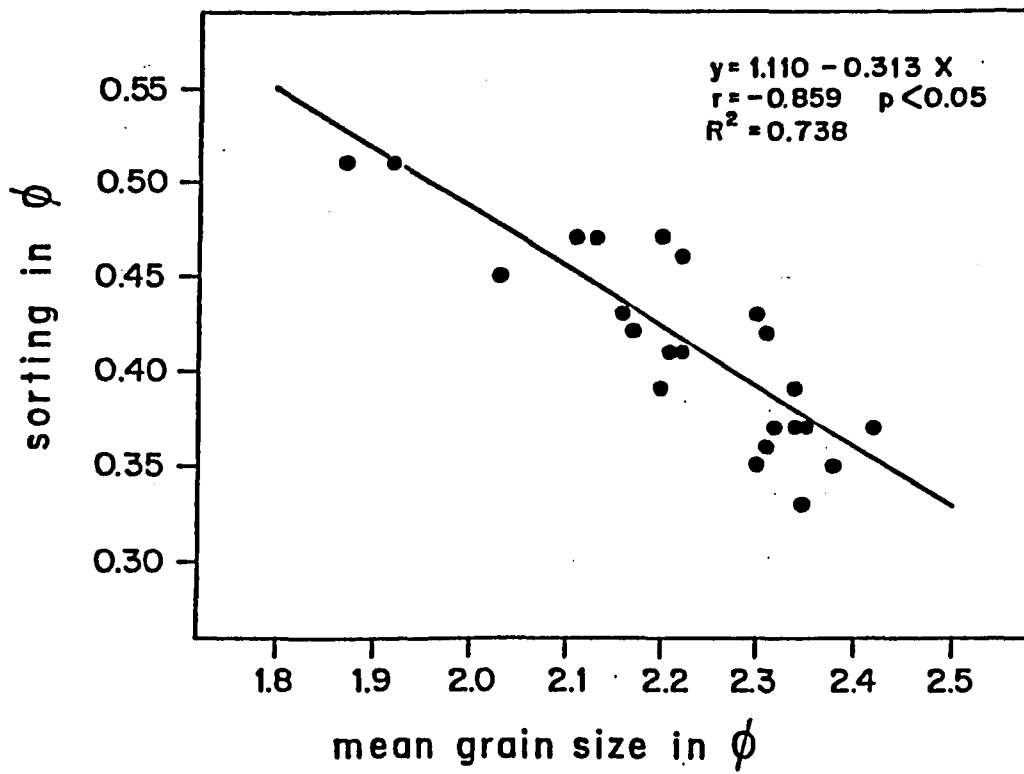


Fig. 12

Fig. 13. Temporal variability in a) temperature, b) water content, and c) penetrability of the sediments at Mehuín Beach during May, 1978 to April, 1980.

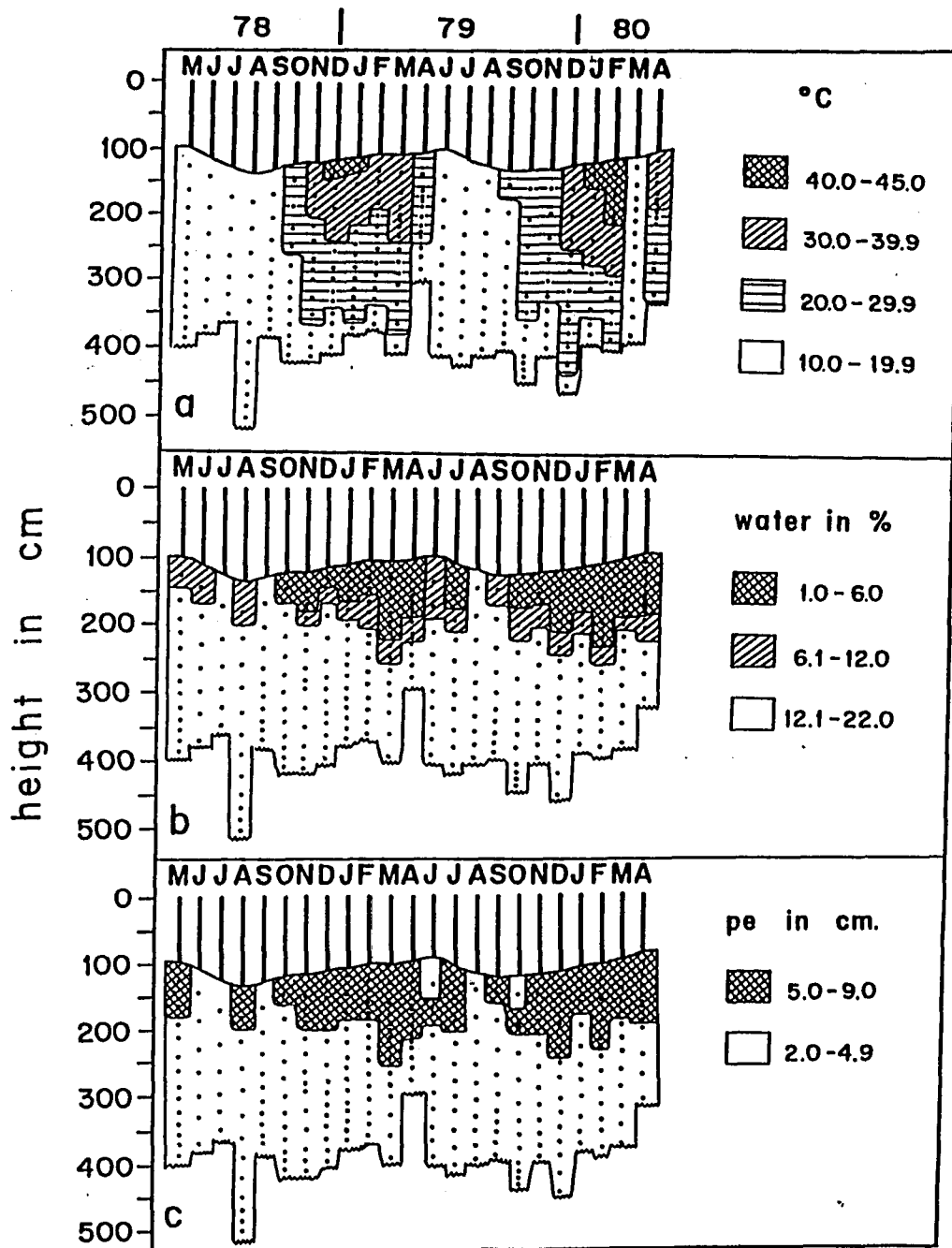


Fig. 13

**Fig. 14.** Relationships between a) the monthly averages of water content and temperature, and b) penetrability and water content of the sediments at Mehuín Beach during May, 1978 to April, 1980.

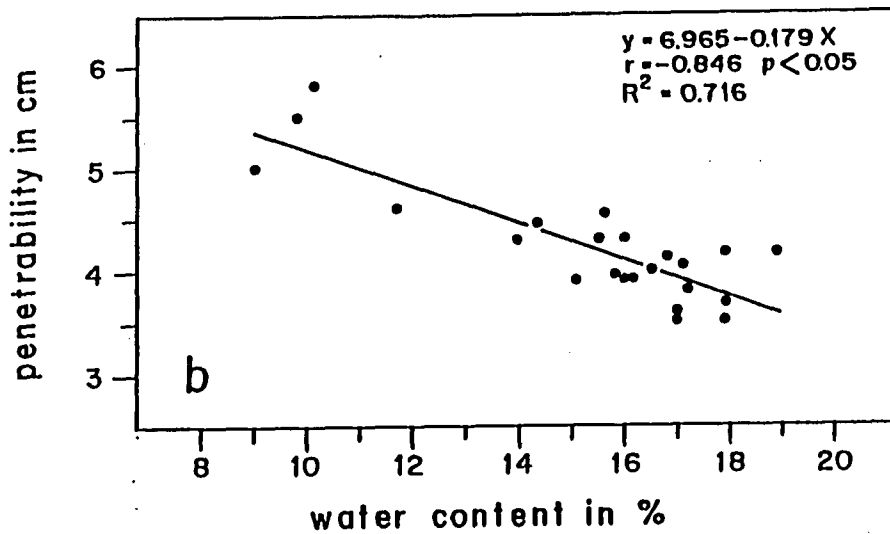
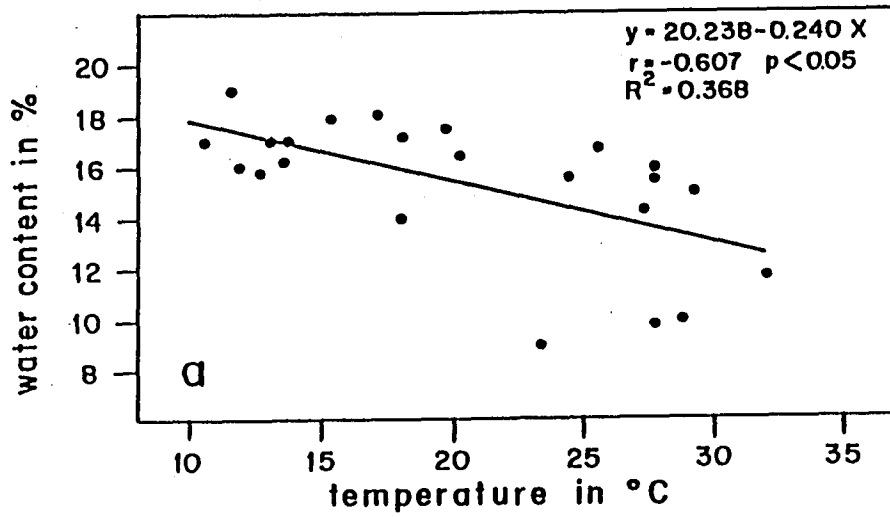


Fig. 14

Fig. 15. Ordination of the stations sampled at Mehuín Beach during May, 1978 to April, 1980 based on the values of mean grain size, sorting, temperature, water content and penetrability of the sediments. The first component is represented by the horizontal axes, while the second is represented by the vertical ones.

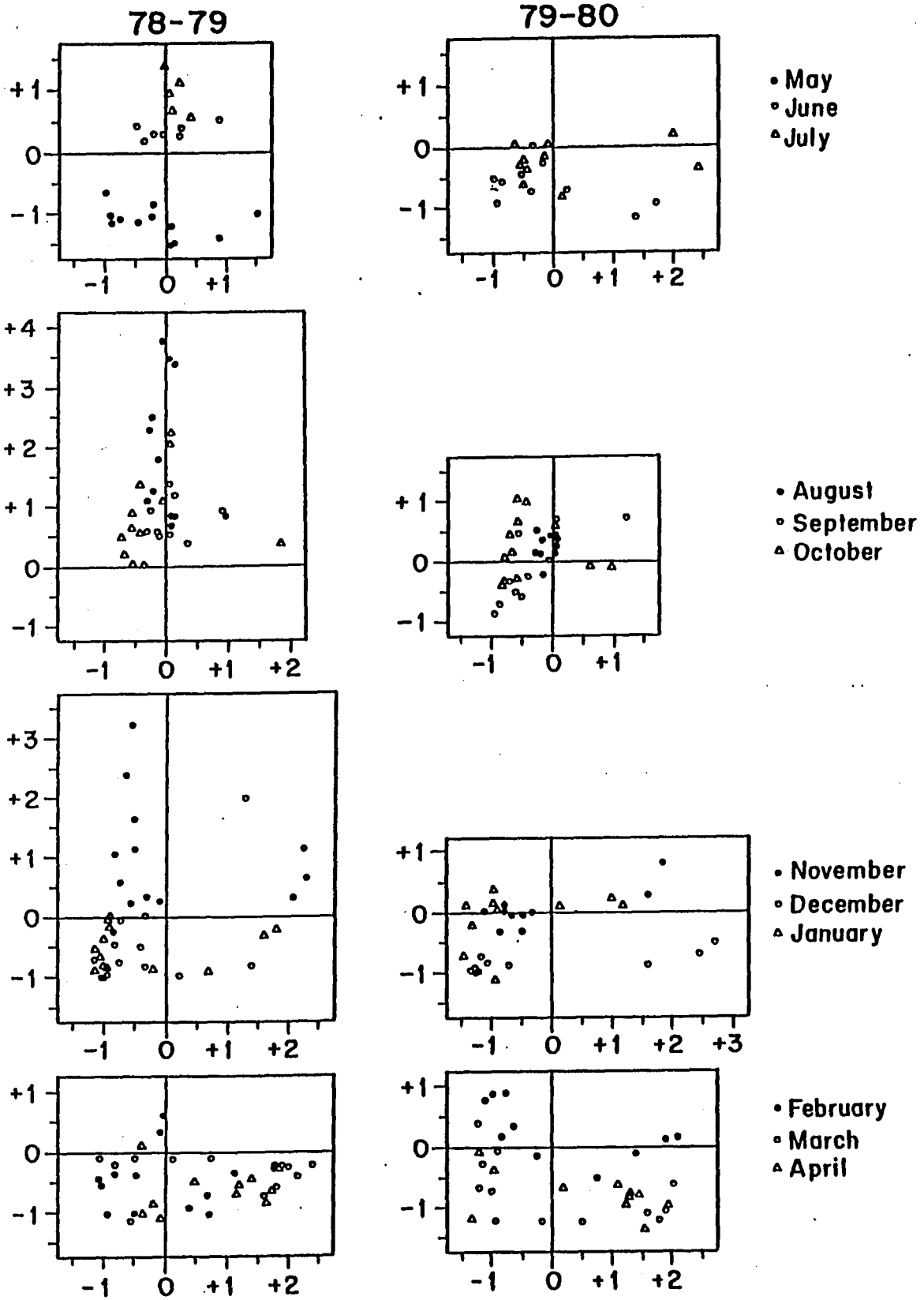


Fig. 15



Fig. 16. Temporal variability in the mean macroinfaunal abundances at Mehuín Beach during May, 1978 to April, 1980.

