

Temporal and spatial comparison of the relative abundance of macroalgae across the Mariana Archipelago between 2003 and 2005

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Past studies have argued that macroalgae serve as useful bioindicators that herald possible environmental changes to reef ecosystems because they are often opportunistic, having high growth rates and responding quickly to environmental changes, such as increased nutrient availability, grazing pressures, or storm activity. In this study, we test their usefulness as reef monitoring management indicators. We investigated the spatial and temporal variability of the relative abundance of macroalgae (RAM) at the genus level in the Mariana Archipelago between two surveys in 2003 and 2005. Islands vary drastically across the archipelago (carbonate vs volcanic, populated vs unpopulated, small vs large) and often experience considerable storm activity. We showed that the diversity of macroalgal genera was generally highest at the southern end of the archipelago, probably because of increased habitat heterogeneity around these geographically larger islands. At the northern end of the archipelago, only Pagan and Maug were large enough or contained enough environmental diversity to exhibit macroalgal diversity similar to that of the southern carbonate islands. Despite the ubiquitous nature of turf algae, crustose coralline red algae, and the green alga *Halimeda* (Bryopsidales) across the archipelago, multivariate analyses revealed RAM to differ among islands with northern, unpopulated, volcanic islands grouping together and differing from southern, populated, carbonate islands. Also, RAM showed significant variability at the local scale (among sites within an island) and over time. We hypothesize that this variability results principally from differing oceanographic conditions such as sea surface temperature, human impacts such as fishing and pollution, typhoons, and volcanic activity across the archipelago. These results provide a baseline for future monitoring studies in the Mariana Archipelago and suggest that rapid ecological assessments of macroalgae in the field at the genus level are a reliable indicator that can be used to monitor change over time.

KEY WORDS: Algae, Coral reef, Mariana Archipelago, Northwestern Hawaiian Islands, Relative abundance, Spatial variability, Temporal change

INTRODUCTION

In tropical reef ecosystems, algal functional groups including crustose coralline red algae, turf algae, and fleshy macroalgae are abundant and widely distributed, contributing to the reef framework, sedimentation, and the food chain (Adey 1998; Chisholm 2003). Both healthy (Vroom *et al.* 2005a) and degraded (Lapointe *et al.* 2004; Fabricius *et al.* 2005) reefs where macroalgal communities dominate serve as sinks for atmospheric CO₂ because of high rates of net primary production (Kayanne *et al.* 1995; Gattuso *et al.* 1996a, b, 1997; Kraines *et al.* 1996). Because algal functional groups are often opportunistic (Adey 1998), having high growth rates and responding quickly to environmental changes (Thacker *et al.* 2001; Hallock 2005) such as increased nutrient availability (Hunter & Evans 1995; Fabricius *et al.* 2005; Lapointe *et al.* 2005a, b), grazing pressures (Adey 1998; Szmant 2002), or storm activity (Vroom *et al.* 2005b), they may serve as useful bioindicators that herald possible environmental changes to coastal ecosystems (Le Bris *et al.* 1998; O'Shanahan *et al.* 2003; Barile 2004).

To better understand and conserve tropical reefs as a whole, remote ecosystems with little anthropogenic activity can serve as models for comparison with disturbed reef environments. In remote areas such as the northern Mariana Islands, algal functional groups have been poorly studied. Examining algal populations in these areas can (1) provide researchers with a

glimpse of the constitution of algal communities in healthy tropical reef environments and (2) serve as a direct point of comparison with reefs around heavily populated islands located at the southern end of the archipelago. Although our phycological knowledge of Guam is well established (Merten 1971; Tsuda 1972a, b, 1974, 1977, 2003; Tsuda & Kami 1973; Gordon *et al.* 1976; Paul & Van Alstyne 1988, 1992; Lobban *et al.* 2002), the remote location and challenging working conditions around many of the northern Mariana Islands have greatly limited phycological studies. Only two lists of macroalgal species that include all 15 islands in the archipelago are available (Tsuda & Tobias 1977a, b; Tsuda 2003). These studies report a total of 332 species of benthic marine macroalgae, with most species known only from Guam and Saipan (Tsuda 2003). The number of species collected from the unpopulated islands of the archipelago ranges from 1 (for Saipan) to 52 (for Maug) and will increase substantially as additional marine algae collected during our expeditions are taxonomically identified (R. Tsuda, personal communication).

In October 2003 and October 2005, as part of the NOAA Coral Reef Conservation Program's Mariana Archipelago Reef Assessment and Monitoring Program (MARAMP), the Coral Reef Ecosystem Division (CRED), Pacific Islands Fisheries Science Center of the NOAA Fisheries Service, conducted algal surveys at all islands and several submerged banks in the Mariana Archipelago. These efforts are the first to provide quantitative algal data for the entire archipelago and investigate the variability of the relative abundance of

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macroalgae (RAM) at the genus level at 15 islands and banks over a two-year period (2003–2005). Our objectives were to (1) determine RAM at each island in the Mariana Archipelago for both 2003 and 2005, (2) deduce if RAM differed spatially among sites/islands within each sampling period, and (3) examine if RAM changed among sites/islands over time.

