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Marine Phytogeography of the Juan Fernández Archipelago: A New Assessment[1]

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ABSTRACT: A new assessment of the geographic affinities of the marine algae of the Juan Fernández Archipelago indicates a flora with a small number of species and very high endemism (about 30%) as compared to other oceanic islands of similar age, size, origin, and abiotic conditions. The flora also contains many widely distributed species (45%) and a small group of species with circumpolar-subantarctic affinities (about 13.5% of the flora). The potential algal species sources for this flora seem to be distant localities in the southern Pacific, including the southern tip of South America, southern Australia, New Zealand, and several subantarctic islands. Considering effective dispersal distances of marine benthic algae, the Juan Fernández Archipelago appears as more isolated than Easter Island, which previously was supposed to be the most isolated point in the Pacific basin. An analysis of the endemic components suggests that there has been speciation but no radiation in these islands. Some species originating in the archipelago might have migrated across the Pacific to continental South America, perhaps via El Niño/Southern Oscillation (ENSO).

BASED ON THE SEAWEEDS collected by the Swedish expedition to Juan Fernández and Easter Island, Levring (1941) and Skottsberg (1943*a*,*b*) made what amounts to be the only phytogeographic characterization of the marine algae of the Juan Fernández Archipelago. They distinguished eight floristic groups among the nearly 100 seaweed species reported from the islands. Endemic elements were most abundantly represented in the flora (32%), followed by subcosmopolitan (20%), and subtropical species widely distributed in warm waters (14%). They also noticed the presence of a small (10%) Australasian-Neozelandian element that did not belong to the circumpolar group known also from southern Chile and Magellania, and a few (about 5% of the flora) subantarctic species. Both Levring and Skottsberg were impressed with the absence in the islands of the large kelps and bull kelps that are so common in the southern part of Pacific South America and by the abundance of subtropical elements, which were common in Perú and northern Chile. Therefore, Skottsberg (1943*a*) concluded that the island flora was more like that of Perú and northern Chile than that of the continental flora farther south.

Even though Skottsberg (1943*a*) recognized that the West Wind Drift and the Chile-Perú Current (Humboldt Current) was the route probably followed by a large number of species, he considered that the abundance of subtropical elements in this insular flora was greater than what could be attributed to temperature conditions alone. He (Skottsberg 1943*a*) further suggested that historical causes had been influential. Considering that the fossil land flora of southern Chile and Antarctica showed that during the Tertiary the climate was considerably warmer than now, Skottsberg supported the idea that Juan Fernández was formerly connected with South America. He disregarded a neovolcanic, oceanic origin of the Juan Fernández Islands because seemingly it did not allow enough time for the evolution of strongly marked endemic forms and because a majority of the endemic species belong to genera

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regarded by Skottsberg (1943*a*) as having tropical and subtropical affinities.

In the 50 yr following Skottsberg's proposal, several expeditions have visited the islands, increasing the geological, oceanographic, and floristic knowledge of the archipelago. It is now accepted that the Juan Fernández Islands are entirely volcanic in origin and apparently have never been connected to the mainland (Stuessy et al. 1984, González-Ferrán 1987). The Nazca Plate is moving from west to east and apparently new islands are produced as the plate moves eastward over a "hot spot." The absolute ages are estimated at 3.8 to 4.2 million years (My) for Masatierra Island and 1 to 2.4 My for Masafuera Island. The known spreading rates for the margin of the Nazca Plate (8.8 cm yr^{-1}) agree well with the observed distance separating Masatierra and Masafuera (150 km) and their known ages. Therefore, present geological data do not support Skottsberg's (1943*a*) proposal of a land connection of the Juan Fernández Islands with South America, and the argument cannot be used to explain the geographic affinities of the marine flora of the islands with that of the continent.

Oceanographic studies have concluded that the surface waters surrounding the Juan Fernández Islands are mainly of subantarctic origin. The most superficial layer, and down to 200 m depth, corresponds to the subantarctic water mass, with temperature ranges from 10 to 19°C and salinities between 34.0‰ and 34.2‰. Furthermore, the ocean circulation around the islands, between 75° W and 78° W, is under the influence of the strong northward flow of the Humboldt Oceanic Branch, also called the Chile-Perú Current (Figure 1). Between 78° W and 80° W, there is a strong southward flow that may correspond to the Perú Oceanic Countercurrent; beyond 81° W, a current flowing to the north with low velocity and small volume transport has been identified (Arana 1987).

On at least one occasion this general subantarctic influence was found to be altered: the most superficial 50 m around the islands was found in April 1973 to be occupied by waters of the subtropical water mass, with higher temperatures and salinities (Silva and Sievers 1973). According to Arana (1987) this modification could have been related to the aperiodic El Niño/Southern Oscillation (ENSO), which was exceptionally strong that year.

Marine floristic studies have added new perspectives to the biogeographic affinities of the flora. Even though new collections (Etcheverry 1960, Earle 1969, Hawkes and Johnson 1981) have added few records to the islands, floristic studies elsewhere have modified the known geographic distribution of several of the species found in the Juan Fernández Archipelago. Several of the subtropical elements considered as most important by Skottsberg (1943*a*) are now regarded as widespread both in temperate and tropical waters. Some of these taxa also have been found in southern South America (see review by Ramírez and Santelices 1991), increasing the floristic affinities between the Juan Fernández Archipelago and localities in southern South America, New Zealand, and Australia.

