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Patterns and breaking points in the distribution of benthic algae along the temperate Pacific coast of South America

Patrones y puntos de quiebre en la distribución de algas bentónicas a lo largo de la costa Pacífica de Sudamérica

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ABSTRACT

According to biogeographic studies made two decades ago, marine benthic algal species of the Pacific temperate coast of South America could be grouped into five components according to their geographic affinities. Each of these components was distributed differentially along the coastline between 4° and 56°S and thus, their contribution to the overall flora varied depending on the latitude. Species composition changed at specific latitudes in such a way that three groups could be observed: from 4 to 6°S, from 6 to 30°S and from 30 to 55°S. Since 1980, new information on marine algae along this coastline allows a review of the previous phytogeographic characterization. The presence/absence of algal species, separated by division and geographic affinity, was recorded for each degree of latitude from 4° to 56°S and used to analyze the similarity in species composition and possible changes in distribution patterns. Results show the same five geographic components detected 20 years ago with similar distributions. Differences observed are a further southward intrusion of subtropical elements, a decrease in endemic species number and relative contribution to the flora at the southern tip of South America, and two breaking points in species composition at 12° and 42°S. Another two breaking points occur at 20°S and at 33°S in Phaeophyta and Rhodophyta species composition respectively. The inclusion of single-record species does not affect significantly the distribution of species along this coastline.

Key words: Distribution patterns, breaking points, species composition, temperate Pacific.

RESUMEN

De acuerdo a estudios biogeográficos realizados hace 20 años, las especies de algas marinas bentónicas de la costa temperada del Pacífico de Sudamérica se agrupan en 5 componentes de distinta afinidad geográfica. Cada uno de estos componentes posee una distribución diferencial a lo largo de estas costas entre los 4° y los 55°S. De esta forma su contribución a la flora varía dependiendo de la latitud. La composición de las especies cambia en determinadas latitudes de manera que se pueden reconocer tres grupos: uno se encuentra de 4° a 6°S, otro de 6° a 30°S y el tercero de 30° a 55°S. A partir de 1980, el aporte de nuevos estudios en algas ha permitido una revisión de esta caracterización fitogeográfica. La presencia /ausencia de las especies, separadas dentro de cada división por afinidad geográfica, fue registrada para cada grado de latitud entre los 4° y los 56°S, y usada para analizar la similitud en la composición de especies y los posibles cambios en sus patrones de distribución. Los resultados muestran los mismos 5 componentes geográficos encontrados 20 años atrás con distribuciones similares. Las diferencias observadas consisten en: una incursión más al sur de elementos subtropicales, una disminución en el número de especies endémicas y en su contribución relativa en el extremo sur de Sudamérica y, la presencia de dos puntos de quiebre en la composición de las especies, a los 12° y a los 42°S. Otros dos puntos de quiebre se presentan en las Phaeophyta a los 20°S y en las Rhodophyta a los 33°S. La inclusión de especies con un solo registro no afectan significativamente la distribución de las especies a lo largo de estas costas.

Palabras clave: Patrones de distribución, puntos de quiebre, composición de especies, Pacífico temperado.

INTRODUCTION

The last two decades have been characterized by an extensive number of studies focused on the distribution of marine organisms along the temperate coasts of the Southeastern Pacific (see Lancellotti & Vásquez 1999). A number of these deal with macroalgae, most of them mainly related to recognition of taxa (Acleto 1980, 1981, 1984, Etcheverry et al. 1980, Westermeier 1981, Ramírez 1982, Santelices & Montalva 1983, Contreras et al. 1984, Santelices & Abbott 1985, Westermeier & Rivera[1] 1986, Ramírez & Rojas 1988, Pinto 1989, Santelices et al. 1989, Benavente 1994, Meneses

[1] WESTERMEIER R & PJ RIVERA (1986) Caracterización ficológica del intermareal rocoso de la X región (Valdivia, Osorno, Llanquihue y Chiloé) y de la XII región (Islas Diego Ramírez), Chile Actas II Congreso de Algas Marinas Chilenas 125 – 144.

