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Diversity in Intertidal Habitats: An Assessment of the Marine Algae of Select High Islands in the Hawaiian Archipelago[1]

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ABSTRACT: Quantitative and qualitative sampling of intertidal algal assemblages on a limestone bench (O'ahu) and basalt benches (O'ahu and Hawai'i) resulted in enumeration of more than 100 species of macrophytic and turf species on O'ahu and over 60 species of primarily turf algae on Hawai'i. These assemblages are diverse and of a mosaic type and represent subcosmopolitan species, pantropical species, West Pacific species, and apparent endemic species. The algal community on Hawai'i shares 40 to 75% similarity with O'ahu populations that in one case shared only 66% similarity with adjacent sites for the same substrate type. It is suggested that the differences in species distributions are associated with age-related substrate effects and possibly settlement shadow effects.

THE HAWAIIAN ARCHIPELAGO presents at least one gradient in physical factors that could influence the distribution of marine organisms. This obvious gradient is complex and related to the ages of the islands themselves: the southeasternmost island, Hawai'i, is the youngest, less than 0.5 million yr old, and is primarily composed of volcanic basalt (McDougall and Tarling 1963, Swanson 1972, Macdonald et al. 1983) with only small reefs located in waters adjacent to older parts of the island.

The island of O'ahu is intermediate in age for the high islands but the east and west shores of the island are markedly different in age. The eastern shores of O'ahu are primarily volcanic basalt from the Ko'olau volcanic series (McDougall 1964, Doell and Dalrymple 1973, Macdonald et al. 1983), about 1.8 to 2.45 million yr old, although recent eruptions less than 35,000 yr ago created new flows and small peninsulas at the easternmost end of O'ahu (Gramlich et al. 1971). The western shores are primarily emerged fossil coral-algal reef that overlies more ancient basaltic flows of the Wai'anae volcanic series, about 2.2 to 3.8 million yr old (McDougall 1964, Funkhauser et al. 1968, Doell and Dalrymple 1973, Macdonald et al. 1983). None of the other Hawaiian islands has emerged reef regions as extensive as those of O'ahu (Macdonald et al. 1983).

The northwesternmost high island, Ni'ihau, is 7.5 million yr old and shows largely detrital sediments in coastal areas (Department of Geography, University of Hawaii 1973, Macdonald et al. 1983). Beyond Ni'ihau, the archipelago extends to the north-northwest with a group of 10 ancient remnants of high islands, the oldest of which is approximately 25 million yr old (Funkhauser et al. 1968, Macdonald et al. 1983). The oldest have calcareous formations that cap their ancient basalt bases. Thus, the ontogeny of oceanic islands appears to start off with, and return to, habitat simplicity while reaching a maximum complexity for those islands of intermediate age that have ancient basalt, recent basalt, and limestone substrates in coastal areas.

Ecological theory predicts that greater numbers of types and complexity of habitats increase the diversity of species (see Ricklefs 1973, Roughgarden 1979). Thus, islands with greater complexity of substrate types should have greater diversity of species. In the Hawaiian archipelago, old and young islands each with one surface type for recruitment

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should support populations that are less diverse than high islands of intermediate age with both basalt and calcareous surfaces in coastal areas.

Here, I examine the hypothesis that algal assemblages could be influenced by age-related factors of oceanic islands and calculate community similarity indices for sites of different ages on O'ahu and Hawai'i.

MATERIALS AND METHODS

Sites on O'ahu

The limestone bench at West Beach on the western shore of O'ahu was selected for this portion of the study in part because it had restricted access and in part because it was one of the longest uninterrupted stretches of bench left on O'ahu—about 2 km long (Figure 1). The bench was subdivided into four sampling regions, sites A to D, and each site was divided into five sampling stations consisting of three 0.4-m^2 quadrats (144 points) randomly placed on a 10-m transect line placed parallel to shore and at the bench height, between 0.5 to 0.75 m tide height. Upon completion of transect work, investigators walked the area again to collect unknown and known algae not included in the transect work. The southern region near site D has been impacted to some degree by construction of a harbor in an adjacent portion of the bench. This fieldwork was carried out during spring low tides in 1988.

For each region, all macroalgae were identified to species in the field or, if unknown, were preserved in 4% formalin in seawater and identified in the laboratory. Microalgae were treated as unknowns, as above. Slides and herbarium specimens were prepared as vouchers for all identifications.

Samplings and random walks to characterize algal communities of basalt surfaces on O'ahu were conducted in spring 1991 in a manner similar to that used for the limestone bench. These basalt sites, Kaloko and Makapu'u, are on the eastern end of O'ahu (Figure 1).