MATERIAL AND METHODS

Location

Wedged between the Philippine Sea to the west and the Pacific Ocean to the east, the Mariana Archipelago contains 15 major islands and numerous banks and shoals that stretch for 750 km along a north-to-south axis (Fig. 1). Fourteen islands belong to the US Commonwealth of the Northern Mariana Islands (CNMI), while the southernmost island belongs to the US Territory of Guam.

Guam, Rota, Tinian, and Saipan represent the largest, southernmost inhabited islands in the archipelago. Although they have a volcanic origin, each island is now capped by a raised carbonate platform protected by barrier and well-developed fringing reefs to the west (leeward side) (Gilman 1997; Richmond *et al.* 2002). Guam, the largest of these islands (560 km²) contains numerous reef habitats (fringing reefs, barrier reefs, reef slopes, and lagoon and patch reefs). Guam also shows high biodiversity with 306 species of macroalgae and 403 species of hard corals reported (Richmond *et al.* 2002). The southern carbonate islands, except Aguijan, which is uninhabited, experience varying levels of anthropogenic stress including fishing, sewage, pollution, dredging, and sedimentation that reduce water quality and smother nearshore corals (Richmond *et al.* 2002; Abraham *et al.* 2004; Bearden *et al.* 2005). Santa Rosa is a submerged carbonate bank located southwest of Guam and is reported to experience some fishing pressure (Abraham *et al.* 2004; personal observation).

The northern nine islands (Uracas, Maug, Asuncion, Agrihan, Pagan, Alamagan, Guguan, Sarigan, and Anatahan) are distinct from their southern counterparts and represent small, uninhabited, active strato-volcanoes that rise steeply from the ocean floor. Although most of these northern islands are volcanic cones, Maug consists of three small islands surrounding a flooded caldera. The coral reefs around most of the northern islands exhibit limited coral development, and some have experienced sedimentation due to deforestation by feral animals and volcanic activity (Richmond *et al.* 2002). The ash fallout from the 2003 and 2005 eruptions at Anatahan Island caused extensive damage to nearshore reef habitats (Bearden *et al.* 2005).

In general, limited *in situ* oceanographic data are available for the Mariana Archipelago. Sea surface temperature (SST) varies seasonally (Fig. 2), ranging between ~24.5°C and 30.5°C at the northern end of the archipelago (Maug), with a smaller range of ~25.5°C to 30.0°C at the southern end of the archipelago (Guam). Between October and November, the northern islands typically experience temperatures at least 1°C cooler than their southern counterparts. October 2005 salinity measurements varied between 34.2 and 34.7 from south to north (R. Hoeke, personal communication). In regard to weather, the Mariana Archipelago experiences frequent typhoons and tropical storms, especially from August to November. For example, between June 2002 and October 2003,

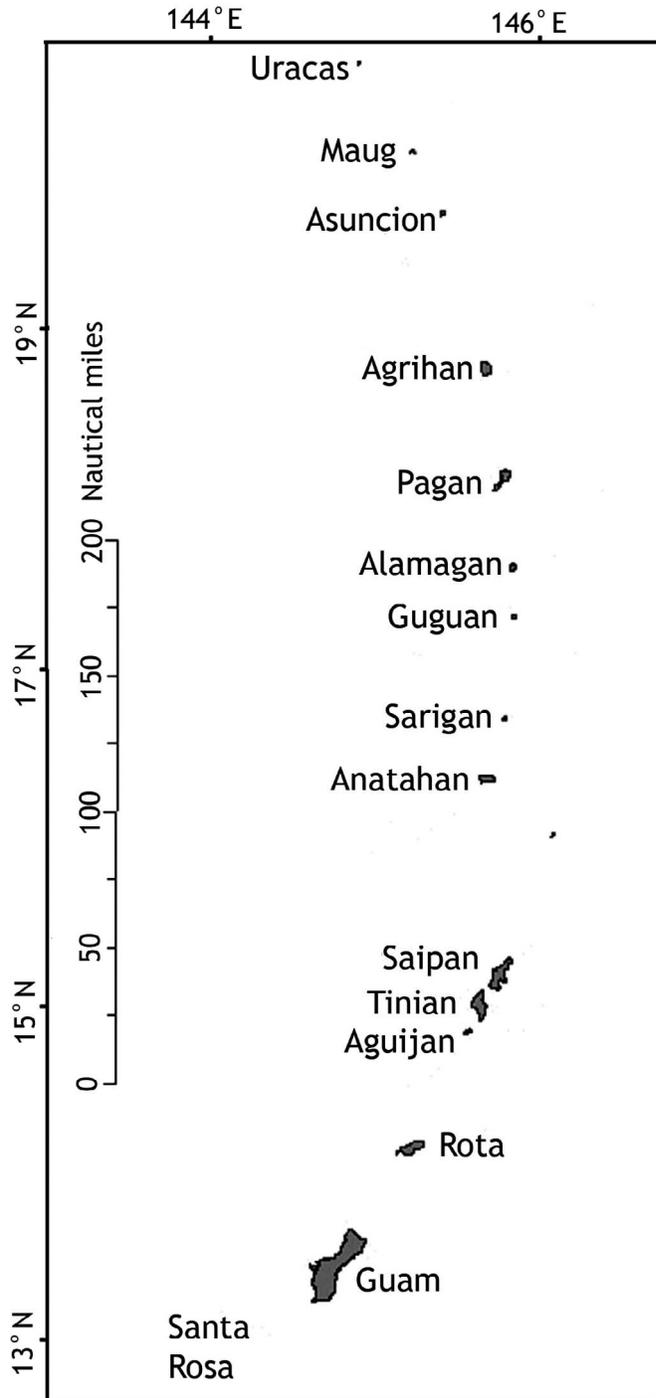


Fig. 1. Map of the Mariana Archipelago.

four typhoons and four tropical storms (Table 1) passed over the archipelago, affecting primarily the southern islands. The last typhoon occurred in August 2005 at the beginning of our research expedition, affecting primarily the islands of Saipan and Tinian.