On the other hand, new data on the flora of Easter Island, another oceanic island of similar age, size, origin, and approximately similar abiotic conditions as those in the Juan Fernández Archipelago, are inconsistent with our present understanding of the relationship among isolation, species richness, and endemism, but are useful for comparison. Easter Island has been found to have about 1/3 more species but only about half the percentage of endemic elements as the flora of the Juan Fernández Archipelago (Santelices and Abbott 1987). All of these island are volcanic and of about the same age (3.0 My, Easter Island, Newman and Foster 1983) and the same size (Masatierra = 93 km^2, Masafuera = 60 km^2, Easter Island = 93 km^2). All are hilly and relatively barren, with coastlines characterized by cliffs; few, small beaches; and few sheltered bays (Stuessy et al. 1984, González-Ferrán 1987). Winds are strong and change directions seasonally and daily (Hajek and Espinoza 1987). Thus, there seem to be no obvious differences in the above determinants of species richness and endemism between the islands in the Juan Fernández Archipelago and Easter Island.

The most important difference between

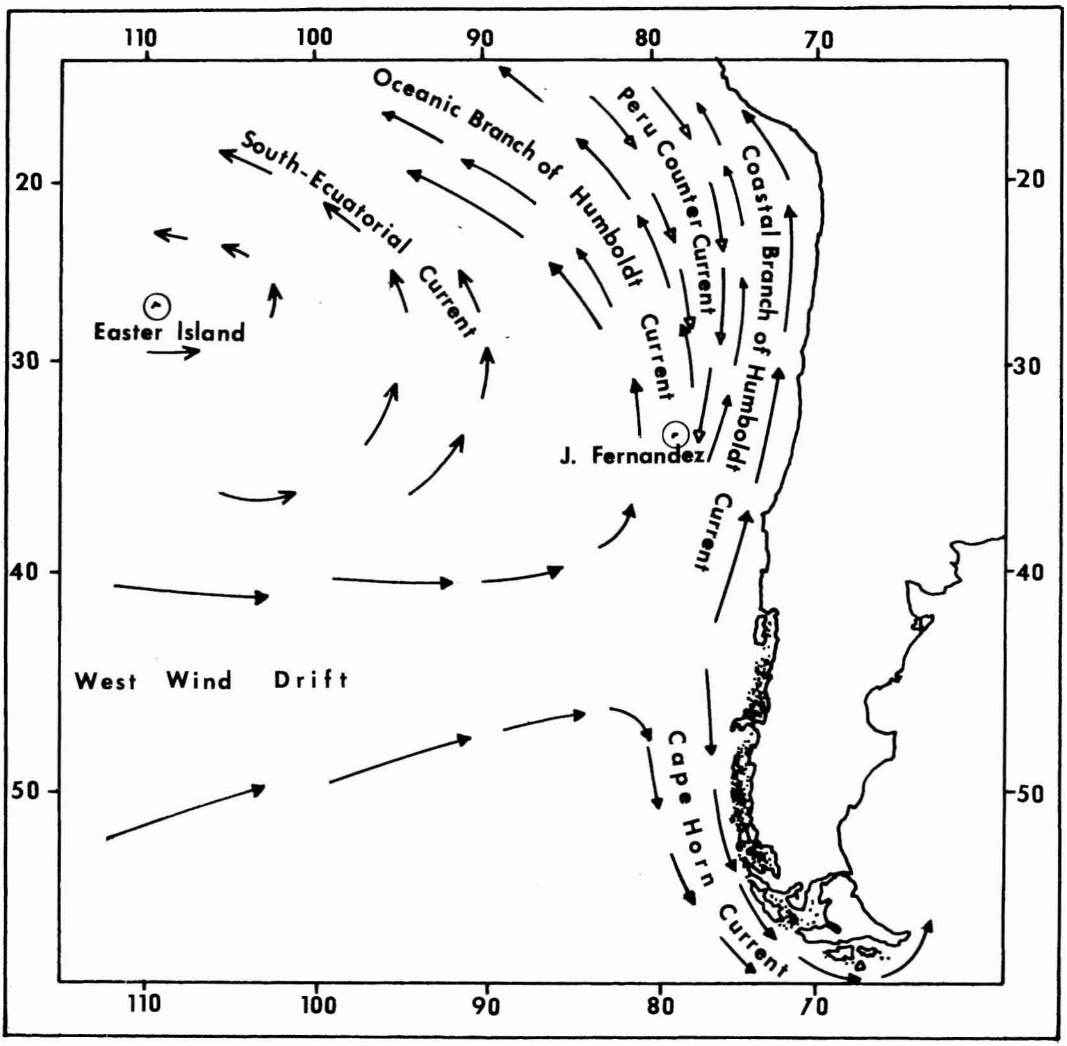


FIGURE 1. Pattern of oceanographic circulation around the Juan Fernández Archipelago (redrawn from Arana 1987).

Easter Island and the islands in the Juan Fernández Archipelago seems to be the degree of isolation. Easter Island is recognized as one of the most isolated points in the Pacific, lying 3250 km away from the South American coast and 2315 km away from the nearest land to the west (Ducie Atoll). The Juan Fernández Archipelago is only 600 km away from the South American continent. Therefore, the degree of isolation of the Juan Fernández Archipelago has traditionally been considered (Briggs 1974) to be considerably less than that of Easter Island. However, the high endemism and the small number of species exhibited by the flora of the Juan Fernández Archipelago as compared to Easter Island are not consistent with their respective degrees of isolation. The degree of endemism and the species richness of Juan Fernández might be explained by dispersion distances and biological isolation several orders of magnitude greater than those in effect on Easter Island. This assumption is

TABLE 1

EXAMPLES OF PATTERNS OF GEOGRAPHIC DISTRIBUTIONS OF BENTHIC ALGAE REPORTED FROM THE JUAN FERNÁNDEZ ARCHIPELAGO AND EASTER ISLAND

