

Variation in algal turf species composition and abundance on two Hawaiian shallow subtidal reefs¹

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Abstract — In the tropics, algal turfs are a key marine community, floristically and ecologically, yet the turf structure and its spatial and temporal variation have seldom been quantitatively assessed. We compared species composition and abundance of turf algae on two shallow subtidal reefs (< 2 m deep) on the island of Hawai'i from September 2000 to July 2002. Of the 102 species of marine algae identified in the algal turf community, 17 belonged to the Chlorophyta, 9 to the Phaeophyta, and 76 to the Rhodophyta. Red algae dominated the turfs at both sites. Species richness, species diversity, and evenness varied between sites and among sampling dates, perhaps due to differences in substratum, precipitation and wave exposure. The most abundant turf species (*Ceramium macilentum* J. Agardh, *Pterocladia caerulescens* (Kützing) Santelices et Hommersand, *Hypnea spinella* (C. Agardh) Kützing, *Coelothrix irregularis* (Harvey) Børgesen, *Amansia glomerata* C. Agardh and *Laurencia brachyclados* Pilger) showed very patchy spatial distributions and variable seasonal abundances. 38 new records for the island of Hawai'i were documented, many of which were common. Although growth form rather than dominant or diagnostic species defines the algal turf community, identification and monitoring of individual species, which have different reproductive and physiological characteristics, are essential to understanding the ecology of the turf.

algal turf / community structure / Hawai'i / species diversity / subtidal

Résumé — **Variation de la composition et de l'abondance des espèces de gazons d'algues de deux récifs infralittoraux peu profonds à Hawaii.** Sous les tropiques, les gazons d'algues constituent une communauté marine clé d'un point de vue floristique et écologique ; leur structure, leur variation spatiale et temporelle ont pourtant été rarement évaluées. Nous avons comparé la composition et l'abondance des espèces de gazons d'algues sur deux récifs infralittoraux de faible profondeur (< 2 m) sur l'île d'Hawaii de septembre 2000 à juillet 2002. Cent deux espèces d'algues marines furent identifiées dans la communauté algale, comprenant 17 Chlorophytes, 9 Phaeophytes et 76 Rhodophytes. Les algues rouges dominaient le gazon des deux sites. La richesse et la diversité spécifiques ainsi que la régularité de présence variaient entre les sites et selon les dates d'échantillonnages, peut-être en raison des différences de substrat, de précipitation et d'exposition aux vagues. De plus, les espèces les plus abondantes (*Ceramium macilentum* J. Agardh, *Pterocladia caerulescens*

1. Dedicated with pleasure to Isabella Aiona Abbott on the occasion of her 85th birthday. *Hau'oli lā hānau, e ke kumu a'o i ho'ānoano a aloha nui 'ia!* Happy Birthday, to our teacher who is greatly respected and much loved!

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(Kützing) Santelices et Hommersand, *Hypnea spinella* (C. Agardh) Kützing, *Coelothrix irregularis* (Harvey) Børgesen, *Amansia glomerata* C. Agardh et *Laurencia brachyclados* Pilger), ont montré des distributions spatiales très inégales et des abondances saisonnières variables. Trente-huit taxons sont signalés pour la première fois pour l'île d'Hawaii, dont beaucoup d'entre eux étaient communs. Bien que la forme de croissance définisse la communauté, plutôt que les espèces dominantes ou caractéristiques, l'identification et le suivi individuel des espèces qui ont des caractères reproductifs et physiologiques différents, sont essentiels pour comprendre l'écologie du gazon d'algues.

diversité spécifique / gazon algal / Hawaii / structure d'une communauté / zone infralittorale

INTRODUCTION

Algal turfs—less than 3 cm in height, densely packed, multispecific assemblages of caespitose or reptant seaweeds—are common in intertidal and subtidal zones throughout the world (Odum & Odum, 1955; Neushul & Dahl, 1967; Dahl, 1972; Lawson & John, 1977; Adey & Steneck, 1985; Asetline-Neilson *et al.*, 1999; Boaventura *et al.*, 2002; Kelaher *et al.*, 2003). The algal community is most often referred to as turf, however other descriptors include mats, lawns, parvosilvosa, and carpets. In tropical waters, turf algae comprise much of the marine flora (Airoldi, 1998), contribute significantly to coral reef productivity (Adey & Goertemiller, 1987; Klumpp & McKinnon, 1989), and serve as an important food source for many herbivorous marine organisms (Wanders, 1976; Brawley & Adey, 1981; Kendrick, 1991; Harmelin-Vivien *et al.*, 1992; Ferreira *et al.*, 1998; Mills *et al.*, 2000).

