

Floristic and Biogeographical Trends in Seaweed Assemblages from a Subtropical Insular Island Complex in the Gulf of California¹

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ABSTRACT: Floristic and biogeographical trends of the seaweed assemblages in subtidal rocky areas were evaluated at 10 sites around Espíritu Santo Island in the Gulf of California. Seasonal sampling in two consecutive years with intensive surveys in a 500-m² area at each site was done. An intensive search was made of previous records from the literature. We found 85 species in the field with an additional 69 species from the literature, for a total 116 species. Species composition was significantly different between sides of the island in the first year, but very similar in the second. Species composition was not influenced by the presence of epiphytes. Phenologically, most species were ephemeral or annual with a low reproductive effort. Biogeographically, tropical elements dominated, but there was an important contribution from temperate species. Our results indicate that Espíritu Santo Island is a dynamic system that is strongly influenced by local oceanographic conditions.

INSULAR SYSTEMS in the eastern Pacific area are poorly known (Stoddart 1992); only a few systems have been studied intensively (e.g., the Channel Islands in California [Murray et al. 1980] in the Northern Hemisphere, Easter Island [Rapa Nui], and the Juan Fernández Archipelago [Santelices and Abbott 1987, Santelices 1992] in the Southern Hemisphere). Those studies were devoted to understanding the organization of the assemblages in a biogeographical context. However, other features may influence the organization and dynamics of the flora, including temporal or spatial patterns in distribution (Neto and Farham 1995), the influence of the epiphytes on the overall biodiversity (Smith 1992), and phenology/reproduction (Mathieson 1989). These features have not been documented for the eastern Pacific.

Studies of insular systems in the Mexican Pacific have been restricted to Guadalupe Island (Stewart and Stewart 1984), the Todos Santos complex (Aguilar-Rosas et al. 1990), Rocas Alijos (Silva et al. 1996), and the Revillagigedo complex (Leon-Tejera et al. 1996). Some of these studies describe the species composition and others the affinities of the flora. None examined the dynamics of seaweed assemblages.

The Gulf of California has a relatively high number of insular areas (Villa 1988) that are increasingly affected by tourism. As a result, the Mexican government is developing strategies for the protection and management of these areas as a priority region (SEDESOL 1994). Prior knowledge of the species distributed in insular systems in the gulf comes primarily from observations made during cruises sponsored by the California Academy of Sciences (Setchell and Gardner 1924) and a few additional contributions by Dawson (1959), Norris (1972), Norris and Bucher (1976), and Riosmena-Rodriguez et al. (1998). More recently, Foster et al. (1997), Reyes-Bonilla et al. (1997), and Riosmena-Rodriguez et al. (1998) have shown that rhodolith beds are widely distributed around the islands in the area. Furthermore, the insular complex Espíritu Santo–La Partida is lo-

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cated in a transitional zone where oceanographic conditions may determine the biogeographical affinities of the marine flora (Dawson 1960). Thus, the goals of this study were to determine the temporal and spatial dynamics of seaweed assemblages of the Espíritu Santo–La Partida complex and to determine their biogeographic affinities.

MATERIALS AND METHODS

Study Area

Espíritu Santo–La Partida is located in the southernmost part of the Gulf of California (24° 30' N, 110° 21' W), northwestern México (Figure 1). The subtropical nature of the region is defined by transitional oceanographic conditions influenced by the cold California Current, the warm eastern tropical Pacific water, and the warm Gulf of California water (Alvarez-Borrego 1983). Overall productivity measurements are representative of an oligotrophic zone (Round 1964). Upwelling events occur along the littoral of the bay during spring (most intensely) and in summer (Marignone 1988). Those events are associated with northwestern winds in spring and with southeastern winds in the summer (Alvarez-Borrego 1983). The western shore of Espíritu Santo Island is protected from gulf waves and has gentle slopes, but the eastern shore has steep slopes exposed to wave action. Ten sampling sites were located along the margins of the insular complex in rocky areas (Figure 1).