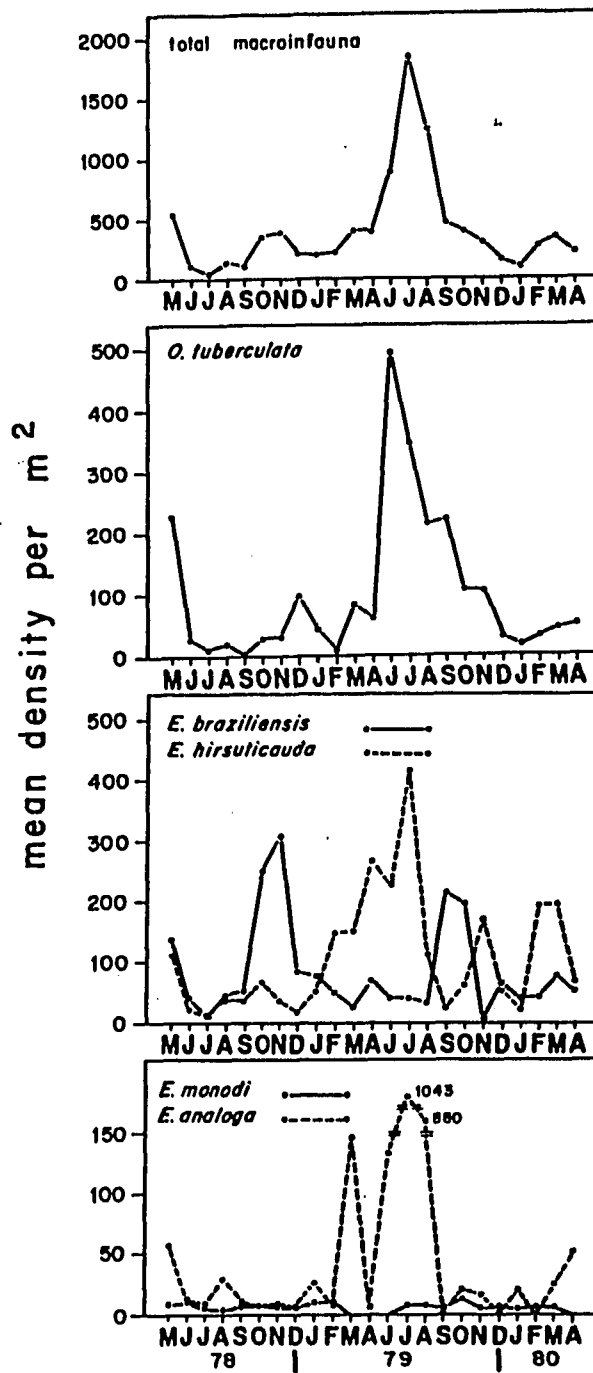


Fig. 16

Fig. 17. Seasonal occurrence of ovigerous females and juveniles of the peracarid species at Mehuín Beach during May, 1978 to April, 1980.

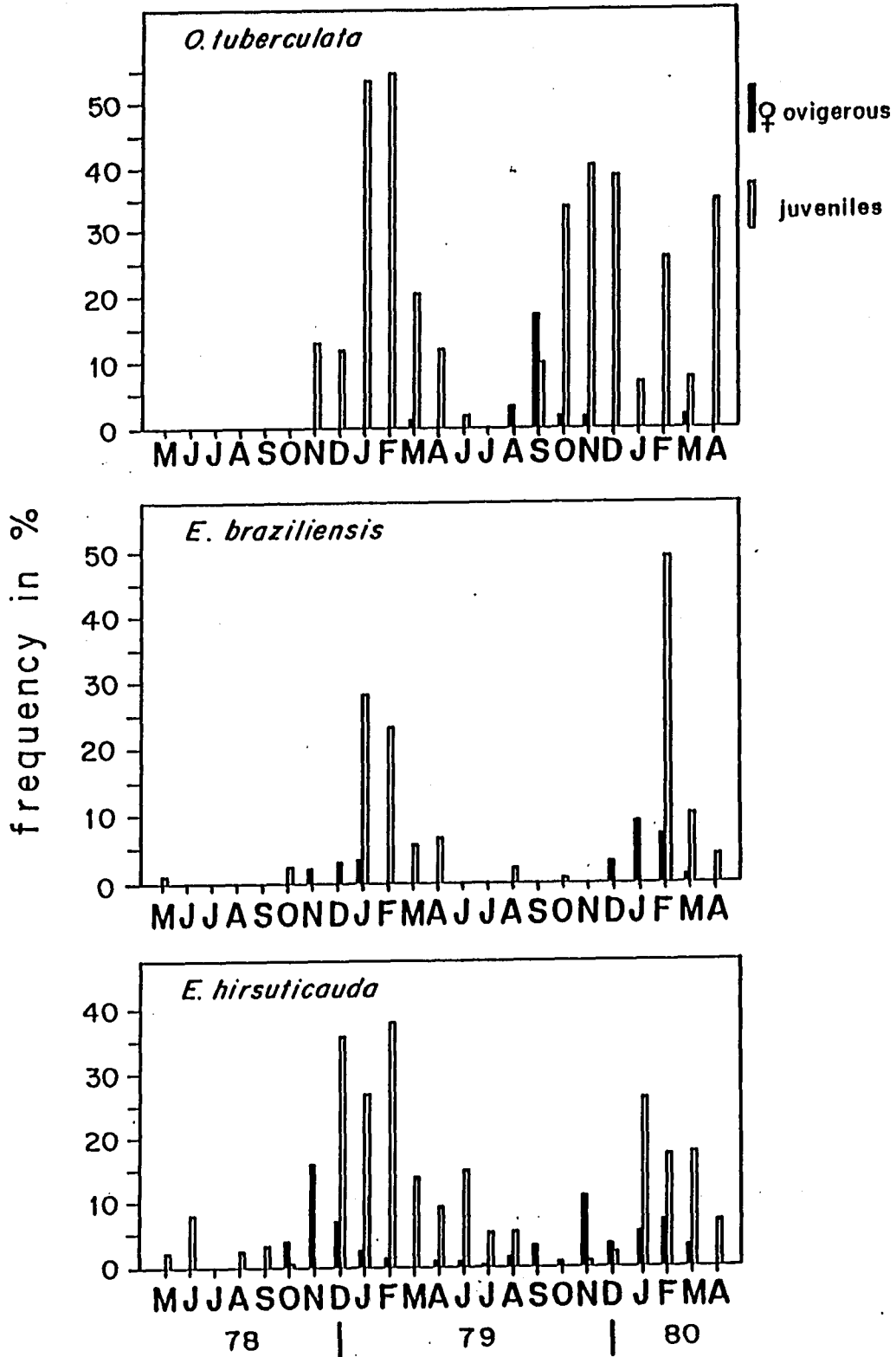


Fig. 17

Fig. 18. Seasonal occurrence of ovigerous females and juveniles of E. analoga at Mehuín Beach during May, 1978 to April, 1980.

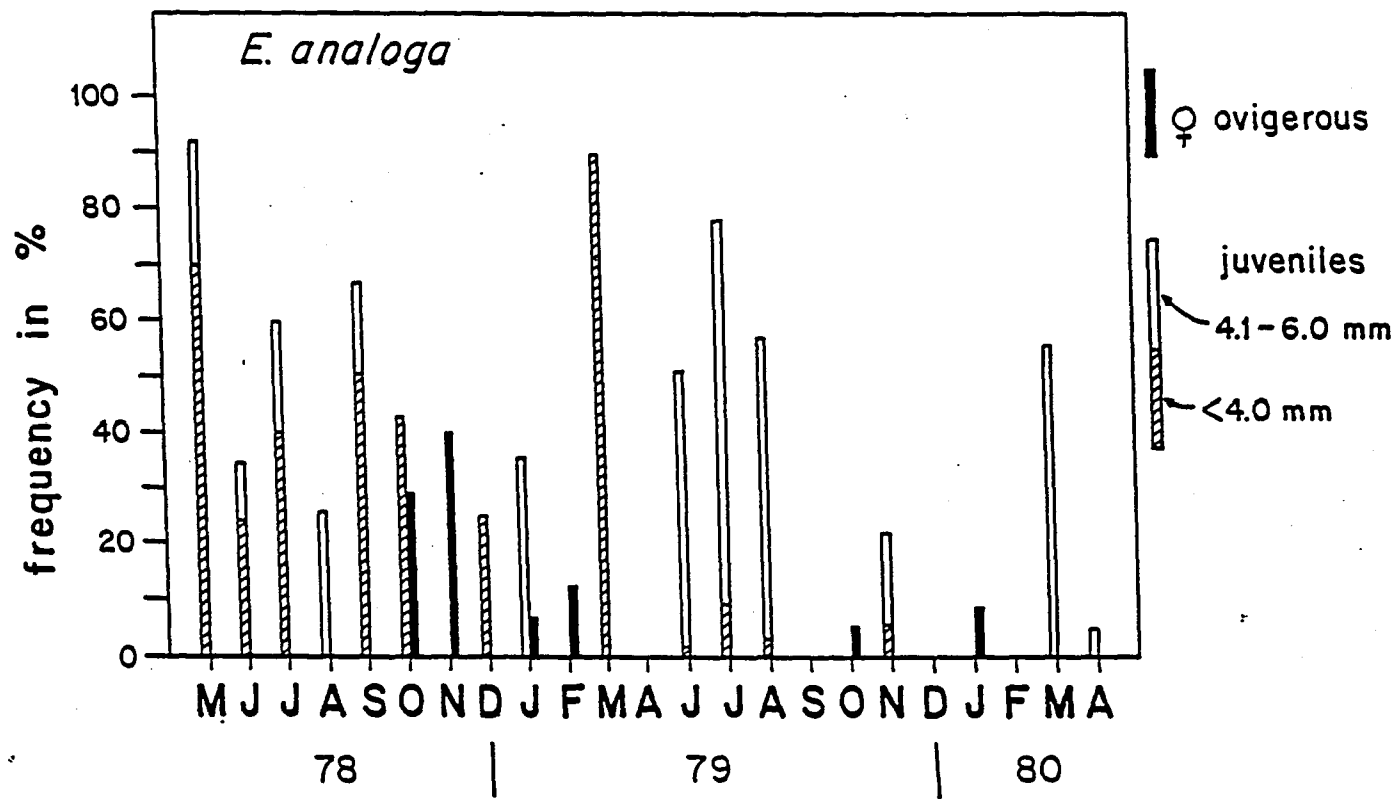


Fig. 18

Fig. 19. Occurrence and intertidal distribution of juveniles and adults of the peracarid species at Mehuín Beach during the recruitment months of May, 1978 to April, 1980.





Fig. 20. Relationships between the mean body length of ovigerous females and the brood size of the peracarid species.

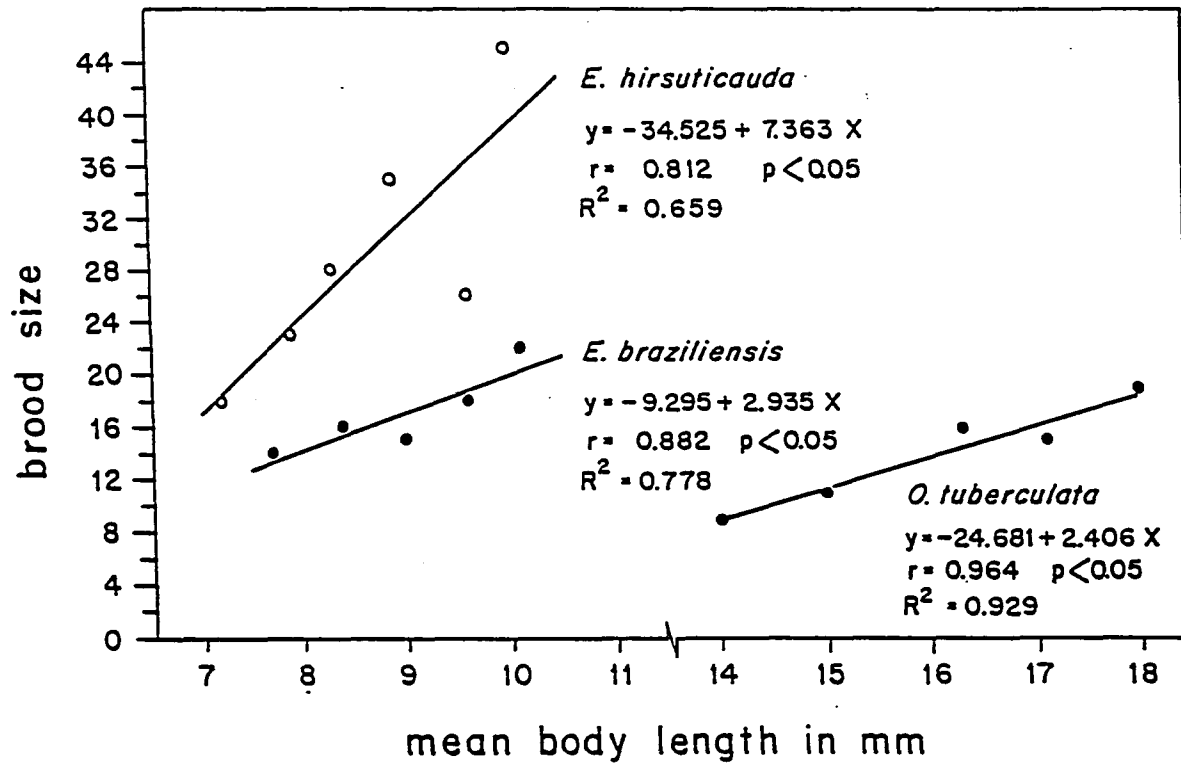


Fig. 20

Fig. 21. Population structure of the peracarid species and E. analoga at Mehuín Beach during May, 1978 to April, 1980. The juveniles of O. tuberculata, E. braziliensis and E. hirsuticauda are included in the size class <4.0 mm, while those of E. analoga are in the first two size classes, <4.0 and 4.0-5.9 mm.