On Hawaiian reefs, turfs can dominate the intertidal zones (McDermid, 1990; Smith, 1992) and reef flats (Cheroske *et al.*, 2000), compete with coral for space on subtidal reef slopes (Smith *et al.*, 2001), affect water flow (Carpenter & Williams, 1993), provide habitat for small invertebrates (Russo, 1991), and contribute to reef productivity through nitrogen fixation (Williams & Carpenter, 1997, 1998). However, few studies have documented taxonomic identities of the individual algal species in the turf community or acknowledged the variability in turf structure. Without this information, a turf remains an ecological “black box.” The goals of our study were to document species diversity within the algal turf, and to assess the seasonal and spatial variation within turf communities on two Hawaiian reefs.

MATERIALS AND METHODS

Study sites

This study was conducted at two sites on opposite sides of the island of Hawai'i (Fig. 1), the southernmost island in the Hawaiian Archipelago. Sampling at both sites took place in the shallow subtidal (< 2 m deep). Lelewi (19.74° N 155.01° W), on the eastern, windward side of the island facing the prevailing north-easterly trade winds, is characterized by a basalt rock shoreline. Puakō (19.97° N

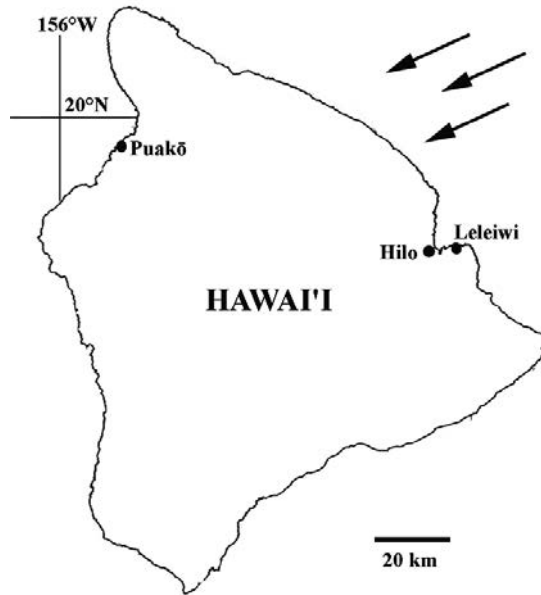


Fig. 1. The island of Hawai'i, showing the two sampling locations: Puakō and Leleiwi. The prevailing northeasterly trade winds are indicated by arrows.

155.85° W), located on the western, leeward side of the island, has a limestone fringing reef. The reef at Leleiwi is exposed to more tradewind-generated wave action than the reef at Puakō, and receives an average annual rainfall of 314.2 cm, whereas Puakō only 24.8 cm/year of rainfall (Juvik & Juvik, 1998). These two locations were chosen due to the differences in substratum, wave action, and freshwater input, as well as shared characteristics of similar depth, low level of human disturbance and 80-100% cover of turf.

Sampling

Sampling while snorkeling occurred seasonally at both sites in September 2000, November 2000, February 2001 and July 2002 along two 10 m transect lines haphazardly positioned perpendicular to the shoreline, greater than 10 m apart. A circular 78.5 cm² (diameter = 10 cm) quadrat was placed along each transect at 1 m intervals (nine samples/transect) except on two occasions, September 2000 at Puakō and November 2000 at Leleiwi, when poor ocean conditions prevented complete sampling. The algal turf within each quadrat was removed intact by hand using a fine-edged blade and placed into a labeled plastic bag. Any remaining thalli or fragments within the quadrat were hand picked. Loss of sample during collection was < 2%. The samples were preserved in a 4 % formalin-seawater solution for later identification and quantification. Point intercept and photo-quadrat methods were not used in this study because *in situ* identification at the species level was not possible due to the small stature and density of the seaweeds. The taxonomy of many turf species requires examination of microscopic features.

Laboratory methods

In the laboratory, the contents of each bag were floated in water in a 10 × 1.5 cm (diameter × height) Petri dish that had been etched with a grid pattern consisting of 12 intersection points. The number of grid intersection points in the Petri dish was determined by a species-sample size curve. Algae over each intersection were collected using fine forceps and mounted as permanent slides (Tsuda & Abbott, 1985). Specimens were identified to lowest taxonomic level possible based on examination of morphological and anatomical characteristics using taxonomic references (Abbott, 1999; DeClerck, 1999; Abbott & Huisman, 2004). Voucher slide specimens were selected and deposited in the Bishop Museum Herbarium in Honolulu (BISH). Cyanobacteria, diatoms and dinoflagellates found in the samples were not included in this report.