Very few prior data concerning reef health are known for most of the archipelago. A major crown-of-thorns starfish (COTS) outbreak was reported in 1978 around Rota, Saipan, and Tinian (Quinn & Kojis 2003), but since that event, the density of COTS has remained low around those islands

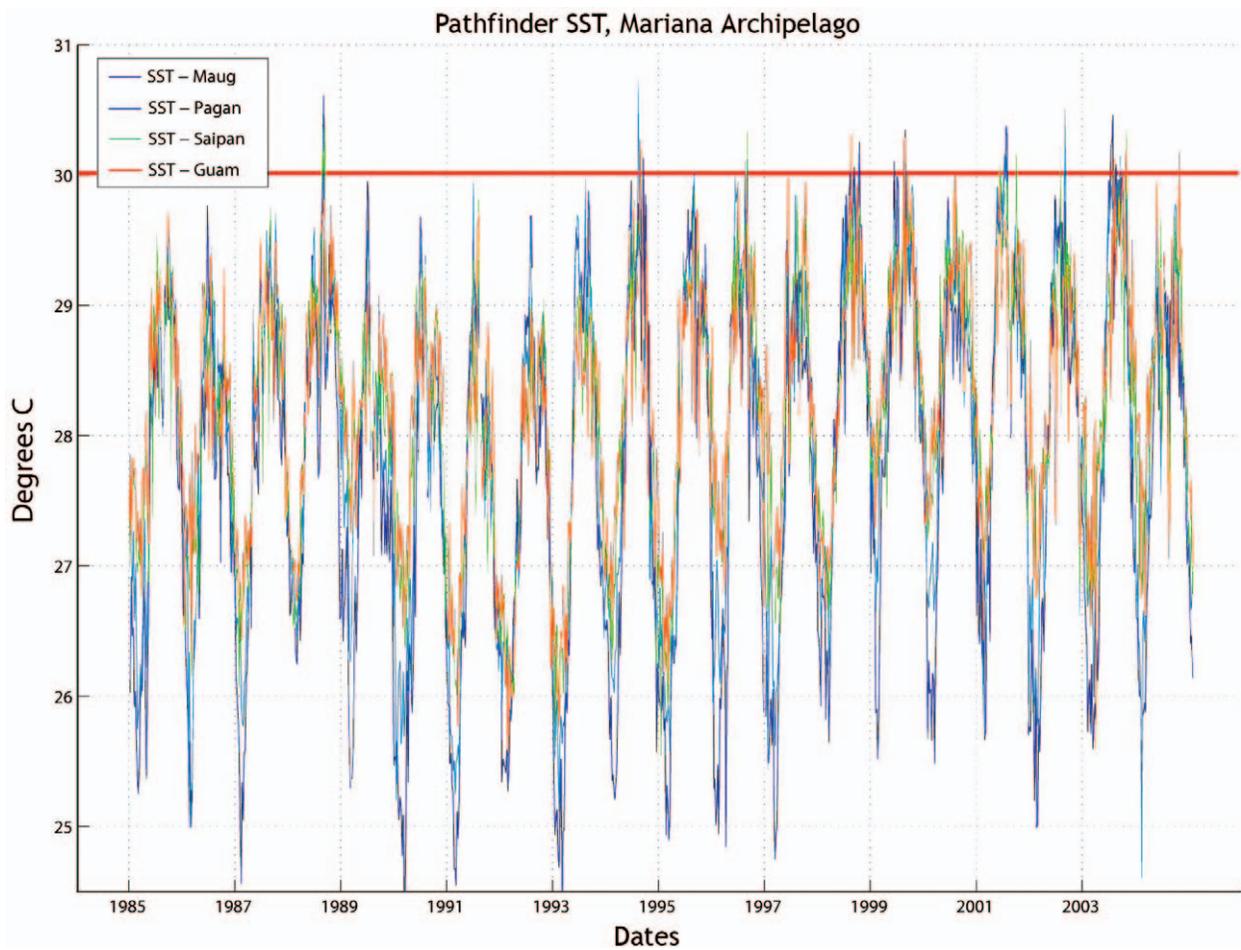


Fig. 2. Pathfinder satellite Sea Surface Temperatures (SST) from Maug, Pagan, Saipan, and Guam: January 1985–January 2005. Red line indicates temperature at which coral bleaching is known to occur. (Figure made by Ronald Hoeke.)

