

Biodiversity and Biogeography of Benthic Marine Algae in the Southwest Pacific, with Specific Reference to Rotuma and Fiji¹

A. D. R. N'YEURT AND G. R. SOUTH²

ABSTRACT: Occurrence and distribution of various species of benthic marine algae in Fiji and Rotuma were investigated, with the resulting floras being subjected to comparison indices (Jaccard) both between themselves and with respect to other neighboring floras in the Southwest Pacific. The Rotuman flora was found to be rather impoverished (106 species) with respect to the Fijian flora (314 species), and the Nauruan and Rotuman flora were most similar, as were the Fijian and Micronesian floras. Dispersal mechanisms for algae in the region were considered, with special attention to the major ocean currents. These currents tend to favor movements of algal species from more northerly locations toward Fiji, and dispersal in the opposite direction seems unlikely. This is assumed to explain the similarities of the Rotuman flora with the Nauruan and Micronesian floras. Peculiar distribution patterns of algae were examined, with one species (*Meristotheca procumbens* P. Gabrielson & Kraft) being found in Rotuma, Lord Howe Island, and New South Wales (Australia), but not in intervening localities. Ecological and geographical factors are invoked to explain this, although unavailability of detailed checklists from many sites in the region impedes an accurate biogeographical analysis.

THE BIOGEOGRAPHY AND biodiversity of the tropical Pacific has been studied by several authors in the past, including Kay (1980), Lüning (1990), and Stoddart (1992). Stoddart (1992) favored a typological approach for the basis of biogeographic regionalization, but Lüning (1990) and van den Hoek (1984) preferred a hierarchical distinction between biogeographic regions. According to van den Hoek (1984), the world can be divided into 22 phytogeographic regions as defined by their temperature regimes (Figure 1). For example, in the North Atlantic interregional latitudinal boundaries coincide with floristic discontinuities, and many "southern" species disappear poleward and are replaced by a few "northern" species. Along the western coast of South America, there is a tendency for flora impoverishment toward the equator (Santelices 1980). However, these latitudinal boundaries need not always coincide with floristic discontinuities. In general, though, the

differentiation of algal floras on a global scale primarily is related to the latitudinal climatic gradient and to historic changes in climate and the distribution of continents and oceans over geologic time (van den Hoek et al. 1990).

There is indirect evidence that long-distance dispersal mechanisms exist for seaweeds, as exemplified by the fact that midoceanic volcanic islands (e.g., Tristan da Cunha) are furnished with well-developed algal floras that could only have come from continental donor areas (van den Hoek 1987). However, long-distance dispersal is the exception rather than the rule, because the world's algal floras are by no means similar in species composition at similar latitudinal gradients (van den Hoek 1987). Usually, dispersal range for most algae is within a few meters only, depending on current. Episodic events such as El Niño currents, tropical cyclones, and tsunamis also play an infrequent, but important part in long-range dispersal of algae.

In islands such as Rotuma, which have had no previous connection with other land masses, all the algal flora must have been imported over long distances from surrounding islands and continents by a number of means. Natural dis-

¹ Paper presented at the Fifth International Phycological Congress, Qingdao, P.R. China, 26 June–7 July 1994. Manuscript accepted 21 March 1996.

² Marine Studies Programme, The University of the South Pacific, Box 1168, Suva, Fiji.