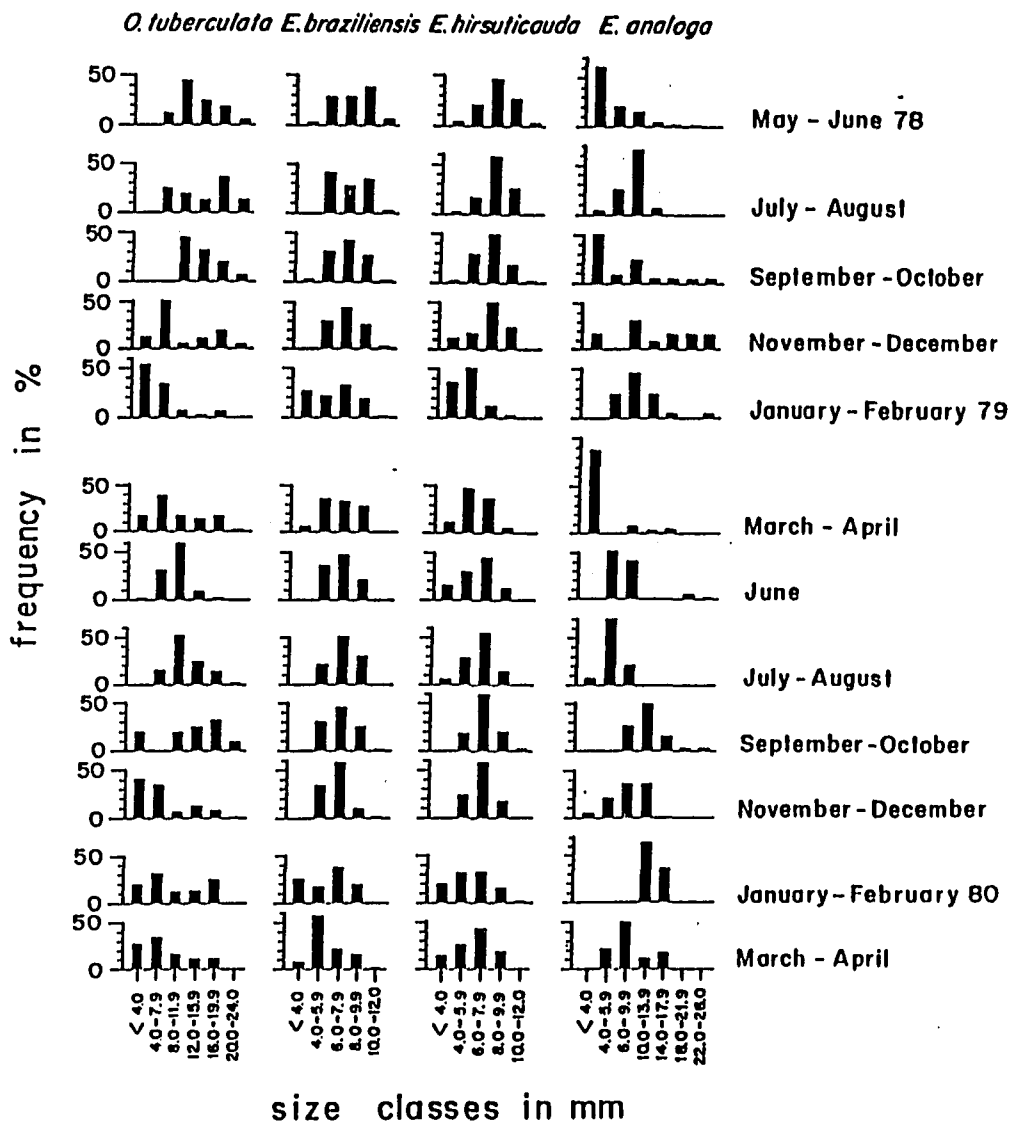


Fig. 21

Fig. 22. Intertidal zonation of the macroinfauna at Mehuín Beach based on the overall mean abundances during May, 1978 to April, 1980.

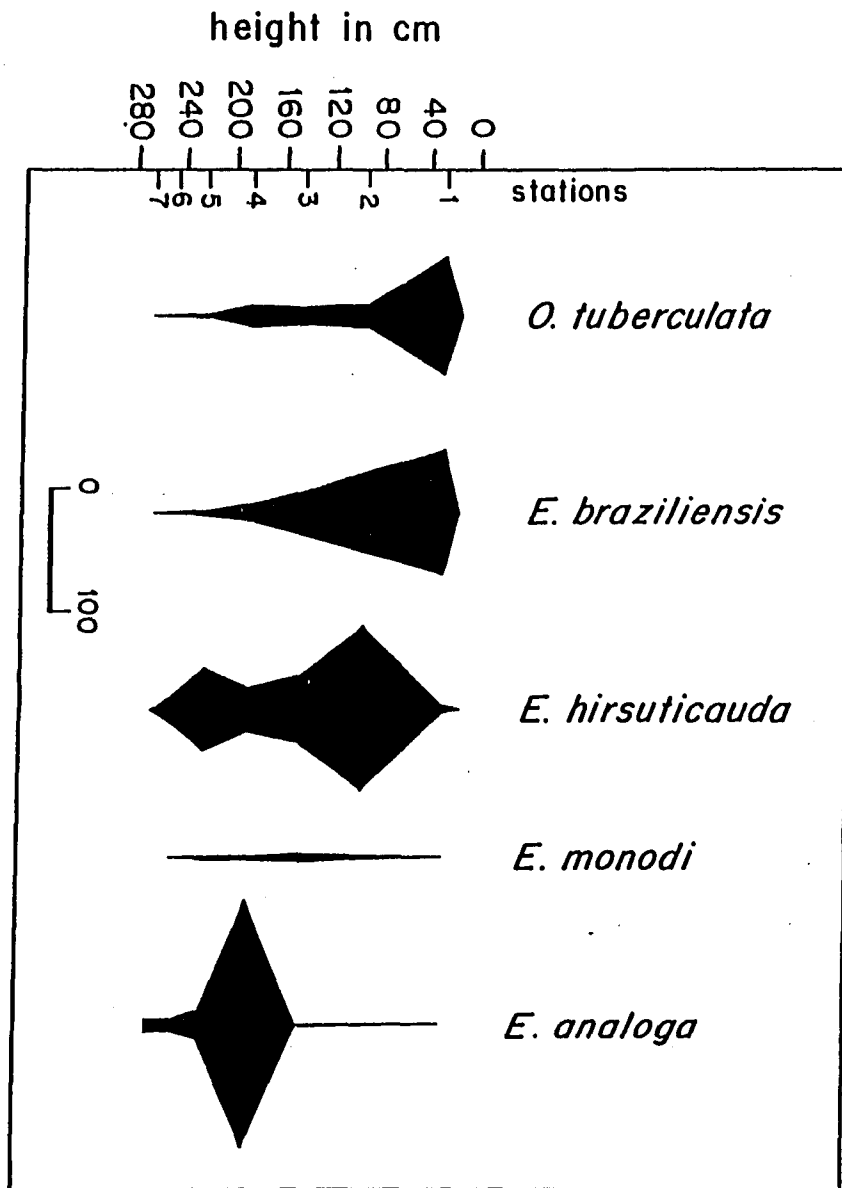


Fig. 22

Fig. 23. Temporal variability in the intertidal zonation of a) O. tuberculata, b) E. braziliensis, c) E. hirsuticauda and d) E. analoga at Mehuín Beach during May, 1978 to April, 1980. The dotted line at the top of each rectangle represents the variability of the sand level on the upper beach, while the black dots represent stations at which no animals were collected. The levels of the stations correspond to their heights in relation to the sand level of the post located on the upper beach.

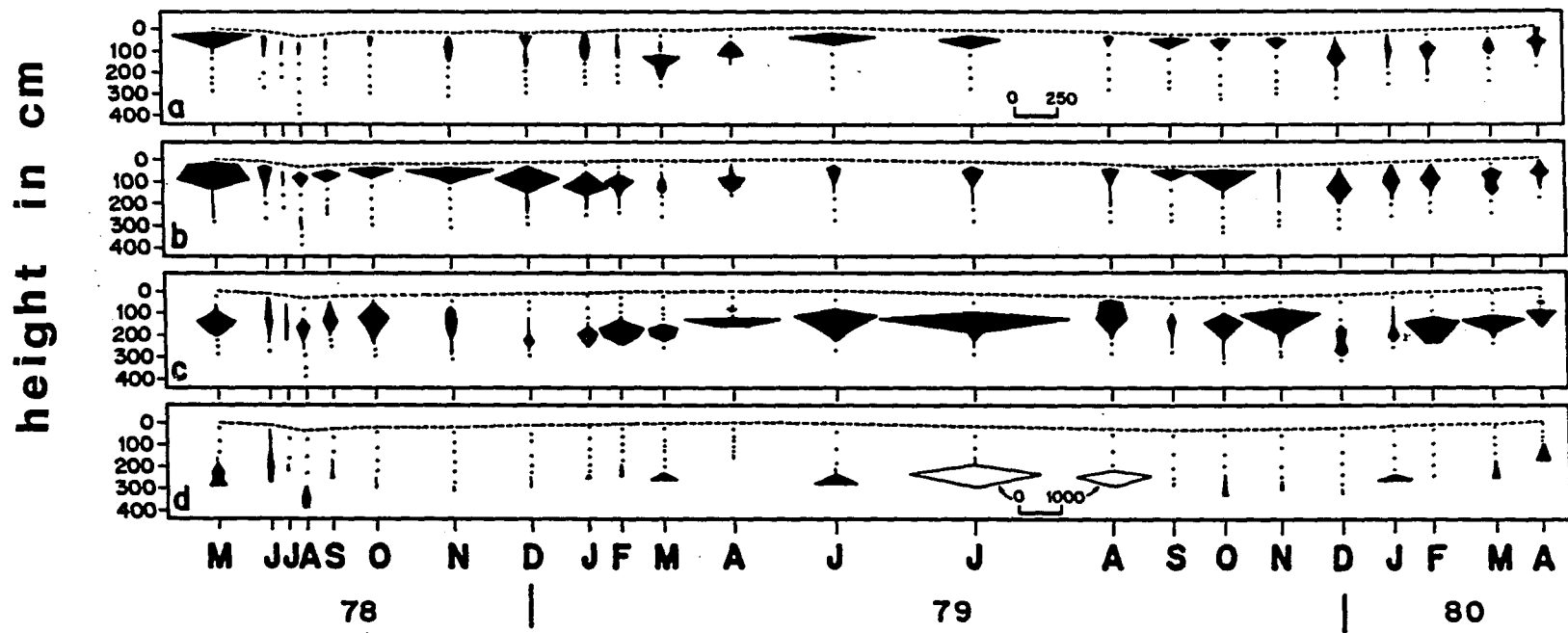


Fig. 23



Fig. 24. Long-term variability in the mean abundances of O. tuberculata, E. braziliensis and E. hirsuticauda at selected intertidal levels of Mehuín Beach through the years 1978-1985.

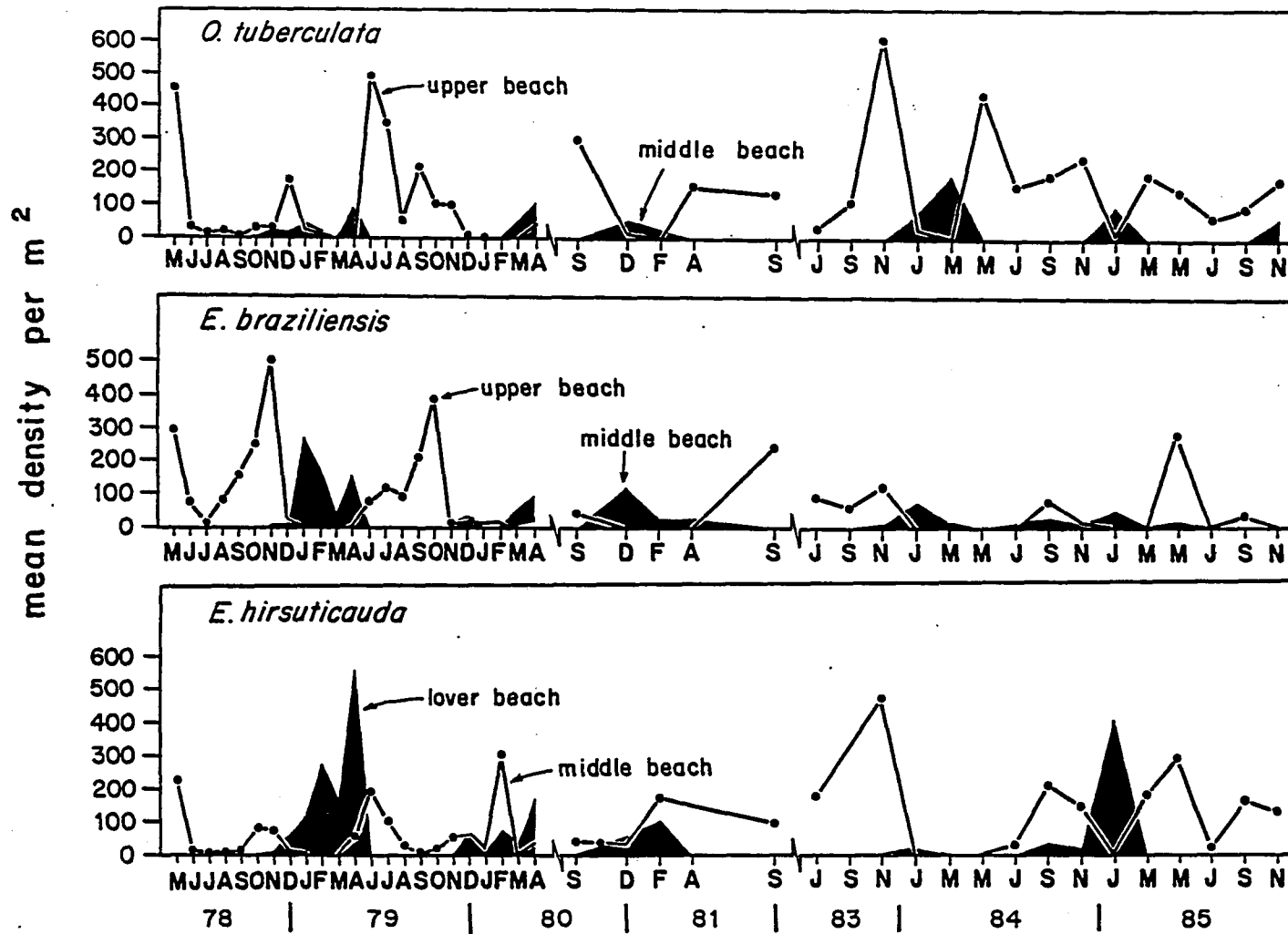


Fig. 24

Fig. 25. Long-term variability of E. analoga at the lower level of Mehuín Beach (station 5) through the years 1978-1985.