Field Work

Seasonal sampling was conducted from April 1990 to October 1991. Winter sampling in 1991 was not carried out because of climatic and logistic problems. Intensive qualitative surveys were made in the intertidal and subtidal zones (to 5 m depth) within an approximately 300-m² area by skin diving during high tide. Special precautions were taken to collect and properly preserve the fragile, filamentous specimens and those epiphytic on other seaweeds. All material was transported to the laboratory, processed, and deposited in

the Phycological Herbarium of the Autonomous University of Baja California Sur (FBCS) according to procedures in Riosmena-Rodriguez and Siqueiros-Beltrones (1994). Historic reports from the area were compiled from the literature (references are cited in Riosmena-Rodriguez and Paul-Chávez 1997). These, and the species collected in this study, are included in a taxonomic list (Appendix) following the systematic arrangement in Riosmena-Rodriguez and Paul-Chávez (1997).

Data Analysis

A presence/absence matrix by locality was constructed based on the collected species. The species distribution among localities and times was determined by season and year for each of the 10 localities. This was based on overall number of species, and by taxonomic division, arranged by green, brown, and red algae. An independent goodness of fit test (chi square) was used to compare species richness by division between the protected and unprotected sites ($n = 10$) by year. Jaccard's index of similarity was used to compare localities by year. The resulting matrix was used in a cluster analysis, to represent the similarity between sites in a dendrogram. Also, the percentage of species in each division per season was plotted from each locality. Because of the clear differences among exposed and protected areas, representative sites for each are presented.

Based on the presence/absence matrix, a longevity category was assigned to each species as defined by Mathieson (1989), and the percentage of each group was plotted for each locality. The reproductive state of each species was also determined by locality/season by a careful external examination of the specimens and with cross sections where necessary. After determining the reproductive state of each specimen, a calculation of the percentage of each state (vegetative or reproductive) was also plotted. Information about habit (epilithic or epiphytic) was recorded and analyzed graphically. Biogeographical affinities of the species were assigned to four categories (tropical [Tr], temperate [T], cos-