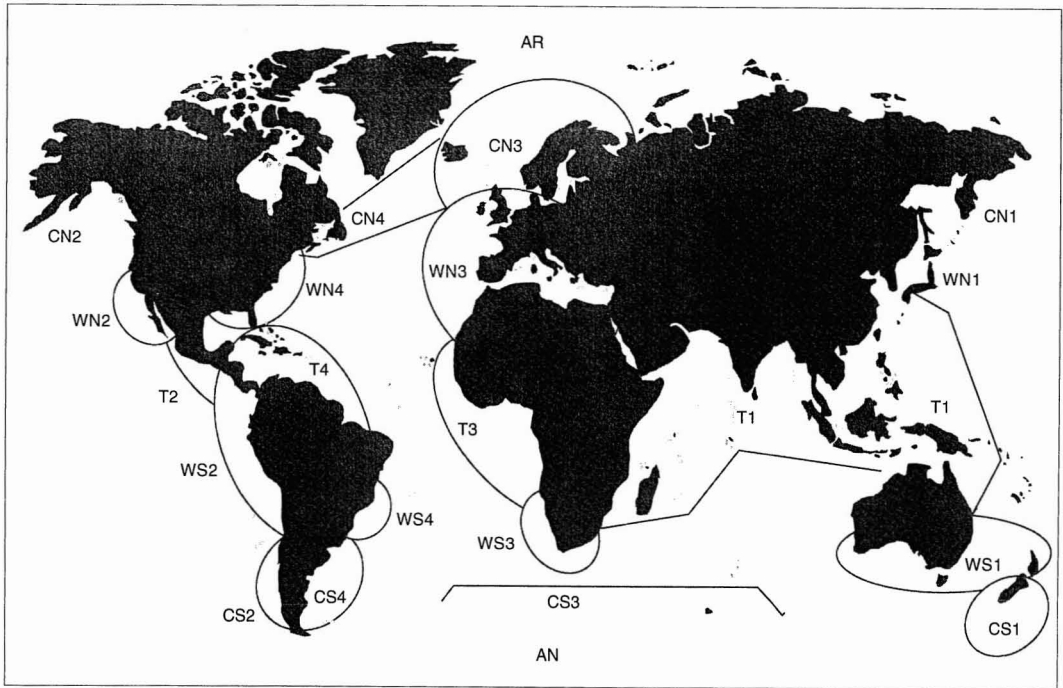


FIGURE 1. Map showing the world's 22 phytobiogeographic regions (adapted from van den Hoek [1984]). AR, Arctic; CN1, cold temperate NW Pacific; CN2, cold temperate NE Pacific; CN3, cold temperate NE Atlantic; CN4, cold temperate NW Atlantic; WN1, warm temperate NW Pacific; WN2, warm temperate NE Pacific; WN3, warm temperate NE Atlantic; WN4, warm temperate NW Atlantic; T1, tropical Indo-West Pacific; T2, tropical E Pacific; T3, tropical E Atlantic; T4, tropical W Atlantic; WS1, warm temperate SW Pacific; WS2, warm temperate SE Pacific; WS3, warm temperate SE Atlantic; WS4, warm temperate SW Atlantic; CS1, cold temperate SW Pacific; CS2, cold temperate SE Pacific; CS3, cold temperate SE Atlantic; CS4, cold temperate SW Atlantic; AN, Antarctic.

persal can occur via ocean currents (floating algae; algae borne on floating pumice, wood, etc.), by animal carriers (birds, fish, planktonic stages of benthic animals, humans), or by spores borne on the wind or on water (coralline algae [van den Hoek 1987]). The time taken for an island to gain a fairly "complete" flora (in terms of the number of species found in relation to its size) depends on the dispersal means available and the presence or absence of such obstacles as countercurrents, unfavorable temperature gradients, etc. Small islands harbor fewer species than larger ones, because the former possess inherently fewer habitats for algal colonization. Also, few species from large donor areas actually manage to "hit" small islands during long-range dispersal (van den Hoek 1987). These observations can be summarized in the four main principles of the Island Theory (MacArthur and

Wilson 1967), which state that: 1) the number of immigrating species increases with island size; 2) the number of immigrating species is reduced with increasing distance from the nearest donor continental area; 3) the amount of endemism on an island is a factor of the island's geological longevity, its size, and its distance from continental donor areas; and 4) high rates of endemism indicate regions of species formation.

The point concerning endemism relative to island size and isolation is debatable. One might expect an isolated island to have a high rate of endemism (for instance, Hawai'i), but there is also the factor of distribution of algae (i.e., the species present in isolated islands tend in actual fact to be those with a wide geographic distribution, owing to their higher dispersion and colonization abilities [which in turn make them common species]). This was demonstrated for

the Easter Island marine flora by Santelices and Abbott (1987), where only 14% endemism was reported. In reality the situation is more complex than the Island Theory might allude to, because other factors such as nutrient input and the height of islands come into play.

In addition, the fact that islands in the central Pacific are mostly chains of geologically short-lived atolls (arranged in a southeast-northwest direction) means that islands in the northwestern end of the atoll are older than islands in the southeastern end, because the island chain is assumed to move northwest with the Pacific Plate, submerging the oldest islands (Lüning 1990). This leads to the necessity for "island hopping" among the fauna and flora of these moving islands, with any endemic species having to readapt to a new set of environmental conditions at each migration. This also means that the geological age of endemic species may be greater than the island they inhabit (Pielou 1979). A similar migration of species from east to west (with bulk water flow) also occurs, except in El Niño years when the direction of bulk flow is reversed. Hence, on islands we have a combination of geographic isolation and dispersal methods via regular and episodic physical events that creates a complex situation.

Algal floras from different sites on an island or between different island groups can be compared using Jaccard's Similarity Index, P (Greig-Smith 1964:136):

$$P = \frac{c}{a + b - c} 100$$

where a is the number of genera or species of flora X , b is the number of genera or species of flora Y , and c is the number of genera or species shared by floras X and Y .

Hierarchical clustering on the indices can then be carried out using agglomerative centroid methods (Sokal and Sneath 1963, Goodhall 1973). Two matched floras are replaced by a centroid, and the similarity coefficients of the centroid with the other floras and groups of floras are derived by arithmetic means. The resulting data may be presented as a dendrogram. Depending on the quality and amount of data used in the analysis, the resulting dendrograms may or may not indicate similarity relationships between the sets of flora. Computer

programs that generate dendrograms from distributive data have been used successfully in the past to derive similarities between floras at different sites (Hooper et al. 1980, Whittick et al. 1989). In our study, however, similarity indices alone have been used to analyze the flora relationships.

One of us (N'Yeurt 1993*a*, 1996*b*) recently carried out a floristic survey of the small, isolated island of Rotuma (12° 30'S, 177° 05'E), which resulted in the first algal checklist for that locality (N'Yeurt 1993*b*). It was felt that this information, along with the data from the latest Fijian algal checklist (South and Kasahara 1992, South et al. 1993) could be used in a broader investigation of the phytobiogeographic relationships of Southwest Pacific algal floras, using available checklists and information for that region.