Table 1. Typhoon activity in Guam and CMNI: June 2002–August 2005. Storm statistics from http://weather.unisys.com/hurricane/w_pacific/.

| Storm | Date | Latitude | Longitude | Wind speed (km h ⁻¹) | Islands closest to storm path |
|---------------------|----------------|----------|-----------|----------------------------------|-------------------------------|
| Typhoon #8 | Jun. 2002 | 13.3 | 145.7 | 167 | Guam |
| | | 13.8 | 144.2 | 176 | Guam |
| | | 14.2 | 143.2 | 200 | Rota |
| Typhoon #10 | Jul. 2002 | 12 | 144.2 | 176 | Santa Rosa, Guam |
| Typhoon #25 | Oct. 2002 | 18 | 145.8 | 120 | Pagan, Alamagan |
| | | 18.6 | 144 | 139 | Pagan, Agrihan |
| Typhoon #31 | Dec. 2002 | 12 | 146.2 | 204 | Guam |
| | | 14.3 | 144.7 | 240 | Rota |
| | | 15.2 | 144.2 | 231 | Saipan, Anatahan |
| Typhoon Tinting | Jul. 2004 | 16.2 | 146.4 | 120 | Anatahan |
| | | 16.8 | 145.7 | 139 | Sarigan |
| | | 17.6 | 144.9 | 139 | Pagan, Alamagan |
| Supertyphoon Chaba | Aug. 2004 | 14.4 | 146.3 | 203 | Rota |
| | | 14.4 | 145.4 | 231 | Rota |
| | | 17.6 | 144.9 | 139 | Aguijan |
| Supertyphoon Songda | Aug./Sep. 2004 | 17.8 | 146.7 | 241 | Pagan, Alamagan |
| | | 18.4 | 146.3 | 231 | Pagan, Agrihan |
| | | 19.6 | 145.4 | 231 | Asuncion |
| Typhoon Haitang | Jul. 2005 | 21.3 | 145.9 | 130 | Uracas |
| | | 20.5 | 144.7 | 139 | Uracas |
| Typhoon Nabi | Aug. 2005 | 15.6 | 146.3 | 167 | Saipan, Tinian |
| | | 16.5 | 145.0 | 176 | Anatahan |

(Quinn & Kojis 2003) and more generally across the archipelago (Richmond *et al.* 2002). Coral bleaching has been noted in CNMI and Guam several times since 1994 (Richmond *et al.* 2002), but no quantitative assessment exploring the spatial extent of these events was made (Bearden *et al.* 2005).

Survey technique

As part of the MARAMP surveys, CRED quantitatively assessed algal populations at 64 sites in 2003 and 70 sites in 2005 at 15 islands and three submerged banks in the Mariana Archipelago (Appendix 1). At each island surveyed, long-term monitoring sites were selected by a multidisciplinary group of researchers to represent a variety of habitat types that could be accessed on a biennial basis regardless of prevailing weather or oceanographic conditions. At each site, phycologists used SCUBA to sample two 25-m transect lines set in a single-file row, with each transect separated by ~10 m. A 0.18-m² sampling quadrat was located at randomly selected points along each transect (three points per transect), and another quadrat was located at a point 3-m perpendicular from each random point in the direction of shallower water; altogether, there were 12 quadrats per site. The usefulness, efficiency, and accuracy of this protocol have been demonstrated by Preskitt *et al.* (2004), Vroom *et al.* (2005a, 2006), and Vroom & Page (2006). Fleishy macroalgae were identified to genus in the field, whereas cyanophytes, branched nongeniculate coralline red algae [e.g. *Neogoniolithon brassica-florida* (Harvey) Setchell & Mason; R. Tsuda, personal communication], crustose coralline red algae, brown algal crusts, orange algal crusts, and turf algae were lumped into functional group categories, their identification being difficult or impossible underwater. Ranks were assigned to each genus or functional group found in each quadrat (1 being the most abundant in terms of number, 2 being the next most abundant, etc., with 10 being the maximum number of genera found in a single quadrat) to determine RAM.

Statistical analysis

To test significant differences of RAM among sites and islands, a matrix was created that included genus and functional group ranks from quadrats surveyed in 2003 and 2005. Each quadrat was treated as an individual replicate within a site for each year ($n = 12$ quadrats/site), and a Bray–Curtis similarity matrix of untransformed rankings by quadrat was created using PRIMER 5.2.9. (Clarke & Warwick 2001). For each year surveyed, a two-way nested analysis of similarity (ANOSIM; 5000 permutations) nesting sites within island ($n = 64$ sites for 2003, $n = 70$ sites for 2005) was conducted to determine if differences in similarities occurred among sites and islands. These analyses were followed by two similar ANOSIMs, one for each year, using only common sites surveyed both in 2003 and 2005 ($n = 46$ common sites; 5000 permutations).

To depict relationships among islands (latitudes) based on RAM, data within the matrices were averaged by island for each year, and a Bray–Curtis similarity matrix of the averaged data was generated. Ordinations of relationships were created *via* nonmetric multidimensional scaling (nMDS; 30 restarts) and these relationships visually compared to geographic maps of the archipelago.

To determine if RAM changed over time across the entire

Mariana Archipelago or within individual islands, several two-way crossed ANOSIMs were conducted. In the first analysis, 46 sites from across the Mariana Archipelago sampled in both 2003 and 2005 were compared (Appendix 1; Factor A = year, Factor B = site; 5000 permutations). In the other analyses, temporal changes were examined at each island independently of other islands (Factor A = year, Factor B = site; 5000 permutations).