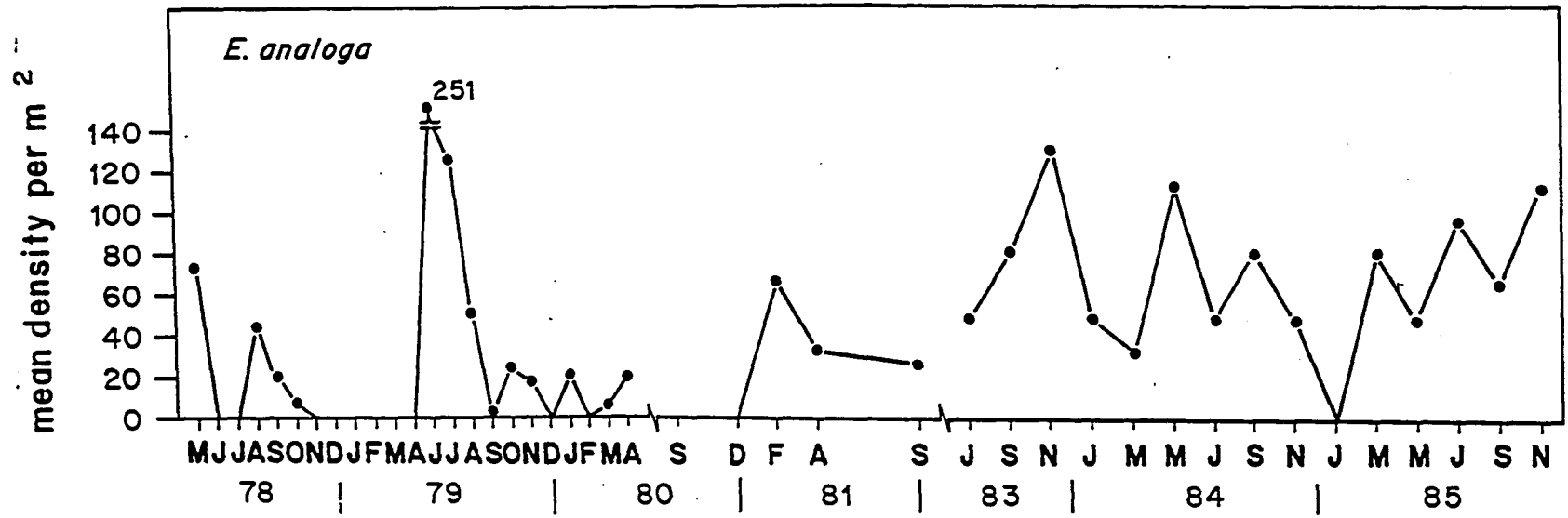


Fig. 25

Fig. 26. Seasonal sand depth distribution of mean grain size ( $\bar{x} \phi$ ) and sorting ( $\sigma\phi$ ) at Mehuín Beach. The variability in the number of stations was due to the seasonal variability in the beach width. No data were obtained during the macroinfaunal sampling of September 1981.

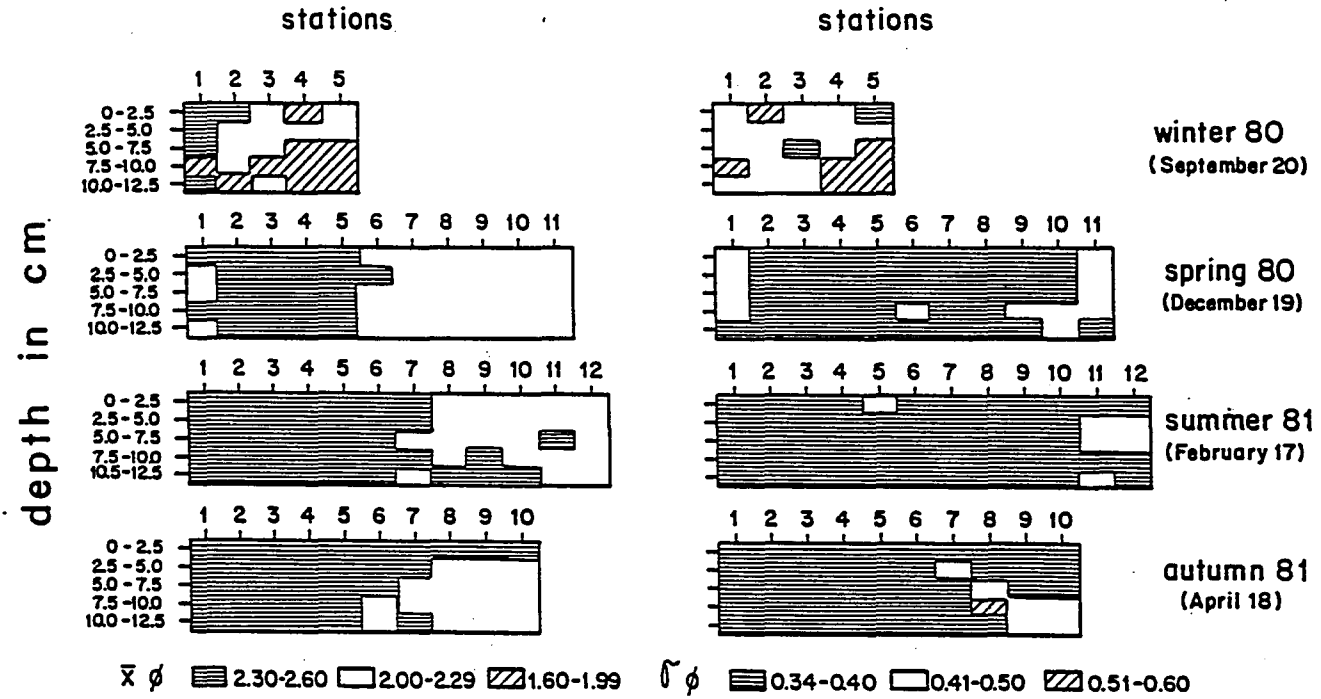


Fig. -26

**Fig. 27. Seasonal sand depth distribution of temperature and water content of the sediments at Mehuín Beach. No data were obtained during the macroinfaunal sampling of September 1981.**

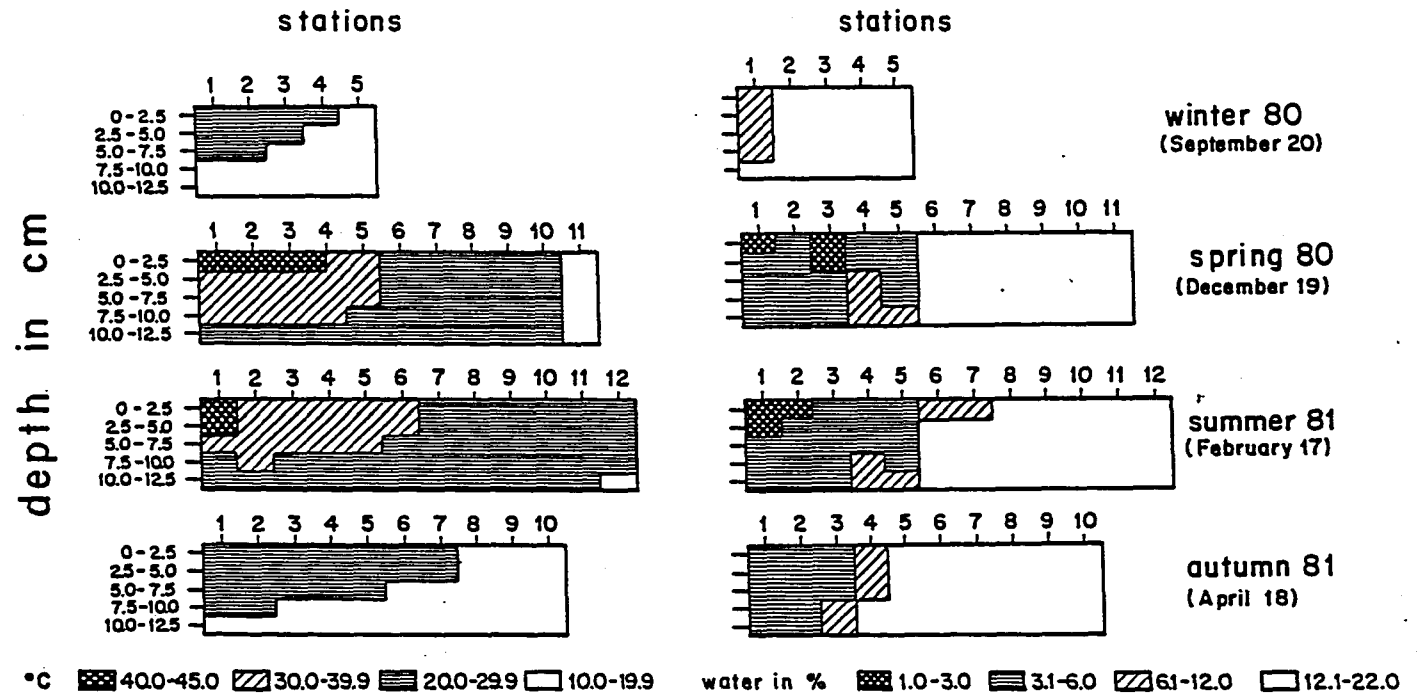


Fig. 27



Fig. 28. Seasonal sand depth distribution of the macroinfauna at Mehuín Beach.

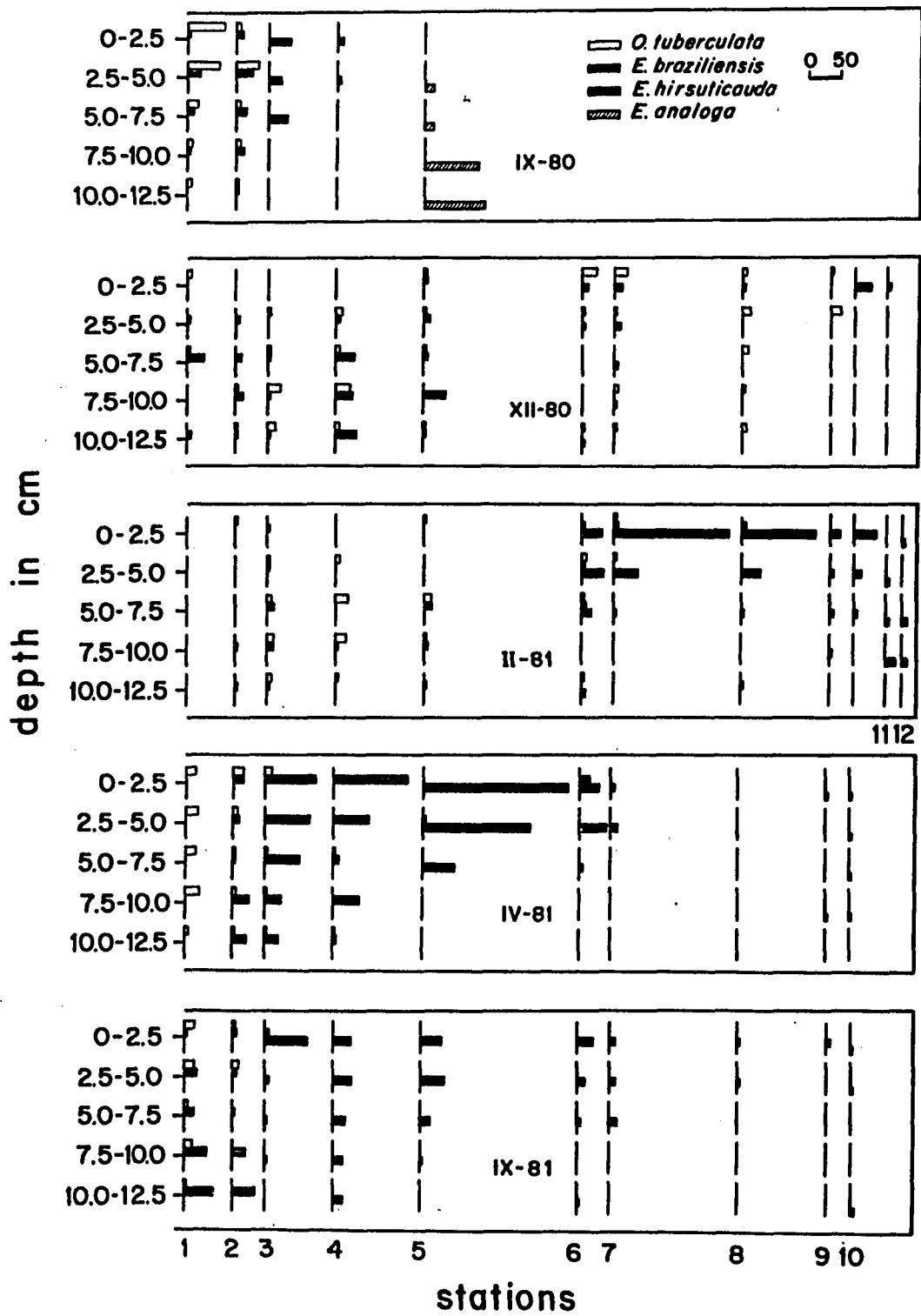


Fig. 28

**Fig. 29.** Relationships between the mean abundances of the macroinfauna and mean grain size and sorting of the sediments in samples from Bahía de Maiquillahue and outlet areas of Río Queule and Río Lingue; February-March, 1983.

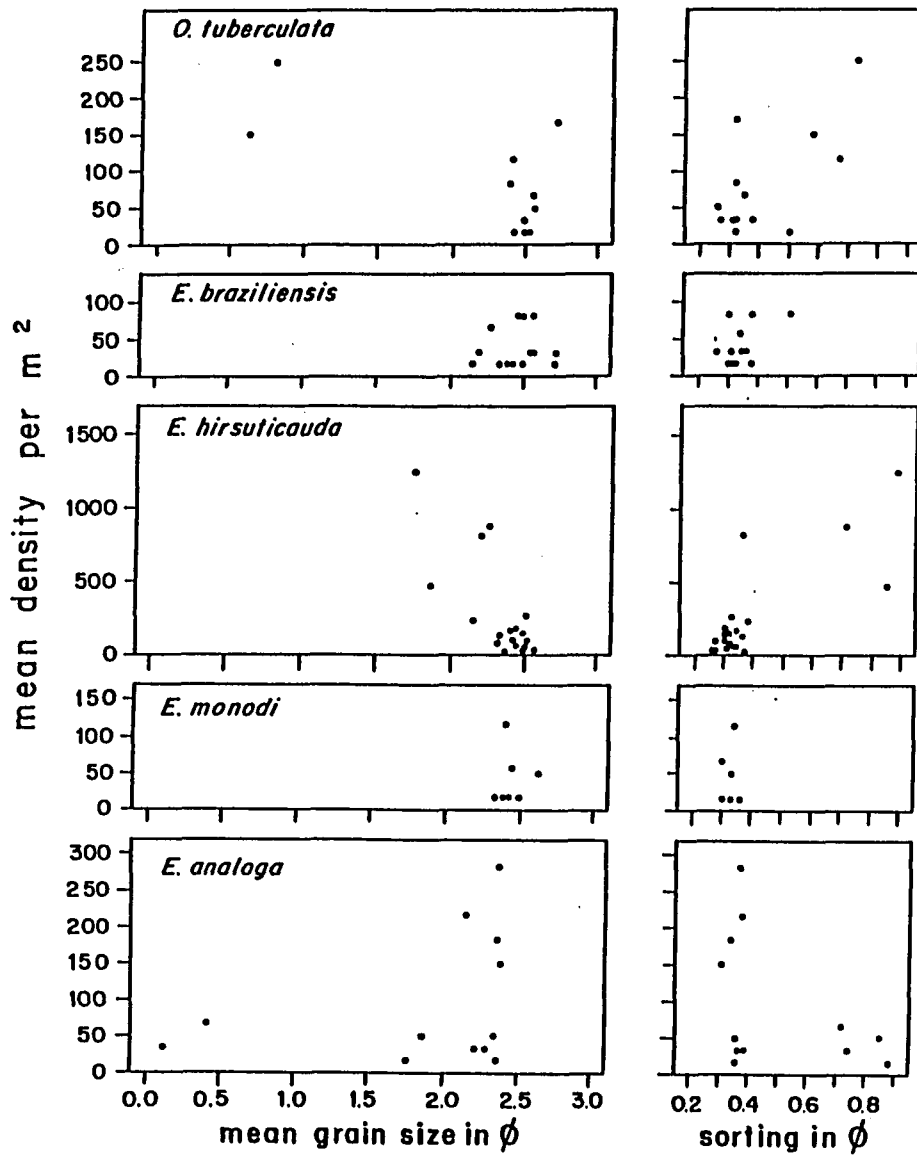


Fig. 29

Fig. 30. Selected intertidal zonation schemes from Bahía de Maiquillahue and outlet areas of Río Queule and Río Lingue.