MATERIALS AND METHODS

Occurrence and distribution data of marine benthic algae for Rotuma (N'Yeurt 1993*a,b*) and Fiji (South and Kasahara 1992, South et al. 1993) were analyzed and entered into a database for the determination of coefficients of similarity (Jaccard indices) as outlined earlier in this paper. Owing to the disputed taxonomy of most Cyanophyceae, they were excluded from this analysis. Similarly, floristic data for the algae of other Southwest Pacific islands were entered into the database for eventual biogeographic comparisons. The floras involved are New Caledonia (Garrigue and Tsuda 1988), the Marshall Islands (Dawson 1956, 1957), Micronesia (Tsuda and Wray 1977, Tsuda 1981), Samoa (Setchell 1924), Tahiti (Payri and Meinesz 1985), Nauru (South and Yen 1992), northern Australia (Lewis 1984, 1985, 1987), the Solomon Islands (Womersley and Bailey 1970), and Lord Howe Island (Lucas 1935, Allender and Kraft 1983, Gabrielson and Kraft 1984, Jones and Kraft 1984, Wynne and Kraft 1985, Millar and Kraft 1993, 1994). It would have been desirable to include the Tuvaluan and Gilbertese floras, but the available checklists for these (Chapman [1955], and Moul [1957, 1959], respectively) are essentially sketchy in nature and were not deemed representative enough for this study. The resulting data

TABLE 1

FLORA COMPARISON DATA BETWEEN ROTUMA AND SEVERAL TROPICAL SITES (EXCLUDING CYANOPHYCEAE)

LOCALITY	FLORA			JACCARD INDICES ^a				
	SPECIES	GREEN	BROWN	RED	P _O	P _G	P _B	P _R
Fiji	302	94	38	170	18.3	27.5	4.4	13.5
Samoa	90	30	12	48	8.0	11.9	10.5	1.9
Nauru	40	16	9	15	24.4	13.9	14.3	40.5
New Caledonia	336	130	59	147	10.4	14.8	6.3	8.3
Tahiti	151	63	29	59	19.4	26.3	15.1	14.6
Micronesia	520	189	56	275	11.0	14.4	16.1	7.6
Solomon Islands	219	71	27	121	18.4	26.8	28.6	11.4
North Australia	1,185	305	252	628	5.0	8.3	2.8	4.2
Lord Howe Island	100	28	21	51	6.6	10.9	0.0	6.2
Marshall Islands	268	106	23	139	13.1	19.0	18.5	8.1

NOTE: Sources given in Materials and Methods.

^a P_O, overall Jaccard index (excluding Cyanophyceae); P_G, Jaccard index for Chlorophyta; P_B, Jaccard index for Phaeophyta; P_R, Jaccard index for Rhodophyta.

were presented in graphic form using computer software (Harvard Graphics; © 1991–1993 Software Publishing Corporation).

RESULTS

Tables 1 and 2 present the results of the biogeographical analysis between the various floras considered in this study.

From Table 1 it can be seen that if we consider the overall algal floras (excluding the Cyanophyceae), the Rotuman flora is most similar to the Nauruan ($P_O = 24.4$), whereas Table 2 shows that the Fijian algal flora is most similar to the Micronesian ($P_O = 26.9$). If we consider the Chlo-

rophyta, Phaeophyta, and Rhodophyta components of the floras separately, the Rotuman algal flora most closely resembles the Fijian, Solomon Islands, and Nauruan floras; and the Fijian algal flora is most similar to the New Caledonian and Micronesian floras.

DISCUSSION

Rotuman Flora

The results of the Rotuman biogeographic analysis show that the flora sampled is quite distinct from most of the other tropical floras used for comparison. Indeed, the highest coeffi-

TABLE 2

FLORA COMPARISON DATA BETWEEN ROTUMA AND SEVERAL TROPICAL SITES (EXCLUDING CYANOPHYCEAE)

LOCALITY	FLORA			JACCARD INDICES ^a				
	SPECIES	GREEN	BROWN	RED	P _O	P _G	P _B	P _R
Rotuma	85	36	9	40	18.3	27.5	4.4	13.5
Samoa	90	30	12	48	5.9	8.9	2.0	5.3
Nauru	40	16	9	15	7.9	13.4	9.3	4.5
New Caledonia	336	130	59	147	20.1	31	14.1	15.3
Tahiti	151	63	29	59	17.7	24.6	21.8	12.3
Micronesia	520	189	56	275	26.9	29	42	23
Solomon Islands	219	71	27	121	24.6	28	27.5	22.3
Lord Howe Island	100	28	21	51	5.0	6.1	18	1.4

NOTE: Sources given in Materials and Methods.

^a P_O, overall Jaccard index (excluding Cyanophyceae); P_G, Jaccard index for Chlorophyta; P_B, Jaccard index for Phaeophyta; P_R, Jaccard index for Rhodophyta.

cient of similarity (Jaccard index) for any aspect of the flora was below forty-one. Only one confirmed endemic species, *Avrainvillea rotumensis* N'Yeurt, Littler & Littler, is reported from Rotuma (N'Yeurt et al. 1996). However, one must view these results with caution because the Rotuman flora sampled was relatively restricted (to intertidal habitats) and consequently incomplete with regard to subtidal species, and many of the floras used in the comparison analysis were themselves far from comprehensive. The high degree of similarity of the Rotuman flora with the Nauruan flora, especially with regard to Rhodophyta ($P_R = 40.5$), probably reflects the close similarity in the collection methods used in these two studies (limited to intertidal benthic habitats) more than anything else. The number of habitats in both locations was also restricted and broadly similar. This resulted in a fairly monotonous composition of the flora from habitat to habitat (N'Yeurt 1993a).