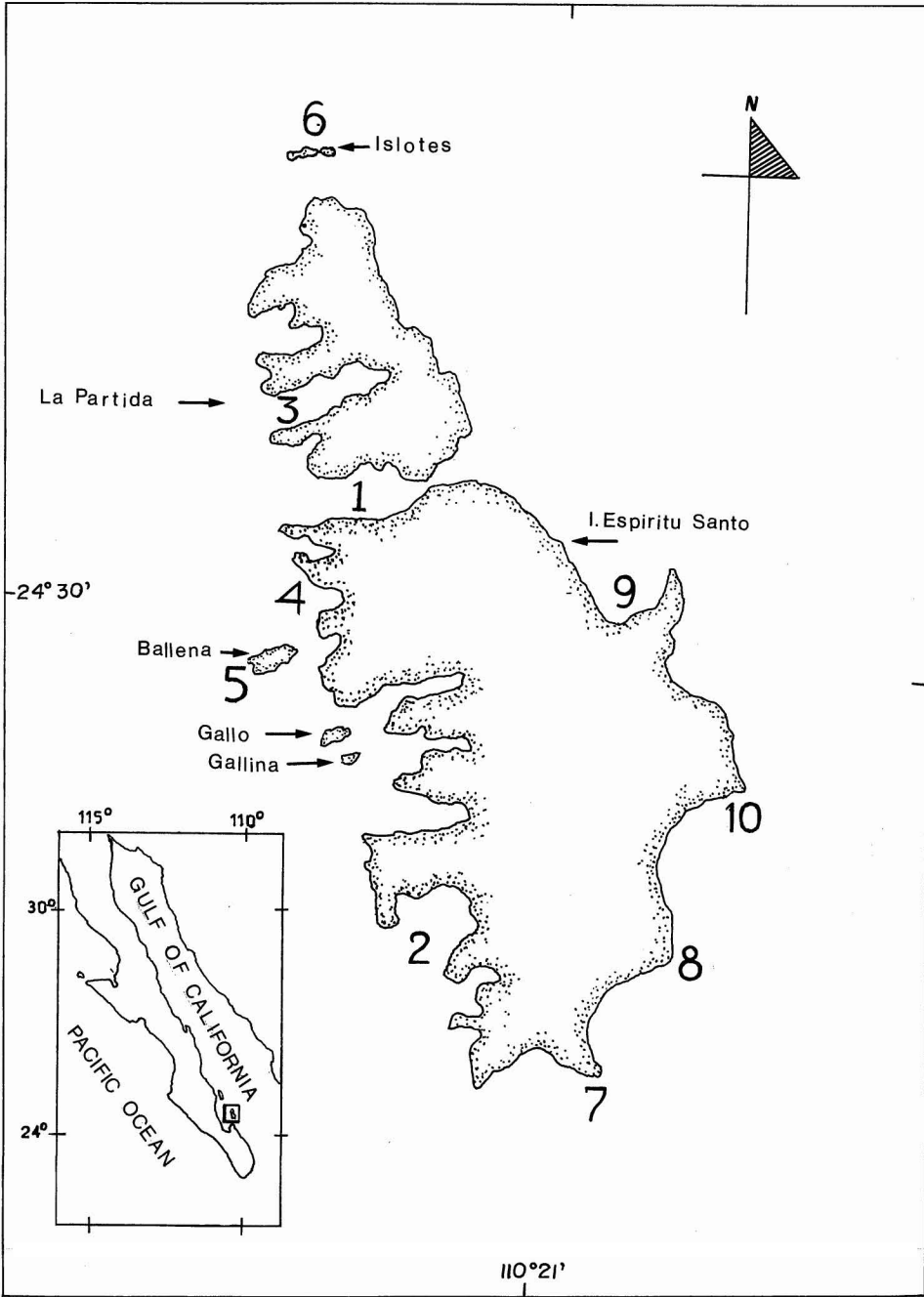


FIGURE 1. Study area and sampling sites (1, La Partida; 2, San Gabriel; 3, El Cardonal; 4, Candelero; 5, La Ballena; 6, La Lobera; 7, Punta Sur; 8, Morrito; 9, El Faro; 10, El Pailebote).

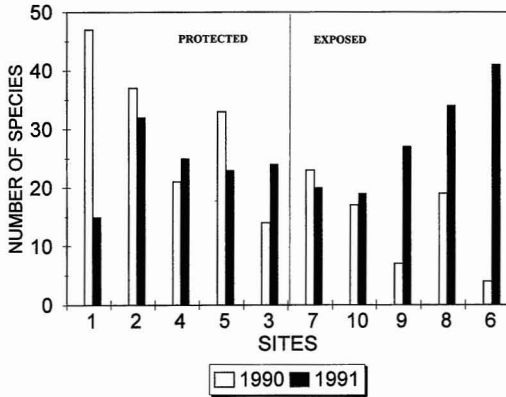


FIGURE 2. Number of species by site (numbers as in Figure 1) and year.

mopolitan [C], and endemic [E]) based on their distribution; then the number of species in each category per year from each division were plotted. The classification of the species list follows the disposition and literature presented by Riosmena-Rodriguez and Paul-Chávez (1997).

RESULTS

A total of 116 species of macroalgae has been collected on the rocky shores of Espíritu Santo-La Partida (Appendix). Comparison of species found in the bibliographic review and our collections yielded 25 species collected previously but not by us, 16 previously and by us. Sixty-nine taxa were identified in our collections and they represent new reports for the area. During 1990–1991, we found 85 species, 11% of which were chlorophytes, 28% phaeophytes, and 61% rhodophytes. The average number of species found per year was lower, with 70 species found in 1990, of which rhodophytes composed 57% of the total. Sixty-eight species were collected in 1991 even though there was no winter survey. Rhodophytes also dominated in 1991, composing 66% of the total.

The observed species richness differed depending on the side of the island and the year. In 1990, more species were found along the protected side (47) versus the exposed side (25) (Figure 2). The inverse was found in

the second year, with 42 species on the exposed side versus 32 for the protected side (Figure 2). This pattern also is clear in the cluster analysis (based on the values of Jaccard's index), with a significant separation (0.8) in the taxonomic composition between the protected and exposed zones in 1990 (Figure 3). The chi square test of independence using species richness by division also indicated significant differences in number of species by division between sides in 1990 ($\alpha = 0.05$, $df = 2$). The distribution was more equitable between exposures in 1991, with no distinct floristic separation (Figure 3).