	JUAN FERNÁNDEZ	EASTER ISLAND	REPRESENTATIVE LOCALITIES ELSEWHERE
Indo-Pacific Distribution			
Cladophora socialis	—	+	Tahiti, Polynesia, Malaysia
Cladophoropsis herpestica	—	+	Vietnam, Japan, southern Australia
Ectocarpus arabicus	+	+	Indian Ocean, India, Malaysia
Feldmannia indica	—	+	Indo-Pacific, Indonesia, Philippines, Hawaiian Islands
Sphacelaria taitensis	—	+	Tahiti
Dictyota crenulata	—	+	Central Pacific, Philippines, Hawaiian Islands
Dictyopteris repens	—	+	Western Pacific, Japan, Philippines, Mariana Islands
Lithophyllum samoense	—	+	Tahiti, Samoa, Hawaii
Ceramium cruciatum	—	+	Indo-Pacific
Polysiphonia savatieri	—	+	Tropical Pacific, Hawaii, Malaysia, Japan
Circumpolar-Subantarctic Distribution			
Scytothamnus australis	+	—	Central southern Chile, Australia, Tasmania, New Zealand
Splachnidium rugulosum	+	—	Tasmania, New Zealand, South Africa
Glossophora kunthii	+	—	Southern Perú to Cape Horn, Chatham Islands, New Zealand
Acrochaetium catenulatum	+	+	Central to southern Chile, Campbell Islands, New Zealand
Gymnogongrus furcellatus	+	—	Central Perú to southern Chile, New Zealand, Australia
Rhodymenia australis	+	—	Australia
Rhodymenia cuneifolia	+	—	Chiloé to Magellan Strait in southern Chile, Falkland Islands, southern Argentina
Phycodris guercifolia	+	—	Central to southern Chile, Falkland Islands, Kerguelen Islands, South Georgia Islands, and Campbell Islands
Schizoseris griffithsia	+	—	Concepción to Magellan Strait, Falkland Islands, New Zealand, Auckland Islands, Chatham Islands, Campbell Islands
Polysiphonia abscissa	+	—	Coquimbo to Magellan Strait, several subantarctic islands
Endemic Species			
	Phaeophila pacifica	*Ectocarpus chnoosporae*	
	Phaeophila ramosa	*Sargassum skottsbergii*	
	Codium fernandezianum	*Erythrocladia laurenciae*	
	Codium cerebriformis	*Erythrocladia repans*	
	Ectocarpus minutissimus	*Acrochaetium discoideum*	
	Distromium skottsbergii	*Acrochaetium ralfsiae*	
	Padina fernandeziana	*Galaxaura paschalis*	
	Leptophyllum fernandezianum	*Botryocladia skottsbergii*	
	Chondriella pusilla	*Ceramium skottsbergii*	
	Hypoglossum parvulum	*Laurencia clavata*	

TABLE 1 (continued)

	JUAN FERNÁNDEZ	EASTER ISLAND	REPRESENTATIVE LOCALITIES ELSEWHERE
Restricted to the Two Island Localities and Temperate Pacific South America			
Chaetomorpha firma	+	+	Valparaíso to Coquimbo in central Chile
Chaetomorpha linoides	+	—	Valparaíso in central Chile
Cladophora perpusilla	+	+	—
Hymenena decumbens	+	—	Valparaíso in central Chile
Gelidium pseudointricatum	+	—	Iquique to Chiloé, Chile
Corallina berteroana	+	—	Valparaíso to Chiloé, central Chile

consistent with the notion that the majority of the floristic elements present in the islands of the archipelago originate in Fuegia-Magellania and the Australasian area, involving dispersal distances of 3000 (Fuegia) to 12,000 km (Australia–New Zealand). This relation was perceived by Skottsberg (1943*a*) but was overlooked by him because he supported a land connection between Juan Fernández and the continent. The abundance of tropical elements in the archipelago, and its general floristic affinity with Perú and northern Chile, can be explained in two ways: (1) Some species of wide distribution could have arrived independently in the islands and the continent; (2) Species restricted to Perú–northern Chile and Juan Fernández could have been transported across the eastern Pacific by aperiodic ENSO events.

In this study these ideas were tested and the geographic affinities of the marine flora of Juan Fernández were reassessed. For comparative purposes, the marine flora of Easter Island has been included in the analysis.

METHODS

This study is restricted to the benthic Chlorophyta, Phaeophyta, and Rhodophyta recorded in the Juan Fernández Archipelago and on Easter Island. Data on the geographic distribution of the species were taken from the literature, most of which has been summarized by Santelices (1987), Santelices and Abbott (1987), and Ramírez and Santelices (1991) for the areas in question. Data were initially recorded for 110 taxa in Juan Fernández and 165 taxa on Easter Island. Taxonomic uncertainties or lack of information on geographic distribution elsewhere reduced the number of species considered to 89 in Juan Fernández and 105 on Easter Island. Our samples represent 80% and 65% of the respective total number of taxa reported for these islands, and the proportion of endemics to total number of species is only slightly different from the values corresponding to the total flora.

The species were grouped according to their patterns of geographic distribution in the

Pacific basin and elsewhere. Table 1 shows a few outstanding examples of each group of species distinguished in each location. Abundance of algae groups among locations was compared by chi-square tests.