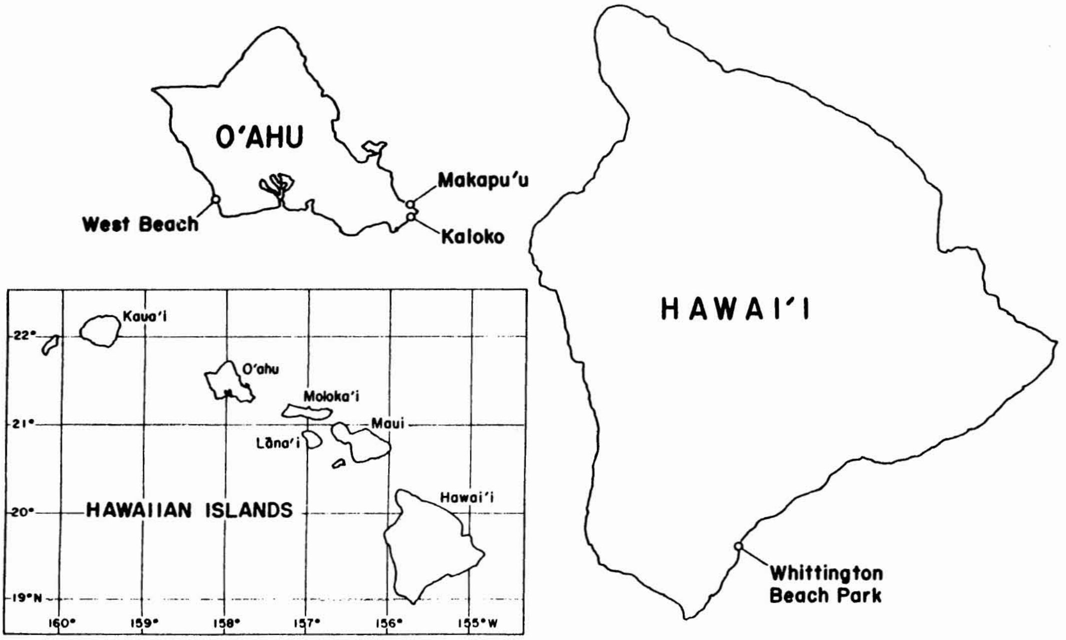

FIGURE 1. The high islands of Hawai'i showing field sites on O'ahu and Hawai'i. "West Beach" represents sites A–D on O'ahu; Makapu'u Beach Park, O'ahu; Kaloko Beach Park, O'ahu; Whittington Beach Park, Hawai'i.

Sites on Hawai'i

Quantitative and qualitative sampling on the island of Hawai'i was carried out primarily at Whittington Beach Park in Ka'ū (Figure 1) during two sampling periods, May 1990 and March 1991. Ten-meter transects were positioned in intertidal regions as described above. Work at this location challenged the procedures employed on O'ahu, primarily because the ecologically dominant algae were unidentifiable turfs. To sample smaller surface areas, the 0.4-m^2 quadrat (described earlier) and a 400-cm^2 (100 points) quadrat were employed along transects (as above). All samples were labeled and fixed in formalin for identification in the laboratory.

Floristic Comparisons

Floristic comparisons among different sampling sites (substrate or island) were made by calculating Sorensen's index of similarity (Sorensen 1948). The output from these analyses was subjected to the weighted-pairs method for cluster analysis with computer-assisted methods (Kovach 1990) following Santelices and Abbott (1987).

Because these samples were collected directly for this study, all but cyanophyte species (not listed in Table l) were employed for the cluster analysis.

RESULTS

The more than 100 species of benthic marine algae collected from intertidal limestone and basalt benches on O'ahu and Hawai'i are listed in Table 1 and ecological dominants in Tables 2–4.

On the limestone benches on O'ahu there is striking evidence for great diversity and a complex mosaic of community organization (Table 2). Red algal species were twice as numerous as the green and brown algae combined for sites A to D even though some sites were dominated by the phaeophyte *Sargassum echinocarpum* with up to 95% cover for individual quadrats. Turf species less than 2 cm in height could account for as little as 1 to 5% cover but could be composed of nine or more species, most of them red algae such as species of *Ceramium*, *Griffithsia*, and *Polysiphonia*, although a conspicuous green, *Cladophora*, and at least two brown algae, *Hincksia* and *Sphacelaria*, also occurred.

At a floristic level, the similarities among species represented at different sites changed depending upon the algal division examined (Figure 2). The highest degree of similarity among red algae was found between the northernmost sites, A and B, with that of the southernmost site, D, closer than that of the actual intermediate site, C (Figure 2). This pattern was different for the brown and green algae. For the dozen or so species of brown and green algae, sites A and B were most similar in species makeup, while sites C and D were closer to each other than to sites A and B (Figure 2).

The marine algal community on basalt benches on O'ahu had substantial percentages of cover by frondose macrophytes. These common macrophtyes include two *Sargassum* species, *S. echinocarpum* and *S. polyphyllum*, as well as *Ulva fasciata* (Chlorophyta) and coralline reds such as *Jania capillacea* and *Haliptylon rosea* (Table 3). Turfs were present at both sites but made up not more than about 25% of the cover from replicate quadrats (Table 3).

On basalt benches on Hawai'i, the turf assemblage is the ecological dominant, with other macrophytic species, *Sargassum echinocarpum*, *Chnoospora minima* (Phaeophyta), *Codium arabicum* (Chlorophyta), *Ahnfeltia concinna* (Rhodophyta), and *Amansia glomerulata* (Rhodophyta) present but at very low levels (Table 4).

In contrast to limestone communities, at a floristic level, the similarities among taxa at different basaltic sites did not change with algal division (Figure 3). Surprisingly, however, given the relative proximity of the sites, the algal communities at the Kaloko and Makapu'u sites appear to be substantially different, as shown by the distance to the node for these two sites (Figure 3). Nonetheless, for the three algal groups examined, the two O'ahu basalt sites were more closely similar in species composition than they were to the

TABLE 1

TAXONOMIC IDENTIFICATION AND PRESENCE/ABSENCE DATA FOR MARINE ALGAE FROM INTERTIDAL SOLUTION BENCH AND TIDE POOLS AT SITES ON O‘AHU AND HAWAI‘I