RESULTS

Diversity

Forty-seven genera of fleshy macroalgae were found at sites sampled across the Mariana Archipelago (35 genera in 2003, 47 genera in 2005; Table 2). Additionally, six algal functional groups including cyanophytes, branched nongeniculate coralline red algae, crustose coralline red algae, brown algal crusts, orange algal crusts, and turf algae (dominated by red algal species of the order Ceramiales) were documented. Southern carbonate islands generally exhibited a higher diversity of macroalgal genera than northern volcanic islands, although there was no statistical difference between islands (Tables 2, 3). In 2003 and 2005, turf algae, crustose coralline red algae, and species of the green algal genus *Halimeda* Lamouroux were the most common algae to occur in quadrats across the Mariana Archipelago (Table 2). Other ubiquitous although less prevalent genera or functional groups included the chlorophyte *Neomeris* Lamouroux, the phaeophyte *Dictyota* Lamouroux, the rhodophyte *Jania* Lamouroux, and nongeniculate branched coralline red algae. *Lobophora* Agardh, a genus of brown algae, commonly occurred around northern islands during both sampling periods but was not observed around southern islands during 2003 and was rarely observed during 2005.

Several differences were observed in algal prevalence within sampled quadrats between 2003 and 2005. *Dictyota* and *Jania*, two genera commonly seen in abundance across the archipelago in 2005, were observed only sporadically in 2003. On a more regional level, cyanophyte populations seemed to decrease in abundance at northern islands between 2003 and 2005 (Table 2). Similarly, *Dictyosphaeria* Decaisne, *Microdictyon* Decaisne, *Galaxaura* Lamouroux, and *Padina* Adanson were common in southern islands during 2003, but by 2005 only *Dictyosphaeria* remained a common component of areas sampled. *Neomeris* was the only genus whose relative abundance increased at southern islands from 2003 to 2005. The chlorophyte *Chlorodesmis* Harvey & Bailey was common at most islands during both research expeditions but was especially abundant in northern islands during the 2005 sampling period.

Spatial variability

The two-way nested ANOSIMs of ranked data from 64 and 70 sites in 2003 and 2005, respectively, showed that RAM did not vary across the archipelago as a whole (no difference among islands, r values ≤ 0.25 and $P < 0.001$; Table 3) but highlighted moderate differences of RAM among sites within islands (r values ≈ 0.4 , $P < 0.001$). The two-way nested ANOSIMs using only sites common to both 2003 and 2005 suggest minimal differences of RAM among islands (r values \approx

Table 2. Percentage of quadrats at each island in which macroalgal genera were found in 2003 and 2005. Year 2003 data are represented by numbers without parentheses; 2005 data are represented by numbers in parentheses. Symbols are used for genera that occurred in < 20% of quadrats; ■ = 2003 data, ◆ = 2005 data. Crust. Coralline, crustose coralline red algae; branch. corall., nongeniculate branched coralline red algae; *Laurencia/Ch. Laurencia/Chondrophycus*; SAN, Santa Rosa; GUA, Guam; ROT, Rota; AGU, Aguijan; TIN, Tinian; SAI, Saipan; SAR, Sarigan; ALA, Alamagan; PAG, Pagan; AGR, Agrihan; ASU, Asuncion; MAU, Maug; URA, Uracas.