Despite the above effects encountered in the biogeographic comparisons, there are some notable differences, especially comparing the Fijian algal flora with the Rotuman. The Fijian flora only falls in fourth place with regard to similarity with the Rotuman, after Nauru, Tahiti, and the Solomon Islands. In particular, species such as *Boodlea coacta* (Dickie) Murray & De Toni, *Chondria simpliciuscula* Weber-van Bosse, *Coelarthrum boergesenii* Weber-van Bosse, *Halimeda micronesica* Yamada, and *Chnoospora minima* (Hering) Papenfuss occur in the tropical central Pacific and the Indo-Pacific Region, but not in Fiji. Also, *Meristotheca procumbens* P. Gabrielson & Kraft occurs in Rotuma and eastern Australian localities (New South Wales, Lord Howe Island), but to date has not been confirmed from Fijian waters. Table 3 presents a summary of the distribution of these algal species.

Fijian Flora

The Fijian algal flora overall is most similar to the Micronesian flora. This is not too surprising, because both these floras have been quite comprehensively reported in the literature, as opposed to the other floras involved. It also agrees with ocean-current dispersal patterns for algae in the Southwest Pacific, discussed in more

TABLE 3

BIOGEOGRAPHIC DISTRIBUTION OF SOME ALGAL SPECIES
IN THE SOUTHWEST PACIFIC

SPECIES	DISTRIBUTION
<i>Coelarthrum boergesenii</i>	Marshall Islands, Rotuma
<i>Meristotheca procumbens</i>	Lord Howe Island, New South Wales, Rotuma
<i>Rhodymenia divaricata</i>	Caroline Islands, Rotuma
<i>Chnoospora minima</i>	Northern Australia, Solomon Islands, Tahiti, Rotuma
<i>Boodlea coacta</i>	Micronesia, New Caledonia, Rotuma
<i>Chondria simpliciuscula</i>	Micronesia, northern Australia, Rotuma
<i>Rhizoclonium africanum</i>	Micronesia, Samoa, New Caledonia, Solomon Islands, Tahiti, Rotuma
<i>Halimeda micronesica</i>	Marshall Islands, Caroline Islands, Solomon Islands, Tahiti, northern Australia, Rotuma

detail further on. It is pertinent to note that the Chlorophyta component of the Fijian flora is most similar to the New Caledonian flora; in most cases this particular group is the most reliably represented in any checklist because it is mostly intertidal in habitat. Moreover much of the Fijian subtidal flora, especially Rhodophyta, is still poorly known, and further discoveries in this area could well change the picture of the current biogeographical results. At least one endemic Fijian species, *Bornetella vitileviana* sp. ined. H. Kasahara (Kasahara 1988), is reported in the literature.

General Observations

Looking at the distribution of some selected species of the Southwest Pacific (Table 3, Figure 2), it can be seen that if we exclude northern Australia and Lord Howe Island (for special reasons discussed below), none of the species mentioned occurs below 17° 30'S (Tahiti), and none is found in Fijian waters. Indeed, most have their southern limits of distribution below, and including, 12° 30'S (Rotuma). Possible reasons for this distribution pattern may be that these species have not yet reached as far south as Fiji