During analysis of the temporal variation within the localities, we found that, as in the spatial scale, seasonal patterns in the assemblages could be grouped as protected versus exposed side; differences were also found related to taxonomic category (division Chlorophyta, Phaeophyta, and Rhodophyta). On the protected side, green algae showed a seasonal change, with highest species number during winter of the first year and in summer of the second (Figure 4). Brown algal species maxima occurred in spring in both years, with minima in summer (Figure 4). For red algae, maximal numbers were in autumn in both years, with a marked increase in the first year and less in the second (Figure 4).

The richness of species was very different on the exposed side of the island between years. In the first year, green and brown algae were only present in spring and winter; red algae appeared in summer and the flora decreased in number in the autumn. In the second year, the maximal numbers of each division occurred in different seasons: summer for green algae, spring for browns, and autumn for reds (Figure 5). The seasonal trends in the second year had a pattern similar to that of the protected side in both years. The observed seasonality could be explained by the phenological patterns observed for most of the localities in both years (Figure 6). Green and brown algae were only represented by sporadic and pseudoperennial (= annual thalli) species, and red algae by both groups and a few perennial. Green algae are the major component in the pseudoper-

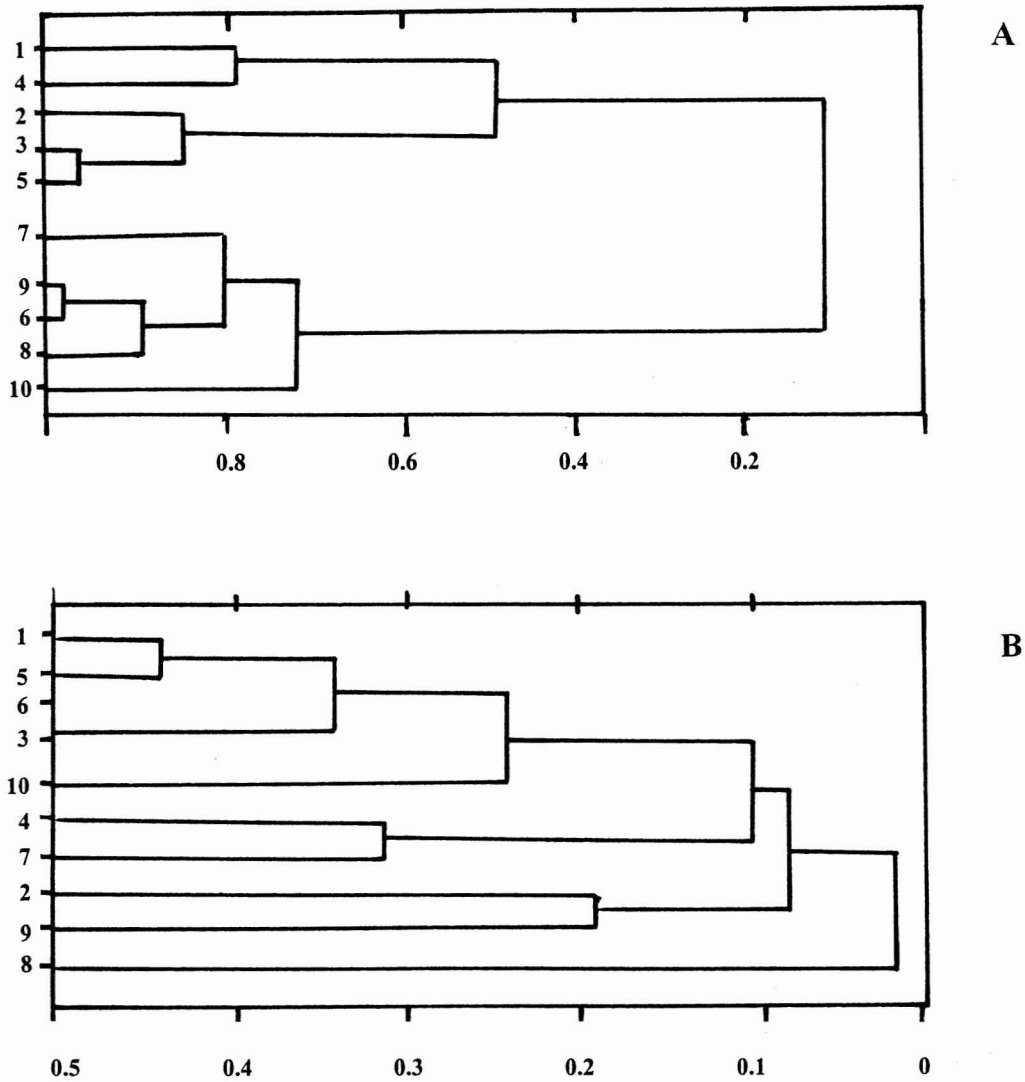


FIGURE 3. Similarity among sites and years for all algae (numbers as in Figure 1). *A*, 1990; *B*, 1991.