| Genus/group | SAN | GUA | ROT | AGU | TIN | SAI | SAR | ALA | PAG | AGR | ASU | MAU | URA |
|--------------------------------|-----------|----------|----------|----------|---------|----------|---------|-----------|---------|---------|---------|---------|----------|
| Island size (km ²) | Submerged | 541 | 85 | 7 | 102 | 120 | 5 | 11 | 48 | 30 | 7 | 2 | 3 |
| Human population | 0 | 168,564 | 3283 | 0 | 3540 | 62,392 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| No. genera | 15 | 34 | 27 | 12 | 24 | 25 | 13 | 11 | 23 | 17 | 12 | 22 | 9 |
| No. functional groups | 2 | 4 | 5 | 6 | 5 | 5 | 5 | 5 | 5 | 5 | 4 | 4 | 2 |
| Functional groups | | | | | | | | | | | | | |
| Branch. corall. | (25) | 27 | ■ | ◆ | 36 ◆ | 54 ◆ | 50 | 25 | 55 ◆ | ■◆ | | 64 ◆ | |
| Brown crusts | | | | ◆ | | | | | | | | | |
| Crust. coralline | | 81 (64) | 46 (47) | 75 (86) | 47 (46) | 47 (73) | (56) | 67 (83) | 42 (75) | 53 (56) | 22 (78) | 43 (43) | 25 |
| Cyanophytes | (58) | 56 (52) | 48 (89) | 38 (61) | ■(64) | 22 (50) | ■ | 44 | 43 (23) | 28 | 50 | 22 | |
| Orange crust | | | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ | ◆ |
| Turf algae | 100 (88) | 98 (100) | 100 (97) | 96 (100) | 89 (97) | 100 (95) | 94 (91) | 100 (100) | 94 (96) | 86 (97) | 97 (97) | 83 (81) | 100 (89) |
| Green algae | | | | | | | | | | | | | |
| <i>Anadyomene</i> | ◆ | | | | | | | | | | | | |
| <i>Avrainvillea</i> | ■(63) | 42 ◆ | ■◆ | | ◆ | | | | ◆ | | | | |
| <i>Boodlea</i> | ■ | ◆ | ■◆ | ◆ | ◆ | | 22 | | 63 | | | | |
| <i>Bornetella</i> | ◆ | | 42 ◆ | | ◆ | | | | | | | | |
| <i>Bryopsis</i> | | ■ | ◆ | | | ◆ | | | | | ■ | ■ | |
| <i>Caulerpa</i> | ■(63) | ■(29) | 21 ◆ | ■◆ | 25 ◆ | ■◆ | | ■◆ | 33 ◆ | 42 ◆ | ■◆ | 58 ◆ | ■◆ |
| <i>Chlorodesmis</i> | | ■◆ | ■◆ | ■◆ | ◆ | ◆ | ■◆ | 79 ◆ | ■◆ | 25 ◆ | ■(31) | 25 ◆ | ◆ |
| <i>Codium</i> | (21) | ◆ | | | | | | | | | | | |
| <i>Dictyosphaeria</i> | 75 (79) | ■◆ | 25 (32) | 25 (39) | ◆ | ◆ | | ■ | 22 ◆ | ■◆ | ◆ | ■◆ | ◆ |
| <i>Halimeda</i> | 58 (92) | 51 (95) | 60 (67) | 33 (31) | 61 (60) | ■◆ | 75 (58) | 44 (30) | 41 | 25 (28) | 25 (32) | ■ | |
| <i>Microdictyon</i> | 100 (67) | | 92 ◆ | 75 ◆ | | ◆ | | | | | | | |
| <i>Neomeris</i> | (38) | 48 (45) | 25 ◆ | | 21 (31) | 33 ◆ | | ■◆ | 50 ◆ | 30 ◆ | ■◆ | ■◆ | ■ |
| <i>Rhipidosiphon</i> | | | | | ◆ | ◆ | ◆ | | ■ | 25 ◆ | ◆ | ■◆ | |
| <i>Trichosolen</i> | | | | | | | ◆ | | | | | | |
| <i>Tydemania</i> | | ◆ | ◆ | | | ■ | | | ◆ | | | | |
| <i>Udotea</i> | 58 (58) | ◆ | ■◆ | | ■◆ | | | | | | | | |
| <i>Valonia</i> | | ■ | | | ◆ | ◆ | | | ◆ | | | ◆ | |
| <i>Ventricaria</i> | | ■ | ■ | ■ | ◆ | ◆ | ■◆ | | ■◆ | ■◆ | 25 | ■◆ | |
| Red algae | | | | | | | | | | | | | |
| <i>Acanthophora</i> | | ◆ | | | | | | | | | | | ◆ |
| <i>Actinotrichia</i> | | | | | ◆ | ◆ | | | ■◆ | | | | |
| <i>Amansia</i> | | ◆ | | | ◆ | ■◆ | ◆ | | | | | | |
| <i>Amphiroa</i> | | ■(48) | (29) | | (42) | 50 ◆ | ◆ | ◆ | (36) | | | ◆ | |
| <i>Asparagopsis</i> | | 50 ◆ | ◆ | | ■◆ | ■◆ | | ■◆ | ■◆ | | | ◆ | |
| <i>Botryocladia</i> | | ■◆ | | | | ◆ | | | | | | | |
| <i>Cheilosporum</i> | | | | | | | | | ◆ | | | | |
| <i>Chondria</i> | | | ◆ | | | | | | | | | | |
| <i>Coelarthum</i> | | | | | | | | | | ■ | | | |
| <i>Crouania</i> | | ■ | | | | | ◆ | | | | | | |
| <i>Dasya</i> | | | | | | | | | ◆ | | | | |
| <i>Galaxaura</i> | | 33 (37) | 25 ◆ | | ■(24) | 25 ◆ | ◆ | ◆ | | | | ◆ | |
| <i>Gelid</i> | 92 | 38 ◆ | ■ | | ◆ | ■ | | | ■◆ | ■ | | ■◆ | |
| <i>Gracilaria</i> | | ◆ | | | | | | | | | | | |
| <i>Halychrysis</i> | | | | ◆ | | | | | | | | | |
| <i>Hypnea</i> | | ◆ | | | | | | | | | | | |
| <i>Jania</i> | | ◆ | ■◆ | ■(30.6) | (27.8) | (45.0) | (52.8) | ■◆ | ■◆ | ■(63.9) | ■◆ | ■◆ | (44.4) |
| <i>Laurencia/ch</i> | (38) | ■◆ | 42 | | | | | | | ■ | | ■ | |
| <i>Liagora</i> | (25) | ■ | | | | | | | | | | | |
| <i>Martensia</i> | | ◆ | | | | ◆ | | | | ◆ | | | |
| <i>Peyssonnelia</i> | | ◆ | ◆ | | (33) | | | | | ■ | | | |
| <i>Porteiria</i> | | ■◆ | ■◆ | | ◆ | | | | | | | | |
| <i>Tricleocarpa</i> | | 50 | | | ■ | ■ | | | ◆ | | | | |
| <i>Wrangelia</i> | | | | | | | | | ◆ | | | | |
| <i>Yamadaella</i> | | | ■ | | | | | | | | | | |
| Brown algae | | | | | | | | | | | | | |
| <i>Dictyota</i> | | ■(44) | 38 (39) | ◆ | (29) | ■(28) | (20) | (25) | ■◆ | ■◆ | ■◆ | 50 (36) | ■◆ |
| <i>Lobophora</i> | ◆ | | ◆ | | ◆ | ◆ | ◆ | 42 ◆ | ■◆ | 83 (81) | 75 (78) | 40 (36) | 71 (78) |
| <i>Padina</i> | | 58 (25) | 25 ◆ | | ◆ | ■◆ | | | | ■◆ | ■◆ | ■ | ■ |
| <i>Turbinaria</i> | | ■◆ | ■◆ | ◆ | ◆ | ◆ | | | | ■ | | 25 ◆ | |