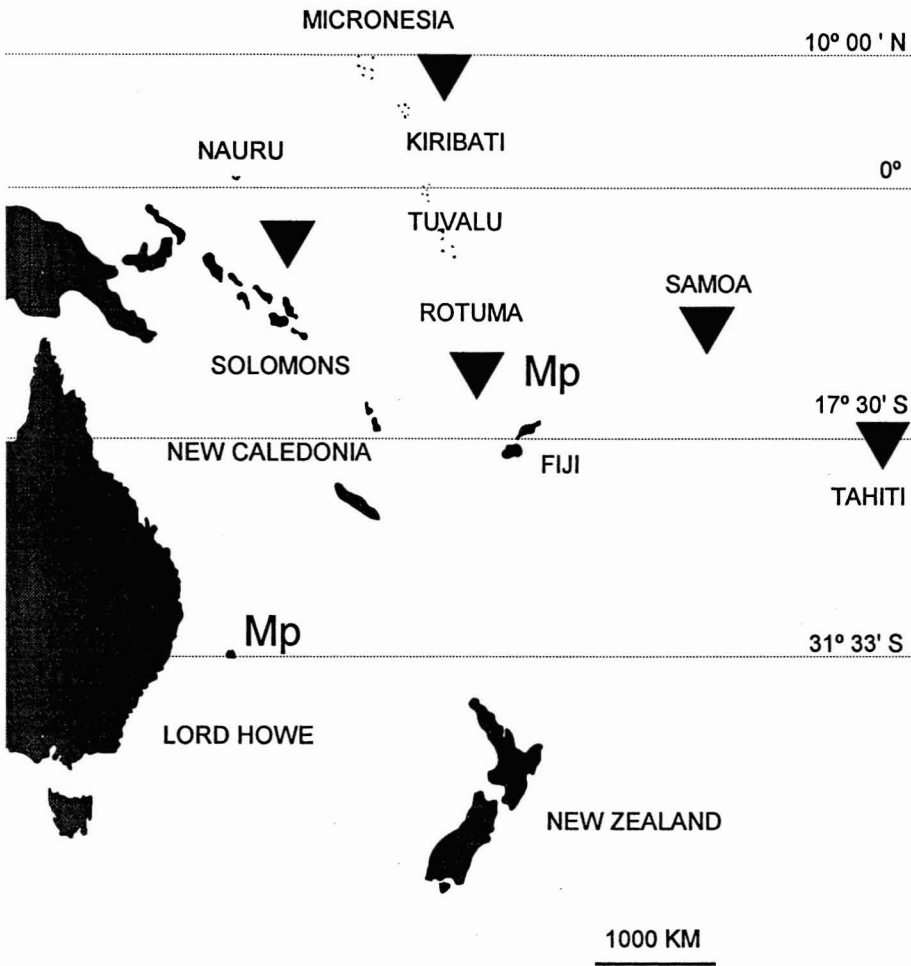


FIGURE 2. Latitudinal distribution of selected Pacific algal species (adapted from N'Yeurt 1993a). Mp, *Meristotheca procumbens*.

or that they do occur in Fijian waters; but have not yet been discovered.

The second hypothesis is plausible, but it is subject to much speculation. However, the first hypothesis could be supported by available distribution data, especially in relation to the prevailing sea currents in the western Pacific Ocean (Figure 3). Ocean currents mostly flow steadily in a westerly direction past Fiji, though in midsummer southeasterly currents in the Solomon Islands region might occasionally penetrate close to Fiji (Ash 1992). The latter route might account for the high similarity of the Fijian flora with the Solomon Island flora ($P_O = 24.6$; sec-

ond to Micronesia). Hence, algal migration routes from the northeast (Samoa, Tahiti) and from the northwest (Solomon Islands, Tuvalu, Rotuma, Micronesia) to Fiji are possible, but movement in the opposite direction is unlikely.

Rotuma Island (12° 30' S) (Figure 3) lies in the direction of the midsummer southeasterly currents, especially from the Solomons region. This might explain the occurrence of shared species (Table 3, Figure 2) between the Solomon Islands and Rotuma, such as *Halimeda micronesica* and *Chnoospora minima*, which do not occur farther south in Fiji. These species, in turn, could have been introduced to the

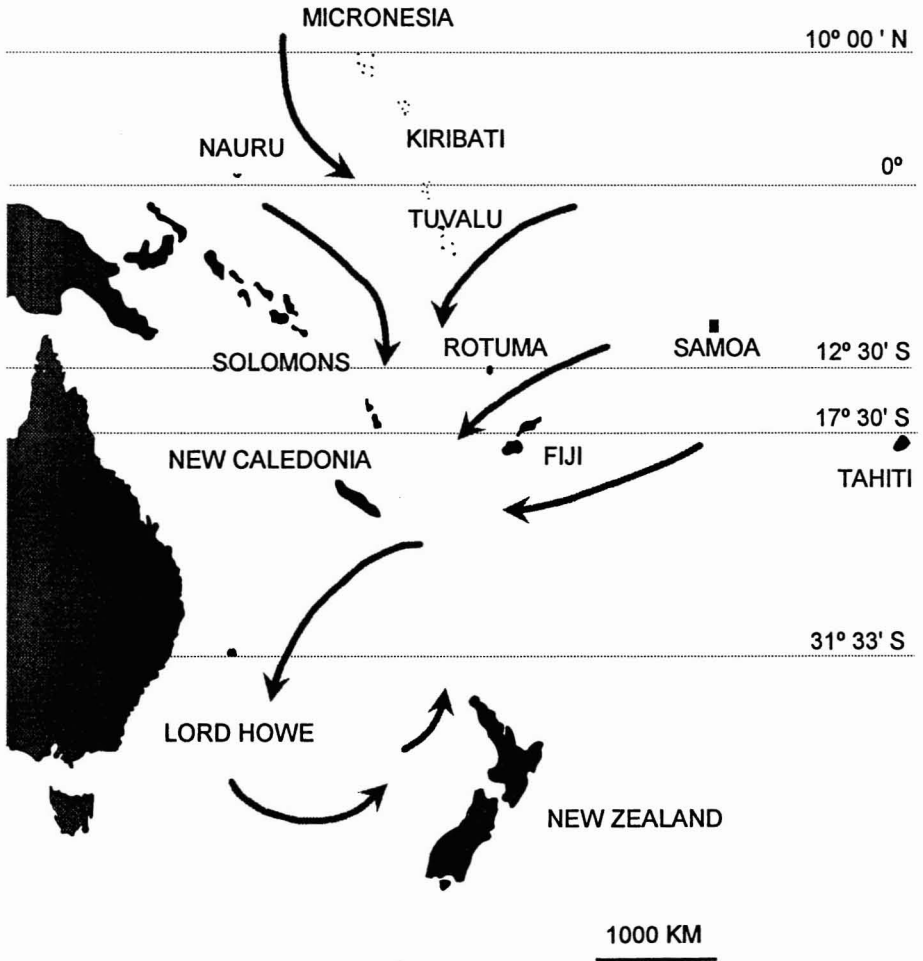


FIGURE 3. Map of the tropical and subtropical western Pacific, showing prevailing ocean currents in January (adapted from Ash 1992).