	O‘AHU						
	WEST BEACH						HAWAI‘I
ALGAE	A	B	C	D	MBP	KBP	WBP
Chlorophyta							
Ulvales							
Enteromorpha intestinalis (L.) Link	+	+	—	—	—	—	—
Ulva fasciata Delile	+	+	+	+	—	+	+
Cladophorales							
Chaetomorpha antennina (Bory) Kütz.	+	+	+	+	—	+	+
Cladophora dotyana Gilbert	+	+	—	—	—	—	+
C. socialis Kütz.	+	+	+	—	+	—	—
C. vagabunda (L.) Hoek	—	—	—	—	—	+	+
Cladophora sp. 1	+	+	+	+	—	—	—
Cladophora sp. 2	+	?	?	?	—	—	—
Siphonocladales							
Boodlea composita (Harv.) Brand	+	+	—	+	+	+	+
Boodleopsis hawaiiensis Gilbert	+	—	—	—	—	—	—
Cladophoropsis membranacea (Hoffm.) Børg.	+	+	+	+	+	+	—
C. herpestica (Mont.) Howe	—	+	—	—	+	+	+
Microdictyon setchellianum Howe	—	+	+	+	+	+	—
Struvea anastomasans (Harv.) Picc. & Grun.	—	+	—	—	—	+	—
Dictyosphaeria cavernosa (Forssk.) Børg.	+	+	+	+	—	+	—
D. versluysii Weber van Bosse	+	+	+	+	+	+	+
Valonia aegagropila C. Ag.	—	—	+	—	—	+	+
V. trabeculata Egerod	—	—	—	—	—	+	+
Codiales							
Codium arabicum Kütz.	—	—	+	—	—	+	+
C. edule Silva	+	—	—	+	—	—	—
Halimeda discoidea Descainse	—	—	—	—	+	—	—
Caulerpales							
Caulerpa ambigua Okamura	—	—	—	—	—	—	+
C. peltata Lamour.	—	—	—	—	—	—	+
C. serrulata (Forssk.) J. Ag.	—	—	+	—	—	—	—
C. racemosa var. *peltata* (Lamour.) Eubank	+	+	+	+	—	—	—
C. taxifolia (Vahl) C. Ag.	+	+	—	—	—	—	—
Chlorodesmis caespitosa Murray & Boodle	—	—	—	—	—	—	+
C. hildebrandtii A. & E. Gepp	+	—	—	—	—	—	—
Dasycladales							
Bornetella sphaerica (Zanard.) Solms-Laubach	—	+	—	—	—	—	—
Neomeris annulata Dickie	—	—	—	—	+	—	—
Number of green algal species	16	16	12	10	8	13	13
Number of green algal genera	11	11	9	9	7	10	10
Phaeophyta							
Ectocarpales							
Hincksia breviarticulata (J. Ag.) Silva	+	+	+	+	—	+	+
H. mitchelliae (Harv.) Silva	—	—	—	—	—	+	—
Mesospora pangoensis (Setch.) Chih. & Tanak.	—	+	—	+	+	+	—
Sphacelariales							
Sphacelaria novae-hollandiae Sonder	—	+	+	—	—	—	—
S. rigidula Kütz.	—	—	—	—	+	+	—
S. tribuloides Meneghini	+	+	+	+	—	—	—

TABLE 1 (continued)

	O‘AHU						
	WEST BEACH						HAWAI‘I
ALGAE	A	B	C	D	MBP	KBP	WBP
Dictyotales							
Dictyopteris plagiogramma (Mont.) Vickers	—	—	—	—	+	+	—
D. repens (Okamura) Børg.	—	—	—	—	+	—	+
Dictyota acutiloba J. Ag.	—	—	—	—	+	—	+
D. bartayresiana Lamour.	+	+	+	+	—	—	—
D. divaricata Lamour.	—	—	—	—	+	—	—
D. friabilis Setch.	—	—	—	—	+	+	+
D. sandvicensis Kütz.	—	+	—	—	—	—	—
Lobophora variegata (Lamour.) Womersley	—	+	—	+	—	+	+
Padina australis Hauck	+	+	+	+	—	—	—
P. japonica Yamada	+	+	+	—	+	+	—
Scytosiphonales							
Colpomenia sinuosa (Roth) Derb. & Sol.	+	—	—	+	+	+	+
Dictyosiphonales							
Chnoospora minima (Hering) Papenfuss	+	+	+	+	+	+	+
Hydroclathrus clathratus (C. Ag.) Howe	—	—	—	—	—	+	—
Fucales							
Sargassum echinocarpum J. Ag.	+	+	+	+	+	+	+
S. obtusifolium J. Ag.	+	+	+	+	—	—	—
S. polyphyllum J. Ag.	—	—	+	—	+	+	—
Turbinaria ornata (Turn.) J. Ag.	+	+	+	+	+	+	—
Number of brown algal species	10	13	11	11	13	14	8
Number of brown algal genera	8	9	7	10	9	12	7
Rhodophyta							
Acrochaetiales							
Acrochaetium catenatulum Howe	—	—	—	—	—	+	—
Erythrotrichia carnea (Dillw.) J. Ag.	—	—	—	—	—	+	—
Nemaliales							
Liagora sp. 1	+	—	—	—	—	+	—
Actinotrichia fragilis (Forssk.) Børg.	—	—	—	—	+	—	—
Galaxaura oblongata (Ellis & Sol.) Lamour.	—	—	—	—	—	+	—
Galaxaura sp.	+	—	—	+	—	—	—
Gelidiales							
Gelidiella acerosa (Forssk.) Feldm. & Hamel	+	+	+	+	+	+	—
G. myrioclada (Børg.) Feldm. & Hamel	—	—	—	—	—	—	+
Gelidium crinale (Turner) Lamour.	—	—	—	—	—	—	+
G. pusillum (Stackhouse) LeJolis	—	—	+	—	—	—	+
Pterocladia caerulescens (Kütz.) Santelices	+	+	+	+	—	—	+
P. capillacea (Gmelin) Bornet	+	+	+	+	—	+	+
Bonnemaisoniales							
Asparagopsis taxiformis (Del.) Coll. & Harv.	+	+	+	+	+	+	+
"Falkenbergia" phase of *A. taxiformis*	—	+	—	+	—	—	—
Cryptonemiales							
Amphiroa beauvoisii Lamour.	—	—	—	—	+	—	+
A. fragillissima (L.) Lamour.	+	+	+	—	+	—	+
Corallina sandvicensis Reinbold	—	—	—	—	—	—	+
Corallina sp. 1	+	—	+	—	—	—	—
Haliptylon rosea	—	—	—	—	+	—	+
H. subulata (Ell. & Sol.) Johansen	—	—	—	—	+	+	—
Hydrolithon reinboldii (W. v. B. & Fosl.) Fosl.	+	+	+	+	—	—	—
Jania capillacea Harv.	+	+	—	+	+	+	+
Jantiella sp.	—	—	—	+	—	—	—
Mesophyllum sp.	—	—	+	+	—	—	—

