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A reassessment of the phytogeographic characterization of Temperate Pacific South America

Una re-evaluación de la caracterización fitogeográfica de la costa temperada del Pacífico de sudamerica

BERNABE SANTELICES & ISABEL MENESES

Departamento de Ecología, Facultad de Ciencias Biológicas, Casilla 114-D, Santiago, Chile, e-mail: bsanteli@genes.bio.puc.cl

ABSTRACT

In 1980, a study of geographic distribution patterns and geographic affinities of benthic algae of temperate Pacific South America (5-55 °S) provided a first characterization of these coasts. High endemism and limited floristic exchange with the Tropical Pacific and with islands in the South Pacific at various distances from the continent were two outstanding features of the marine flora. A partial blockage of species exchange partially accounted for a peculiar latitudinal pattern of species richness that increases with increasing latitudes. In contrast, there was reduced species richness in comparison with other climatically equivalent regions that have contact with more effective routes of migration. Over the last two decades, more than 30 taxonomic and biogeographic studies on this benthic marine flora have been completed, adding a significant number of new records for the area. New studies test the above characterization and indicate that the new data add support to several key aspects of the phytogeographic characterization of this coastline. The relative importance of the various floristic components at different latitudes, the isolated character of this flora and the latitudinal pattern of increasing species richness to higher latitudes are shown.

Key words: benthic phytogeography, isolation, latitudinal patterns, seaweeds, temperate South America.

RESUMEN

El estudio de los patrones de distribución geográfica de las algas marinas bentónicas en la costa temperada de Sudamérica (5-55 °S) permitió en 1980 caracterizar estas costas como con un alto grado de endemismo y con intercambio florístico limitado con localidades situadas en el Pacífico Tropical o con las islas oceánicas del Pacífico Sur dispuestas a distintas distancias de la costa. Este bloqueo parcial al intercambio de especies explicaría la baja riqueza de especies de estas costas en comparación con costas climáticamente equivalentes pero con un número mayor de vías de emigración así como el patrón latitudinal de riqueza de especies que en esta zona muestra un incremento en el número total de especies hacia latitudes mayores. En las últimas dos décadas en esta zona se ha realizado un número cercano a 30 estudios taxonómicos de algas bentónicas y fitogeográficos, agregando un número significativo de nuevos registros para el área. Una puesta a prueba de esta caracterización fitogeográfica a la luz de estos nuevos hallazgos indica que los nuevos datos agregan sustentación a la caracterización biogeográfica, incluyendo la importancia relativa de distintos componentes florísticos a distintas latitudes en estas costas, el carácter aislado de esta flora y el patrón latitudinal de incremento en riqueza de especies hacia latitudes mayores.

Palabras clave: Aislamiento, algas, fitogeografía bentónica, patrones latitudinales, Sud América.

INTRODUCTION

Twenty years ago, Santelices (1980) characterized the benthic phytogeography of the western coast of temperate South America from Northern Perú to Cape Horn in Southern Chile (4-55 °S). This characterization contained two components: a) the study of the floristic affinities of the species registered for the area in order to identify the relative contribution of species with different biogeographic affinities to the marine flora of the region and b) a quantitative study of latitudinal floristic changes along this coastline to define major biogeographic boundaries in the area.

Over the last two decades, a number of floristic studies have added a significant number of new records for the area. This study and a related paper in this volume (Meneses & Santelices 2000) evaluate the validity and significance of the above phytogeographic characterization in light of these new findings. In this report, we foccus on geographic patterns and floristic affinities while Meneses & Santelices (2000) evaluate the latitudinal floristic changes in light of the new evidence.

Phytogeographic characterization of the temperate coast of Pacific South America

The study of the biogeographic affinities of the benthic algal flora of temperate Pacific South America showed (Santelices 1980) a species assemblage of 380 taxa which comprise five different groups (Fig. 1). About 33.2% of the regional flora (some 123 species) were endemic to this coast and only a few of them were also found in geographically close oceanic archipelagos, such as Juan Fernández (with six of these 380 species) or Galapagos (with 13 species). About 34.4% of the temperate Pacific South American benthic flora (130 species) had definite subantarctic affinities, as many of these species had also been reported from the subantarctic islands, New Zealand, Tasmania, Southern Australia and even from the Antarctic Peninsula. Only 3.4% of the flora (13 species) was found to correspond to Central American Pacific species, most of which also had limited latitudinal range extension into South America. A fourth geographic group, comprising 22.8% of the flora (87 species) exhibited wide geographic distribution, being present also in different parts of the world, such as the Atlantic coast of Europe and North America, the Caribbean, Pacific North America, Australia, New Zealand and the subantarctic islands. The fifth group was represented by 27 species (7.1%) endemic to the Pacific coast of America, with anphitropical pattern of distribution in which the species are distributed along the Pacific coast of North and South America, but are absent from Central America.

The relative importance of these five floristic elements varied at different latitudes of the Pacific coast of South America (4-55 °S). The number of endemic species (Fig. 1) for different latitudes was similar across the entire range, with three exceptions. The first of these was a short stretch of coastline north of Paita, Perú (4-5 °S) where the number of endemic species was much reduced. The southern most extreme of South America (53-55 °S) and also Central Perú (11-12 °S) in the region of Callao, exhibited more endemic species, most of which presented short latitudinal distributions and many were known from only a single recorded collection.