RESULTS

Five groups of species can be distinguished when the bulk of algal taxa reported for the Juan Fernández Archipelago and Easter Island is grouped by geographic affinities (Figure 2). The numerically most important group includes species with wide distribution, which compose 45–50% of the flora of these islands. Endemic elements are important in both places, but they are proportionally more important in the Juan Fernández Archipelago. A small group of species that extends to the Pacific coast of South America is also more important in the Juan Fernández Archipelago. The two remaining groups, taxa with Indo-Pacific affinities and species with circumpolar-subantarctic affinities, also are present in both areas but their representation in

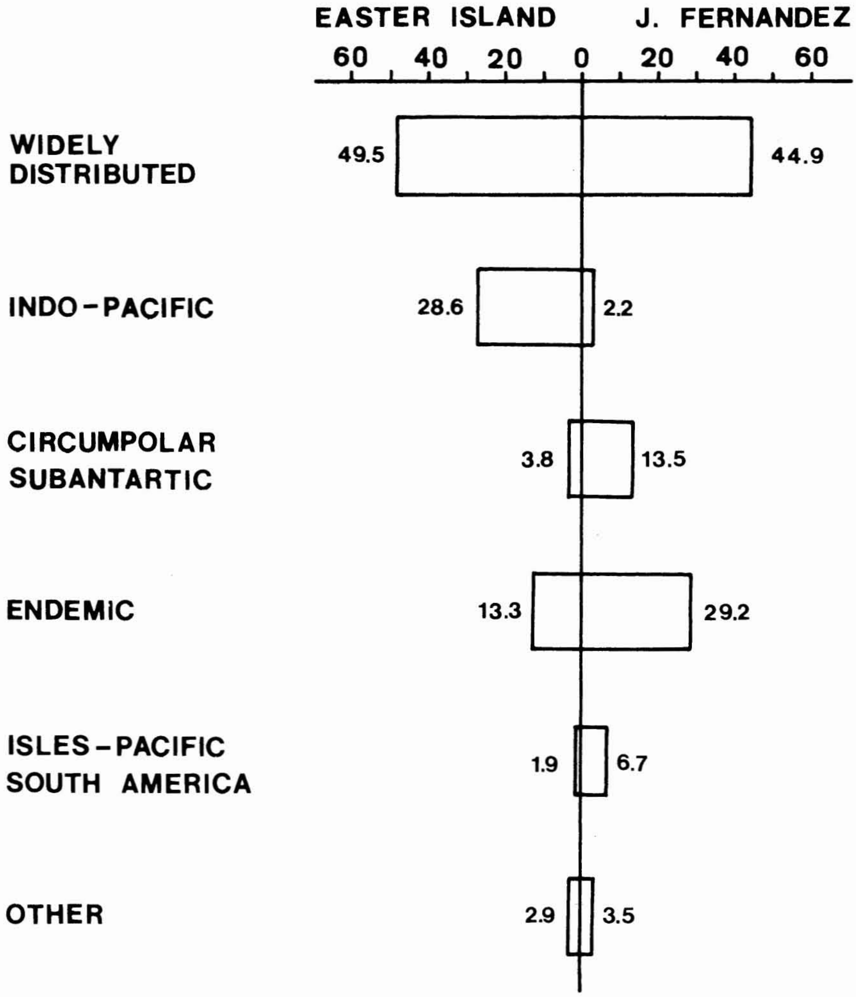


FIGURE 2. Relative importance of several floristic groups with different patterns of distribution in the marine flora of Easter Island and the Juan Fernández Archipelago.