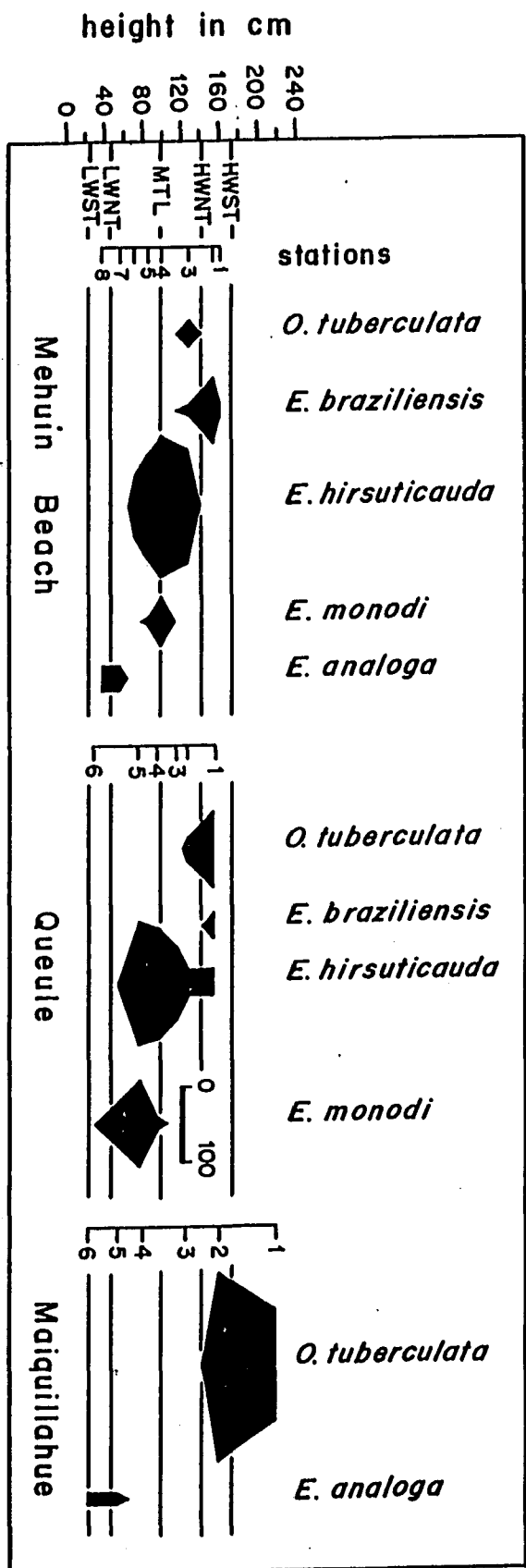


Fig. 30

Fig. 31. Mean mortality of the macroinfauna under different water salinities after a 1-week period.

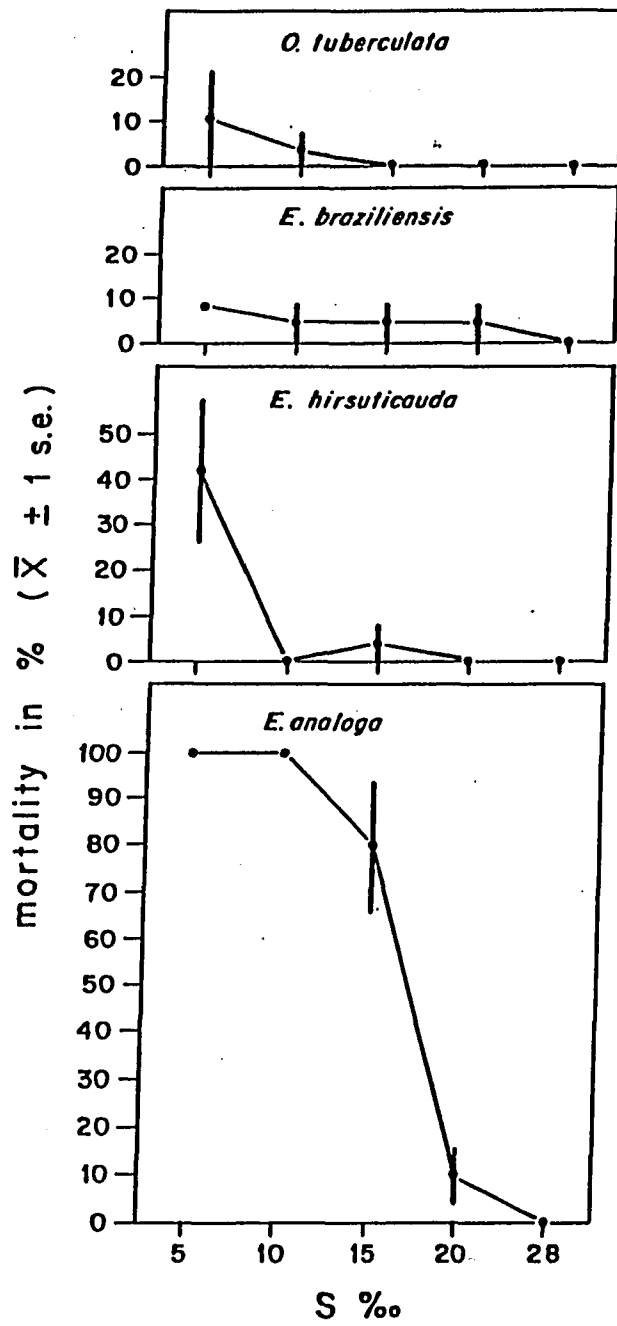


Fig. 31



**Fig. 32. Mean mortality of the macroinfauna under conditions of sand desiccation over a 24-hours period.**

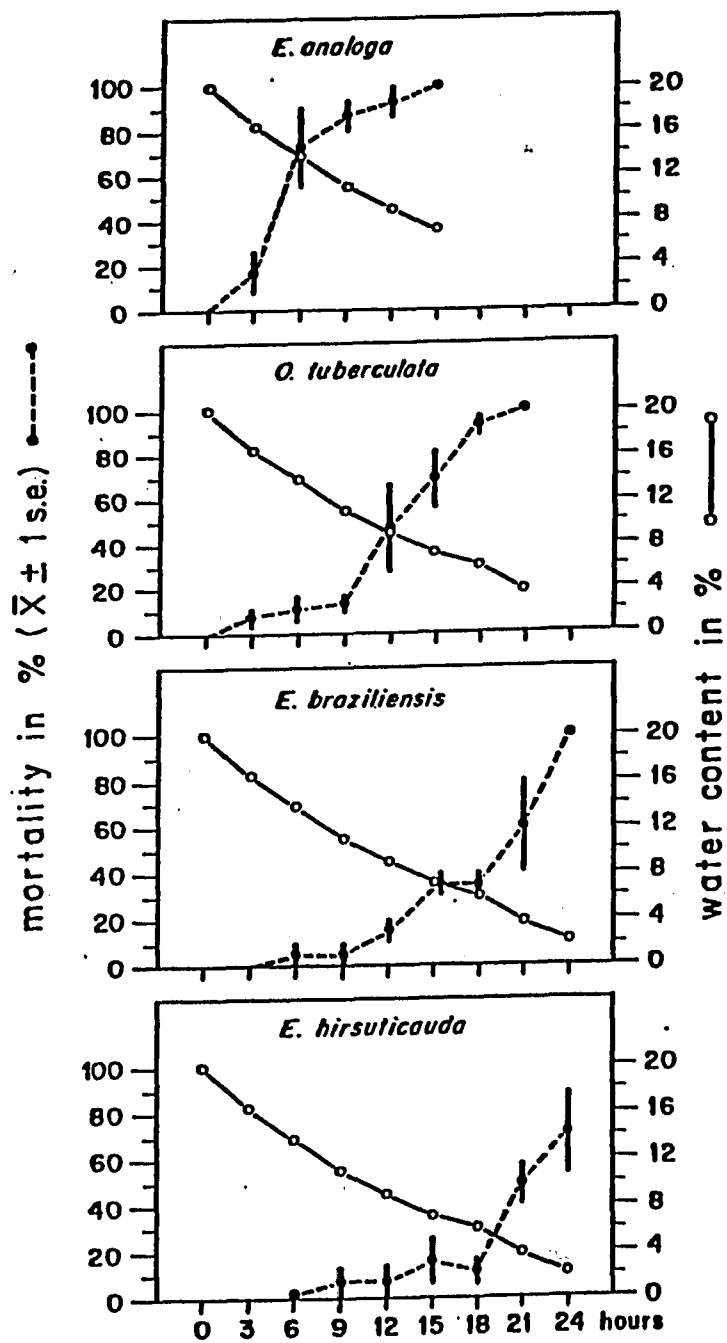
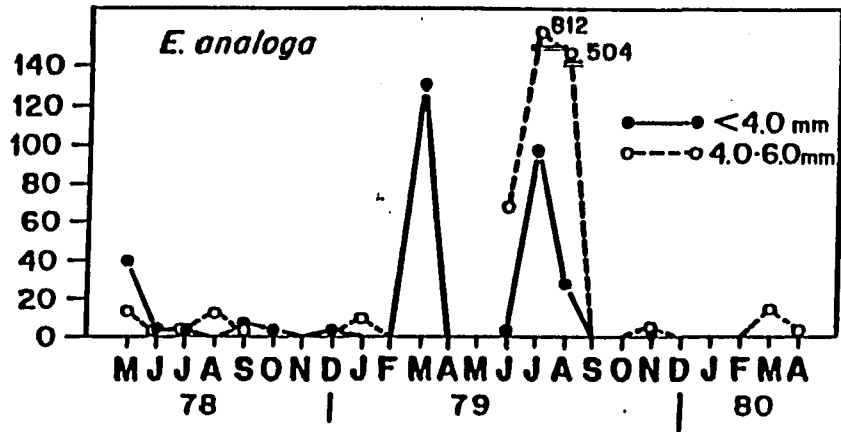


Fig. 32

Fig. 33. Temporal variability in the mean abundance of juveniles of E. analoga during May, 1978 to April, 1980, and shorebirds (C. alba and N. phaeopus) during the years 1983-84.

mean density per m<sup>2</sup>



mean number of shorebirds

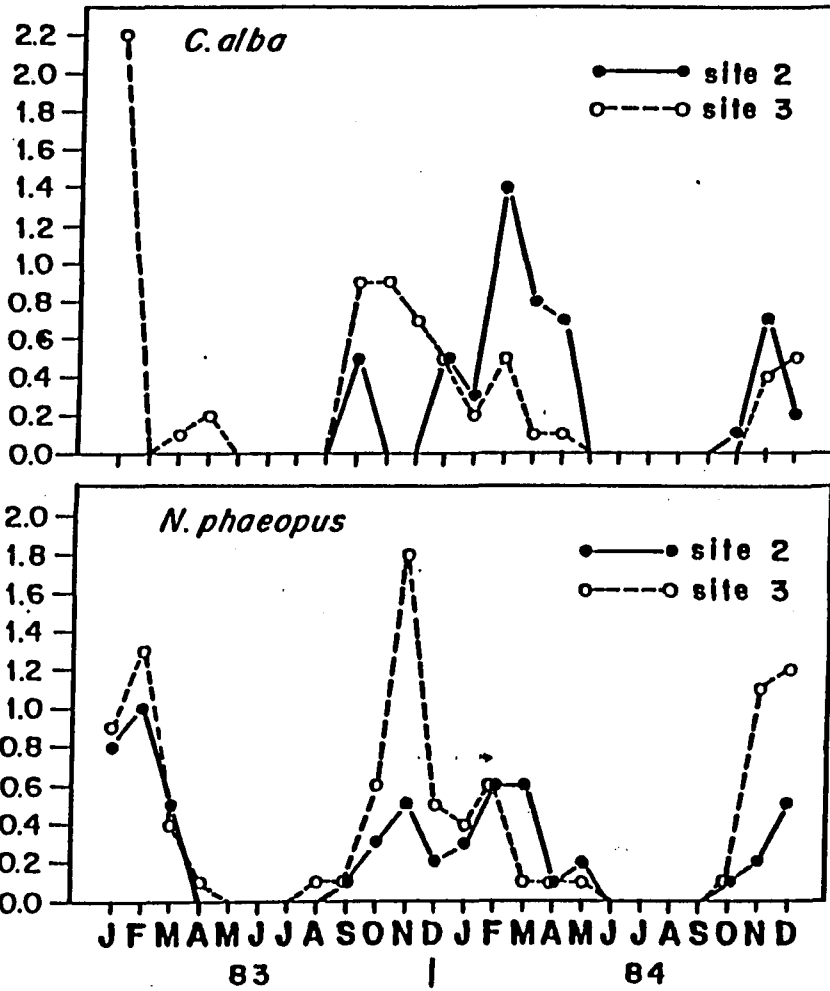


Fig. 33

**APPENDIX**

SANDY BEACH MACROINFAUNA FROM THE CHILEAN COAST: ZONATION PATTERNS AND ZOOGEOGRAPHY.