The numerical importance of the species with subantarctic affinities along the South American coast (Fig. 1) was found to decrease steadily to the north and none were found to extend north of 5 °S latitude nor in the Galapagos. On the other hand, and as indicated above, the contribution of Central American Pacific elements was restricted both in number of species and in latitudinal range (Fig. 1). Only six of these species reached as far as 5 °S, and only two of them extended beyond Callao (c. 12 °S). None were found to extend south of Coquimbo, in Central Chile (30 °S). The latitudinal distributions of the remaining two groups (Fig. 1) were contrastingly different, but numerically complementary. The relative importance of cosmopolitan or widely distributed species increased while the importance of bipolar species decreased to the south.

Since the summation of endemic, bipolar and widely distributed species did not significantly change along temperate Pacific South America, the total species richness at different latitudes along this coastline was heavily influenced by a northward reduction in subantarctic species and a restricted southward incursion of Central American tropical species. The resulting pattern (Fig. 1) was an increase in the total number of species with increasing latitudes.

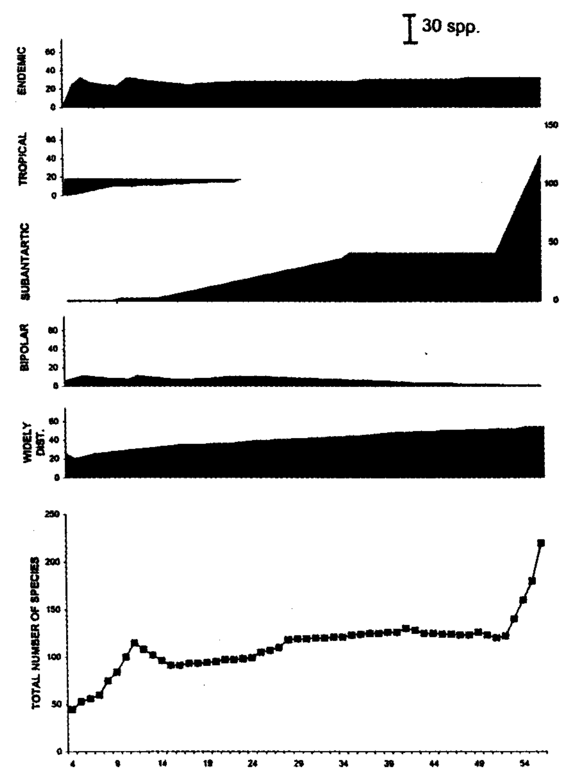

Fig. 1. Numerical importance of the five floristic components of temperate Pacific South America and the latitudinal pattern of species richness with increasing number of species to higher latitudes. Data taken from Santelices (1980).

Importancia numérica de los 5 componentes florísticos del Pacífico temperado de Sudamérica y el patrón latitudinal de riqueza de especies con aumento en el número de especies hacia latitudes altas. Datos tomados de Santelices (1980).

A major phytogeographic generalization that emerged from this study (Santelices 1980) was the apparent isolation of the marine benthic flora of temperate Pacific South America. Floristic exchange across the northern rim of the Perú Current appeared small as the contribution of Central American Pacific species to temperate South America was limited in both number of species and latitudinal range. Floristic exchange between South America and nearby offshore islands (e.g., Juan Fernández or Galápagos) also seemed limited, as indicated by the small number of common elements. This partial blockade to species migration and colonization was thought to explain the high representation of endemic elements and the peculiar latitudinal species diversity gradient found along Pacific South America.

Expanding these findings to species richness, Santelices (1980; 1991) also suggested that the relative isolation of this coastline could partially account for the reduced species richness of this area in comparison to other climatically equivalent regions which generally have greater contact with more effective routes of migration.

Testing the hypothesis

A critical analysis of the data supporting the above hypothesis suggested a rather spotty knowledge of the marine algal flora of the region (Ramírez & Santelices 1981, Santelices 1982). Thus, the geographic patterns observed could reflect incomplete sampling rather than true species absence. Therefore, new taxonomic studies in the region would contribute relevant information to test the above characterization. More complete floristic studies in the northern part of the region (e.g., Northern Chile, Perú) and in the Oceanic Islands (Easter Island and Juan Fernández Archipelago) were thought to be specially critical because they would test the respective absence of species from the Central American Pacific and from the Western Pacific and Central Pacific Islands. If the described pattern was due to incomplete sampling, those taxonomic studies should increase the number of species with tropical affinities in Northern Chile and Perú and the number of species shared between the Continent and the Central Pacific Islands.

Floristic studies in Northern Chile and Perú

Intensive taxonomic studies were carried out (Ramírez & Santelices 1981, Ramírez 1982) between 1976 and 1980 in intertidal and subtidal marine habitats around Antofagasta in Northern Chile (23 °40'S; 70 °25'W). Eight ecologically different sampling stations were regularly sampled over the 4 years, with 60% of the total number of gatherings being collected in subtidal habitats.

A total of 70 species was found, 14 of which constituted new records for the area. The intensive sampling, however, failed to significantly modify the total number of species known for the area or to find species with geographic affinities not considered in the original biogeographic hypothesis (Santelices 1980). Sampling also failed to significantly increase the number of species with tropical affinities. Therefore, the relative representations of algal groups with different geographic affinities remained as predicted by the phytogeographic hypothesis, while the latitudinal pattern of species richness was only slightly modified.

Intensive seaweed sampling was later completed (Pinto 1989) further north, between Iquique (20° 12'S) and Loa River (21 °26'S). A total of 24 sampling sites, including intertidal and subtidal stations (to 10 m depth) were regularly sampled between June 1987 and May 1988, which corresponded to a inter- El Niño period.