Table 3. Two-way nested ANOSIM: *r* values among islands and sites in 2003 and 2005. Each *r* value had a *P* value < 0.001.

| Comp 2003/2005 | 2003 | | 2005 | |
|----------------|-----------------------|---|-----------------------|---|
| | All 64 sites sampled | 46 common sites assessed in 2003 and 2005 | All 70 sites sampled | 46 common sites assessed in 2003 and 2005 |
| Islands | 0.22 (<i>n</i> = 15) | 0.28 (<i>n</i> = 13) | 0.25 (<i>n</i> = 16) | 0.29 (<i>n</i> = 13) |
| Sites | 0.41 | 0.35 | 0.40 | 0.41 |

0.29, $P < 0.001$) and moderate differences among sites within islands (r values = 0.35, 0.41, $P < 0.001$).

Relationships among islands based on RAM were illustrated using nonmetric multidimensional scaling (nMDS) (Fig. 3). The nMDS clustered Santa Rosa, Guam, Rota, Aguijan, Tinian, and Saipan together at one end of the ordination, similar to their geographic location at the southern end of the Archipelago (Fig. 1). Similarly, most volcanic islands clustered together at the

other end of the ordination. Islands that did not follow geographic trends in the nMDS ordination include the volcanic island Pagan, whose algal flora was more similar to Saipan and Tinian than other northern islands, and Alamagan and Guguan, whose algal floras were more closely aligned to the southern island of Aguijan. Finally, Anatahan was situated with the northernmost islands in the nMDS ordination (close to Uracas). Stress values of 0.09 and 0.1 in 2003 and 2005, respectively, indicate a good representation of island relationships in the two-dimensional nMDS ordinations based on RAM (Chapman & Underwood 1999). Because relationships of islands in the nMDS ordinations were similar regardless of sampling year, only the nMDS map for 2003 is presented (Fig. 3).

Temporal variability

The two-way crossed ANOSIM comparing years and sites across the Mariana Archipelago showed differences in RAM among sites (r value = 0.52, $P < 0.001$) and moderate differences over time (r value = 0.39, $P < 0.001$; Clarke & Warwick 2001). Island by island, the two-way crossed ANOSIMs showed similar moderate changes of RAM between 2003 and 2005 (r values = 0.28–0.39, $P < 0.001$) except for Agrihan, Sarigan, Tinian, Rota, Guam, and Santa Rosa, where the change was more statistically significant (r values = 0.43–0.57, $P < 0.001$, Table 4). Aguijan was the only island at which RAM did not change over time (r value = 0.18, $P < 0.001$). The two-way crossed ANOSIMs also highlighted a higher variability of RAM among sites at the southern carbonate islands (average r value = 0.48) than at the volcanic islands (average r value = 0.28, $P < 0.001$; Table 4). No change in RAM was observed among sites at Uracas, Asuncion, and Sarigan.

DISCUSSION

This study provides the first quantitative data of algal genera and functional groups across the entire Mariana Archipelago and lays the groundwork for continued algal monitoring studies. It also represents the second major collection of macroalgal genera from the northernmost Mariana Islands. All 47 genera found had been previously reported for the archipelago (Tsuda & Tobias 1977a, b; Tsuda 2003), and many new species records from these collections are in the process of being documented (R. Tsuda, personal communication).

Spatial variability

As documented in the Hawaiian Archipelago (Vroom *et al.* 2005a; Vroom & Page 2006), habitat variability within single island ecosystems can vary dramatically depending on oceanographic conditions, geomorphology, and island size. In the Mariana Archipelago, the northern volcanic islands contain often poorly developed, steep reefs composed of massive boulders or