& Hoffmann 1994), while others consist of phytogeographic studies restricted either to a specific locality or to a long coastal stretch (Santelices 1980, 1982, Ramírez & Santelices 1981, 1991).

Santelices (1980) gave an overview of the macroalgal patterns of distribution along this long extension of coast, describing five components regarding the geographic affinities of the taxa comprising them: endemic species, subtropical species frequent in other tropical and/or subtropical areas of the world (Indo-Pacific, Caribbean, etc.), bipolar taxa found along the North and Southeastern Pacific (except the central Pacific), widely distributed species around other coasts of the world (although not truly cosmopolitan) and Antarctic and subantarctic species present in Australia, New Zealand, South Africa and the subantactic islands. These components contributed unequally to the algal flora along the coastline with a replacement of species in certain latitudes such as northern Chile characterized by a numerical decrease of subtropical species and a gradual invasion of subantarctic species. It was also claimed that the temperate coast of South America had a high level of endemism, a strong subantarctic component and showed a limited incursion of subtropical species resulting in an overall small number of species in southern Perú and northern Chile.

Whereas previous studies (Ekman 1953, Balech 1954, Knox 1960, Dell 1971) established a classic scheme with two centers of species distribution, one in Perú and northern Chile and the other in southern Chile with an extense transitional zone of species overlapping, the five macroalgal components (Santelices 1980) were distributed differently. The specific latitudinal points at which the replacement of species occurred and thus, the breaking points at which the relative contribution of each component changed, were detected at 6°, 30° and 53°S. The two breaking points in the north were explained by the prevailing oceanographic conditions, result of the northern extension of upwelling regions in Perú and to the southernmost extension of subtropical surface water along central Chile.

In addition, due to the large number of endemic species known from a single collecting record, the data were analyzed with and without these forms (Santelices 1980). When these forms were excluded results showed breaking points at 6° and 42° S. This last point considered by previous studies (Balech, 1954, Knox 1960, Dell 1971) as the southern boundary of the so-called transitional zone.

It was recognized at that time that some of these patterns could be the result of the lack of intensive sampling that would alter the distribution boundaries of many species as well as increase the number of new records with different geographic affinities. The studies carried on in the last twenty years have added plenty of information to test the biogeographic patterns established by Santelices (1980) and to clarify the occurrence of specific breaking points where changes in species composition take place. Therefore, the following study is an update of the macroalgal patterns of distribution observed along this continental coastline and a comparison of its results with those obtained in 1980.

MATERIALS AND METHODS

Species records were registered for each one degree of latitude, from 4° to 56° S (including records of Diego Ramírez Archipelago), along the entire Pacific temperate coast of South America. Presence/absence at each latitude for a particular species was recorded as 1 or 0 respectively. Jaccard´s similarity index was used to build a matrix as the basis for UPGMA (Unweighted pair group method using arithmetic averages) cluster analysis (Sneath & Sokal 1973) applying NTSYS-PC program (Exeter Software‰). Cluster analysis was applied in order to evaluate possible breaks in the species distribution along the coast indicating different biogeographic provinces. The entire analysis was done including and excluding single-record species. Species were also grouped according to Division (Chlorophyta, Phaeophyta and Rhodophyta).

The basic list of species used was that published in the Catalog of Benthic Marine Algae from the Pacific temperate coast of South America by Ramírez and Santelices (1991), adding a number of other references reporting algal records (Westermeier & Ramírez 1978, Ramírez & Santelices 1981, Westermeier 1981, Ramírez 1982, Contreras et al. 1983, Westermeier & Rivera 1986, Ramírez & Peters 1992, Santelices 1992, Benavente 1994 among others). A careful revision of possible misidentifications, uncertain records and synonymies was performed reducing the total number of species included in these analyses. Single-record species are excluded from the plots of distribution.

RESULTS

Distribution patterns

According to the recent incorporation of new algal records since a similar study was conducted

(Santelices 1980), the original five groups of species according to their distribution patterns: endemic, widely distributed, subantarctic, bipolar and subtropical, remain the same.

A total number of 576 specific records were gathered during the course of this study excluding taxonomic uncertainties, 283 are single-record species in the temperate coast of Pacific South America.