Sampling in this case yielded 89 species, 19 of which represented range extensions. Similar to the Antofagasta study (Ramírez & Santelices 1981) and in spite of the new additions, the geographic affinities of the flora found near Iquique agreed well with the proposed phytogeographic characterization of temperate Pacific South America.

No special intensive sampling programs to increase taxonomic knowledge have been undertaken in any locality along the Peruvian coastline that would provide data to test the role of sampling effort on the above phytogeographic characterization. However, Acleto (1988) completed a preliminary analysis of the phytogeographic affinities of the Peruvian flora. Integrating results of the most important taxonomic contributions to the Peruvian littoral (Howe 1914; Collins 1915; Taylor 1947; Dawson et al. 1964; Acleto 1973, 1980; Acosta 1976; Acleto & Endo 1977), Acleto (1988) recorded 225 species extending between 3°30'S and18 °30'S. A total of 28 species (12.4%) was recognized as endemic to Perú, 15 species (6.6%) had affinities with the marine flora of Chile and the subantarctic region; 24 species (10.6%) had tropical and subtropical affinities with the American Pacific, 26 species (11.5%) exhibited bipolar distribution and the remaining 132 species (58.6%) had widespread geographic distribution. Acleto (1988) concluded that the distribution of the marine flora of Perú agreed well with the previous (Santelices 1980) phytogeographic characterization done of the area.

Intertidal sampling in specific places of the Peruvian littoral generally yields low numbers of species. For example, Acosta (1976) listed 67 species for the Pisco Province in Central Perú. More recently, Benavente (1994) found only 36 species of benthic macroalgae in intertidal habitats of Caleta Yasila, south of Paita (5°S). Interestingly most of these species were endemic to the area (32.3%). Species with wide distributions or bipolar distributions had roughly similar importance (23.5% and 20.6% respectively) while the species with subantarctic affinities (5.9%) were the least abundant. Although species with tropical affinities were proportionally more abundant than in localities further south (17.65%), their quantitative significance still was very minor.

In summary, results of floristic studies conducted in Northern Chile and Perú over the last 20 years are consistent with several aspects of the original phytogeographic predictions made by Santelices (1980) for the area.

Floristic studies with Islands in the Central Pacific

A new taxonomic survey of the intertidal and shallow subtidal marine algal flora of Easter Island (27°07'S; 109°22'W) was undertaken (Santelices & Abbott 1987) to test whether increase in sampling effort would increase the total number of species known for the island and later, how this increase in species richness would affect the level of floristic similarity between the island and the South American Continent.

The survey (Santelices & Abbott 1987) yielded 107 identified species, 61.7% of which (66 spp.) represented new records. Adding these to previously known records (Börgesen 1924; Levring 1941; Etcheverry 1960) a total of 144

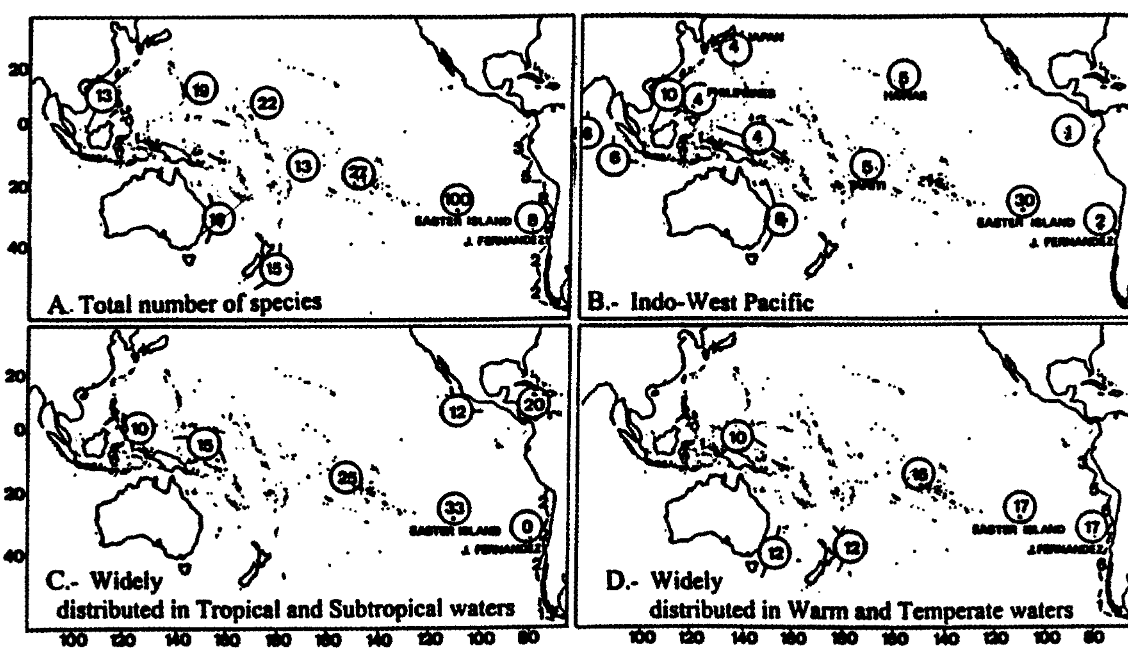

Fig. 2. The floristic affinities of the marine flora of Easter Island. A) Pattern of distribution across the Pacific of 100 species collected in Easter Island. B) Species from Easter Island (30 spp) with Indo-West Pacific pattern of distribution. C) Pattern of distribution of species collected in Easter Island and in other tropical and subtropical waters. D) Pattern of distribution of species collected in Easter Island and in other warm and temperate waters. Note that the number of species in A) results from the addition of data in B), C) and D) plus 14 endemic species and 6 other species with distribution in other places (see Figs. 3B and 3D).