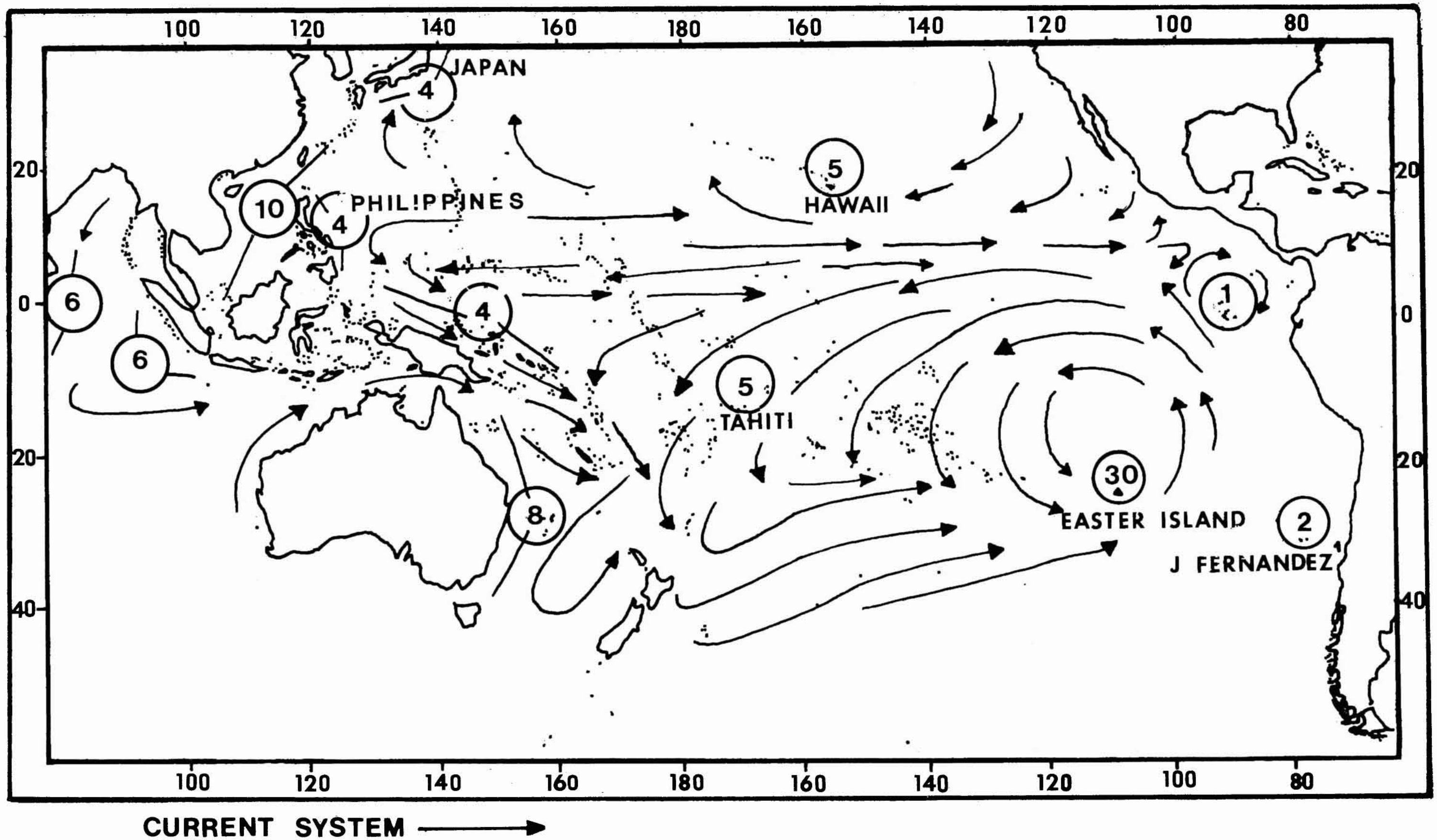


FIGURE 3. Distribution of 30 species of benthic algae with affinities in the Indo-Pacific. Number in circles represents the mean number of species present.

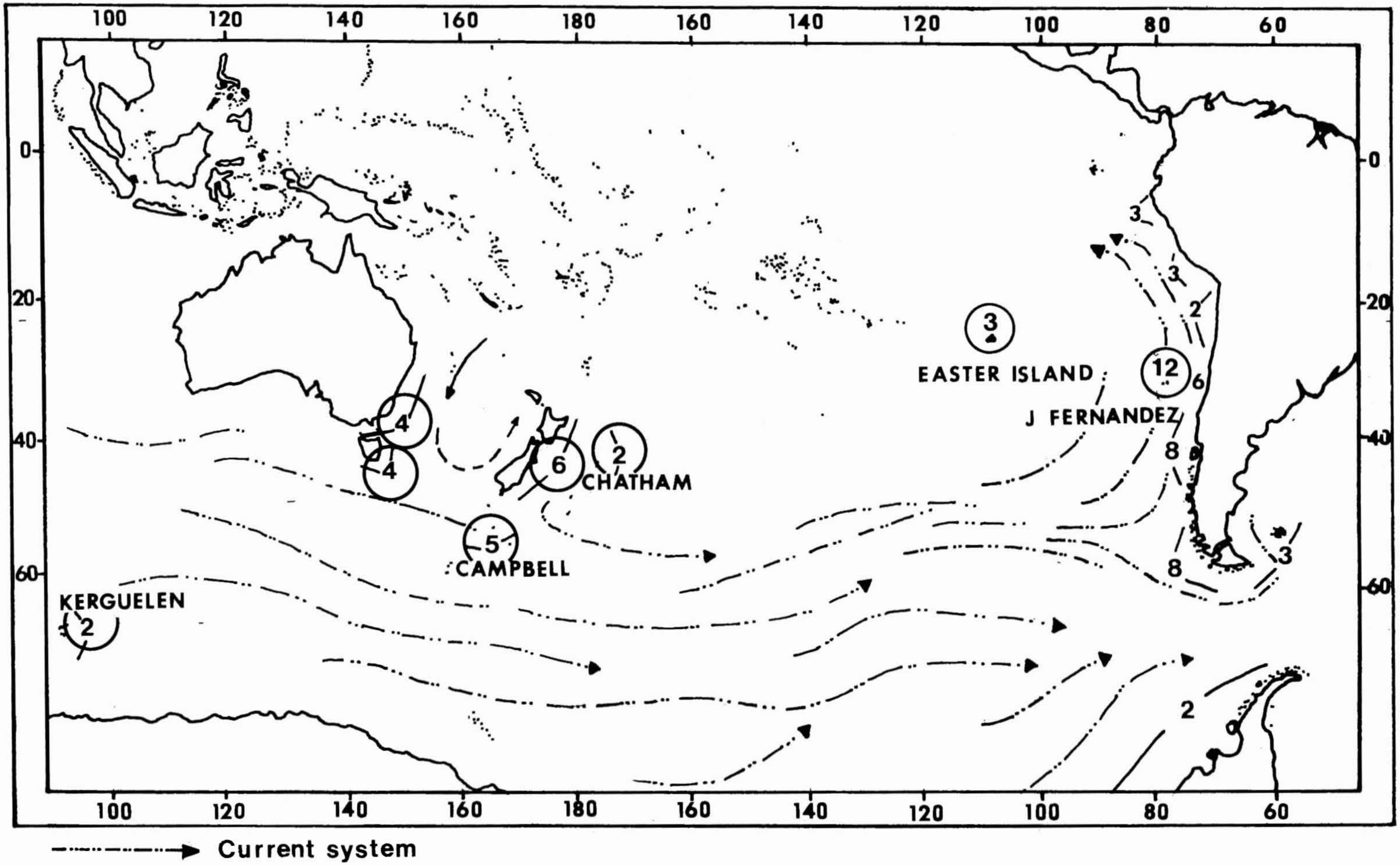


FIGURE 4. Pattern of distribution of 12 species of benthic algae with subantarctic-circumpolar distribution. Number in circles represents the mean number of species present.

each place is very different. The Indo-Pacific elements are very abundant on Easter Island; those with circumpolar-subantarctic affinities are more abundant in Juan Fernández. Although the endemic elements usually are regarded as highly characteristic of a given area, these last two groups, with differential representation and strong asymmetry among the islands, may better reflect the geographic affinities of the local floras. They will therefore be considered first.