Data analysis

Percent abundance values were obtained using a point system. For example, when a species occurred at an intersection it was given a score of 1. If more than one species were sampled at an intersection, then each species was given a fractional score for that intersection (i.e. three species at one intersection were each scored as 1/3). Percent abundance for each species in a quadrat was calculated by summing the intersection scores and dividing the total by 12. For each species, the average of these quadrat abundances on a given sampling date was defined as the mean percent abundance for that species. Species richness (S), evenness (J'), and species diversity (H') were determined based on these mean percent abundance values using Primer[®] software. An index of dispersion (variance-to-mean ratio; Krebs, 1999) was calculated to assess the spatial pattern of selected species in the algal turf communities. Abundance of each species at each site was calculated by averaging the mean transect percent abundances during the sampling period (n = 7 for both sites). Data were arc-sine transformed to achieve homogeneity of variances. Differences in species abundance between sites were evaluated using a non-parametric Kruskal-Wallis test or one-way ANOVA for species that had equal variances. Variation in species abundance among sampling dates was assessed using one-way ANOVA after Bartlett's test confirmed equal variances. Tukey's pairwise comparison was employed to determine where the differences existed between sampling dates.

RESULTS

One hundred-two species (17 Chlorophyta, 9 Phaeophyta, and 76 Rhodophyta) were recorded in the algal turf as well as 15 taxa identified to genus only (Table 1). Thirty-eight new records were found for the island of Hawai'i (8 Chlorophyta, 1 Phaeophyta, and 29 Rhodophyta) (Table 1). Of these new records, approximately one-third was either common or abundant at one or both sites, for example, *Bryopsis pennata* var. *pennata*, *Ceramium cingulum*, *Champia parvula*, *Cladophora vagabunda*, and *Hypnea spinella*. Taxa had thallus diameters generally less than 2 mm, and included filamentous, fleshy, foliose, and some calcified forms. Turf communities at Lelewi and Puakō were dominated by red algae. Sixty percent of the taxa reported in the algal turf were considered rare (mean abundance ≤ 0.5%), and roughly one tenth of the species were labeled

Table 1. List of species and their abundance in turf communities at Leleiwi and Puakō on the island of Hawai'i. Abundance at each site was calculated by averaging the mean transect percent abundances during the sampling period (n = 7). R = rare ($\leq 0.5\%$). Species not found at a site are indicated with a "—". Values of p and F for ANOVA are listed, unless indicated otherwise: ^a p-value from non-parametric Kruskal-Wallis test, ^b H value. DF = 13 for ANOVA, 1 for Kruskal-Wallis. * new records for the island of Hawai'i.

Algae	Abundance			
	Leleiwi	Puakō	p value	F
Chlorophyta:				
<i>Boodlea composita</i> (Murray) Brand*	—	R		
<i>Bryopsis pennata</i> Lamouroux var. <i>pennata</i> *	1.04	R	0.074 ^a	3.20 ^b
<i>Caulerpa peltata</i> Lamouroux	R	R		
<i>Caulerpella ambigua</i> (Okamura) Prud'homme van Reine <i>et</i> Lokhorst*	—	R		
<i>Chaetomorpha capillaris</i> (Kützing) Børgesen	R	1.30	0.009 ^a	6.74 ^b
<i>Chlorodesmis caespitosa</i> J. Agardh	R	R	0.948	0.00
<i>Cladophora laetevirens</i> (Dillwyn) Kützing	R	R	0.940	0.01
<i>Cladophora sericea</i> (Hudson) Kützing	—	R		
<i>Cladophora vagabunda</i> (Linnaeus) Hoek*	0.61	0.67	0.779	0.08
<i>Codium edule</i> P.C. Silva in Egerod	R	—		
<i>Dictyosphaeria cavernosa</i> (Forsskål) Børgesen*	—	R		
<i>Dictyosphaeria</i> sp.	—	R		
<i>Enteromorpha paradoxa</i> (C. Agardh) Kützing	R	0.96	0.007 ^a	7.18 ^b
<i>Enteromorpha</i> sp.	R	R	0.216	1.71
<i>Percursaria</i> sp.	—	R		
<i>Phyllocladon anastomosans</i> (Harvey) Kraft <i>et</i> Wynne*	R	R	0.188	1.95
<i>Ulvella setchellii</i> Dangeard*	R	R	0.534 ^a	0.39 ^b
<i>Uronema marinum</i> Womersley*	—	R		
<i>Valonia aegagropila</i> C. Agardh	R	R	0.692	0.16
<i>Ventricaria ventricosa</i> (J. Agardh) Olsen <i>et</i> West	—	R		
Phaeophyta:				
<i>Asteronema breviarticulatum</i> (J. Agardh) Ouriques <i>et</i> Bouzon	R	—		
<i>Bachelotia antillarum</i> (Grunow) Gerloff	—	R		
<i>Chnoospora implexa</i> J. Agardh	R	R	0.677	0.18
<i>Cutleria</i> sp.	R	—		
<i>Dictyota ceylanica</i> Kützing	4.08	R	0.003 ^a	8.95 ^b
<i>Dictyota crenulata</i> J. Agardh	—	R		
<i>Dictyota friabilis</i> Setchell	1.85	0.98	0.159	2.26
<i>Padina</i> sp.	—	R		
<i>Sargassum</i> sp.	R	—		
<i>Sphacelaria novae-hollandiae</i> Sonder	1.43	0.87	0.532	0.41
<i>Sphacelaria rigidula</i> Kützing	R	—		
<i>Sphacelaria tribuloides</i> Meneghini*	R	—		
<i>Sphacelaria</i> sp.	R	0.90	0.033 ^a	4.54 ^b
Rhodophyta:				
<i>Acanthophora spicifera</i> (Vahl) Børgesen	1.69	R	0.063 ^a	3.46 ^b
<i>Acrochaetium catenatum</i> Howe	—	R		
<i>Acrochaetium robustum</i> Børgesen*	—	R		