The bipolar component of this flora (approximately 16%) consists of 46 species endemic to the eastern Pacific coasts on both hemispheres but absent from the Central Pacific. This component (Fig.1A) contributes between 12° and 32°S up to 20% of the total flora and has one major reduction at 32°S and another at 42°S. The bipolar component is more important among Phaeophyta (Fig. 1C) than in the other two divisions of macroalgae (Fig. 1B, D). In Phaeophyta it represents between 30 and 40% of the total species of brown algae until 33°S, then it is drastically reduced to 10% and then again at 42°S to less than 5%. Bipolar species are more variable in their contribution to Chlorophyta, representing less than 10% of the species of this division at low latitudes (Fig.1B). Then, at 9°S they increase in number to represent more than 20% of the total species of Chlorophyta. This value is approximately kept until 30°S where the component is reduced to approximately 10% and remains there until 56°S. On the other hand, bipolar Rhodophyta contribute uniformly with less than 20% to the total species of this division until 42°S where it reduces its contribution to approximately 5% remaining at the same level until Cape Horn.

The subantarctic component of this flora is defined as formed by all those species with records on subantarctic islands, New Zealand, Tasmania, South Africa, and southern coasts of Australia. It contributes with 32% of the species (94 species) and shows the inverse pattern of endemic taxa (Fig.1A) increasing gradually from 5% at the northern extreme of this coastline up to 70% at the southern tip of South America. Rhodophyta (Fig.1D) follow exactly this pattern with a gradual and continuous increase from 15.4% of the total red algae present at 4°S up to 73.3% at 56°S. The subantarctic elements in Phaeophyta (Fig.1C), begin with a 12.5% contribution at 5°S and decrease to 6-7% between 12 to 17°S. At 18°S subantarctic Phaeophyta increase abruptly to 22.2% and keep a gradual increase until 56°S where they contribute with 68% of the total number of species. In Chlorophyta the subantarctic component is less abundant (Fig.1B) than in the other two groups, and more variable in its distribution. With a contribution of 8-9% at 5°S, green subantarctic elements have the same reduction as brown

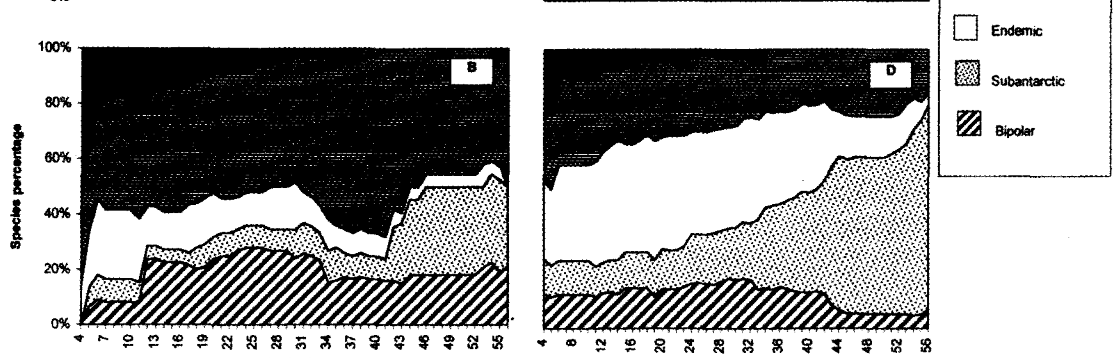

Fig. 1. Relative importance of each phytogeographic component along the Pacific temperate coast of South America. A) All macroalgae divisions; B) Cholophyta; C) Phaeophyta; D) Rhodophyta.

Importancia relativa de cada componente fitogeográfico a lo largo de la costa Pacífica temperada de Sudamérica. A) Todas las divisiones de macroalgas; B) Clorifita; C) Feofita; D) Rodofita.

representatives; decreasing to 4% from 12 to 17°S. They reach again values close to 11% at 30°S and then have a second abrupt decrease between 36 to 41°S. Southwards from 42°S they fluctuate contributing with approximately 30% of the total of green species present along these coasts.