TABLE 1 (continued)

	O‘AHU						
	WEST BEACH						HAWAI‘I
ALGAE	A	B	C	D	MBP	KBP	WBP
Porolithon onkodes (Heydrich) Foslie	+	+	+	+	—	—	—
Peysonnelia rubra (Grev.) J. Ag.	+	+	—	—	+	+	—
Portieria hornemanni (Lyngb.) Silva	+	+	+	+	+	—	+
Rhodopeltis gracilis Yamada & Tanaka	—	—	—	—	+	—	—
Grateloupia phuquoensis Tanaka & Pham-Hoang	+	+	—	+	+	—	+
Gigartinales							
Ahnfeltia concinna J. Ag.	—	—	—	—	+	—	+
Gelidiopsis intricata (C. Ag.) Vickers	—	—	—	—	—	+	+
G. scoparia (Mont. & Mill.) Schm.	+	+	+	+	—	—	—
Gracilaria coronopifolia J. Ag.	+	—	—	—	—	—	—
Gymnogongrus flabelliforme Harv.	+	—	—	—	—	—	—
Gymnogongrus sp.	—	—	—	+	—	—	—
Sarcodia sp.	—	—	—	—	+	—	—
Hypnea cervicornis J. Ag.	+	—	+	—	—	—	—
H. chordacea Kütz.	+	+	+	+	+	+	—
H. musciformis (Wulfen) Lamour.	+	+	+	—	+	+	—
H. pannosa J. Ag.	—	—	—	—	—	+	+
H. spinella (C. Ag.) Kütz.	—	—	+	—	+	—	+
Rhodymeniales							
Botryocladia skottsbergii (Børg.) Levr.	+	+	+	+	+	—	—
Champia parvula (C. Ag.) Harv.	+	+	—	+	+	—	+
Coelothrix irregularis (Harv.) Børg.	+	+	—	—	—	+	—
Ceramiales							
Anotrichum tenue (C. Ag.) Naegeli	—	—	—	—	—	+	+
Centroceras clavulatum (C. Ag.) Montagne	+	+	+	+	—	+	+
Centroceras sp.	—	—	—	—	—	—	+
Ceramium aduncum Nakamura	—	—	—	—	—	+	+
C. affine Setch. & Gard.	—	—	—	—	—	+	+
C. clarionense Setch. & Gard.	—	—	—	—	—	—	+
C. fimbriatum Setch. & Gard.	+	+	+	—	—	—	+
C. flaccidum (Harv.) Ardiss.	+	+	—	—	—	+	+
Ceramium sp.	+	?	+	+	—	—	—
Ceramothamnion hanaense Norris & Abbott	—	—	—	—	—	—	+
Griffithsia heteromorpha Kütz.	+	+	+	+	?	—	+
G. metcalfii Tseng	+	—	—	—	—	—	—
G. ovalis Harv.	+	—	—	—	+	—	—
Griffithsia sp.	—	—	+	—	+	—	+
Haloplegma duperreyi Montagne	—	—	—	—	—	+	—
Spyridia filamentosa (Wulfen) Harv.	+	+	+	+	+	+	—
Wrangelia penicillata C. Ag.	—	—	—	—	+	+	—
Dasya corymbifera J. Ag.	+	—	+	—	—	—	—
Eupogodon iridescens Schlech	+	+	+	+	—	+	—
Heterosiphonia crispella (C. Ag.) Wynne	+	—	—	—	—	—	—
Lophosiphonia sp.	—	—	—	—	—	—	+
Martensia fragilis Harv.	+	—	+	+	+	+	—
Taenioma perpusillum (J. Ag.) J. Ag.	—	+	+	+	—	—	+
Acanthophora pacifica (Setch.) Kraft	—	—	—	—	—	+	—
A. spicifera (Vahl) Børg.	+	+	+	+	—	+	—
Amansia glomerata C. Ag.	+	+	+	+	+	—	+
Chondria dasyphylla (Woodw.) C. Ag.	—	—	—	—	—	—	+
C. repens Børg.	+	+	+	+	?	—	—
Chondria sp. 1	+	?	+	+	—	—	?
Chondria sp. 2	+	?	—	—	+	—	—

TABLE 1 (continued)