Species with Indo-Pacific Affinities

This group of species is the second most numerous on Easter Island (Figure 2), amounting to 28.6% of the flora in the sample considered for this study. This group combines species previously characterized by Santelices and Abbott (1987) as having a western Pacific pattern of distribution and a few taxa previously included among those widely distributed in warm waters. Some of the species in the group (Figure 3) are restricted to a few islands in Polynesia; others are present also in Malaysia, northeastern Australia, Vietnam, Japan, and the Philippines, and a few reach northern New Zealand. Thirty of these species are found on Easter Island, but only two of them are found in the Juan Fernández Archipelago. Furthermore, one of these two taxa (*Laurencia clavata*) could have arrived in the archipelago through the West Wind Drift and the Chile-Perú Current system, because it is also found in southern Australia. The difference in the number of species of this group represented on Easter Island and in the Juan Fernández Archipelago emphasizes the influence of the Humboldt system on Juan Fernández, which with its cold temperature and northern flow acts as a powerful barrier to dispersal for a majority of species from Easter Island.

Species with a Circumpolar-Subantarctic Pattern of Distribution

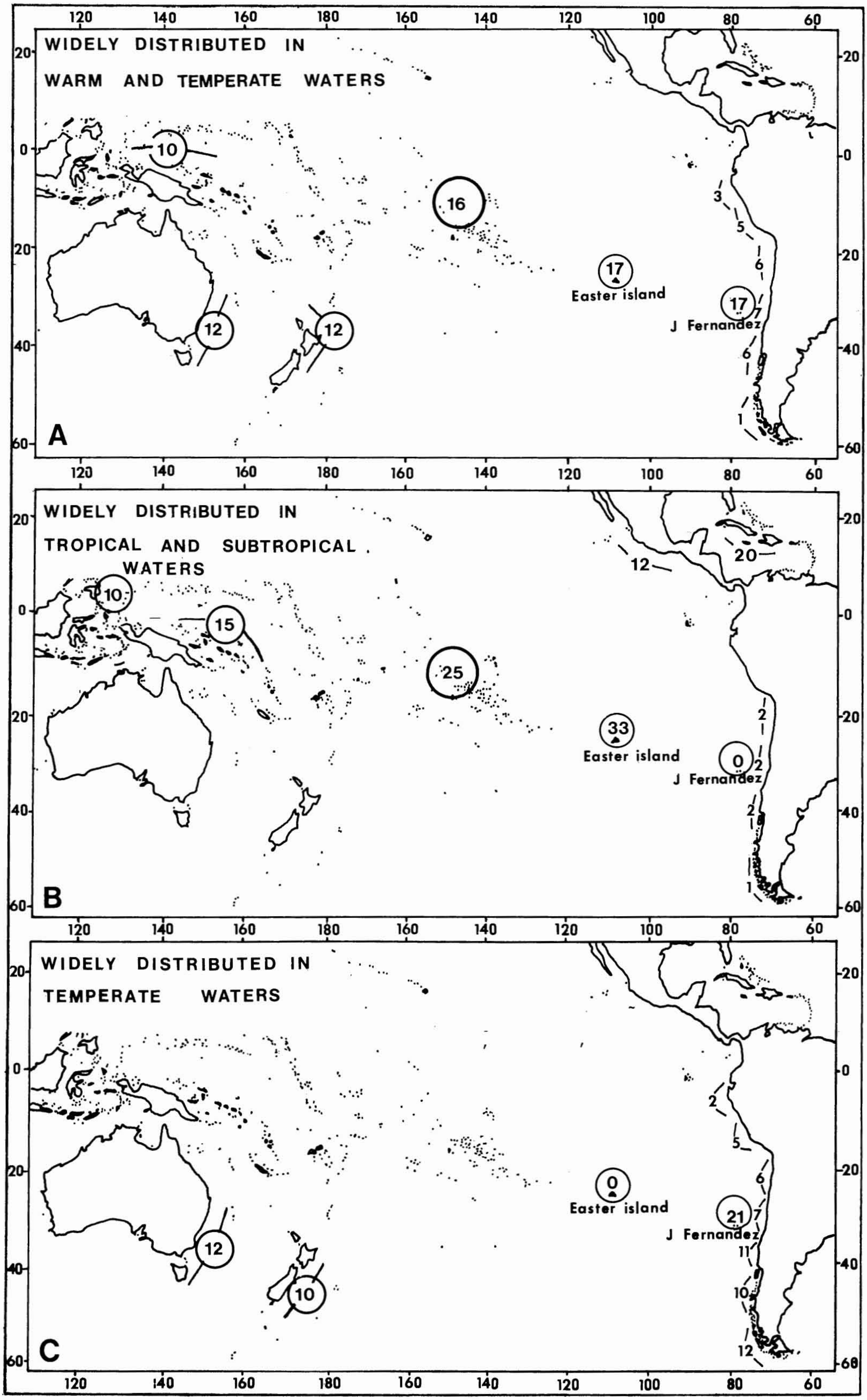
The Juan Fernández Archipelago contains a group of 12 species with geographic affinities in distant places in the southern hemisphere, a pattern of distribution that is closely associated with the West Wind Drift and the Chile-Perú Current systems (Figure 4). Eight of these species are found both at localities in southernmost Chile and in distant places in the southern Pacific Ocean, including southern Australia, New Zealand, Campbell Islands, and Chatham Islands. Four other species occur in these distant localities in the Pacific, but have not been found in southern South America. Because all of these species seem to have a similar dispersal route and only a few are restricted to localities in Australasia or the subantarctic, it is unnecessary to distinguish subgroups such as subantarctic and Australasian-Neozelandian as Skottsberg (1943*a*) did. Moreover, only two or three of these species are also found in northern Chile and Perú, showing a higher similarity between Juan Fernández and southern Chile than with more northern localities. In fact, the presence of these species in northern Chile and Perú does not require a circulation system between the islands and the continent because they could have reached there from southern localities by means of currents along the continental margins.