Twenty-seven per cent (79 species) are endemic to these coasts with a variable contribution to the regional flora from 25 to 30% between 4 to 42°S (Fig.1A). An abrupt reduction in endemic species occurs at 42°S, which corresponds to the northward extreme of Chiloé island, and their number decreases further toward higher latitudes, becoming a minor component at the southern tip of the continent. This general distribution pattern is well represented by red algae (Fig.1D).

Brown algae show a sudden reduction of its endemic component at 12°S followed by a gradual decrease until 32°S and then a second decrease until 44°S (Fig.1C). Green algae have a similar reduction at 27°S (Fig. 1B).

Macroalgae with wide distribution include those species that are found on other coasts around the world, although most of them seem to be not entirely cosmopolitan but restricted to specific areas such as Mediterranean, East coast of North America, Indo-Pacific and so on. Approximately 24% (71 species) show this distribution pattern which is highly uniform along the eastern South Pacific (Fig.1) for the three divisions contributing in higher proportion to green algae than to red and brown algae.

Species with subtropical affinity are a minor contribution to these coasts, although they indicate the entry of species at the northern boundary of the Humboldt Current. They can reach up to 50% (in the case of Phaeophyta) at its northern limit (Fig.1C). This component never reaches further southern latitudes than 37°S. This distribution pattern is repeated in the three divisions. In Chlorophyta (Fig.1B), subtropical taxa contribute with 37% of the total number of species, show an abrupt decrease to 10% at 8°S and continue gradually decreasing until disappearing at 37°S. On the other hand, 50% of total Phaeophyta taxa (Fig.1C), are subtropical at 4°S. This component decreases to 20% at 5°S and reaches a minimum of 3% at 34°S. These taxa contribute less to the entire Rhodophyta representatives present along these coasts (Fig.1D), than to the other two divisions with a maximum of 19% at 4°S, 10% at 6°S and 5% at the end of its contribution at 33°S.

Similarity patterns in species composition

Three main species-conglomerates appear in Chlorophyta without considering 4°S which has no species in common with the rest of the coast under study (Fig.2A). From North to South the coastline from Piura (5°S) to Callao (11°S) is characterized by subtropical elements, and a general low number of species. The second large group comprises from 12°S to 41°S (Chiloé) with 41 species of green algae most of them of wide and bipolar distribution. The last southern strip of coast from 42°S to the tip of South America (56°S) is characterized by the occurrence of subantarctic elements absent northwards and a reduction in subtropical and widely distributed species.

In Phaeophyta four groups can be distinguished. Again as in Chlorophyta, elements at 4°S show a minor similarity with those reported for the rest of this coast (Fig.2B). A tight group (Similarity =1.0) between 5°S and 12°S (Callao) is detected with mainly subtropical elements, bipolar and widely distributed species, but low endemism and no subantarctic elements. A second group that extends until 20°S (Iquique) where there are few subantarctic taxa and an increasing number of bipolar and widely distributed species. Both groups show a low number of species compared with the southermost coasts. The third group may be subdvided into two sub-groups; one between 21° and 30°S, mainly because at this latitude records of bipolar and subtropical species are reduced, and the second group from 31°S to 43°S where bipolar taxa practically disappear and the subtropical taxa are not represented, while the importance of subantarctic elements increase significantly (Fig.2B). The entire cluster may be considered a transition zone at least for the Phaeophyta. The last and most southern group is, as in the Chlorophyta, a group formed by 60% of subantarctic taxa , and approximately 30% of species of wide distribution with a remnant of endemic taxa.

In Rhodophyta the breaking points are somewhat different (Fig.1C), although the distance in similarity with those species recorded at 4°S is more marked. A small group with high similarity among its elements ($J > 0.80$) is detected between 5°S and 11°S. This group is characterized by having a uniform contribution of all elements but a low abundance of representatives. A second larger group is observed between 12°S (Callao) and 32°S (north from Valparaíso). This group has a larger number of species than the northern one and increases the contribution of endemic, subantarctic and bipolar species to the total flora (Fig.2C). The breaking points that limit the third group are Valparaíso (33°S) on the north and Chiloé (42°S) on the south. This coastal extension presents an increase in the abundance of all groups except the subtropical species that disappear and