	O'AHU						
	WEST BEACH						HAWAI'I
ALGAE	A	B	C	D	MBP	KBP	WBP
Chondria sp. 3	+	?	—	—	—	—	—
Chondria sp. 4	+	?	—	—	—	—	—
Herposiphonia arcuata Hollenb.	—	—	+	—	—	—	—
H. crassa Hollenb.	—	—	+	+	—	—	—
H. dendroidea Hollenb.	—	—	+	+	—	—	—
H. parca Setch.	—	—	—	—	—	+	—
H. tenella f. *secunda* (C. Ag.) Hollenb.	—	+	—	—	—	—	—
Herposiphonia sp.	—	+	—	?	?	—	?
Laurencia brachyclados Pilger	—	—	—	—	—	—	+
L. crustiformans McDermid	+	+	+	+	—	—	—
L. dotyi Saito	+	+	+	+	+	—	—
L. majuscula (Harv.) Lucas	+	—	—	+	+	+	—
L. nidifica J. Ag.	+	—	—	+	+	+	—
L. parvipapillata Tseng	—	—	—	—	+	—	—
L. succisa Cribb	—	+	—	+	—	—	—
L. surculigera Saito	—	—	—	—	—	—	+
L. yamadana Howe	+	+	+	+	+	—	+
Laurencia sp. "green"	+	—	+	—	+	+	—
Laurencia sp.	—	—	+	—	—	—	—
Polysiphonia quadrata Hollenb.	—	—	+	—	—	—	—
P. scopulorum Hollenb.	—	—	—	—	—	—	+
P. sparsa (Setch.) Hollenb.	—	—	—	—	—	+	—
P. sphaerocarpa Hollenb.	—	—	+	—	—	—	+
P. tuberosa Hollenb.	—	—	+	—	—	—	—
P. villum Hollenb.	—	—	—	—	—	—	+
Polysiphonia sp. 1	+	+	?	+	—	+	?
Polysiphonia sp. 2	+	?	?	?	—	—	—
Tolypiocladia glomerata (C. Ag.) Schmitz	—	—	—	—	—	—	+
Number of red algal species	50	35	42	38	32	33	40
Number of red algal genera	33	27	27	29	22	25	25
Total number of algal species	76	64	65	59	53	60	61
Total number of algal genera	52	47	43	48	38	47	42

NOTE: MBP, Makapu'u, O'ahu; KBP, Kaloko, O'ahu; WBP, Whittington Beach Park, Hawai'i; + = present; — = absent.

basalt community on the island of Hawai'i (Figure 3).

For all sites sampled, Figure 4 shows that analysis of red algae alone does not change the arrangements of earlier clustering shown in Figures 2 and 3. The West Beach limestone communities are most similar, the O'ahu basalt community intermediate, and the Hawai'i basalt community is least similar.

For the brown algae, the algae at Whittington Beach are about equally distantly related to the algae of the basalt or limestone surfaces on O'ahu (Figure 4). For the green algae, the community on the basalt at Whittington Beach is more similar to those of the limestone benches at site B, West Beach, O'ahu. The algae at Kaloko and Makapu'u are now outliers to the algae community on limestone surfaces (Figure 4).

A preliminary biogeographical analysis suggests that there are at least four groups or patterns of distribution among the algae species cited here: (1) subcosmopolitan, including such species as *Hincksia mitchelliae*; (2) a

TABLE 2

CONTRIBUTIONS TO COVER OF A LIMESTONE BENCH BY ALGAE, WEST BEACH, O'AHU

LOCALITY	COMMON SPECIES (MEAN > 10% COVER)	% COVER (RANGE)	TURF SPECIES
Site A	52 genera with 76 species		
	Acanthophora spicifera	0 to 24.5	*Centroceras clavulatum*
	Laurencia dotyi	2 to 48.8	*Ceramium flaccidum*
	Laurencia nidifica	0 to 29.0	*Chondria* sp. 1–4
	Hypnea musciformis	0 to 34.6	*Griffithsia heteromorpha*
			Hincksia breviarticulata
			Jania capillacea
			Polysiphonia sp. 1 & 2
			Sphacelaria tribuloides
Site B	47 genera with 64 species		
	Acanthophora spicifera	0 to 26.9	*Centroceras clavulatum*
	Gelidiella acerosa	14.6 to 25.5	*Ceramium fimbriatum*
	Laurencia succisa	2.9 to 14.6	*Chondria repens*
	Laurencia yamadana	26.4 to 30.8	*Cladophora* sp. 1
	Sargassum echinocarpum	8.3 to 13.3	*"Falkenbergia" (A. taxiformis)*
	Ulva fasciata	4.7 to 26.4	*Griffithsia heteromorpha*
			Herposiphonia tenella
			Hincksia breviarticulata
			Polysiphonia sp. 1
			Pterocladia caerulescens
			Sphacelaria novae-hollandae
			Taenioma perpusillum
Site C	43 genera with 65 species		
	Dictyosphaeria versluysii	0 to 29.9	*Ceramium* sp.
	Hincksia breviarticulata	0 to 56.8	*Chondria repens*
	Laurencia yamadana	0 to 28.5	*Chondria* sp. 1
	Sargassum echinocarpum	0 to 95.1	*Cladophora* sp. 1
	Turf assemblage	0 to 27.0	*Griffithsia heteromorpha*
			Herposiphonia arcuata
			H. crassa
			H. dendroidea
			Hypnea spinella
			Polysiphonia quadricata
			P. tuberosa
			Pterocladia caerulescens
			Sphacelaria novae-hollandae
			S. tribuloides
			Taenioma perpusillum
Site D	48 genera with 59 species		
	Cladophoropsis membranacea	3.3 to 16.9	*Centroceras clavulatum*
	Laurencia dotyi	10.0 to 19.0	*Ceramium* sp. 1
	Laurencia nidifica	21.1 to 28.7	*Chondria repens*
	Turf assemblage	0 to 40.0	*Chondria* sp.
			Cladophora sp. 1
			Griffithsia heteromorpha
			Herposiphonia crassa
			H. dendroidea
			Jania capillacea
			Jantiella sp.
			Polysiphonia sp. 1
			Pterocladia caerulescens
			Sphacelaria tribuloides
			Spyridia filamentosa
			Taenioma perpusillum