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Instituto de Zoología  
Universidad Austral de Chile  
Valdivia, Chile

RESUME. - La zonation de la macrofaune des plages sableuses est étudiée en trois régions de la province Peruvo-Chilienne. Les niveaux inférieures des trois régions sont caractérisés par Emerita analoga (Anomura), Nephtys impressa (Polychaeta) et Mesodesma donacium (Bivalvia). Dans les niveaux moyens une réduction est constatée dans le nombre des espèces d'Isopodes cirolanides du sud au nord, et dans certaines plages elles sont absentes. Une Cirolanide (Excirolana braziliensis) et un Insect (Phalerisidia maculata) sont présents dans la zone supérieure de toutes les plages étudiées. Des Crabes (Ocypode gaudichaudii) ne sont présents que dans la zone supérieure dans la partie nord du Chili, des espèces d'Isopodes terrestres (Tylos spinulosus) dans le nord de la région centrale et un Amphipode (Orchestoidea tuberculata) dans toute la région centrale chilienne. Cette distribution géographique est analysée en fonction des conditions hydrographiques et climatiques particulières de la côte chilienne. L'hypothèse avancée repose sur l'absence de courant ou des barrières de température à la surface de l'eau ce qui favorise la similitude de la composition taxonomique dans les zones inférieures de

toutes les plages étudiées. L'accroissement des précipitations du nord au sud et la différence de température de l'air et du sédiment, du sud au nord, expliquent les différences qui apparaissent dans les compositions taxonomiques de la macrofaune dans les zones supérieures.

ABSTRACT. - The zonation of the sandy beach macroinfauna was studied at three areas of the Peruvian-Chilean Province. The low beach levels (below MTL) of the three areas were characterized by: Emerita analoga (Anomura), Nephtys impressa (Polychaeta), and Mesodesma donacium (Bivalvia). The middle (MTL to MHWNT) and high (above MHWNT) beach levels showed significant changes in species composition with latitude. At middle levels there is a decrease in the number of cirolanid isopod species (Excirolana spp.) from south to north, and at some northern beaches they were absent altogether. One cirolanid (Excirolana braziliensis), and an insect (Phalerisidia maculata), inhabited high beach levels of all the beaches studied. Ocypodid crabs (Ocypode gaudichaudii) were found only at high beach levels of northern Chile, oniscoid isopods (Tylos spinulosus) only at northern central Chile, and talitrid amphipods (Orchestoidea tuberculata) at northern central and southern central Chile. The pattern of geographic distribution is analyzed in relation to some hydrographic and climatic conditions along the Chilean

coast. It is hypothesized that the general absence of current or temperature barriers in the surface waters, allows similar species composition at low beach levels at all locations. On the other hand, an increase in rainfall from north to south, and differences in air and sediment temperatures from south to north, are associated with different taxonomic composition of fauna at high beach levels. The zonation patterns of the Peruvian-Chilean macroinfauna are very similar to those noted by Dahl (1952) and Trevallion et al. (1970).

#### INTRODUCTION

Investigations of the sandy beach macroinfauna of the Chilean coast are rather limited. The first mention of macroinfaunal zonation is that of Dahl (1952) who analyzed the intertidal distribution of Crustacea at Montemar (central Chile), Isla Tenglo (southern central Chile), and Punta Arenas (southern extreme of Chile). At northern central Chile, Sanchez et al. (1982) studied the community structure and zonation schemes of a semi-exposed beach and compared their zonation results with the schemes of Dahl (1952), Pichon (1967), and Trevallion et al. (1970). For this area of the Chilean coast, Castilla et al. (1977) and Castilla (1983) analyzed changes in the typical zonation pattern and community structure of sandy beaches affected by an oil spill and by copper mine tailings, respectively. Zonation of species living in sandy areas of central Chile



were mentioned by Nunez *et al.* (1974) and Osorio *et al.* (1967), while distributional patterns in southern central Chile were studied by Bertrán (1984), Epelde-Aguirre and Lopez (1975), and Jaramillo (1978). The last two studies also provided comparisons with world-wide zonation schemes. All of these earlier studies were carried out mainly in the central area of the Chilean littoral (from approximately 30 to 40° S). The Chilean coast is quite extensive (about 4,000 km) ranging from approximately 18° 30' S to 55° S latitude, covering about 36 degrees of latitude. Zoogeographical boundaries were discussed by several authors (e.g. Balech, 1954; Brattstrom and Johanssen, 1983; Castilla, 1976; Dahl, 1960; Dell, 1971; Knox, 1960; and Viviani, 1979). In general, most workers agree that two regions can be distinguished: a northern warm-temperate (from about 18 to 42° S latitude), the Peruvian or Peruvian-Chilean Province, and a southern cold-temperate (from about 42 to 55° S latitude) or Magellanic/Patagonic Province. A transitional zone has also been suggested, located approximately between 30 and 40° S, where many species from both regions co-exist (Balech, 1954; Brattstrom and Johanssen, 1983; and Dell, 1971).

The purpose of this study was to analyze the species composition and zonation patterns of the sandy beach macroinfauna inhabiting three areas of the Peruvian-Chilean

Province. Northern Chile corresponds approximately to an area between 18 and 25° S, northern central Chile between 25 and 35° S, and southern central Chile between 35 and 45° S.

#### MATERIALS AND METHODS

The faunal data examined for this paper represent samples from ten sandy beaches along the Chilean coast (Fig. 1). Sites in northern and southern central Chile were sampled in the period January to December, 1977, while the site in northern central Chile was sampled during November, 1980. The macroinfauna were sampled during spring low tides at a series of stations along transects extending from low water level to the back border of each beach (defined by foredunes, cliffs or drift lines). At each station, a 0.1 m<sup>2</sup> box quadrat (33 x 33 cm) was pressed into the sand 15 cm. The sediment was washed through a 1 mm sieve, and the animals were removed and preserved in 10% formalin. Ghost crab (Ocypode gaudichaudii Milne Edwards) distribution was recorded by the number of burrows.

Density values per 1 m<sup>2</sup> were calculated (except for Ocypode gaudichaudii) and used to draw kite diagrams and describe zonation patterns. To analyze the zonation of species associations, macroinfaunal samples were subjected to numerical classification. The taxonomic similarity between pairs of samples was calculated with Jaccard's Index (after Saiz, 1980), and dendrograms were obtained after the Weighted Pair Group Method (Sokal and Sneath, 1973). Multivariate analyses were performed with the

program ACOM (Navarro, 1984) on a DECSYSTEM-2020 computer at the Centro de Información y Computación, Universidad Austral de Chile, Valdivia.

Beach profiles were constructed according to the method of Emery (1961). The slope of each transect was measured by the coefficient  $\frac{a}{L} \times 100$ , where  $a$  is the difference in height between the highest and lowest station (low water line), and  $L$  is the distance between these two points. Sand samples (15 cm deep) were taken for grain size analysis at the high, middle, and low levels of each beach. The three samples were mixed, washed, dried at  $105^{\circ}\text{C}$  for 24 hours, and then subsampled randomly to obtain a cumulative 100 gram sample. The samples were passed through a series of sieves of 2,000, 1,000, 500, 250, 106, and 53 microns; a mechanical shaker was used for 20 minutes on each sample. Graphic mean and inclusive graphic standard deviation values were calculated from cumulative curves drawn with the percentages of sand in each size fraction (after Folk, 1980). The results for each beach are expressed in phi units ( $\phi = -\log_2 \text{ mm}$ ).

Analyses of environmental conditions on the Chilean coast were based on several features: (1) examination of hydrographic characteristics given by Brattstrom and Johanssen (1983) and Viviani (1979), and comparisons of sea water temperatures compiled from Ahumada and Chuecas (1979), Bretos et al. (1983), Pizarro (1973), and the daily

data of the Marine Biology Station of the Universidad Austral de Chile at Mehuín, (2) comparisons of surface sand temperatures (about 0.5 cm depth) of sandy beaches in northern and southern central Chile, and (3) inspection of climatic characteristics given by Brattstrom and Johanssen (1983), and Walter's climatic diagrams (1957) presented by di Castri and Hajek (1976) for selected coastal localities.

## RESULTS

### The Beaches

The sandy beaches studied here are located on the exposed coast of the Chilean littoral (Fig. 1) having moderate tidal amplitudes (1.2 - 2.2 m at spring tides) and unequal tidal height (twice) each 24 hours (Brattstrom and Johanssen, 1983).

In northern Chile, Colorado, Cavanca and Huaiquique were the narrowest beaches with the steepest profiles (highest slope values). The other two beaches of this area, Aguila and Guanillo, were the widest beaches and had the shallowest profiles (lowest slope values, cf. Table I and Fig. 1). Punta Choros, a beach sampled in northern central Chile, had a steep profile (Fig. 1). In southern central Chile, the four beaches studied had similar widths. Niebla and Muicolpue were the steepest, while Ronca and Mehuín had more gentle slopes (cf. Table I and Fig. 1). Colorado in the north and Niebla in the south had medium sand sediments (1-2  $\phi$ ), while the other beaches showed fine

sand sediments (2-3  $\phi$ , cf. Folk, 1980). Colorado and Niebla had moderately well sorted sediments (0.50 - 0.71  $\phi$ ), while all the rest fit the range of well sorted sediments (0.35 - 0.50  $\phi$ , cf. Folk, 1980). The relationship between slope and grain size ( $\phi$ ) is shown in Fig. 1. In general, the steepest beaches had the coarsest sediments; however, the correlation coefficient ( $r = -0.58$ ) between these paired observations was not significant.

#### Currents and Sea Water Temperature

The following summary of the oceanic current system near the Chilean coast is based on the comprehensive account given by Brattstrom and Johanssen (1983). For this study only some of the currents involved in this system (Fig. 2) are discussed.

Near 80-90° W longitude off the coast of southern Chile the Westwind Drift Current (circumantarctic) gives rise to a northern and a southern branch (Fig. 2). The Perú Oceanic Current transports subantarctic waters to the north, while the Cape Horn Current flows to the southern tip of South America along the Chilean archipelagos. At about 40-48° S and close to the coast, the Cape Horn Current produces the Humboldt or Perú Coastal Current which carries to the north subantarctic waters in origin and colder than those in the Perú Oceanic Current. The Humboldt Current leaves the coast at about 30° S, near the southern boundary of the most significant upwelling area on the Chilean coast (Viviani, 1979).

The combined effect of the northerly transport of cold water by the Humboldt Current and the upwelling occurring along the central and northern littoral, explain why the sea temperature differences between northern and southern Chile are smaller than expected for this long coastline (Brattstrom and Johanssen, 1983; Viviani, 1979). Therefore, no abrupt temperature barriers are found, and the temperature increases gradually from south to north (Brattstrom and Johanssen, 1983). The following examples give support to these general statements. Brattstrom and Johanssen (1983) mention that the sea surface temperature during October-March (spring-summer) is 15-20 °C off Arica (18° 28'S latitude), 16-18 °C at Coquimbo (about 29° 20'S) and 12-16 °C at Valdivia (39° 48'S). During April-September (fall-winter), similar temperatures are 14-18 °C at Arica, about 13-14 °C at Coquimbo, and 10-11 °C at Valdivia. Thus, the difference between both latitudinal extremes (about 2,500 km apart) is only 8 °C for both seasonal periods. These values are quite similar to those from other sources. Mean sea surface temperature at Huaiquique (20° 17'S) varied between 15 and 17.5 °C during 1979-80; however, higher temperatures have been measured (up to 25 °C) here (Bretos *et al.*, 1983; Viviani, 1979) during years when El Niño, a tropical south-flowing current affects especially northern and central Chile. At Montemar (32° 58'S), Bahía de Concepción (36° 40'S) and Mehuín (39° 26'S), the mean values fluctuate in a similar manner between approximately 12 and

14 °C over a number of years (Ahumada and Chuecas, 1979; Pizarro, 1973 and data from the Marine Biology Station of Universidad Austral de Chile).

### Climate

From approximately 18 to 30 °S latitude (Arica to Coquimbo), there is a very low and irregular rainfall (di Castri and Hajek, 1976). Brattstrom and Johanssen (1983) consider this area the dry zone of Martin (1923) with a desert coast and a mean monthly air temperature of 18-22 °C in the summer and about 12-17 °C in the winter. The area between 30 and 38 °S latitude (Coquimbo to Isla Mocha) corresponds closely to Martin's (1923) warm zone where the mean temperature for the warmest month varies from about 15 to 22 °C, and for the coldest month from 10-13 °C. Furthermore, Brattstrom and Johanssen (1983) state that the yearly rainfall increases from about 110 mm at Coquimbo to 760 mm at Talcahuano (Isla Quiriquina) and still higher farther south. Finally, Brattstrom and Johanssen (1983) claim that the area between about 38 to 56 °S (Isla Mocha to Cabo de Hornos) closely corresponds to the rainy zone and the Patagonia-Tierra del Fuego zone of Martin (1923). The mean annual temperature here decreases approximately linearly from 12.5 °C at about 38 °S south to 5.4 °C at Cabo de Hornos.

These climatic characteristics are graphically displayed by Walter's climatic diagrams. In this display

(Fig. 3, left side), the abscissa represents the months of the year, while the two ordinate axes represent temperature and rainfall. Aridity (dotted area) is indicated when the rainfall curve lies below the temperature curve. The humid period is conventionally represented by vertical lines, with the exception of periods exceeding 100 mm rainfall which are black; the dry period is represented by a dotted surface (di Castri and Hajek, 1976). Arica is typical of the dry zone, with aridity during the entire year. La Serena, Zapallar, and Lebu are located in the warm zone delimited by Brattstrom and Johanssen (1983), where the arid period decreases from north to south, coincidental with an increase of the humid period. Aridity ceases south of Lebu; Punta Galera and Puerto Aysén show an excess of rainfall during at least half of the year. These two localities and Punta Arenas are included in the so-called rainy zone.

#### Sand Temperature

The data obtained during the autumn of 1977 from beaches of northern Chile (Colorado, Cavancha, Huaiquique, Aguila and Guanillo) show that the sand temperature values were similar to those measured during summer at the sandy beach of Mehuín in southern central Chile. At these beaches, temperatures ranged from approximately 18 to 45 °C, with values above 33 °C at the highest beach levels, i.e. above MHWST. At Mehuín, sediment temperatures varied between approximately 14 and 19 °C in May 1978, 17 and 29 °C



in April 1979, and 21 and 34 °C in April 1980. During the autumn of 1979 and 1980, the temperature values measured at the highest beach levels of Mehuín were quite similar to those measured at the middle levels of the beaches in northern Chile.

#### The macroinfauna

The highest number of species and total densities were found in sandy beaches of northern central and southern central Chile (Table II). In northern Chile (with the exception of Colorado) the highest densities per station, and the highest density of the dominant species as the anomuran crab Emerita analoga (Stimpson) (Hippidae), occurred near the low water line (Table II). At Punta Choros, the highest density per station was estimated for the highest level of that beach, while in southern central Chile, stations located at the middle levels (MHWNT to MTL or MTL) of Mehuín and Muicolpue yielded the highest densities (Table II). The isopod Excirolana hirsuticauda Menzies (Cirolanidae) was the most abundant species in both of these areas with the exception of Muicolpue in the south, where the amphipod Orchestoidea tuberculata Nicolet (Talitridae) was the most abundant species.