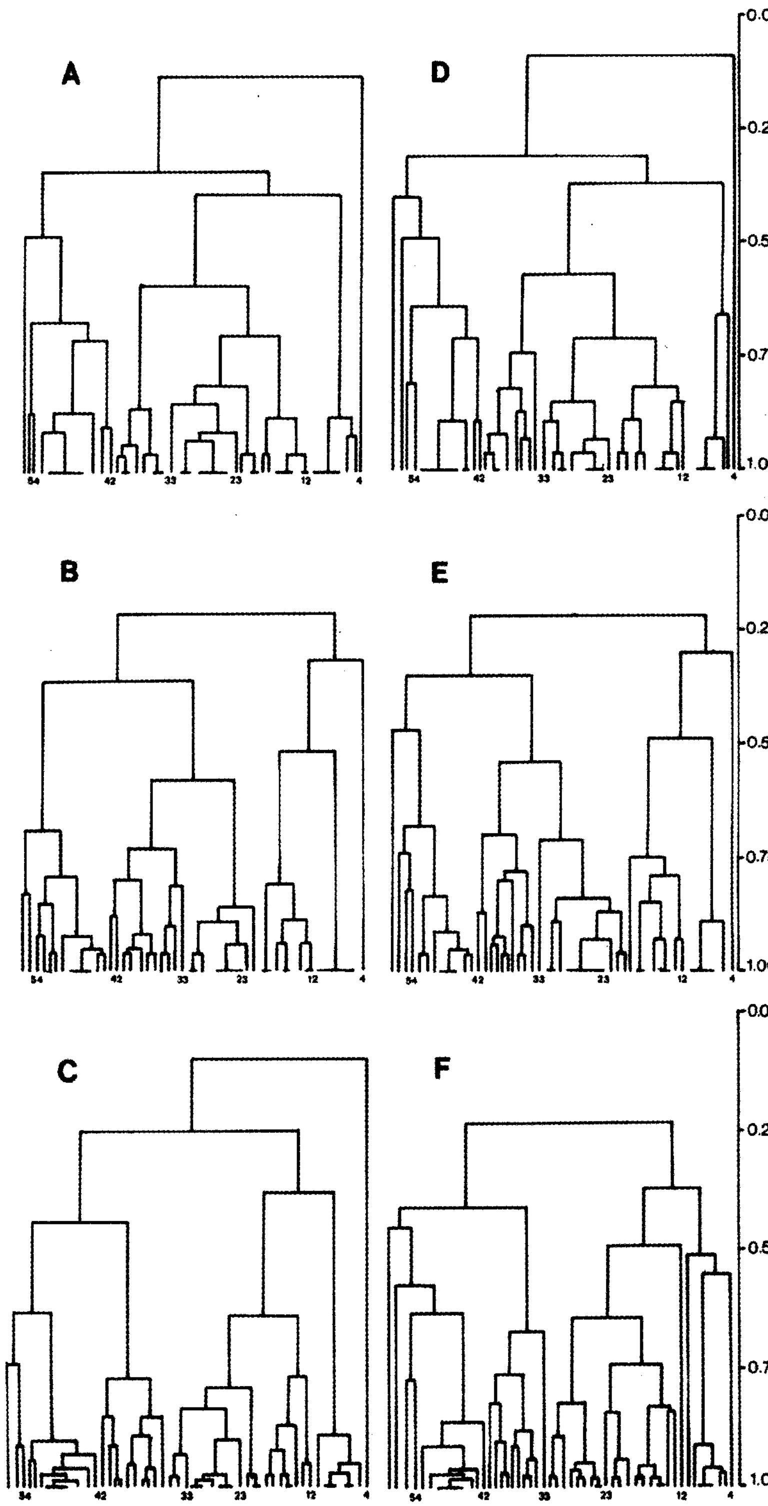

Fig. 2. Dendograms that describe species similarity between adjacent latitudinal degrees along the continental coast from 4° to 5° S, and on the Diego Ramírez (56° S) islands. A – C) data that does not include species only once recorded. D – F) date that includes species only once recorded. A and D) Chlorophyta; B and E) Phaeophyta; C and F) Rhodophyta.