Solomon Islands via the same current patterns emanating from Micronesia. Similarly, southerly currents from Micronesia to Rotuma might explain the occurrence of such species as *Coelarthrum boergesenii* Weber-van Bosse, *Rhodymenia divaricata* Dawson, and *Rhizoclonium africanum* Kützing, which occur both in Rotuma and Micronesia, but not in Fiji or the Solomon Islands (flora comparison data for Fiji and Rotuma are given in Tables 4 and 5 and Figure 2).

Hence, it appears that the fundamental difference between the Fijian and Rotuman flora might result from the direction of the prevailing

ocean currents, which favor migrations from the western central Pacific to Rotuma, which is situated substantially farther north than Fiji. A possible explanation for the absence of many Fijian algal species in Rotuma is its isolation and the lack of suitable habitats for establishment on that island (which is much smaller and has exposed fringing reefs), because most Fijian species would probably have been introduced via ocean currents that flowed past Rotuman latitudes. The Indo-Pacific element is most pronounced in the Rotuman flora sampled (N'Yeurt 1993a). However, as stated earlier, the lack of subtidal Rotuman collections imposes limitations on this

TABLE 4
NUMBERS OF ALGAL SPECIES: FIJI AND ROTUMA

FLORA	FIJI ^a	ROTUMA	NEW RECORDS	SHARED SPECIES	% SHARED SPECIES
All species	314	106	45	66	15.7
Cyanophyceae	12	21	15	6	18.2
Chlorophyceae	94	36	11	28	21.5
Phaeophyceae	38	9	2	7	14.9
Rhodophyceae	170	40	15	25	11.9

^a Excludes species occurring in Rotuma and not in Fiji.

analysis. Such collections might present a different picture of the Rotuman flora, which may be more similar to the Fijian one, especially with respect to subtidal Rhodophyta. The low level of endemism in both floras could be a reflection of the relatively young age of the islands concerned; however, once again a more complete knowledge of the floras might change the current picture. It is pertinent to note that yet unpublished research will add many new records to the Fijian flora and that the dynamic nature of the species composition makes definite comparisons difficult.

The Australian and Lord Howe Island floras present interesting aspects. It is pertinent to note that most Rotuman algal species occur in northern Australia, despite the low similarity coefficients (Jaccard indices; Table 3) between the two floras (which is mainly a result of the wide disparity in the number of species of the respective floras, coupled with a lack of Rotuman subtidal collections). In Figure 3, we can see that the mostly constant westerly ocean currents flowing across the South Pacific become disturbed around Australian, New Guinean, and Solomon Island waters, mainly as a consequence of the presence of land masses in the western South Pacific and the seasonal intrusion of southeast-

erly currents. Hence, there appear to be many possible migratory routes from the Indo-Pacific (the accepted center of origin of most tropical Pacific algal species) to Australia, which might account for the richness of the Australian algal flora, in addition to the large variety and extent of algal habitats present there.

The Lord Howe Island flora, on the other hand, lies in the path of the main westerly ocean currents, which tend to get recirculated into a gyre pattern between the southeastern coast of Australia and New Zealand (Figure 3). Hence, possible donor areas for the Lord Howe Island algal flora could include tropical islands to the northeast (Cook Islands, French Polynesia), seasonal long-range input from the north (Fiji, Solomons, Rotuma, Micronesia), and some from the southeastern Australian coast (via "recirculated" ocean currents). The notable occurrence of *Meristotheca procumbens* P. Gabrielson & Kraft, so far only known from Lord Howe Island (Gabrielson and Kraft 1984), eastern Australia (Millar and Kraft 1993), and Rotuma (N'Yeurt 1993a, 1996a), poses some interesting biogeographical questions. Indeed, *M. procumbens* does not, to date, occur in the intervening islands of Solomons, Fiji, New Caledonia, or anywhere else in the central or South Pacific. (There is a chance that this species may occur in the Suva Lagoon, Fiji, but rarely, because a single specimen of possibly *M. procumbens* was found in deep water [A.D.R.N., unpubl. data].) Considering the prevailing ocean currents (and hence the possible migratory routes for this species), it could only have come from floras farther north or east (*M. procumbens* has not been recorded from northern Australia to date). Because it is highly unlikely that this species would only be found

TABLE 5

FLORA COMPARISONS: FIJI AND ROTUMA

FLORA	JACCARD INDEX (<i>P</i>)
All species	18.3
Cyanophyceae	N/A
Chlorophyceae	27.5
Phaeophyceae	4.4
Rhodophyceae	13.5

in such vastly distant locations as Rotuma and New South Wales, there remain two possible explanations: this species does occur in intervening islands, and possibly in the central Pacific, but has not yet been discovered; or the species migrated south across the intervening island groups, but did not become permanently established for lack of suitable habitat.