The zonation of the species from each area of the Chilean coast is shown in Fig. 4. The insect Phalerisidia maculata Kulzer occurred on the high beach levels of all the beaches studied. The ghost crab Ocypode gaudichaudii

Milne Edwards (Ocypodidae) occurred only in northern Chile. Tyloid isopods (Tylos spinulosus Dana) were not collected in northern Chile, nor in southern central Chile, but only at Punta Choros in northern central Chile. Talitrid amphipods (Orchestoidea tuberculata) were absent at northern Chile, and cirolanid isopods were more diverse at southern central Chile (Excirolana hirsuticauda, Excirolana braziliensis Richardson and Excirolana monodi Carvacho). Emerita analoga, the polychaete Nephtys impressa Baird (Nephtyidae), and the clam Mesodesma donacium (Lamarck) were collected at the low levels (below MTL) of most of the beaches.

Three major station groups, linked by a very low value of similarity (0.04), are recognizable in the dendrogram produced by the cluster analysis (Fig. 5). The groups (A, B and C) represent tidal levels, while the subgroups within them represent groups of stations from different geographical areas. Group A includes levels inhabited by insects, ocypodids, talitrids, cirolanid (E. braziliensis) and tyloid isopods. Group B has cirolanids as the main component and group C includes E. analoga, N. impressa, and M. donacium.

#### DISCUSSION

The analysis of the zonation patterns and cluster analysis of the macroinfauna from the Chilean coast show that significant changes in species composition occur at

middle and high beach levels, while similar species occur at low beach levels (Fig. 6). At middle beach levels, there is a northward reduction in the number of cirolanid isopod species, and an absence of cirolanids at some beaches in northern Chile. At high beach levels, talitrid amphipods occur in southern central and northern central Chile, while in northern Chile ocypodid crabs occupy similar levels. On the other hand, oniscoid isopods only occur in the northern central area of the Chilean coast.

The hydrographic analyses of Brattstrom and Johanssen (1983) and Viviani (1979) show that no abrupt sea water temperature or current barriers are typically found on the Chilean coast. This may explain why the same species, Emerita analoga, Nephtys impressa, and Mesodesma donacium, characterize the low beach levels in sands that are water saturated most of the time. These abiotic factors could readily favor widespread distribution of benthic animals with pelagic larvae. The presence of upwelling waters bringing higher primary production to the northern coast (Viviani, 1979) may explain the higher abundance of E. analoga in northern Chile (Fig. 2). Higher abundances than those presented here were also observed for this species and another suspension feeder (M. donacium) in a beach near Coquimbo (personal observations).

Other physical factors such as air and sediment temperatures, and rainfall show a different pattern. This pattern is characterized by wide latitudinal changes,

especially rainfall (Fig. 3). These climatic factors can be important for organisms living higher on the shore (Brattstrom and Johanssen, 1983). The progressive increase of rainfall toward the south is an effective barrier in the southward distribution of many littoral species common in northern Chile (Viviani, 1979) and may explain the absence in southern central Chile of some echinoderms and grapsid crabs, species that are common in the littoral of northern central Chile (Viviani, 1975). Similar ideas can be hypothetically applied to the distribution of ocypodid crabs and oniscoid isopods (Fig. 6). The increase in rainfall from La Serena southward (Fig. 3) may be a significant obstacle to the southward distribution of both groups, by lowering the salinity of surface and interstitial water on the beach. If the upper layers of sandy beaches have freshwater flowing over or falling on them, the situation may not be tolerated by those animals that are mostly active in the surface sediments. The increase in pore water due to the increase in rainfall may adversely affect the stability of the burrows of ghost crabs and oniscoid isopods; the sediment may become too fluid to support burrows.

Lack of rainfall, together with high temperatures in the sediment, may act as barriers for the northward distribution of talitrids and oniscoids (Fig. 6). Other factors, for example, predation by ocypodids as a regulating mechanism in the distribution of these

peracarids, have not been reported, although in other littoral areas, predaceous habits have been mentioned for these crabs (e.g. Ansell et al., 1972; Koepcke and Koepcke, 1953; Wolcott, 1978). On the Chilean coast, Viviani (personal communication) has observed the coexistence of ocypodids and oniscoids in sandy beaches of Bahía Salada (27° 38'S, 70° 58'W) and near Punta Choros. In both areas, the densities of the ghost crab populations were very low in comparison to those of Tylos spinulosus, and no predator activity was observed.

The harsh conditions at high beach levels of northern Chile do not necessarily preclude the presence of all the peracarids characteristic of these levels in other areas of the Chilean coast. For example, the cirrolanid Excirrolana braziliensis inhabited most of the beaches studied in northern Chile and also occurs throughout the tropical and subtropical areas of the east coast of the Americas (Glynn et al., 1975). This species was restricted to the high or highest middle levels in most of the beaches in northern Chile, and in two sites (Colorado, Cavanha), it did not occupy the middle levels at all. The presence of E. braziliensis in northern Chile suggests that significant differences exist between this species and Orchestoidea tuberculata and Tylos spinulosus related to tolerance to desiccation and high environmental temperatures. In fact, high tolerances to warm waters (30-40°C) have been experimentally shown for one population of E. braziliensis

from Naos Island, Panama (Dexter, 1977), while in desiccation tolerance experiments carried out with animals from Mehuin, E. braziliensis showed higher tolerances than O. tuberculata (E. Jaramillo, unpubl. data). Another factor that speaks to the harshness of the high beach levels of northern Chile as compared with those of northern central and southern central Chile, concerns the location of the highest macroinfaunal abundances. In northern Chile, these were typically at low beach levels, while in the other two areas they were at middle or high beach levels (Table II). Consequently, the environmental harshness gradient discussed above (sediment temperature-rainfall) would function along two gradients (i.e. latitudinal and tidal) (Fig. 6, top).

The discussion so far does not help to explain the absence of macroinfauna at the middle and slightly low levels in some beaches of northern Chile. Aguila and Guanillo exhibit similar width, beach slope and grain size; however, middle and slightly low tidal levels were lacking macroinfauna at Aguila, while they were occupied by Excirolana braziliensis at Guanillo. Colorado, Cavanha and Huaiquique had similar width, but different slopes and grain sizes. On the other hand, Colorado differed from the other beaches due to its high degree of anthropomorphic influence (fishing industry nearby). However, all of these beaches exhibited the same lack of macroinfauna at the mentioned tidal levels. It remains an enigma. A similar

situation was reported by Epelde-Aguirre and Lopez (1975) for the middle beach levels of Playa Blanca in southern central Chile.

Several attempts have been made to build zonation schemes for worldwide application, or at least, for littoral sandy areas over wide latitudinal ranges. Among them, those of Dahl (1952) and Trevallion et al. (1970) are the most comprehensive schemes. The zonation patterns described above for the Peruvian-Chilean Province are very similar to those noted by Dahl and Trevallion et al., but with some important differences. The presence of cirolanid isopods at higher beach levels (Dahl's subterrestrial fringe) of all the beaches studied, talitrid amphipods in the middle beach levels (Dahl's midlittoral) of southern central Chile, cirolanids in the lower beach levels (Dahl's sublittoral) of that same area, and anomuran crabs (Hippidae) in the lower beach along all the shores studied, are the main differences with the scheme of Dahl (1952). Similar differences were also found in other studies carried out on the Chilean coast (Castilla et al., 1977; Epelde-Aguirre and Lopez, 1975; Jaramillo, 1978; Sanchez et al., 1982) and in other areas of the world. More similarities are found when zonation patterns are compared with Trevallion's et al. (1970) scheme. In the specific case of the littoral studied here, the main difference with Trevallion's scheme is the absence of bivalves of the genus Donax, gastropods and echinoids from the Chilean coast.

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TABLE I. Transect width in meters, slope in % and grain size values (graphic mean in  $\phi$  =  $\phi$ ) at each beach.

NORTHERN CHILE		width	slope	$\phi$
Colorado	(20 <sup>o</sup> 11'S, 70 <sup>o</sup> 09'W)	35	5.5	1.88
Cavanca	(20 <sup>o</sup> 14'S, 70 <sup>o</sup> 10'W)	30	6.5	2.48
Huaiquique	(20 <sup>o</sup> 17'S, 70 <sup>o</sup> 08'W)	35	5.8	2.18
Aguila	(20 <sup>o</sup> 50'S, 70 <sup>o</sup> 11'W)	75	3.5	2.40
Guanillo	(21 <sup>o</sup> 12'S, 70 <sup>o</sup> 06'W)	90	3.3	2.22
NORTHERN CENTRAL CHILE				
Punta Choros	(29 <sup>o</sup> 14'S, 71 <sup>o</sup> 29'W)	40	6.4	2.03
SOUTHERN CENTRAL CHILE				
Ronca	(39 <sup>o</sup> 23'S, 73 <sup>o</sup> 14'W)	45	3.6	2.53
Mehuín	(39 <sup>o</sup> 26'S, 73 <sup>o</sup> 09'W)	50	4.0	2.32
Niebla	(39 <sup>o</sup> 52'S, 73 <sup>o</sup> 24'W)	30	6.8	1.72
Muicolpue	(40 <sup>o</sup> 34'S, 73 <sup>o</sup> 46'W)	30	7.7	2.02

TABLE II. Number of species and density values (number per 1 m<sup>2</sup>) of the total macroinfauna and the dominant species. Mean densities are in relation to the number of stations with animals. The ghost crab *Ocypode gaudichaudii* is included in the number of species living in the sandy beaches of Northern Chile, but not in the density figures.

	no. spp.	total density $\bar{x}$	highest density	tidal level (station)	dominant species	density $\bar{x}$	highest density	tidal level (station)
NORTHERN CHILE								
Colorado	3	29	56	above MHWST (1)	<i>P. maculata</i>	30	56	above MHWST (1)
Cavancha	5	43	83	MLWST (7)	<i>E. analoga</i>	56	65	MLWST (7)
Huaiquique	6	140	250	MLWST (8)	<i>E. analoga</i>	158	176	MLWST (8)
Aguila	7	149	704	MLWST (13)	<i>E. analoga</i>	477	602	MLWST (13)
Guanillo	6	103	231	MLWNT (9)	<i>E. analoga</i>	95	185	MLWNT (9)
NORTHERN CENTRAL CHILE								
Punta Choros	8	874	1500	above MHWST (1)	<i>E. hirsuticauda</i>	1111	1389	MLWNT (5)
SOUTHERN CENTRAL CHILE								
Ronca	8	71	204	MHWNT (5)	<i>E. hirsuticauda</i>	69	185	MHWNT (5)
Mehuín	8	189	417	MHWNT-MTL (6)	<i>E. hirsuticauda</i>	118	352	MHWNT-MTL (6)
Niebla	4	94	287	MHWNT-MTL (5)	<i>E. hirsuticauda</i>	84	194	MLWNT (7)
Muicolpue	6	145	389	MTL (5)	<i>O. tuberculata</i>	111	222	MTL (5)

Fig. 1. Study areas showing beach profiles at each site. The relationship between grain size (graphic mean in  $\phi$ ) and slope (%) is shown in the inserted panel on the right. The beaches are Colorado (Co), Cavancha (Ca), Huaiquique (Hu), Aguila (Ag), Guanillo (Gu), Punta Choros (Pu), Ronca (Ro), Mehuin (Me), Niebla (Ni) and Muicolpue (Mu).



Fig. 2. Some of the oceanic currents off the Chilean coast. 1: Westwind Drift Current, 2: Peru Oceanic Current, 3: Cape Horn Current, 4: Humboldt or Peru Coastal Current, and 5: Peru Counter Current. The dotted area indicates the region of the upwelling system. Based on Brattstrom and Johanssen (1983) and Viviani (1979).



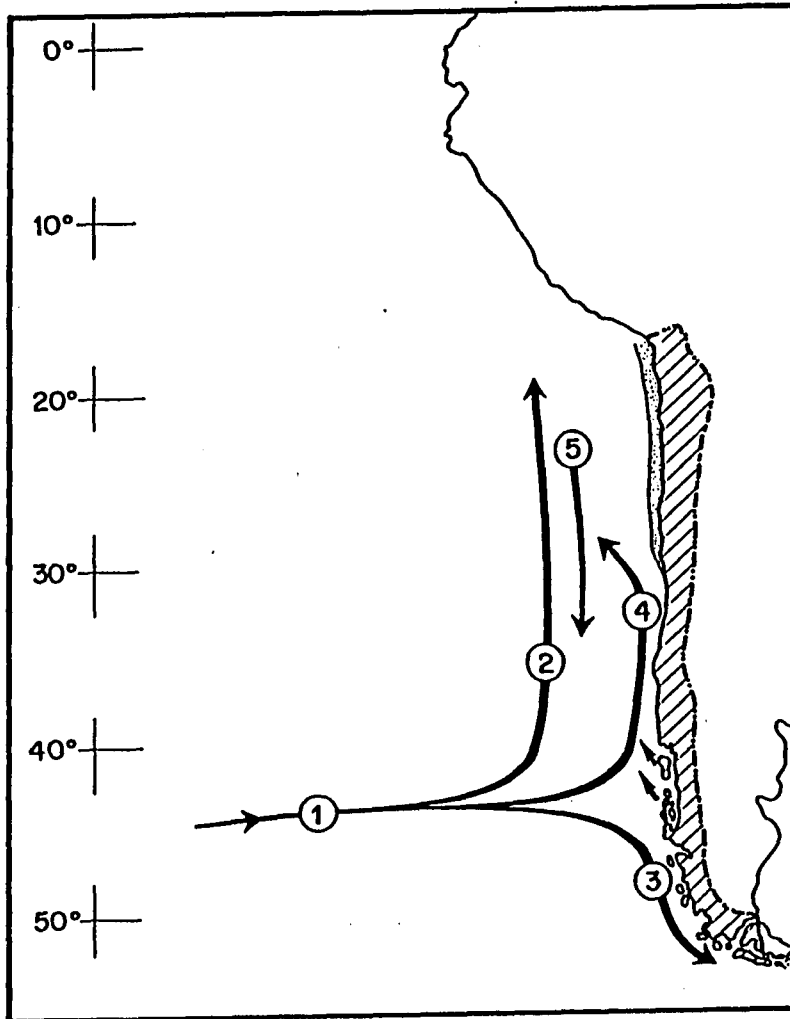


Fig. 2

Fig. 3. Walter's climatic diagrams (temperature and rainfall) of selected coastal localities along the Chilean coast (figures taken from di Castri and Hajek, 1976). The scales of this representation are shown in the inserted diagram on the left side of the figure.