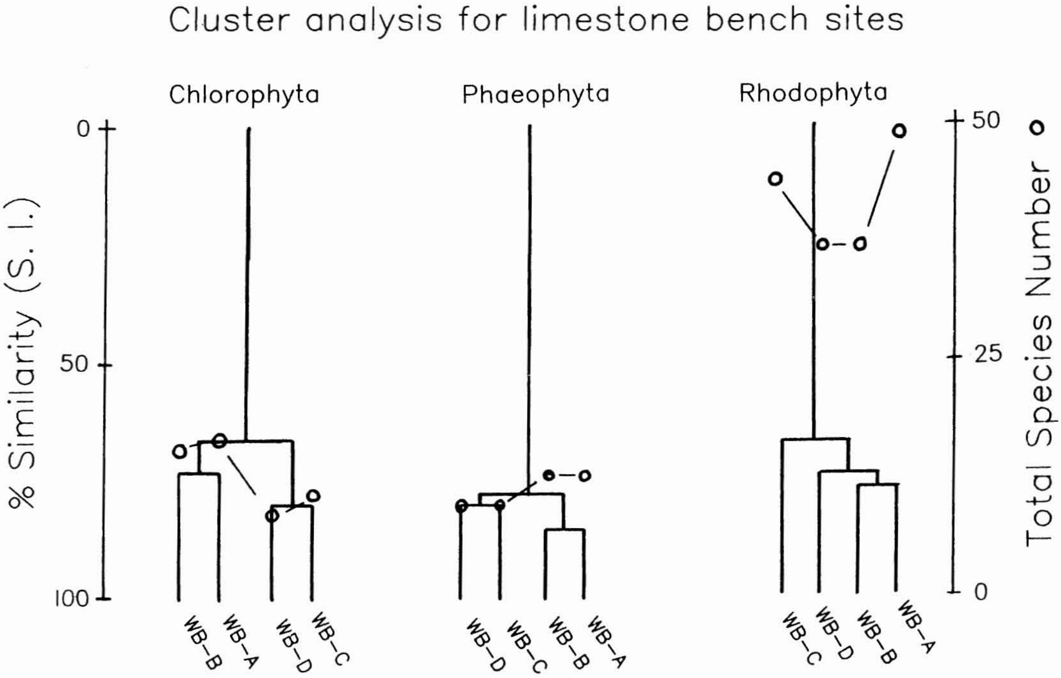

FIGURE 2. Floristic analysis and numbers of species of the intertidal algae on limestone benches at sites at West Beach, O'ahu (WB-A, WB-B, WB-C, and WB-D).

pantropical element, especially of *Acanthophora spicifera*, *Hydroclathrus clathratus*, and *Halimeda discoidea*; (3) several Pacific basin species such as *Botryocladia skottsbergii*, *Padina japonica*, and *Microdictyon setchellianum*; and (4) at least six species endemic to the Hawaiian Islands (Table 5).

DISCUSSION

The hypothesis that stimulated this study suggests that younger oceanic islands have fewer algal species than islands of intermediate age, based on habitat diversity. The work carried out for this study showed that these algal assemblages within one island or between a young and intermediate-aged island are quantitatively and qualitatively distinct at a surprising level. There is as much difference for the O'ahu limestone bench as has been reported among different sites on Easter Island (Santelices and Abbott 1987).

The overall morphology of algal communities examined here also differs across the age-related gradient. Taxa making up the limestone bench community were generally larger plants (up to 30 cm for *Sargassum*). The turf on Hawai'i possesses compact and procumbent morphologies generally under 5 cm. These turfs act as anchor species and offer structural as well as moist environments for crustaceans, micromollusks, polychaete annelids, nematodes, and cyanobacteria, none of which was analyzed as part of this study. Epiphytic algal species are common and occur in nearly a 1:1 relationship (O'ahu basalt) to anchor species. On Hawai'i, anchor species are already diminutive and average about three epiphyte species, especially in the genera *Ceramium* and *Polysiphonia*. Collections from Hawai'i, Maui, and O'ahu have recently led to recognition of two new species of *Ceramium*; a new species of *Ceramothamnion* from the Puna and Ka'ū districts of Hawai'i, 'Āhihi Bay and Hāna, Maui, and O'ahu; and a new species of *Corallophila* from the Puna and Kailua-Kona districts of Hawai'i (Norris and Abbott 1992).

TABLE 3

CONTRIBUTIONS TO COVER OF BASALT BENCHES BY ALGAE, MAKAPU‘U AND KALOKO BEACHES, O‘AHU

LOCALITY	COMMON SPECIES (MEAN > 10% COVER)	% COVER (RANGE)	TURF SPECIES
Makapu‘u Beach Park Site	38 genera with 53 species		
	Jania capillacea	0 to 18	*Amphiroa fragillissima*
	Haliptilon rosea	0 to 15	*Champia parvula*
	Sargassum echinocarpum	0 to 50	*Chondria* sp. 2
	Sargassum polyphyllum	0 to 25	*Dictyopteris repens*
	Turf assemblage	0 to 25	*Griffithsia* sp.
			Hypnea spinella
			Laurencia yamadana
			Sarcodia? sp.
Kaloko Beach Park Site	47 genera with 60 species		
	Sargassum echinocarpum	0 to 90.0	*Anotrichum tenue*
	Ulva fasciata	0 to 95.0	*Centroceras clavulatum*
	Turf assemblage	0 to 10	*Ceramium aduncum*
			C. affine
			C. flaccidum
			Jania capillacea
			Herposiphonia parca
			Hincksia breviarticulata
			H. mitchelliae
			Hypnea chordacea
			H. pannosa
			Laurencia majuscula
			L. nidifica
			Polysiphonia sparsa
			Polysiphonia sp.
			Spyridia filamentosa

The marked species diversity seen in these intertidal regions may be related in part to the high degree of disturbance that prevails in these wave-washed habitats (see McDermid 1988) combined with strongly seasonal exposure and low rates of tissue dehydration when exposed. Many of the adjacent subtidal areas for these intertidal sites had very little frondose biomass (pers. obs.). Thus, intertidal benches may offer a tidal refuge for many "subtidal" species that thereby escape herbivory.