Three species with circumpolar-subantarctic affinities occur on Easter Island. Interestingly, two of them (*Codium pocockiae* and *Dasya villosa*) are absent from the Juan Fernández Archipelago, illustrating the very limited exchange between Easter Island and this archipelago.

Species with Wide Distribution

In both insular floras discussed here the numerically most important group of species are taxa with wide geographic distribution (Figure 5A). About 17 of these species are subcosmopolitan, including Juan Fernández and Easter Island, and their geographic distributions do not provide additional clues on their geographic origins and dispersal. Another 33 species are found on Easter Island but not in Juan Fernández (Figure 5B). They exhibit wide distribution, in tropical and

FIGURE 5. Regional affinities of insular species of benthic algae widely distributed in warm and temperate waters in the Pacific basin and elsewhere. Number in circles represents the mean number of species present.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subtropical waters, including localities in the western Pacific, the Caribbean, and Pacific Central America. The Juan Fernández Archipelago also contains widely distributed species (Figure 5C), but they occur in rather temperate waters. None has yet been found on Easter Island. As was the case with the group of species with a circumpolar-subantarctic pattern of distribution, only a quarter of these last species are present in central Chile and that representation decreases northward along the continent. The geographic affinities of this group of species are much higher with southern South America, New Zealand, and southern Australia.

Endemic Species

The number of endemic species per algal division found in each island locality is shown in Table 2. In both localities the number of endemic Rhodophyta is higher than the number of endemic Chlorophyta and Phaeophyta. However, in comparison with the total number of species of each group found in each locality, the proportion of endemic taxa is similar among the three different algal divisions. A chi-square test failed to find significant differences ($\chi^2 = 3.8; 0.25 \leq P \leq 0.10$) in abundance of endemic species among the three algal divisions in the two localities. Results, however, were significantly different ($\chi^2 = 48; 0.05 \leq P \leq 0.025$) when comparing abundance of endemic species among islands.

In both sites the genera/species ratio is close to 1, meaning that most endemic species belong to different genera. Four of the five genera exhibiting more than one endemic species are epiphytic or endophytic taxa (Table 2).

Species Restricted to the Islands and Temperate Pacific South America

A small group of species exhibits a peculiar geographic distribution pattern. They occur only in the two island localities and in temperate Pacific South America (Figure 6). The occurrence of this small group of species, whose relative importance on the continent and in the islands is only minor, is the only evidence of species transfer in this part of the Pacific, across the northward flow of the Chile-Perú Current system. The number of these species is higher in the Juan Fernández Archipelago than in either Easter Island or continental South America. The pattern of distribution of these species on the continent is conspicuously different from the patterns exhibited there by species with a circumpolar-subantarctic distribution and species with wide distribution. In this small group of species, all occur only in central and northern Chile. None has been reported north of Chile or south of Chiloé.

TABLE 2

SOME CHARACTERISTICS OF ENDEMISM IN THE JUAN FERNÁNDEZ ARCHIPELAGO AND EASTER ISLAND

	JUAN FERNÁNDEZ ARCHIPELAGO			EASTER ISLAND		
	ENDEMIC SPECIES	TOTAL NUMBER OF SPECIES	%	ENDEMIC SPECIES	TOTAL NUMBER OF SPECIES	%
Chlorophyta	5	21	24	0	25	0
Phaeophyta	5	25	20	3	23	13
Rhodophyta	16	43	37	11	57	19
Total number of species	26	89	29	14	105	13
Genera/species ratio		0.85			0.86	
Genera with more than one endemic species		*Phaeophila* *Codium* *Pterosiphonia*			*Erythrocladia* *Acrochaetium*	