Las afinidades florísticas de la flora marina de Isla de Pascua. A) Patrón de distribución a lo largo del Pacífico de cien especies colectadas en la Isla de Pascua. B) Especies de Isla de Pascua (30 spp) con patrón de distribución del Pacífico Indooccidental. C) Patrón de distribución de especies colectadas en Isla de Pascua y en otras aguas tropicales y subtropicales. D) Patrón de distribución de especies colectadas en Isla de Pascua y en otras aguas cálidas y temperadas. Nótese que el número de especies en A) es el resultado de la suma de los datos en B), C) y D) más 14 especies endémicas y 6 otras especies con distribución en otros lugares (ver Figs. 3B y 3D).

species was reached, 69.4% of which (100) were considered for further geographic analysis (Fig. 2). Thirty three species exhibited wide distribution in tropical and subtropical waters (Fig. 2C), 17 were widely distributed in warm and temperate waters (Fig. 2D), 30 species had an Indo-West Pacific affinity (Fig. 2B); 14 were endemic to Easter Island and six species corresponded to taxa found only in a few other localities (e.g., Juan Fernández). When these 100 species are mapped according to their representation in other localities of the Pacific (Fig. 2A), it becomes evident that the number of species the island has in common with another locality decreases as distance increases. However, even the most remote Western Pacific locality considered (Nha Trang in Vietnam) maintained a higher similarity value with Easter Island than nearby Juan Fernández. Thus, this new survey (Santelices & Abbott 1987) characterized the flora of Easter Island as having a greater affinity with islands in the West Pacific and almost no relationship with islands in the East Pacific or with Continental Chile, regardless of distance and despite the significant increase in new records and species numbers achieved through the study.

A later survey on the benthic marine algae from Easter Island was undertaken by Ramírez & Müller (1991), in which the authors made collections on three opportunities at different localities around the island. They added six new records and confirmed the affinities and biogeographical patterns established by Santelices & Abbott (1987), likewise concluding that the flora of this island is very different from that of the nearest Pacific South America coasts.

These marine flora findings of Easter Island motivated a new assessment of the geographic affinities of the marine flora of the Juan Fernández Archipelago (Santelices 1992), a group of islands located at about 650 km to the west of Central Chile (33°45'S; 79°22'W). Data were initially recorded for 110 taxa. However, taxonomic uncertainties and lack of information on geographic distribution of species elsewhere reduced the number of species for further consideration to 89 (Fig. 3A). This flora exhibited a high degree of endemism (about 30%), a large number of widely distributed species (45%; Fig. 3D) and a small group of species with circumpolar-subantarctic affinities (about 13.5%; Fig. 3B). The sources for this flora, therefore, seem to be distant localities in the Southern Pacific, including the southern tip of South America, Southern Australia, New Zealand and several subantarctic islands. The West Wind Drift and the Humboldt Current appeared as the route most probably followed by many species reaching the islands. Thus, the geographic affinities of this flora are as high with Southern Chile (19-21 of the 89 species) as with Central and Northern Chile (19-23 species) and higher than with Perú (12-19 common species). Considering effective dispersal distances of marine algae, the Juan Fernández Archipelago appears to be more isolated than Easter Island, which explains the very different number of endemic species found in both islands (14% in Easter Island; 29.2% in Juan Fernández). These results also are consistent with predictions of limited species exchange across the northward flow of the Chile-Perú current system. The presence of 5 species that only co-occur in the Archipelago and in Central Chile (Fig. 3C) attests to the possibility of migration across the Chile-Perú current system. But, the low number of these species suggests that although the possibility exists, its frequency is low. Rock lobster fishing boats moving between the Archipelago and the continent or ENSO events of such an intensity as to reach the Archipelago (e.g., 1973; Silva & Sievers 1973; Arana 1987) are potential transporting mechanisms between the Juan Fernández Archipelago and Central Chile.

More recently, Meneses & Hoffmann (1994) studied drift and hand collected materials from the Desventuradas Archipelago (26°20'S, 80°'W). They added 10 new records to the 12 previously known species (Levring 1942; Etcheverry 1960). Although these islands are located 972 km from the Chilean coast, only five of the 22 species found there also occur in the continent. On the other hand, six of the species found in the islands also occur in temperate zones of the South Pacific (South Africa, Australia, Tasmania, New Zealand) reproducing the pattern found for Juan Fernández. Meneses & Hoffmann (1994) stressed the floristic similarity between the Desventuradas and the Juan Fernández Archipelago and the potential transport and introduction of marine algae by lobster fishing boats that roam among these islands.

In summary, results with the new floristic studies of the oceanic islands off Central Chile support the prediction of a very limited floristic exchange between the islands and the continent. These studies also have characterized phytogeographically the marine flora of these islands, described the large floristic differences between them and called attention to effective dispersal ranges, which seem to be much more extensive for Juan Fernández than for Easter Island, regardless of their respective distance from the Continent.

Latitudinal patterns of species richness

In addition to the taxonomic studies mentioned above, others (Etcheverry et al. 1980; Acleto 1981, 1984, 1986; Westermeier 1981; Santelices & Montalva 1983; Contreras et al. 1984; Ramírez & Rojas 1986, 1988; Ramírez et al. 1986; Westermeier & Rivera 1986; Villouta & Santelices 1986; Santelices & Abbott 1985; Bird et al. 1987; Wynne 1988; Santelices et al. 1989) have added new records and described new species for the coast of Perú and Chile. It is therefore pertinent to evaluate whether or not these additions have significantly modified the pattern of species richness along temperate Pacific South America.