Dendrogramas que describen la similitud de especies algales entre grados de latitud adyacentes a lo largo de la costa continental, desde los 4° a los 5° S, y en las islas Diego Ramírez (56° S). A – C) Datos no incluyen especies con un solo registro. D – F) Datos que incluyen especies con un solo registro. A y D) Clorofita; B y E) Feofita; C y F) Rodofita.

the widely distributed species that remain constant. Further south from Chiloé, the fourth group is distinguished by the reduction in the endemic and bipolar components concomitant with an increase in subantarctic elements and an overall reduction in the total number of species.

Similarity patterns in species composition including single-record species

The addition of single-record species slightly modifies the above patterns. Green algae or Chlorophyta show the same three main groups indicated above when single-record species are included in the analysis (Fig. 2D). At 5°S a number of species not recorded further south tends to isolate this particular point, while the main middle group from 12°S to 41°S remains almost the same. At the southernmost extreme, the addition of single-record species separates the Magallanes and Tierra del Fuego region from the rest of the continent.

Phaeophyta keeps the four groups without including the single-record species (Fig. 2E). As in the Chlorophyta, the southernmost region of Magallanes and Tierra del Fuego are separated further from the neighboring areas as a result of the addition of new records.

In Rhodophyta the four original groups remain almost the same (Fig. 2F). The differences observed are in the northernmost and southernmost groups of species. Rhodophyta species composition at 4°S becomes more similar to the nearest latitudes and the species composition at 5°S decreases in similarity with the others of the group because a larger number of species is recorded only until this latitude and do not occur further south. At the southern tip of the distribution, differences become more noticeable at the southernmost latitudes due to new records in the area of Magallanes and Tierra del Fuego.

DISCUSSION

Distribution patterns

Basically no big changes have been made to our understanding of the phytogeographic patterns in the temperate Pacific coast of South America since 1980. The circumscription of the five components according to their geographic affinities is supported, as is their relative importance along the latitudinal gradient. New records from particular areas (Westermeier 1981, Ramírez 1982, Westermeier & Rivera 1986, Pinto 1989, Santelices et al. 1989, Benavente 1994) along this coast have refined the limits of distributional ranges in certain species and highlight slight differences from the previous studies (Santelices 1980).

The first difference seen from the new records is the pattern of distribution and abundance of endemic species. While previously found to be similar in number of species along these coasts (except for being reduced north of Paita, 4°S - 5°S), the new records indicate clearly how this component is reduced in number of species. Their relative importance southward in the three divisions of macroalgae is also reduced. This is the combined consequence of including neither single-record species nor taxa with unclear identification. Most of those records correspond to taxa collected once during the first expeditions that explored this coastline (Skottsberg 1907, 1921, 1923, Gain 1912, Kylin & Skottsberg 1919) and not reported again in the literature. Despite this different distribution pattern, endemic algae are still one of the important components of the west coast of South America, contributing 27% of the total number of species compared to 32.3% obtained in the previous study (Santelices 1980).

The second difference along this coastline, unknown until this study, is the presence of a few taxa considered to be of tropical and/or subtropical origin extending further their latitudinal range. In fact, the initially described breaking point at 6° S for algae of subtropical affinity has moved to 12° S due to the new records reported from Perú (Benavente 1994). A few other species reported at 30° S (Coquimbo) now have been reported to reach to 37° S. Although this is still a minor component of this marine flora, it is likely to produce some changes in the future. The adding of species records as a result of a more exhaustive sampling (including less noticeable species), and the studies focused on particular groups (Chordariales, Delesseriaceae) should contribute to the possible changes in this component. The inclusion of filamentous, tiny taxa, such as those belonging to the order Ectocarpales among brown algae and / or Ceramiales among red algae, which could be of tropical origin, will increase the relative importance of this group.