ennial group and the reds in the sporadics (Figure 6). Reproductive structures (sporophytic and gametophytic) on all the species during the study period were rare (<10%) in 1990, and even rarer in the second year (~2%). The species found to be reproductive were brown and red algae; no reproductive structures were observed in green algae with our sampling regime. The percentage of species reproducing decreased during the first

year. By the summer of 1991 there was no reproduction, and then a small increase occurred in fall, but not more than 2%.

The proportion of species found as epiphytes was only around 15%. Few species were observed growing both epilithically and epiphytically. No epiphytes were observed in the autumn of either year. In 1990, most epiphytic species occurred in winter (Figure 7). In both years spring and summer had low

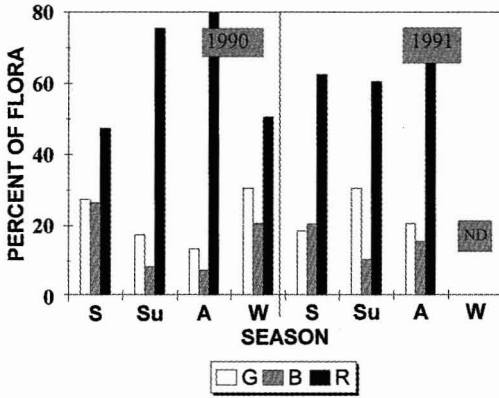


FIGURE 4. Seasonal change of species (S, spring; Su, summer; A, autumn; W, winter) between years of the major algal divisions on the exposed side (G, green algae; B, brown algae; R, red algae).

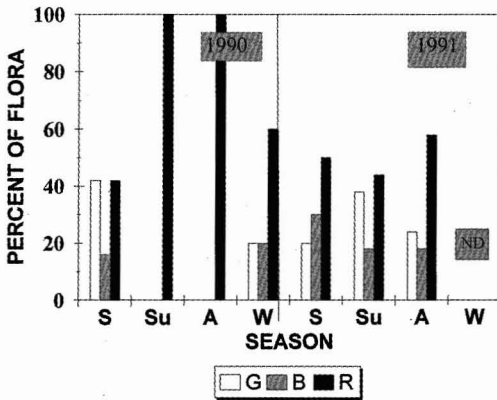


FIGURE 5. Seasonal change of species on the protected side (keys as in Figure 4).

proportions of epiphytes (10% or less of the species).

Biogeographical affinities of the flora in the insular complex were similar spatially and between years, but not between the major taxa considered; most of the groups have a major proportion of tropical elements with similar values (Figure 8). The proportion of cosmopolitan species was larger in greens and reds. The difference between these groups is that in the greens the percentage of temperate elements is similar to that of cos-

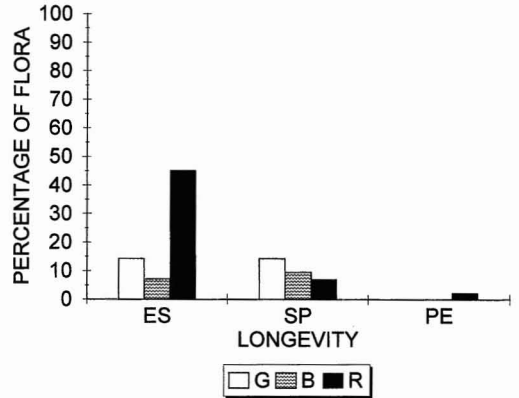


FIGURE 6. Major phenological groups (ES, sporadic; SP, pseudoperennial or annual; PE, perennial) among algal divisions (keys as in Figure 4).