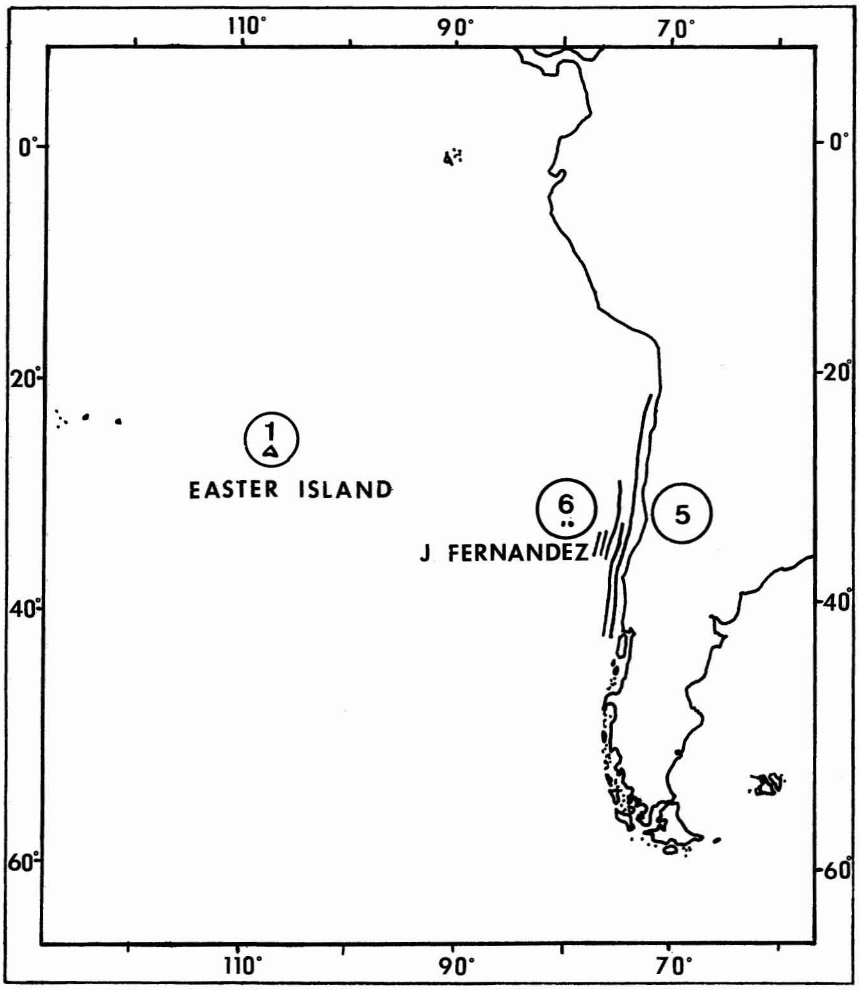

FIGURE 6. Benthic algal species restricted to the Juan Fernández Archipelago, Easter Island, and continental South America. Number in circles represents the mean number of species present.

DISCUSSION

The phytogeography of the marine benthic flora of the Juan Fernández Archipelago is best characterized as one of a very high degree of isolation. This marine flora appears to be more isolated than the flora of Easter Island, since the potential sources of algal species for the archipelago seem to be distant localities in the southern Pacific, including southern South America, southern Australia, New Zealand, and several subantarctic islands. It is difficult to estimate the length of the dispersal routes, as many species can be found in more than one of these southern localities. However, the total distance between the southern tip of South America and the archipelago is about 6000 km. The estimated distance from New Zealand to Juan Fernández is 9000 to 12,000 km (Hawkes and Johnson 1981). As anticipated by Skottsberg (1943*a*), the West Wind Drift and the Chile-Perú Current (Humboldt Current) appears as the route most probably followed by a large number of species, such as those with circumpolar-subantarctic distribution and those widely distributed in temperate waters. Together these two groups compose close to 40% of this marine flora.

The present analysis failed to find the abundance of subtropical elements in the archipelago that so much impressed Levring (1941) and Skottsberg (1943*a*,*b*), and that convinced Skottsberg of the general similarity of this flora with that of Perú and northern Chile and supported his views of a former Juan Fernández land connection with South America. It is true that the flora of these islands contains about 20% of species widely distributed in tropical latitudes, but they also occur in temperate waters and could have reached Juan Fernández from either New Zealand, Australia, or southern Chile. This seems to be the case for species such as *Colpomenia sinuosa*, *Gelidium pusillum*, *Centroceras clavulatum*, *Chaetomorpha anteninna*, *Hincksia mitchelliae*, *Ralfsia expansa*, *Hydroclathrus clathratus*, and *Laurencia obtusa*. The advance in knowledge of the taxonomy and distribution of benthic marine algae gained since Skottsberg's time undoubtedly has contributed to the change in our notions of the temperature tolerances of many of these species, regarded by Skottsberg as strictly subtropical.

The set of endemic species in both the Juan Fernández Archipelago and Easter Island suggests some interesting conclusions. It appears that 3 to 4 My of island age is enough time for benthic algae to have speciated in isolated places such as these islands. However, although speciation has occurred, radiation seems to have been minimal. There is only one species in each of the two endemic genera reported for the islands. Most endemic species belong to different genera and those genera with more than one endemic species correspond to endophyts and epiphyts. This contrasts with the land flora of these islands in which some genera (both endemic and nonendemic) contain up to six endemic species (Hoffmann and Marticorena 1987) and the genus to species ratio therefore is about 0.60. These differences are perhaps related to more heterogeneity of habitats in land as compared to the shallow marine environment in these islands or to the different reproductive modes of land and marine plants.

The small group of species restricted to the islands and to continental South America did not appear in Skottsberg's (1943*a*) analysis. However, this is a group whose geographic distribution would require a transport system across the eastern Pacific. Migration across the Chile-Perú Current appears to offer enormous difficulties. Nevertheless, there are at least two types of transport mechanisms that could enhance such a dispersal. Rock lobster fishing boats have been commercially active over the last 200 yr, frequently crossing between central Chile (Valparaíso) and the Juan Fernández Archipelago. On the other hand, strong ENSO should be able to reach the archipelago (Silva and Sievers 1973). Given its antiquity (ca. 5000 yr, Rollins et al. 1986) and frequency (range = 2–10 yr; $\bar{x} = 4$ yr; Cane 1983), ENSO could play important roles in the dispersal and gene flow of some of these species. Because most of these species occur in Juan Fernández and only a few in continental Chile, and considering the established pattern of distribution in central Chile, I suggest that these species might have originated in the archipelago and migrated to Easter Island on one side and to the continent on the other side. If this is the case, the degree of endemism of the marine flora of the archipelago is still higher than generally accepted, and, more important, Juan Fernández could be considered a source of algal species for continental South America.

The possibility that ENSO reaches the Juan Fernández Archipelago is important because it could have additional effects on the flora. The numerous changes in oceanographic conditions associated with ENSO may reduce the survival potential of populations originating in the cold waters of the circumpolar-subantarctic circulation, contributing to the low species richness of the archipelago. Alternatively it may accelerate the differentiation of the population stocks in the islands, speeding the speciation process.

A general problem emerging from this study is our poor understanding of long-range dispersal in the seaweeds. The geographic affinities of the flora of Easter Island and of the Juan Fernández Archipelago require dispersal distances of several thousand kilometers. They suggest dispersal times of hundreds of days under free-floating conditions. However, as discussed elsewhere (Santelices 1990), such problems have been rarely studied and are poorly understood in marine algae.

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