The separated analysis of the three macroalgal divisions, although showing some differences in their distribution patterns, keeps the basic five components structure. Slight changes noted may reflect physical as well as biological responses, as yet un-measured, and the following trends: 1) A tropical/subtropical component strong in green algae that represents an incursion from northern latitudes with warmer waters, 2) a bipolar component which is reduced towards the South, 3) an endemic component with stronger contribution of red algae, 4) a widely distributed component with a fairly constant contribution along the entire coastline, 5) a subantarctic component reduced in the north that becomes gradually more important southwardly until contributing half of the total number of species at the tip of South America with mainly red and brown taxa.

Breaking points

Twelve degrees South is one of the important breaking points in species composition for the three macroalgal divisions along the Pacific temperate coast of South America. This latitude corresponds to the southern boundary of an important number of subtropical species. This fact could be the result of two factors: 1) the characteristics of warm surface waters that extend South until this point that possibly facilitates growth and reproduction for these species, and 2) this latitude corresponds to the harbor of Callao, an area intensively sampled over the years in comparison with neighboring localities.

The second breaking point, 30°S appears only for Phaeophyta although it has been reported before for several algae that seem to end their distributional range (either southern or northern) at this point. Apparently several of the algae (at least reds) that extend South to this latitude do not complete the entire life-cycle, a fact attributed to the cold temperatures present in the area due to upwelling processes during the summer months (Acuña et. al. 1988).

Another breaking point that appears to affect only Rhodophyta distribution is 32-33°S, latitude that corresponds to the locality of Valparaíso and adjacent areas heavily sampled over the years. Nevertheless, at this point winter temperatures average less than five degrees than northern latitudes (Servicio Hidrográfico y Oceanográfico de la Armada de Chile 1996) and this fact may affect the formation of reproductive structures which often occurs during late winter.

The marked breaking point at 42° S (Chiloé) has been discussed (Brattström & Johansen 1983, Lancellotti & Vásquez 1999) and explained as the change in water conditions (low salinity, less wave exposure) and topographic diversity between the adjacent areas regarding marine fauna although it has been dismissed in certain cases (Lancellotti & Vásquez 1999). In macroalgae the first studies (Stephenson & Stephenson 1972) indicated that the zonation patterns north from Puerto Montt (approximately 42°S) were significantly uniform and differed from those of southern Chiloé (Santelices 1979). One attempt has been made to gather information on the local flora found at the two sides of this breaking point (Westermeier & Rivera 1986) suggesting that no such differences occur at least in terms of zonation patterns and in those groups of species that compose these vertical zonation bands. Nevertheless, the authors make clear that between the two areas studied (39° 24'S – 42°30'S and 56° 36'S), mostly consisting of exposed areas, there is an extensive geographic region where no information is available. Also, no tiny, filamentous or crustose algal types were considered at the specific level and this could well make the difference in species diversity between these zones.

The slight changes recorded in the similarity of the different groups along the coastline with and without single - record species indicate a very stable pattern with almost no influence of these isolated records. The three divisions of macroalgae behave in the same way. The changes observed basically affect the patterns at the southern tip of South America which coincides with the previous results obtained in 1980. This is due to a number of new records at the Magallanes and Tierra del Fuego regions. A possible explanation is that these records belong to species which are not only present at one single locality but, that they have a much more extended distribution in the area. Ramirez (1998) estimated 237 species in the area based on collections made by her between 1985 and 1997, records that have not been included in this study. She established that this region flora has 79.83% of similarity with the flora of Antarctica, which supports the hypothesis that there is some sort of biogeographical continuity (John et al.1994) between these masses of land either due to the previous union between continents during the Mesozoic (Crame 1992, Clayton 1994) or, due to the possible dispersal of propagules by the Circunpolar Antarctic Current. Thus, either the continuous arrival of propagules or, the more effective use of those particular climatic conditions by algae of subantarctic affinity could be the reason for the decrease in endemic species towards these regions. We expect that the present results will change once the large stretch of coastline between Magallanes and Tierra del Fuego in the south and Chiloé on the north is thoroughly sampled and these findings reported, which has not occurred until now.

In summary, the addition of new records to the temperate west coast of South America has not changed the previous view of five biogeographic components along this coastline. Possible breaking points that could indicate different biogeographic provinces require attention in order to explain the possible factors that determine them. Coastal oceanographic characteristics should be finely tuned with growth and reproductive events of those species in their distribution boundaries.

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