A third possibility could include artificial introduction (by humans, because this is an edible species); however, this is highly unlikely because this alga is not reported as being consumed on Lord Howe and in eastern Australia, and furthermore there have not yet been any substantiated reports of algae being propagated by humans from one island to another. The temperature difference between Rotuma and Lord Howe Island (the latter is much cooler) adds a further element of mystery to this strange distribution pattern.

Finally, the results of this investigation seem to favor a typological basis for the demarcation of biogeographic regions, as advocated by Stoddart (1992), where there must be a fundamental congruity between the items grouped in a particular zone. Viewed in this perspective, the close similarity of the Rotuman and Nauruan floras is not surprising, because both islands have broadly similar habitats and are comparable in terms of size and isolation. The latter observation further reinforces the idea that the Fiji Islands and Rotuma should be placed in separate biogeographic regions, with the Fiji Islands being more comparable to such similarly high volcanic islands as New Caledonia and the Solomon Islands, and Rotuma more comparable to smaller and isolated locations such as Nauru and possibly Tuvalu and Kiribati. The high degree of similarity between the Fijian flora and the Micronesian, however, could be a result of other factors such as the large number of heterogeneous habitats and the availability of fairly comprehensive checklists for both of those areas.

From our analysis, we conclude that the most probable donor area for the Fijian and Rotuman floras is the Micronesian region, with probable input from the Solomon Islands region via seasonal current patterns. This agrees with the general patterns of current flow in the region, which favor dispersal from northerly donor areas to more southerly islands, assuming that such long-

range dispersal is the main method by which these isolated islands acquired their floras. However, many of the floras involved in this study are still incompletely known, and several (including the Tuvaluan and Gilbertese floras) are essentially sketchy in the literature, and it would be highly desirable to have more information on these to enable a more accurate and complete understanding of the phytobiogeography of the region. Although the results tend to favor a typological basis for biogeography in the region, it must be emphasized that the two main theories in existence currently might be oversimplistic to describe the actual situation, which appears to be governed by complex sets of variables, both physical and biological.

LITERATURE CITED

- ALLENDER, B. M., and G. T. KRAFT. 1983. The marine algae of Lord Howe Island (New South Wales): The Dictyotales and Cutleri-ales (Phaeophyta). *Brunonia* 6:73-130.
- ASH, J. 1992. Vegetation ecology of Fiji: Past, present, and future perspectives. *Pac. Sci.* 46:111-127.
- CHAPMAN, V. J. 1955. Algal collections from Funafuti Atoll. *Pac. Sci.* 9:354-356.
- DAWSON, E. Y. 1956. Some marine algae of the southern Marshall Islands. *Pac. Sci.* 10:25-66.
- . 1957. An annotated list of marine algae from Eniwetok Atoll, Marshall Islands. *Pac. Sci.* 11:92-132.
- GABRIELSON, P. W., and G. T. KRAFT. 1984. The marine algae of Lord Howe Island (N.S.W.): The Family Solieriaceae (Gigartinales, Rhodophyta). *Brunonia* 7:217-251.
- GARRIGUE, C., and R. T. TSUDA. 1988. Catalog of marine benthic algae from New Caledonia. *Micronesica* 21:53-70.
- GOODHALL, D. W. 1973. Numerical classification. Pages 575-617 in R. H. Whittaker, ed. *Handbook of vegetation science V. Ordination and classification of communities*. Junk, The Hague.
- GREIG-SMITH, P. 1964. *Quantitative plant ecology*. Butterworths, London.
- HOOPER, R. G., G. R. SOUTH, and A. WHITTICK. 1980. *Ecological and phenological*