<i>Algae</i>	<i>Lelewi</i>	<i>Abundance</i>		<i>F</i>
		<i>Puakō</i>	<i>p value</i>	
<i>Acrochaetium seriatum</i> Børgeesen	—	R		
<i>Amansia glomerata</i> C. Agardh	4.59	—		
<i>Amphiroa</i> sp.	0.95	R	0.065 ^a	3.39 ^b
<i>Amphiroa valonioides</i> Yendo*	R	—		
<i>Anotrichium tenue</i> (C. Agardh) Nägeli	1.45	R	0.517	0.45
<i>Asparagopsis taxiformis</i> (Delile) Trevisan	0.86	—		
<i>Caulacanthus ustulatus</i> (Turner ex Mertens) Kützing	R	0.75	0.203 ^a	1.62 ^b
<i>Centroceras clavulatum</i> (C. Agardh) Montagne	3.56	2.81	0.786	0.08
<i>Centroceras corallophilloides</i> R.E. Norris*	R	R	0.937	0.01
<i>Centroceras minutum</i> Yamada	R	R	0.678	0.18
<i>Ceramium aduncum</i> Nakamura*	R	R	0.174 ^a	1.85 ^b
<i>Ceramium cingulum</i> Meneses*	0.72	—		
<i>Ceramium clarionensis</i> Setchell et Gardner	1.99	R	0.002 ^a	9.77 ^b
<i>Ceramium codii</i> (Richards) G. Mazoyer	R	R	0.173	2.10
<i>Ceramium fimbriatum</i> Setchell et Gardner	R	R	0.031	6.01
<i>Ceramium flaccidum</i> (Kützing) Ardissonne	1.97	2.04	0.999	0.00
<i>Ceramium hanaense</i> R. E. Norris et Abbott	R	0.77	0.003 ^a	8.95 ^b
<i>Ceramium macilentum</i> J. Agardh	0.77	7.72	0.002	9.8
<i>Ceramium serpens</i> Setchell et Gardner*	0.57	0.61	0.877	0.02
<i>Ceramium vagans</i> Silva	R	2.36	0.001 ^a	10.62 ^b
<i>Ceramium womersleyi</i> R. E. Norris et Abbott	R	—		
<i>Champia parvula</i> (C. Agardh) Harvey*	0.75	1.13	0.101	3.15
<i>Chondria dangardii</i> Dawson*	R	—		
<i>Chondria minutula</i> Weber-van Bosse	1.29	—		
<i>Chondria polyrhiza</i> Collins et Hervey	R	—		
<i>Chondria simpliciuscula</i> Weber-van Bosse	0.70	1.83	0.108	3.02
<i>Chondria</i> sp.	R	—		
<i>Coelothrix irregularis</i> (Harvey) Børgeesen	1.11	5.00	0.001	17.00
<i>Corallophila apiculata</i> (Yamada) R. E. Norris	—	R		
<i>Corallophila huysmansii</i> (Weber-van Bosse) R. E. Norris*	R	—		
<i>Corallophila itonoi</i> (Ardrée) R. E. Norris*	R	R	0.422	0.69
<i>Crouania minutissima</i> Yamada*	R	—		
<i>Gelidiella acerosa</i> (Forsskål) Feldmann et Hamel	R	R	0.470	0.56
<i>Gelidiella antipai</i> Celán	—	R		
<i>Gelidiella machrisiana</i> (Børgeesen) Feldmann et Hamel	R	0.66	0.130	2.64
<i>Gelidiella myrioclada</i> (Børgeesen) Feldmann et Hamel	—	R		
<i>Gelidiopsis variabilis</i> (J. Agardh) Schmitz	0.75	3.89	0.047 ^a	3.96 ^b
<i>Gelidium pusillum</i> (Stackhouse) Le Jolis	R	—		
<i>Gelidium</i> sp.	R	R	0.389	0.80
<i>Griffithsia heteromorpha</i> Kützing	R	0.72	0.028	6.28
<i>Herposiphonia crassa</i> Hollenberg	R	R	0.262 ^a	1.26 ^b
<i>Herposiphonia delicatula</i> Hollenberg*	R	R	0.066	4.11
<i>Herposiphonia nuda</i> Hollenberg*	R	R	0.756	0.10
<i>Herposiphonia obscura</i> Hollenberg*	1.57	R	0.035 ^a	4.46 ^b
<i>Herposiphonia parca</i> Setchell	1.67	R	0.001 ^a	10.62 ^b
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn	R	R	0.018	7.50
<i>Herposiphonia</i> sp.	R	R	0.513	0.45