The emerging pattern of latitudinal species richness varies slightly when single findings are included or excluded (Fig. 4). If only repeated findings are considered (Fig. 4B) there is a gradual increase of species richness from 4°S to 42°S, species richness decreases between 42°S and 44°S, and it remains stable down between 42°S and the southernmost tip of South America. Considering the number of species involved, these data indicate that it would be expected to find 50-70 species in representative habitats between 5°S and 10°S, around 90-95 species between 12°S and 20°S; 120-130 species between 20°S and 32°S and 130-140 species at latitudes between 33 and 40°S, decreasing thereafter to 120-130 species south of 42°S (Chiloé).

The inclusion of single findings (equivalent to one degree findings; Fig. 4C) slightly modifies the above pattern. Along the Peruvian and Chilean coastline there is a larger number of species in places where more intensive taxonomic studies have been completed, suggesting that the species richness of the whole area is perhaps higher and

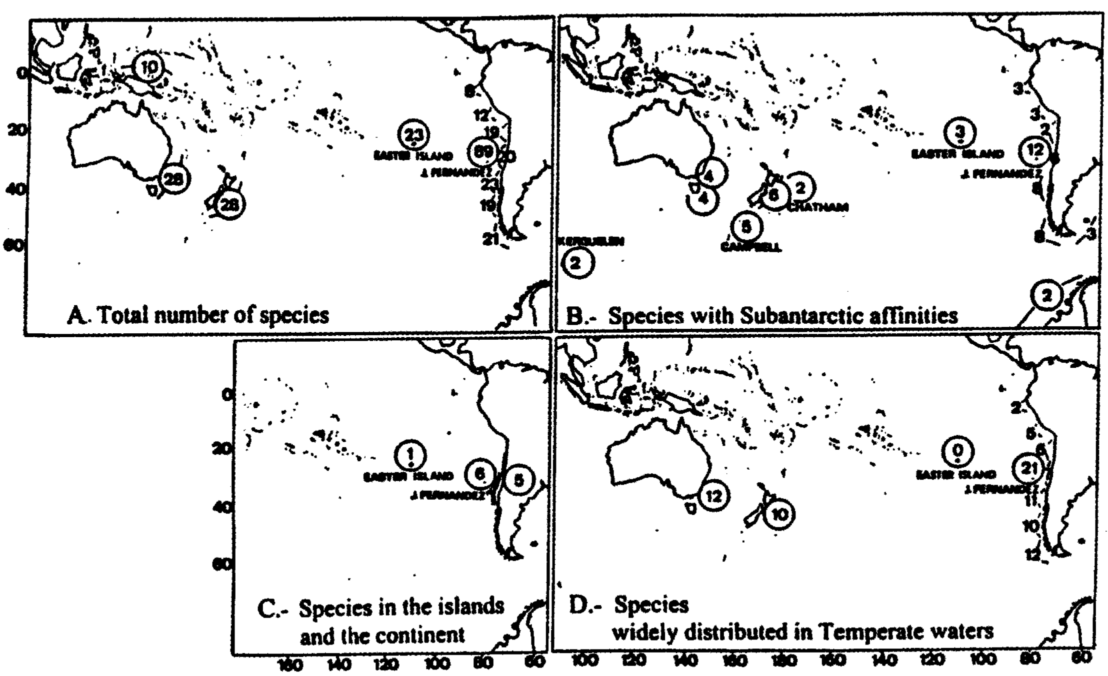

Fig. 3. The floristic affinities of the marine flora of Juan Fernández. A) Pattern of distribution across the Pacific of 89 species collected in Juan Fernández. B) Species (12 spp.) from Juan Fernández with circumpolar-subantarctic affinities. C) Species (6) from Juan Fernández that only co-occur in the Archipelago and in Central Chile (5) or in Easter Island (1). This group attests for the possibility of migration across the Chile-Perú current system. D) Species from Juan Fernández (21 spp.) widely distributed in temperate waters. Note that the number of species in A) results from the addition of data in B), C), D) plus 27 endemic species and 23 other species in warm and temperate waters (see Figs. 2B and 2D).

Las afinidades de la flora marina de Juan Fernández. A) Patrón de distribución a través del Pacífico de 89 especies colectadas en Juan Fernández. B) Especies (12 spp) de Juan Fernández con afinidades circumpolares - subantárticas. C) Especies (6) en Juan Fernández que sólo se encuentran presentes en el Archipiélago y en Chile Central (5) o en Isla de Pascua (1). Este grupo indica la posibilidad de migración a través del sistema de la corriente Chile - Perú. D) Especies de Juan Fernández (21 spp) ampliamente distribuidas en aguas temperadas. Nótese que el número de especies en A) es el resultado de la suma de los datos en B), C) y D) más 27 especies endémicas y 23 otras especies de aguas cálidas y temperadas (ver Figs. 2B y 2D).

that many of these single gatherings could become more extended ranges with more intensive sampling along the entire coast. Still, the increments are slight in most places and follow the general latitudinal pattern already discussed. Thus, as many as 100 species, rather than 50-70, may be expected between 5 and 10°S; up to 120 species may occur between 12 and 20°S; and up to 200 species between 33 and 40°S. The high values gathered for 54 and 55°S are especially important.