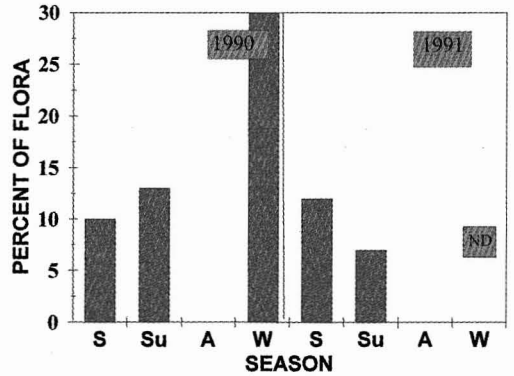


FIGURE 7. Seasonal variation in proportion of epiphytic species (keys as in Figure 4).

mopolitan ones, but in reds there is a proportion of temperate and endemic elements present. In the case of brown algae, temperate elements represent the second major group followed by the endemics and with the lower proportion present in the cosmopolitan species (Figure 8).

DISCUSSION

The rocky areas of the Espiritu Santo-La Partida complex have about 45% of the total species reported for La Paz Bay (Riosmena-

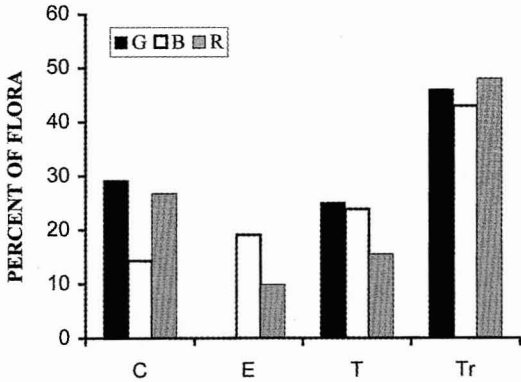


FIGURE 8. Proportion of the major biogeographic components (C, cosmopolitan; E, endemic; T, temperate; Tr, tropical).

Rodriguez and Paul-Chávez 1997). The overall number of species (116) in this complex is similar to that in the Todos Santos complex (Aguilar-Rosas et al. 1990), but much lower than that in Guadalupe Island (180 in Stewart and Stewart 1984) or the Revillagigedo complex (232 in Leon-Tejera et al. 1996).

Santelices and Abbott (1987) have shown that other insular systems in the eastern Pacific with a similar geological age have similar numbers of species. The major differences between the number of species registered in our study and that of most of the islands previously studied are related to the number of sites and habitats sampled, the search effort, and the size of the island. At Espíritu Santo Island, we only sampled rocky areas. But recent surveys in mangrove areas (R.R.R. and L.P.C., unpubl. data) and rhodolith beds (Riosmena-Rodriguez 1996) indicated that these habitats may contribute at least 72 more species.

The assemblages were clearly different in protected and exposed areas the first year, but not in the second (Figures 2 and 3). Seasonal trends were similar in both years on the protected side, with a clear maxima in one season (Figure 4). Seasonal trends were dissimilar on the exposed side in both years (Figure 5), but the sides were more similar spatially in the second year. Seaweed assemblages in the Espíritu Santo-La Partida

complex show strong changes in space and time. This has been suggested in the literature (Pielou 1981), but only a few pieces of evidence are related to seaweed assemblages (Neto and Farham 1995).

The above pattern may be explained based on the high proportion of sporadic or pseudoperennial (= annual sensu Mathieson 1989) species observed (Figure 6). This is in contrast to other seaweed assemblages in the northwestern areas of La Paz Bay, where most of the sporadic and pseudoperennial species are epiphytes and play a major role in the seasonal fluctuations of the flora (Riosmena-Rodriguez et al. 1995). Furthermore, this pattern is also clearly different from that of other insular systems where the relationship of epiphyte:epilithic taxa is about 50% (Smith 1992). In our case the influence of epiphytes on the overall biodiversity and its spatial and temporal variation was lower than 20% during most of the study period (Figure 7). The heterogeneity observed in the floristic composition in the first year and the homogeneity in the second year may result from emigration of some species from the protected to the exposed side and from recruitment. However, this is only a partial explanation because of a low proportion of fertile taxa in both years, suggesting patterns resulting from the regeneration of holdfasts or by immigration from other areas (Santelices 1990).