Algae	Leleiwi	Abundance		F
		Puakō	p value	
<i>Heterosiphonia crispella</i> (C. Agardh) Wynne	—	R		
<i>Hypnea pannosa</i> J. Agardh*	1.94	1.55	0.532	0.41
<i>Hypnea spinella</i> (C. Agardh) Kützing*	1.55	5.35	0.003	13.28
<i>Jania adhaerens</i> Lamouroux	2.31	3.90	0.068	4.03
<i>Jania</i> sp.	0.68	3.37	0.000	27.58
<i>Laurencia brachyclados</i> Pilger	4.51	2.61	0.277 ^a	1.18 ^b
<i>Laurencia dotyi</i> Saito*	R	1.51	0.161	2.23
<i>Laurencia majuscula</i> (Harvey) Lucas	R	R	0.250	1.46
<i>Laurencia mariannensis</i> Yamada	R	R	0.588	0.31
<i>Laurencia nidifica</i> J. Agardh*	0.95	R	0.117	2.85
<i>Laurencia parvipapillata</i> Tseng	R	R	0.917 ^a	0.01 ^b
<i>Laurencia undulata</i> Yamada*	R	—		
<i>Laurencia yamadana</i> Howe*	—	1.05		
<i>Laurencia</i> sp.	R	R	0.627	0.25
<i>Liagora</i> sp.	R	—		
<i>Liagora valida</i> Harvey	—	R		
<i>Polysiphonia delicatula</i> Hollenberg*	R	R	0.114	2.91
<i>Polysiphonia homoia</i> Setchell et Gardner	R	—		
<i>Polysiphonia poko</i> Hollenberg	R	—		
<i>Polysiphonia rubrorhiza</i> Hollenberg*	R	—		
<i>Polysiphonia saccorhiza</i> (Collins et Hervey) Hollenberg*	R	—		
<i>Polysiphonia scopulorum</i> Harvey	R	R	0.232	1.58
<i>Polysiphonia subtilissima</i> Montagne*	R	R	0.402	0.75
<i>Polysiphonia triton</i> Silva	R	—		
<i>Polysiphonia upolensis</i> (Grunow) Hollenberg*	1.57	R	0.008 ^a	7.08 ^b
<i>Polysiphonia</i> sp.	R	R	0.076	3.77
<i>Pterocladia bulbosa</i> (Loomis) Santelices*	R	—		
<i>Pterocladia caeruleascens</i> (Kützing) Santelices et Hommersand	0.79	6.99	0.025 ^a	5.04 ^b
<i>Pterocladia caloglossoides</i> (Howe) Santelices*	R	—		
<i>Ptilothamnion cladophorae</i> (Yamada et Tanaka) Feldmann-Mazoyer*	R	R	0.465	0.57
<i>Stylonema alsidii</i> (Zanardini) Drew*	R	R		
<i>Taenioma perpusillum</i> (J. Agardh) J. Agardh	1.65	1.45	0.774	0.09
<i>Tiffaniella saccorhiza</i> (Setchell et Gardner) Doty et Meñez	R	—		
<i>Tolyptocladia glomerulata</i> (C. Agardh) Schmitz	1.62	R	0.034	5.74