A second gradient over the high islands is, on a long-term average, a westward flow of surface waters around the Islands that is a complex of a permanent flow plus several components: (1) reversing tidal currents in coastal areas, (2) large eddies (32 to 80 km across) in permanent flow downstream, and (3) deflection of water masses by island mass (Laevastu et al. 1964, Wyrtki et al. 1969). From late spring to early fall, instantaneous current flow generally produces a net westward flow (see discussion in Kenyon 1992) from as far away as North and Central America to Hawai‘i. Because this circulation nets occasional input of new waters to the archipelago, it is a possible mechanism for introductions of new entities to the Hawaiian Islands even though the distances traveled are longer than from southern hemisphere locations (Kay 1980).

Recent ecological studies have identified settlement shadows of larvae in coastal waters. A shadow results from more larvae settling on the first rocks they encounter offshore than on inshore rock surfaces (Bernstein and Jung 1979, Gaines and Roughgarden 1985, Gaines et al. 1985, Roughgarden et al. 1988). From this earlier research, we would expect that the number of propagules in an oceanic current is a finite pool. As propagules are delivered to the Hawaiian Islands via the net seasonal flow

TABLE 4

CONTRIBUTIONS TO COVER OF A BASALT BENCH BY ALGAE, WHITTINGTON BEACH PARK, HAWAI'I

LOCALITY	COMMON SPECIES (MEAN > 10% COVER)	% COVER (RANGE)
Whittington Beach Park Site	42 genera with 61 species	
	Turf species:	80 to 100
	Amphiroa fragillissima	
	Anotrichum tenue	
	Centroceras clavulatum	
	Ceramium aduncum	
	C. affine	
	C. clarionenses	
	C. fimbriatum	
	C. flaccidum	
	Champia parvula	
	Chondria dasyphylla	
	Dictyopteris repens	
	Griffithsia sp.	
	Jania capillacea	
	Hincksia breviarticulata	
	Hypnea pannosa	
	H. spinella	
	Laurencia brachyclados	
	L. surculigera	
	L. yamadana	
	Polysiphonia scopulorum	
	P. sphaerocarpa	
	P. villum	
	Taenioma perpusillum	
	Tolypiocladia glomerata	

discussed above, a settlement shadow could be created across the high islands, with the youngest islands enjoying greater success in recruitment.

These expectations are supported by earlier work in island biogeography that demonstrated that rates of immigration are lower for more distant islands than those closer to a propagule source (MacArthur and Wilson 1963). In the Hawaiian archipelago, the younger islands are somewhat closer to continents, but, more important, they are the first surfaces on which propagules from North and Central America can settle for 3200 km. For these younger islands, there could exist greater input rates of propagules and different species assemblages than for older islands.

Settlement shadows may be the explanation for differential distribution of *Ceramothamnion hanaense* (Table 5) and two other epiphytic red algae described in this issue by Norris and Abbott (1992) as new species. *Ceramothamnion hanaense* was collected on the southeast shore of Hawai'i about 3.2 km northeast of Whittington Beach Park (during fieldwork for an expansion of this study) and has also been found at two other basalt locations on the eastern side of Maui and at one site on O'ahu (Norris and Abbott 1992). A species of epiphyte *Ceramium*, *C. womersleyi*, has been collected only from basalt sites on Maui (Norris and Abbott 1992). A new species of the rare genus *Corallophila*, *C. ptilocladioides*, has been collected only at basalt sites on Hawai'i (Norris and Abbott 1992). Characterization of the flora of Kaua'i, Maui, and the Northwestern Hawaiian Islands will no doubt broaden our perspective of these patterns for many other species.

Age of islands, circulation patterns, and settlement shadows appear to have combined to create dynamic and complex forces generating diverse algal communities for at least two high islands. A model that incorporates these results and current oceanographic perspectives follows: Variations in patterns of flow of water to/around the islands may seasonally bring in new propagules from the eastern, southern, or northwestern parts of the chain and then hold them in these waters via eddies and gyres (Laevastu et al. 1964, Wyrtki et al. 1969, Kenyon 1992); islands in the western part of the high island chain have more types of habitats (basalt, limestone, caves, coral reefs, etc.) available than do young high islands (basalt) or ancient low islands (ancient coral reefs, shoals, sand plains). These combine to allow an island of intermediate age to have more species than a younger island. Differential distribution of species in part reflects the path by which they came to the islands. With time, we may be able to distinguish those new species that are products of speciation within island populations from those that are additions from afar.

Thus, the diversity and distributional patterns of intertidal marine algae on two high islands are high and highly complex, respectively. Age-related factors appear to allow more species on intermediate-aged islands like O'ahu, but there is still a diverse algal flora on