Smith (1992) suggested that oceanographic variation influences the arrival of new elements to insular systems and changes in water masses influence the survival of individuals in the assemblages (Mathieson 1989). The influence of the major water masses in the Gulf of California varies among years (Bray 1988), producing changes in the intervals in which particular temperatures can be present in the area. In "cold" years the difference in temperature between summer and winter is 16°C and in "warm" years the difference may be only 5°C (Jimenez-Illescas 1996). Furthermore, the changes in water masses also produce episodic nutrient availability depletion (Alvarez-Borrego 1983). The heterogeneous nature of the seaweed assemblages in the insular com-

plex no doubt reflects the prevailing oceanographic conditions, including upwelling related to wind patterns (Marignone 1988, Fernández et al. 1994).

Oceanographic conditions may have had a major effect on the biogeographical affinities of the island, with the predominance of elements from tropical areas within the major groups present (Figure 8). The proportion of endemics was low (~14%) in both years, similar to other coastal (Murray et al. 1980, Littler et al. 1991) and some oceanic islands (Santelices and Abbott 1987, Leon-Tejera et al. 1996). This is in contrast to the Juan Fernández complex, where the proportion of endemic species is high (~30%), although species richness is low (116 species) and thus similar to the Espíritu Santo-La Partida complex, suggesting that dispersion distance for species to colonize islands is also combined with the degree of oceanographic isolation, and not only with their age and geographical position (Santelices 1992).

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- APPENDIX
SYSTEMATIC LIST OF SEAWEEDS OF THE ESPÍRITU
SANTO-LA PARTIDA COMPLEX
- Division Chlorophyta
Class Ulvophyceae
Order Bryopsidales
Family Bryopsidaceae
Bryopsis pennatula J. Agardh.
Family Caulerpaceae
Caulerpa racemosa (Forskål) J. Agardh.
C. sertularioides (Gmelin) Howe
C. vanbosseae Setchell & Gardner
Family Codiaceae
Codium cuneatum Setchell & Gardner
C. setchellii Gardner
C. simulans Setchell & Gardner
Family Udoteaceae
Halimeda discoidea Decaisne
Order Cladophorales
Family Cladophoraceae
Cladophora colombiana Collins
C. hesperia Setchell & Gardner
C. microcladioides Collins
Lola lubrica (Setchell & Gardner) Hamel & Hamel
Rhizoclonium riparium (Roth) Harvey
Family Siphonocladaceae
Dictyosphaeria versluysii Weber-vanBosse
Ernodesmis verticillata (Kützling) Boergensen
Family Valoniaceae
Valoniopsis cladophoracea Martens
V. pachynema (Martens) Boergensen
Order Dasycladales
Family Dasycladaceae
Acetabularia calyculus Quoy & Gaimard
Order Ulvales
Family Ulvaceae
Enteromorpha clathrata (Roth) Greville
E. compressa (Roth) Greville
E. intestinalis (Roth) Greville
E. ramulosa var. *acanthophora* (Kützling) Chapman
Ulva dactylifera Setchell & Gardner
U. lactuca Linnaeus
U. lobata (Kützling) Setchell & Gardner
Division Phaeophyta
Class Phaeophyceae
Order Dictyotales
Family Dictyotaceae
Dictyota crenulata J. Agardh
D. dichotoma (Hudson) Lamouroux
D. flabellata (Collins) Setchell & Gardner
D. johnstonii Setchell & Gardner
D. volubilis Kützling sensu Vikers
Padina conrescens Thivy
Padina mexicana Dawson
Order Ectocarpales
Family Ectocarpaceae
Ectocarpus acutus Setchell & Gardner
E. bryantii Setchell & Gardner
E. gonodioides Setchell & Gardner
Family Ralfsiaceae
Ralfsia californica Setchell & Gardner
R. confusa Hollenberg
Order Fucales
Family Sargassaceae
Sargassum horridum Setchell & Gardner
S. lapazeanum Setchell & Gardner
Order Scytosiphonales
Family Chnoosporaceae
Chnoospora minima (Hering) Papenfuss
Family Scytosiphonaceae
Hydroclathrus clathratus (Bory) Howe
Colpomenia sinuosa (Martens ex Roth) Derbes & Solie
C. tuberculata Saunders
Roseningea cf. *intricata* (J. Agardh) Boergensen
Order Sphacelariales
Family Sphacelariaceae
Sphacelaria brevicorne Setchell & Gardner
S. rigidula Kützling
Division Rhodophyta
Class Rhodophyceae
Order Ahnfeltiales
Family Ahnfeltiaceae
Ahnfelfthia plicata (Hudson) Fries
Order Bangiales
Family Bangiaceae
Bangia atropurpurea (Roth) C. Agardh
Porphyra pendula Dawson
P. thuretii Dawson
Order Bonnemaisoniales
Family Bonnemaisoniaceae
Asparagopsis taxiformis (Delile) Trevisan
Order Ceramiales
Family Ceramiaceae
Antithamnion sublittorale Setchell & Gardner
Antithamnionella breviramosa (Dawson) Womersley & Bailey
Centroceras clavulatum (C. Agardh) Montagne
Ceramium caudatum Setchell & Gardner
C. clarionense Setchell & Gardner
C. equisetoides Dawson
C. fimbriatum Setchell & Gardner
C. flaccidum Ardissonne
C. horridum Setchell & Gardner
C. paniculatum Okamura
C. procumbens Setchell & Gardner
Digenia simplex (Wulfen) C. Agardh
Griffithsia pacifica Kylin
Spyridia filamentosa (Wulfen) Harvey
Family Dasyaceae
Dasya baillouiana (Gmelin) Montagne
D. sinicola (Setchell & Gardner) Dawson
Heterosiphonia crispella (C. Agardh) Wynne
Taenioma perpusillum J. Agardh
Family Delesseriaceae
Myriogramme caespitosa Dawson
Family Rhodomelaceae
Chondria californica (Collins) Kylin
Herposiphonia spinosa Dawson
H. secunda f. *tenella* (C. Agardh) Wynne