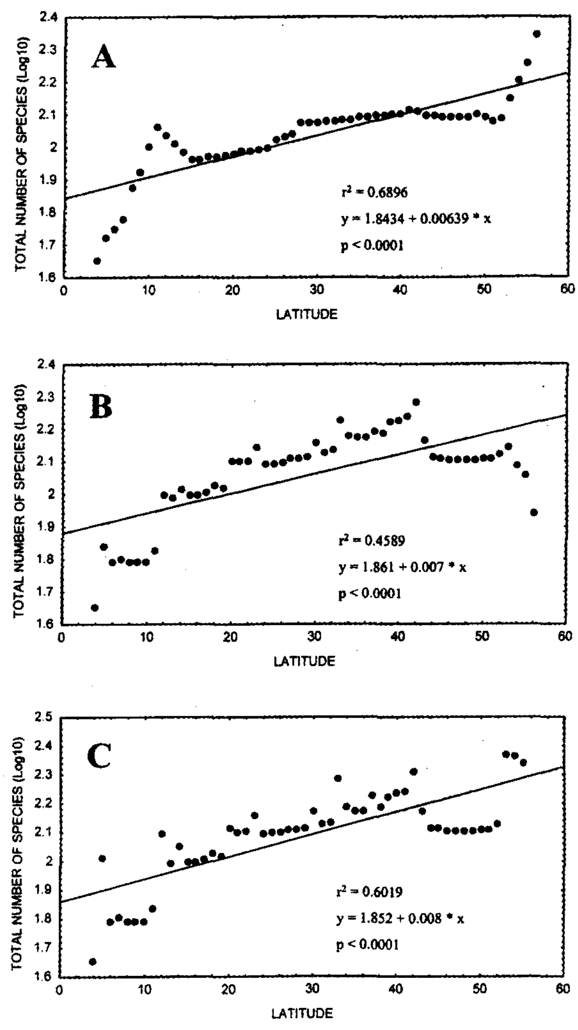

Fig. 4. Latitudinal pattern of species richness along temperate Pacific South America. A) Corresponds to the data base used in Santelices 1980. B) Corresponds to present data but excluding single findings (one degree findings). C) Data includes single findings.

Patrón latitudinal de la riqueza de especies a lo largo del Pacífico temperado de Sudamérica. A) Corresponde a la base de datos usadas en Santelices (1980). B) Corresponde a los datos actuales excluyendo registros únicos (registros de 1 grado). C) Datos incluyen registros únicos.

South of Chiloé (41°S) the coastal geomorphology typically corresponds to an erosional tectonic pattern of fjords with glaciated and unglaciated hinterlands (Araya-Vergara, 1976). The central valley between the Andean Cordillera and the coastal ranges is here covered by the sea. Between this coastline and the open sea, a number of offshore islands provide protected waters, forming sheltered channels. Due to the obvious differences in wave impact, types of substratum, salinity and temperature between the open coast and the sheltered sounds of these islands, a pronounced habitat diversification occurs south of 42°S as compared to the rest of the coastline northward (Santelices 1991). Therefore, the single gatherings at 54-55°S that increase species richness close to 250 species per locality, perhaps are representative of the marine flora of all the stretch of coast south of 42°S. Studies by Westermeier and co-workers south of Puerto Montt and Chiloé (Westermeier & Ramírez 1978; Westermeier 1981; Westermeier & Rivera 1986) have been especially useful to understanding the species pools that form in wave exposed and sheltered rocky habitats so typical of Central and Southern Chile. Here, they are complemented by a diversity of taxa representative of the sheltered sounds that become ecologically important south of 42°S.

Regression analyses of the latitudinal trends in species richness (Fig. 4) in all cases indicate significant increases in species richness to the south. Compared to the distributional data used 20 years ago (Fig. 4A), the taxonomic data added over the last 20 years (Fig. 4B) has slightly reduced the r^2 value but have not modified the statistical significance of the pattern ($p < 0.0001$). Incorporation of single findings (one degree-species) further increases the statistical significance of the southward increase in species number (Fig. 4C).

In summary, the additional data contributed by taxonomic studies in Perú and Chile, have supported the hypothesis that the number of benthic algal species increases to the south in temperate Pacific South America, in sharp contrast to the widely accepted paradigm of increased species richness to the tropics. Compared to the data available 20 years ago, new species additions and phytogeographic registries additions have allowed for statistical analyses supporting the pattern. Further sampling between 41°S and 53°S now appears to be most important to complete the overall picture of species richness along temperate Pacific South America.

Relative importance of geographically different groups in the marine flora of temperate South America

Given the addition of new records and species to this marine flora, it is necessary to evaluate whether or not the relative contribution of geographically different groups of species to this flora has changed in relation to the pattern predicted by Santelices (1980).

Compared to the original characterization (compare Fig. 5 with Fig. 1), endemic and bipolar species now show a reduction in species abundance towards the northermost and southermost distribution limits. Species with wide geographic distribution remains equally represented along temperate Pacific South America. The very unequal representation of tropical species versus the abundance of species with subantarctic affinities is notable and still appears as the principal factor determining the latitudinal pattern of species richness. The new collections have increased the latitudinal extent of species with tropical affinities in the area, but have not increased their numerical importance.