- aspects of the marine phytobenthos of the island of Newfoundland. Pages 395–423 in J. H. Price, D. E. G. Irvine, and W. F. Farnham, eds. The shore environment. Vol. 2. Ecosystems. Systematics Association Special Volume 17b. Academic Press, London.
- JONES, R., and G. T. KRAFT. 1984. The genus *Codium* (Codiales, Chlorophyta) at Lord Howe Island (N.S.W.). *Brunonia* 7:253–276.
- KASAHARA, H. 1988. Description and illustrations of marine Chlorophyceae collected at Viti Levu, Suva, Makuluva and Ovalau, Fiji [in Japanese]. Mimeographed.
- KAY, E. A. 1980. Little worlds of the Pacific. An essay on Pacific Basin biogeography. H. L. Lyon Arboretum Publication 9. University of Hawai'i and Lyon Arboretum, Honolulu.
- LEWIS, J. A. 1984. Checklist and bibliography of benthic marine macroalgae recorded from northern Australia. I. Rhodophyta. Department of Defense: Defense Science and Technology Organisation Materials Research Laboratories Report MRL-R-912. Melbourne.
- . 1985. Checklist and bibliography of benthic marine macroalgae recorded from northern Australia. II. Phaeophyta. Department of Defense: Defense Science and Technology Organisation Materials Research Laboratories Report MRL-R-962. Melbourne.
- . 1987. Checklist and bibliography of benthic marine macroalgae recorded from northern Australia. III. Chlorophyta. Department of Defense: Defense Science and Technology Organisation Materials Research Laboratories Report MRL-R-1063. Melbourne.
- LUCAS, A. H. S. 1935. The marine algae of Lord Howe Island. *Proc. Linn. Soc. N.S.W.* 60:194–232, pls. 5–9.
- LÜNING, K. 1990. Seaweeds. Their environment, biogeography, and ecophysiology. John Wiley & Sons, New York.
- MACARTHUR, R. H., and E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.
- MILLAR, A. J. K., and G. T. KRAFT. 1993. Catalogue of marine and freshwater red algae (Rhodophyta) of New South Wales, including Lord Howe Island, South Western Pacific. *Aust. Syst. Bot.* 6(1): 1–90.
- . 1994. Catalogue of marine brown algae (Phaeophyta) of New South Wales, including Lord Howe Island, South Western Pacific. *Aust. Syst. Bot.* 7:1–46.
- MOUL, E. T. 1957. Preliminary report on the flora of Onotoa Atoll, Gilbert Islands. Scientific Investigations in Micronesia, Pacific Science Board, Rutgers University.
- . 1959. The *Halimeda* and *Caulerpa* of Onota, Gilbert Islands. *Bull. Torrey Bot. Club* 86(3): 159–165.
- N'YEURT, A. D. R. 1993a. A floristic survey of the intertidal and shallow benthic marine algae of Rotuma. M.S. thesis, The University of the South Pacific.
- . 1993b. A preliminary checklist of the marine benthic algae of Rotuma. *Univ. South Pac. Mar. Stud. Prog. Tech. Rep.* 93/2.
- . 1996a. *Meristotheca procumbens* P. Gabrielson et Kraft (Gigartinales, Solieriaceae): An edible seaweed from Rotuma Island. *South Pac. J. Nat. Sci.* 14:243–250.
- . 1996b. A survey of the marine benthic algae of Rotuma Island. *Aust. Syst. Bot.* 9(3): 361–490.
- N'YEURT, A. D. R., D. S. LITTLER, and M. M. LITTLER. 1996. *Avrainvillea rotumensis* sp. nov. (Bryopsidales, Chlorophyta), a peltate species from the South Pacific. *Phycol. Res.* 44(2): 81–84.
- PAYRI, C. E., and A. MEINESZ. 1985. Algae. *Proc. 5th Int. Coral Reef Symp.* 6:498–518.
- PIELOU, E. C. 1979. Biogeography. Wiley, New York.
- SANTELICES, B. 1980. Phytogeographic characterization of the temperate coast of Pacific South America. *Phycologia* 19(1): 1–12.
- SANTELICES, B., and I. A. ABBOTT. 1987. Geographic and marine isolation: An assessment of the marine algae of Easter Island. *Pac. Sci.* 41:1–20.
- SETCHELL, W. A. 1924. Vegetation of Tutuila Island. *Carnegie Inst. Washington, Dep. Mar. Biol. Annu. Rep.* 20(341).
- SOKAL, R. R., and P. H. A. SNEATH. 1963. Principles of numerical taxonomy. Freeman, San Francisco.
- SOUTH, G. R., and H. KASAHARA. 1992. A preliminary checklist of the benthic marine algae of the Fiji Islands, South Pacific. *Micronesica* 25(1): 41–70.

- SOUTH, G. R., and S. YEN. 1992. Notes on the benthic marine algae of Nauru, Central Pacific. *Micronesica* 25(1): 123-131.
- SOUTH, G. R., A. D. R. N'YEURT, and R. A. RAJ-PRASAD. 1993. Additions and amendments to the benthic marine algal flora of Fiji, including the island of Rotuma. *Micronesica* 26(2): 177-198.
- STODDART, D. R. 1992. Biogeography of the tropical Pacific. *Pac. Sci.* 46:276-293.
- TSUDA, R. T. 1981. Bibliography of marine benthic algae of Micronesia: Addendum. *Micronesica* 17(1-2): 213-218.
- TSUDA, R. T., and F. O. WRAY. 1977. Bibliography of marine benthic algae in Micronesia. *Micronesica* 13(1): 85-120.
- VAN DEN HOEK, C. 1984. World-wide latitudinal and longitudinal seaweed distribution patterns and their possible causes, as illustrated by the distribution of rhodophytan genera. *Helgol. Meeresunters.* 38:227-257.
- . 1987. The possible significance of long-range dispersal for the biogeography of seaweeds. *Helgol. Meeresunters.* 41:261-272.
- VAN DEN HOEK, C., A. M. BREEMAN, and W. T. STAM. 1990. The geographic distribution of seaweed species in relation to temperature: Present and past. Pages 55-67 in C. van den Hoek, A. M. Breeman, W. T. Stam, and J. J. Beukema, eds. *Expected effects of climatic change on marine coastal ecosystems.* Kluwer Academic Publishers, Holland.
- WHITICK, A., R. G. HOOPER, and G. R. SOUTH. 1989. Latitude, distribution and phenology: Reproductive strategies in some Newfoundland seaweeds. *Bot. Mar.* 32:407-417.
- WOMERSLEY, H. B. S., and A. BAILEY. 1970. Marine algae of the Solomon Islands. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 259(B830): 257-352, 26 figs, pls. 24-27.
- WYNNE, M. J., and G. T. KRAFT. 1985. *Hypoglossum caloglossoides* sp. nov. (Delesseriaceae, Rhodophyta) from Lord Howe Island, South Pacific. *Br. Phycol. J.* 20:9-19.