- Laurencia glandulifera* (Kützing) Kützing
L. johnstonii Setchell & Gardner
L. pacifica Kylin
L. papillosa var. *pacifica* (C. Agardh) Greville
Polysiphonia decussata Hollenberg
P. simplex Hollenberg
Veleroa subulata Dawson
- Order Corallinales
- Family Corallinaceae
- Amphiroa beauvoisii* Lamouroux
A. misakiensis Yendo
A. rigida Lamouroux
A. vanbosseae Lemoine
Corallina vancouverensis Yendo
Heteroderma gibbsii Dawson
Jania adhaerens Lamouroux
J. longiartha Dawson
Lithophyllum decipiens Foslie
L. hancockii Dawson
L. imitans Foslie
L. margaritae (Hariot) Heydrich
L. sonorensis Dawson
Neogoniolithon trichotomun Setchell & Mason
- Order Erythropeltidales
- Family Erythropeltidaceae
- Erythrotrichia carnea* (Dillwyn) J. Agardh
- Order Gelidiales
- Family Gelidiaceae
- Gelidium johnstonii* Setchell & Gardner
Pterocladia capillacea (Bornet & Thuret)
 Santelices & Hommersan
- Family Gelidiellaceae
- Gelidiella acerosa* (Forskål) J. Feldmann & Hamel
- Order Gigartinales
- Family Halymeniaceae
- Cryptonemia guaymanensis* Dawson
Grauteloupia dactylifera Dawson
Halymenia abyssicola Dawson
H. templetonii (Setchell & Gardner) Abbott
Prionitis abbreviata Dawson
- Family Hypneaceae
- Hypnea cervicornis* J. Agardh
H. valentiae (Turner) Montagne
- Family Nemastomataceae
- Predaea masonii* (Setchell & Gardner) J. De Toni
- Family Peyssonneliaceae
- Peyssonnelia rubra* (Greville) J. Agardh
- Family Phylloporaceae
- Ahnfeltiopsis gigartinoides* (J. Agardh) Silva & DeCew
- Family Wurdemanniaceae
- Wurdemannia miniata* (Draparnaud) Feldmann & Hamel
- Order Gracilariales
- Family Gracilariaceae
- Gracilaria crispata* Setchell & Gardner
G. pachydermatica Setchell & Gardner
G. spinigera Dawson
G. textorii (Suringar) J. Agardh
- Order Nemaliales
- Family Galaxauraceae
- Galaxaura arborea* Kjellman
Liagora californica Zeh
Tricheogleocarpa oblongata (Ellis & Solander)
 Lamouroux
- Order Rhodymeniales
- Family Champiaceae
- Champia parvula* (C. Agardh) Harvey