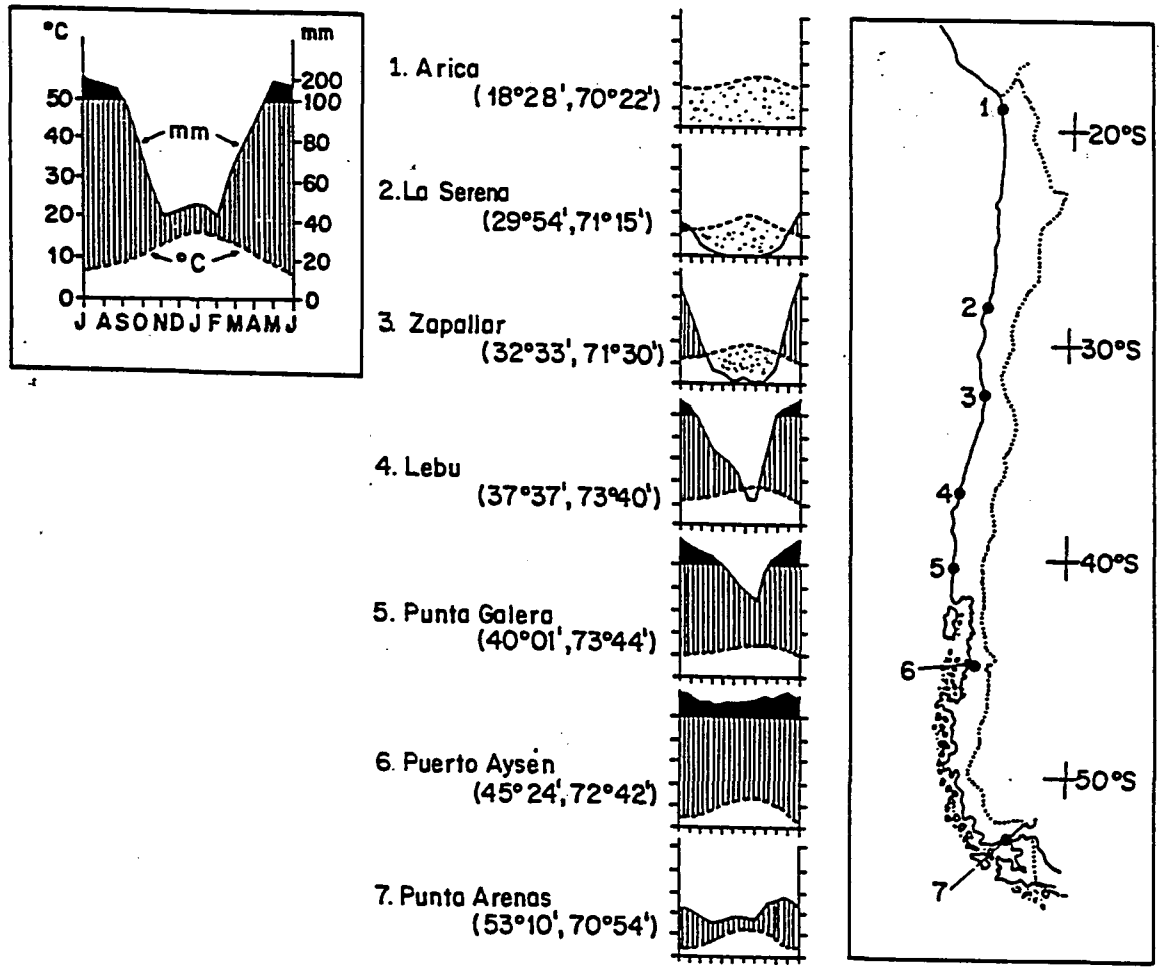


Fig. 3

Fig. 4. Zonation of the macroinfauna at each beach. The distribution, but not the density of Ocypode gaudichaudii is indicated.

SOUTHERN CENTRAL CHILE

NORTHERN CENTRAL CHILE

NORTHERN CHILE

height in cm

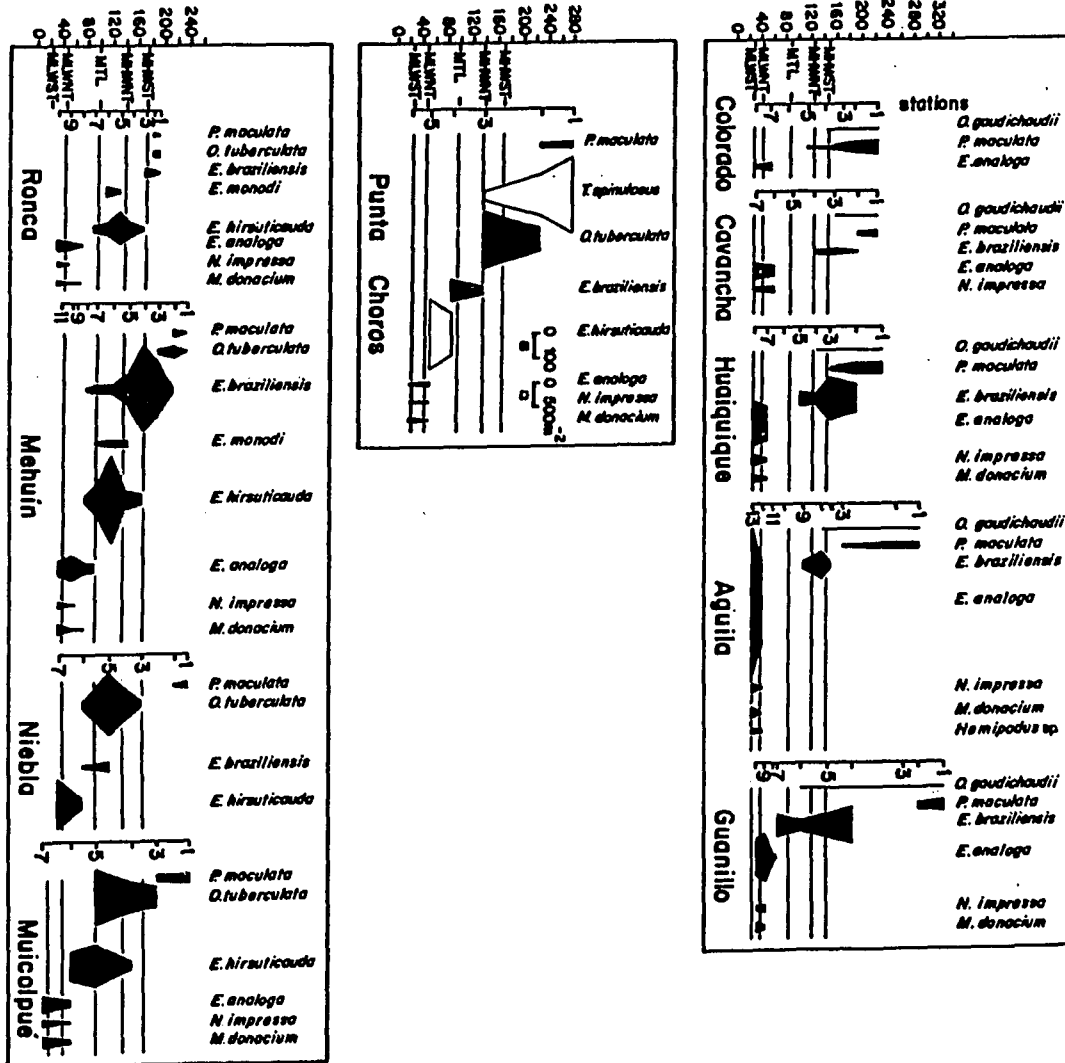


Fig. 4

Fig. 5. Dendrogram showing clustering of stations in three main groups. A: high beach levels, B: middle beach levels and C: low beach levels. Numbers to the right of the dendrogram refer to station numbers as in Fig. 4, while letters refer to the beaches as in Fig. 1.

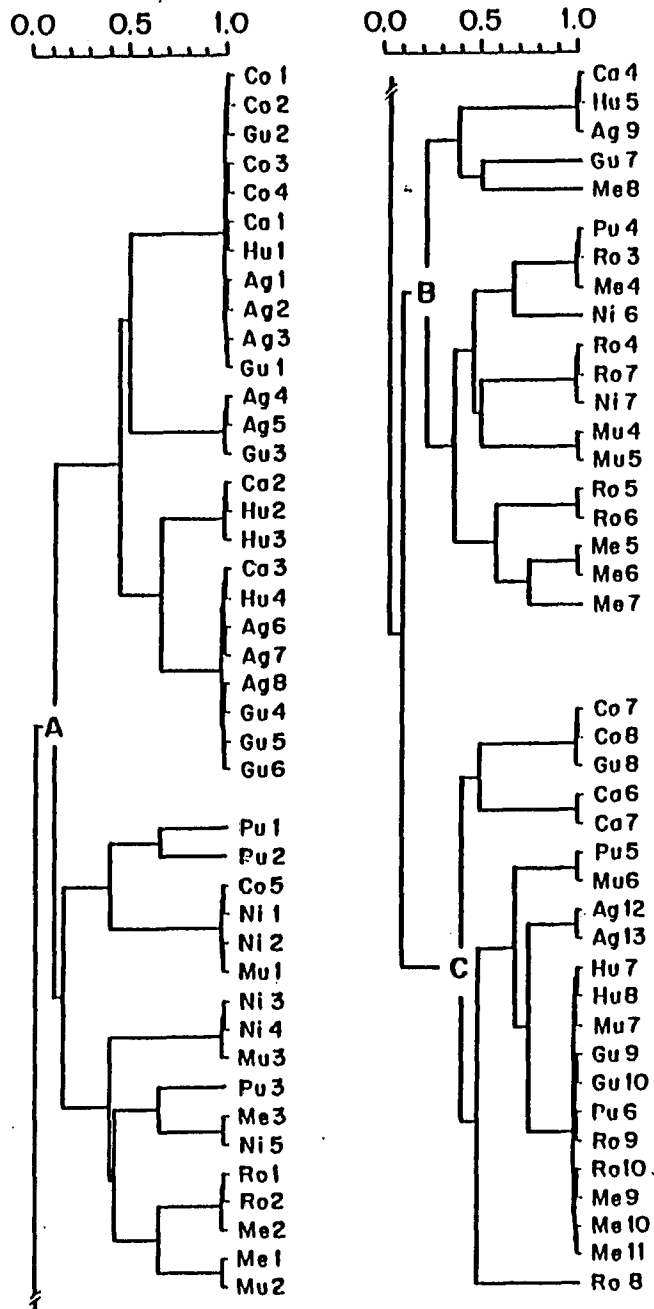


Fig. 5

Fig. 6. Composition of the intertidal sand macroinfauna in the three areas studied. Hypothetical restraints of environmental conditions to the dispersion (northward, southward, or both) of ocypodids, talitrids, and oniscoids are shown by arrows.



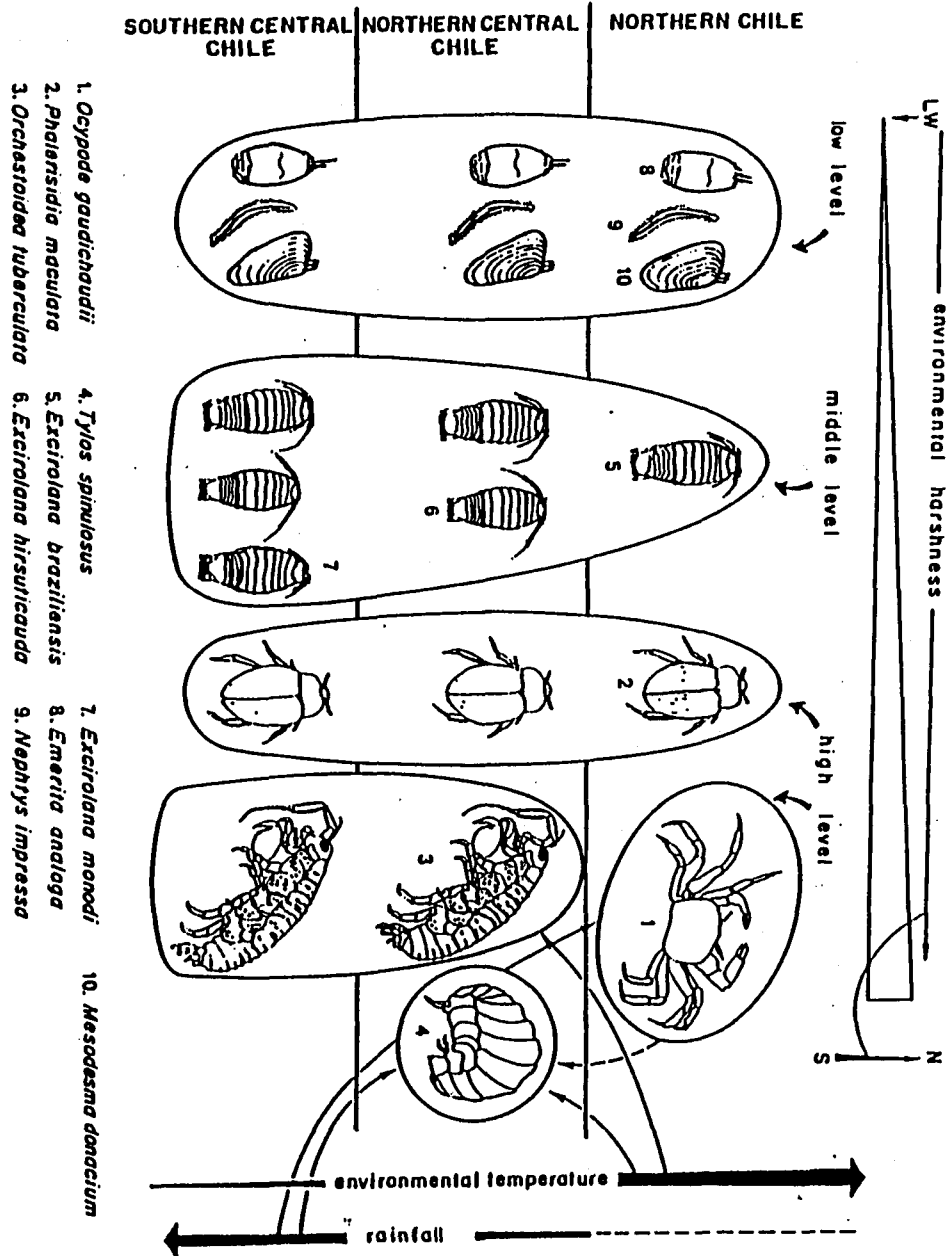


Fig. 6