common with mean abundance between 0.5% and 3%. Only 4% of the species at Leleiwi and 6% of species at Puakō were considered abundant (mean abundance $\geq 3\%$). No species were ranked as abundant at both sites. The abundance of 18 species differed significantly ($p < 0.05$) at Leleiwi versus Puakō (Table 1). Species richness (ranging from 35 to 69 species) was similar at both sites (Table 2). Both sites exhibited similar levels of turf species diversity ($H' > 1$; Table 2); however, evenness was generally higher for Leleiwi than for Puakō turf assemblages (Table 2).

Table 2. Data on the total number of species (S) collected, species diversity (H'), and evenness (J') for each sampling date at Leleiwi and Puakō. $H' = -\sum_i p_i \log(p_i)$ $J' = H' / H'_{max} = H' / \log S$.

	<i>Leleiwi</i>				<i>Puakō</i>			
	Sept. 2000 (n = 17)	Nov. 2000 (n = 9)	Feb. 2001 (n = 18)	July 2002 (n = 18)	Sept. 2000 (n = 8)	Nov. 2000 (n = 18)	Feb. 2001 (n = 18)	July 2002 (n = 18)
Richness (S)	62	35	53	69	45	55	55	52
Diversity (H')	1.53	1.32	1.53	1.60	1.35	1.42	1.40	1.50
Evenness (J')	0.85	0.86	0.89	0.87	0.82	0.82	0.80	0.87

Table 3. Variance-to-mean ratio (I) for the most abundant species at each sampling time at Leleiwi and Puakō. Dispersion patterns are defined as aggregated if $I > 1$, random if $I = 1$ and uniform if $I < 1$.

<i>Species</i>	<i>Site</i>	<i>Sampling Date</i>	<i>I</i>
<i>Laurencia brachyclados</i>	Leleiwi	September 2000	7.50
<i>Ceramium macilentum</i>	Puakō	September 2000	5.76
<i>Dictyota ceylanica</i>	Leleiwi	November 2000	9.75
<i>Hypnea spinella</i>	Puakō	November 2000	25.27
<i>Amansia glomerata</i>	Leleiwi	February 2001	37.17
<i>Pterocladia caerulescens</i>	Puakō	February 2001	8.48
<i>Coelothrix irregularis</i>	Leleiwi	July 2002	24.67
<i>Laurencia dotyi</i>	Puakō	July 2002	32.76

At both sites, mean percent abundance of the three most abundant species showed fluctuations over time (Figs 2 and 3). At Leleiwi, no significant difference in abundance was detected in *Amansia glomerata*, *Dictyota ceylanica* nor *Laurencia brachyclados*. At Puakō, only *Pterocladia caerulescens* abundance differed significantly over time ($p = 0.029$, $F = 13.92$, $DF = 13$), and only the values in February and July were significantly different from each other (Fig. 3).

Species' distributions within the turf were patchy. At Leleiwi, the number of species/quadrats ranged from 3 to 24, and at Puakō from 1 to 23. Samples taken on the same transect on the same sampling date often varied greatly over short distances, for instance, at Leleiwi in July 2002, the number of species/quadrat ranged from 5 to 16 in quadrats 1 m apart (Fig. 4). The index of dispersion for each of the most abundant species for each sampling date at both sites (Table 2) indicated that these species were clumped or aggregated ($I > 1$), not randomly or uniformly distributed within the algal turf.