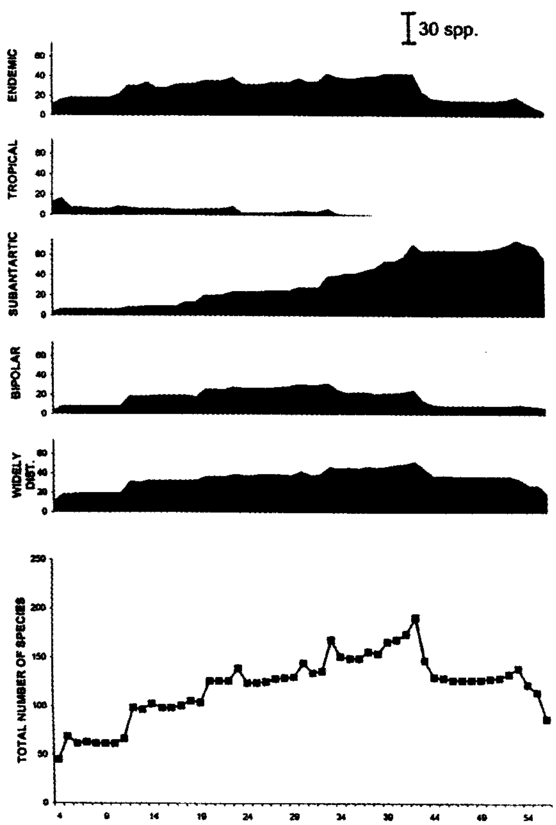

Fig. 5. Numerical importance of the five floristic components of temperate Pacific South America and the latitudinal pattern of species richness. Single findings are excluded.

Importancia numérica de 5 componentes florísticos del Pacífico temperado de Sudamérica y el patrón latitudinal de riqueza de especies. Los registros únicos están excluidos.

CONCLUSIONS

Over the last 20 years, close to 30 biogeographic and floristic studies on the seaweeds of Perú and Chile have been published. The additions of new phytogeographic records and new species resulting from these studies have added support to several key aspects of the phytogeographic characterization formulated 20 years ago for this coastline. This coastline appears to be effectively isolated from the Western Pacific, the Central Pacific Islands and the Eastern Tropical Pacific and presents very unequal contribution of tropical and subantarctic elements. These regional characteristics are likely to have noticeable effects on the biodiversity and ecology of these algae, some of which have been explored elsewhere (Santelices 1980, 1982, 1991).

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LITERATURE CITED

ACLETO C (1973) Las algas marinas del Perú. Boletín de la Sociedad Peruana de Botánica 6: 1-164.

ACLETO C & J ENDO (1977) Las especies peruanas de *Porphyra* (Rhodophyta, Bangiales). I Taxonomía y distribución geográfica. Publicaciones del Museo de Historia Natural "Javier Prado", Serie B 29: 1-9.

ACLETO C (1980) Notas sobre las algas marinas del Perú. Nuevos registros. Publicaciones del Museo de Historia Natural "Javier Prado", Botánica, Serie B 30: 1-33.

ACLETO C (1981) Estado de nuestro conocimiento acerca de la flora marina del Perú. Phycologia Latinoamericana 1: 26-30.

ACLETO C (1984) Las especies peruanas de *Porphyra* (Rhodophyta, Bangiales). II. *Porphyra crispata* Kjellman, un nuevo registro para nuestra flora. Publicaciones del Museo de Historia Natural "Javier Prado", Serie B 31: 1-8.

ACLETO C (1986) Algas marinas del Perú de importancia económica. Publicaciones del Museo de Historia Natural "Javier Prado", Depto. Botánica. Serie de Divulgación Nº 5, 106 pp.

ACLETO C (1988) Aspectos fitogeográficos y taxonómicos de las algas marinas del Perú. Gayana, Botánica (Chile) 45: 143-146.

ACOSTA PJ (1976) Estudio morfológico y anatómico de tres especies de Phaeophyceae. Publicaciones del Museo de Historia Natural "Javier Prado", Serie de Divulgación Nº 6: 1-6, 25.

ARANA P (1987) Perspectivas históricas y proyecciones de la actividad pesquera realizada en el Archipiélago de Juan Fernández, Chile. In: Castilla JC (ed) Islas Oceánicas Chilenas: Conocimiento Científico y Necesidades de Investigación: 319-353. Ediciones Universidad Católica de Chile, Santiago.

ARAYA-VERGARA JF (1976) Reconocimiento de tipos e individuos geomorfológicos regionales en la costa de Chile. Informe Geográfico (Chile) 23: 9-30.

BENAVENTE MJ (1994) Macroalgas Bentónicas de la Caleta Yasila-Piura, Perú. Tesis para optar al título profesional de Biólogo con mención en Botánica. Universidad Nacional Mayor de San Marcos, 108 pp.

BIRD CJ, JL McLACHLAN & EC OLIVEIRA (1987) *Gracilaria chilensis* sp. nov. (Rhodophyta, Gigartinales), from Pacific South America. Canadian Journal of Botany 64: 2928-2934.

BOERGESEN F (1924) Marine algae from Easter Island. In: Skottsberg C (ed) The Natural History of Juan Fernández and Easter Island 2: 247-309. Almquist & Wiksells, Upsala.

COLLINS FS (1915) Algae from the Chincha Islands. Rhodora 17: 89-96.

CONTRERAS D, R SCHLATTER & C RAMIREZ (1984) Flora ficológica de las Islas Diego Ramírez (Chile). Instituto Antártico Chileno, Serie Científica. 13-26 pp.

DAWSON EY, C ACLETO & N FOLDVIK (1964) The seaweeds of Perú. Nova Hedwigia, Beih. 13: 1-111, 80 pls.

ETCHEVERRY DH (1960) Algas marinas de las Islas Oceánicas Chilenas (Juan Fernández, San Félix, San Ambrosio y Pascua). Revista de Biología Marina 10: 83-138.