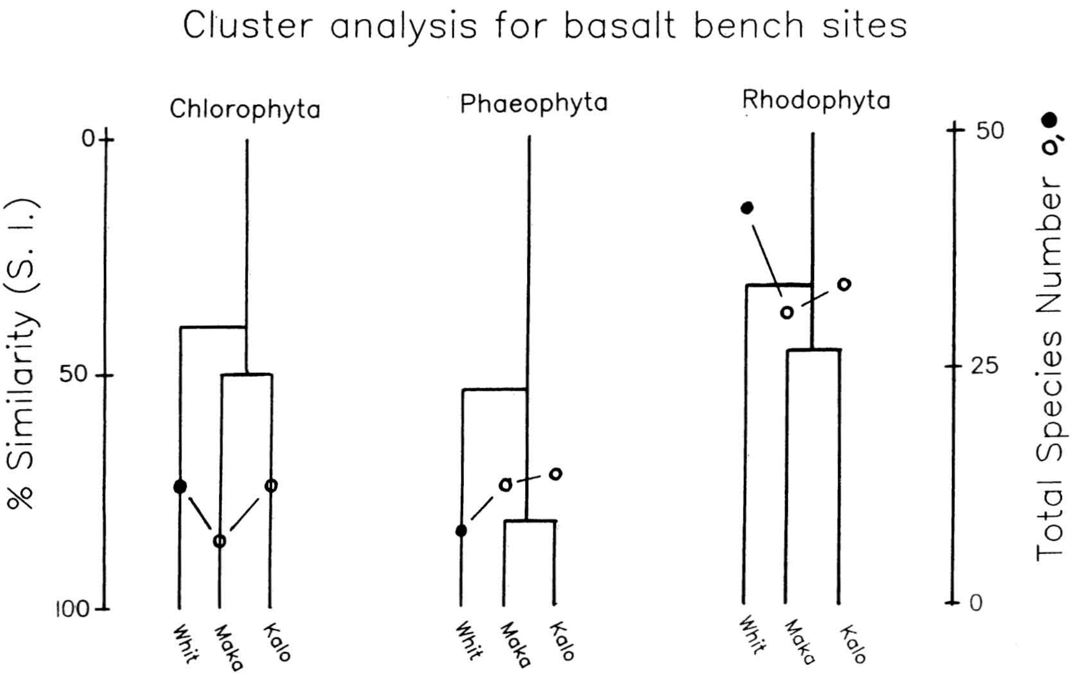

FIGURE 3. Floristic analysis and numbers of species of the intertidal algae on basaltic benches at Whittington Beach Park, Hawai'i (Whit), Makapu'u Beach Park, O'ahu (Maka), and Kaloko Beach Park, O'ahu (Kalo).

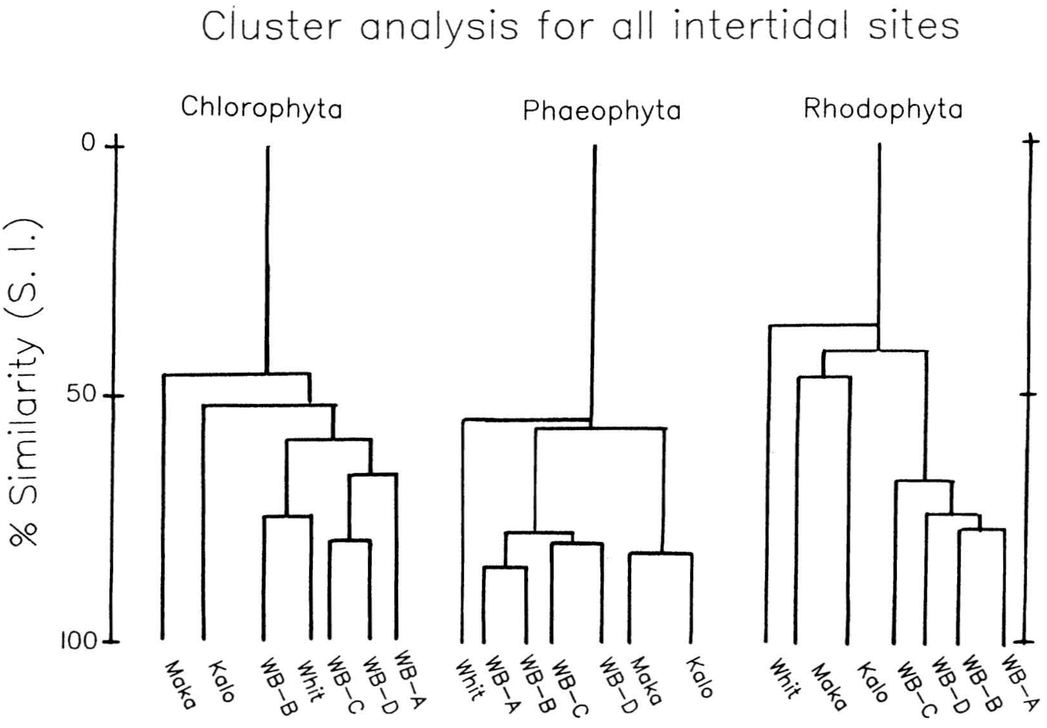

FIGURE 4. Floristic analysis of intertidal algae from all sites. Abbreviations for sites as described in previous figures.

TABLE 5

EXAMPLES OF GEOGRAPHIC DISTRIBUTION OF INTERTIDAL ALGAE

GROUP 1 SUBCOSMOPOLITAN—WIDE PATTERN OF DISTRIBUTION	GROUP 2 PANTROPICAL PATTERN OF DISTRIBUTION	GROUP 3 PACIFIC PATTERN OF DISTRIBUTION	GROUP 4 "ENDEMIC" TO HAWAIIAN ISLANDS
Centroceras clavulatum	*Acanthophora spicifera*	*Botryocladia skottsbergii*	*Boodleopsis hawaiiensis*
Champia parvula	*Asparagopsis taxiformis*	*Chondria repens*	*Ceramothamnion hanaense*
Colpomenia sinuosa	*Boodlea composita*	*Cladophora socialis*	*Sarcodia*? sp.
Erythrotrichia carnea	*Chnoospora minima*	*Cladophoropsis herpestica*	*Sargassum echinocarpum*
Gelidium pusillum	*Halimeda discoidea*	*Chlorodesmis caespitosa*	*S. obtusifolium*
Hincksia mitchelliae	*Hydroclathrus clathratus*	*Microdictyon japonicum*	*S. polyphyllum*
Peyssonellia rubra	*Laurencia majuscula*	*Padina australis*	*Valonia trabeculata*
Pterocladia capillacea	*Lobophora variegata*	*Padina japonica*	
	Porolithon onkodes	*Sphacelaria tribuloides*	
	Sphacelaria novae-hollandiae	*Ulva fasciata*	

*Following Setchell 1924, 1926, Dawson 1954, 1956, 1957, Payri and Meinesz 1985, Santelices and Abbott 1987, Abbott 1989, pers. comm.

the youngest high island in the archipelago. In addition, some components of the younger islands' flora shown here and in Norris and Abbott (1992) are not found on all older islands, as if dispersal is still under way.

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