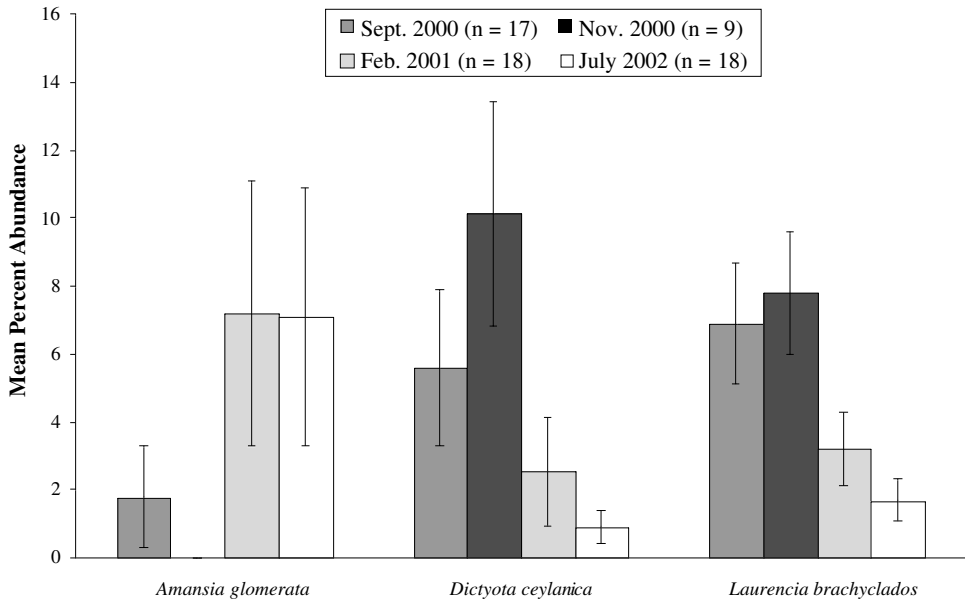


Fig. 2. Variation in mean percent abundance of the three most abundant turf species at Lelewi. Bars indicate the standard error (SE) of the mean.

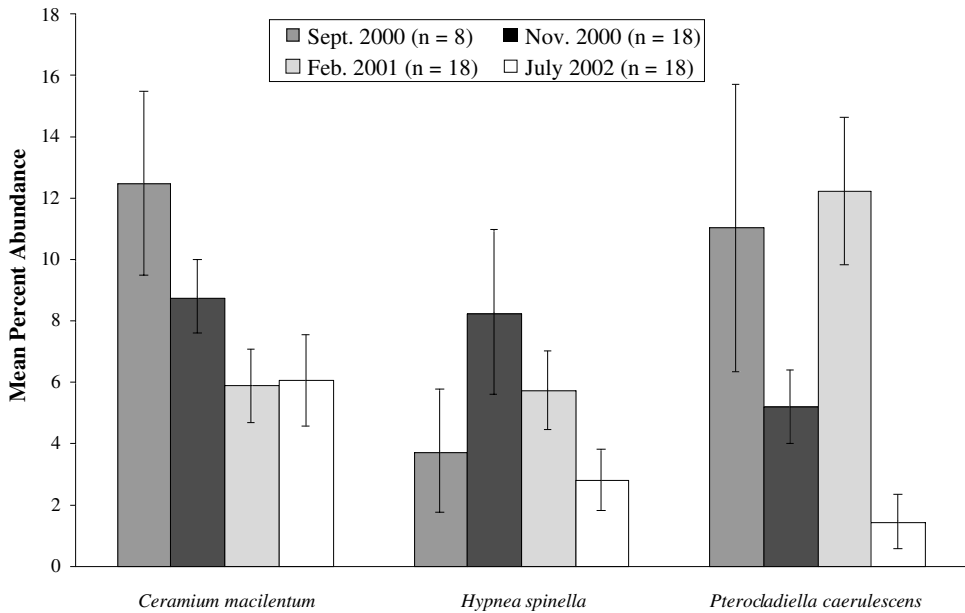


Fig. 3. Variation in mean percent abundance of the three most abundant turf species at Puakō. Bars indicate the standard error (SE) of the mean.