ETCHEVERRY H, E COLLANTES & V RIOS (1980) Taxonomic and biological studies on species of *Iridaea* Bory in Central Chile. Proceedings of International Seaweed Symposium 10: 163-173.

HOWE MA (1914) The marine algae of Perú. The Torrey Botanical Club Memoirs 15: 1-185, 66 pls.

LEVRING T (1941) Die Meeresalgen der Juan Fernández Inseln. In: Skottsberg C (ed) The Natural History of Juan Fernández and Easter Island. Vol. 2, Part 5, Nº 22. Almqvist & Wiksells, Uppsala.

LEVRING T (1942) Einige Meeresalgen van den Inseln San Ambrosio und San Félix. Bot. Not. 1942: 60-62.

MENESES I & AJ HOFFMANN (1994) Contribution to the Marine Algal Flora of San Félix Island, Desventuradas Archipelago, Chile. Pacific Science 48(4): 464-474.

MENESES I & B SANTELICES (2000) Patterns and breaking points in the distribution of benthic algae along the temperate Pacific coasts of South America. Revista Chilena de Historia Natural 73: 615-623.

PINTO R (1989) Caracterización de la flora algológica del área de Iquique, Norte de Chile. Vultur (Botanica) 1: 1-16.

RAMIREZ ME (1982) Nuevos registros de algas marinas para Antofagasta (Norte de Chile). Boletín Museo de Historia Natural de Chile 39: 11-26.

RAMIREZ ME & B SANTELICES (1981) Análisis biogeográfico de la flora algológica de Antofagasta (Norte de Chile). Boletín Museo de Historia Natural de Chile 38: 5-20.

RAMIREZ ME & DG MÜLLER (1991) New records of benthic marine algae from Easter Island. Botanica Marina 34: 133-137.

RAMIREZ ME & G ROJAS (1986) El género *Stenogramme* (Rhodophyta, Gigartinales) en la costa temperada del Pacífico sur-oriental. In: Westermeier R (ed) Actas del Segundo Congreso sobre Algas Marinas Chilenas: 191-200. Universidad Austral de Chile, Valdivia.

RAMIREZ ME & G ROJAS (1988) Nuevos registros de algas marinas para la costa de Chile I. Boletín del Museo de Historia Natural 41: 17-31.

RAMIREZ ME & B SANTELICES (1991) Catálogo de las algas marinas bentónicas de la costa temperada del Pacífico de Sudamérica. Monografías Biológicas 5. Ediciones Universidad Católica de Chile, Santiago. 437 pp.

RAMIREZ ME, DG MÜLLER & AF PETERS (1986) Life history and taxonomy of two populations of ligulate *Desmarestia* (Phaeophyceae) from Chile. Canadian Journal of Botany 64: 2948-2954.

SANTELICES B (1980) Phytogeographic characterization of the temperate coast of Pacific South America. Phycologia 19: 1-12.

SANTELICES B (1982) Caracterización fitogeográfica de la costa temperada del Pacífico de Sudamérica. Verificación de hipótesis y consecuencias ecológicas. Archivos de Biología y Medicina Experimentales (Chile) 15: 513-524.

SANTELICES B (1991) Littoral and sublittoral communities of Continental Chile. In: Mathieson AC & PH Nienhuis (eds) Intertidal and Littoral Ecosystems of the World. Vol. 24. in the Series "Ecosystems of the World": 347-369. Elsevier Publishing Co., USA.

SANTELICES B (1992) Marine phytogeograpy of the Juan Fernández Archipelago. A new assessment. Pacific Science 46: 438-452.

SANTELICES B & IA ABBOTT (1985) *Gelidium rex* sp. nova (Gelidiales, Rhodophyta) from Central Chile. In: Abbott IA & J Norris (eds) Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species: 33-36. California Sea Grant College Program, La Jolla, California.

SANTELICES B & IA ABBOTT (1987) Geographic and marine isolation. An assessment of the marine algae of Easter Island. Pacific Science 41: 1-20.

SANTELICES B & S MONTALVA (1983) Taxonomic studies on Gelidiaceae (Rhodophyta) from Central Chile. Phycologia 22: 185-196.

SANTELICES B, ME RAMIREZ & IA ABBOTT (1989) A new species and new records of marine algae from Chile. British Phycological Journal 24: 73-82.

SILVA N & H SIEVERS (1973) Condiciones oceanográficas de primavera y otoño de las aguas circundantes a las islas Robinson Crusoe y Santa Clara. Investigaciones Marinas 4: 158-179.

TAYLOR WR (1947) Algae collected by the "Hassler" "Albatross" and Schmitt Expeditions, III. Marine algae from Perú and Chile. Paper of the Michigan Academy of Sciences, Arts and Letters 31: 57-90.

VILLOUTA E & B SANTELICES (1986) *Lessonia trabeculata* (Phaeophyta) a new kelp from Chile. Phycologia 25: 81-88.

WESTERMEIER R (1981) The marine seaweed of Chile's Tenth Region (Valdivia, Osorno, Llanquihue and Chiloé). Proceedings of the International Seaweed Symposium 10: 215-220.

Invited Editor J.C. Castilla

WESTERMEIER R & C RAMIREZ (1978) Algas marinas de Niebla y Mehuín (Valdivia-Chile). Medio Ambiente 3: 44-49.

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.

WYNNE MJ (1988) Notes on *Branchioglossum* Kylin (Delesseriaceae, Rhodophyta) in the eastern Pacific. Cryptogamie Algologie 9: 53-64.