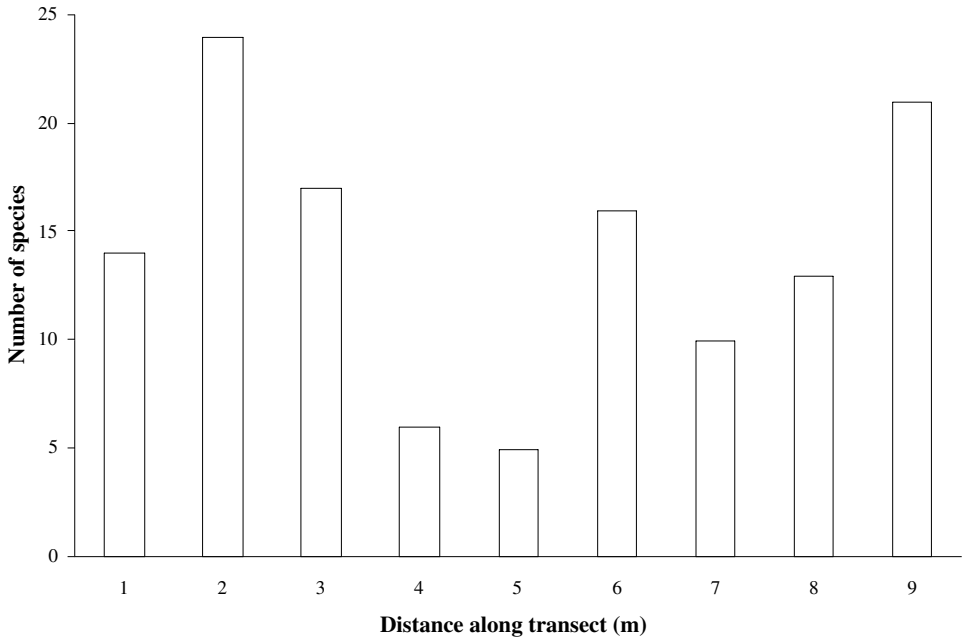


Fig. 4. Number of algal taxa found within each quadrat along one transect at Leleiwi in July 2002.

DISCUSSION

Algal turfs are common on reefs in the tropics, and yet the identities of the algal components are rarely documented or monitored. The species documented in this study comprise 20% of the known flora for the Hawaiian Islands (Abbott, 1999; Abbott & Huisman, 2004), which underscores the preeminence of turf algae despite their small stature (< 3 cm tall). Many of the new records for the island of Hawai'i were the most abundant species in the turf. The short, dense, tangled growth form of turfs may be an adaptive form on tropical reefs (Lobban & Harrison, 1994), but is not restricted to plants from a single functional-form group (Littler *et al.*, 1983). The turf communities at Leleiwi and Puakō included members of the Filamentous Group (e.g. *Asteronema*, *Centroceras*, *Ceramium*, *Chaetomorpha*, *Polysiphonia*, and *Sphacelaria*), the Sheet Group (i.e. *Dictyota* and *Enteromorpha*), the Jointed Calcareous Group (i.e. *Jania*), as well as fleshy, branched species (i.e. *Amansia*, *Chnoospora*, *Codium*, *Coelothrix*, *Laurencia*, and *Pterocladia*).

Both sites showed similar species richness values (S) and a dominance of red algal species. The Puakō turf community contained more taxa in the Chlorophyta than Leleiwi. The algal turf communities at Leleiwi and Puakō consistently showed high species diversity with average Shannon-Weiner diversity indices (H') of 1.5 and 1.4, respectively, when compared to the theoretical maximum for H' ($\log S = 1.9$ for both sites; Krebs, 1999). The greater level of evenness

of species at Leleiwi may have contributed to the higher H' at that site. Differences in species composition and abundance in the two communities may be due to the contrasting environmental conditions at the two sites, including aspect, substratum, tradewind-swell patterns, and rainfall.

Spatially, many of the algal species had aggregated distributions within the turf, which indicates that these communities are not homogenous lawns, but are complex, three-dimensional quilts of algal patches. The turf community concept of perennial basiphytes or anchor species (Stewart, 1982) hosting ephemeral epiphytes was not supported by our observations. For example, *Hypnea spinella* in some patches was the basiphyte for *Ceramium* and *Polysiphonia* species, but in other patches it grew epiphytically on *Pterocliadiella caerulescens*.

Different species dominated the turf at each site and at each sampling date. These two turf communities are more dynamic with more variable species dominance patterns than reported in other algal communities (Sousa, 1979; Santelices *et al.*, 1981; Dethier, 1984; McDermid, 1988; Karez & Chapman, 1998). Although Klumpp & McKinnon (1989) measured biomass turnover in turfs as rapid as once every 4-12 days, species turnover rates need to be determined by high frequency sampling (e.g. weekly during a month). In previous studies, sedimentation, desiccation, water motion, substratum slope, nutrient levels and/or grazing influenced turf distribution, standing crop, and productivity (Hay, 1981; Stewart, 1982; Hatcher & Larkum, 1983; Whorff *et al.*, 1995; Airolidi & Virgilio, 1998). On Hawaiian coasts, variability in rain run-off, nutrient levels, wave action, water temperature, light intensity, daylength, and grazing pressure probably contribute greatly to species distributions and interactions within the turf.

Unlike *Macrocystis*-forests or *Spartina*-marshes, turf communities are not characterized by a dominant or diagnostic species, but are defined by their recognizable short, dense, and tangled growth form. In addition, other traits of turfs, i.e. high species diversity without clear dominants, spatial heterogeneity, and temporal variability, must be taken into account to more fully understand turf community function, reef productivity, fish herbivory patterns, and even coral recruitment. The members of an algal turf community can differ in functional-form, life history, phenology, and photosynthetic activity, which emphasizes the importance of identification and monitoring of individual species.

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