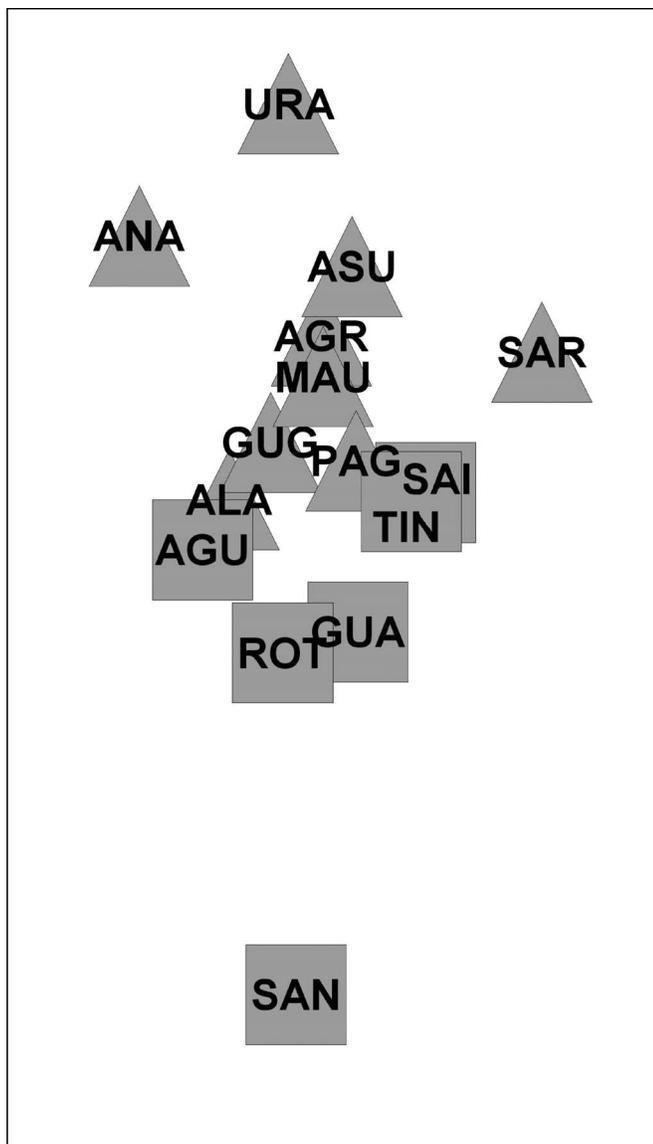


Fig. 3. nMDS plot mapping relationships among islands based on average genus ranks in 2003. Stress = 0.09. Island abbreviations are listed in Appendix 1. Squares represent southern carbonate islands; triangles represent northern volcanic islands.

Table 4. Two-way crossed ANOSIM: *r* values between years and among sites within individual islands. *n* = number of common sites visited at each island in 2003 and 2005. Each *r* value had a *P* value < 0.001.

| Island | Santa Rosa | Guam | Rota | Aguijan | Tinian | Saipan | Sarigan | Alamagan | Pagan | Agrihan | Asuncion | Maug | Uracas |
|------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| <i>r</i> -values | (<i>n</i> = 1) | (<i>n</i> = 6) | (<i>n</i> = 5) | (<i>n</i> = 2) | (<i>n</i> = 3) | (<i>n</i> = 3) | (<i>n</i> = 2) | (<i>n</i> = 3) | (<i>n</i> = 6) | (<i>n</i> = 3) | (<i>n</i> = 3) | (<i>n</i> = 7) | (<i>n</i> = 3) |
| Years | 0.49 | 0.46 | 0.43 | 0.18 | 0.47 | 0.34 | 0.57 | 0.38 | 0.36 | 0.46 | 0.39 | 0.32 | 0.28 |
| Sites | xx | 0.44 | 0.61 | 0.25 | 0.36 | 0.72 | 0.13 | 0.4 | 0.29 | 0.34 | 0.24 | 0.37 | 0.21 |

large plains of black sand, although some of the larger islands exhibit calmer lagoon-like or reef flat areas. Southern carbonate islands contain broader reef flats or shallow regions that typically extend ~1 km from shore, providing considerably more reef heterogeneity than at northern locales. Thus, it is not surprising that the two-way crossed ANOSIM revealed that larger islands, containing greater habitat diversity, exhibited higher diversity among sites than smaller islands. However, in nMDS ordinations, Pagan (the largest of the northern, volcanic islands) clusters closely to the southern, carbonate islands because its larger size likely allows for higher generic macroalgal diversity (23 genera and five functional groups). Similarly, although Maug has a surface area of only 2 km², it also clusters close to larger islands because its unique geomorphology (three small islets surrounding a large flooded caldera) allows for a wider variety of habitats and, accordingly, relatively high algal richness (22 genera and four functional groups). Habitat differences make each island unique, and higher abundance of certain algae over others at each island is reflected through RAM. Two-way nested ANOSIMs revealed moderate differences in RAM when all sites surveyed across the archipelago were considered simultaneously. Such results are expected as algal genus composition changes from habitat to habitat within a single island ecosystem (e.g. wave-exposed fore-reefs vs calm lagoonal reefs; Vroom *et al.* 2005a).

The nMDS plot generated using RAM for each island closely resembled a geographical map of the Mariana Archipelago. This confirmed that detectable differences in genus presence and rank exist among islands and mirrored geographic relationships (Figs 1, 2). Rapid ecological algal assessments using data from the Northwestern Hawaiian Islands (Vroom & Page 2006) revealed a similar trend between geographic orientation and relationships among islands based on RAM. In this study, turf algae, crustose coralline red algae, and the green algal genus *Halimeda* were ubiquitous across the archipelago, a finding in line with similar studies of US coral reefs across the Pacific (Adey 1998; National Marine Fisheries Service 2004, 2005; Vroom *et al.* 2005a; Vroom & Page 2006). Yet despite the relative homogeneity of macroalgal genera across the archipelago, southern islands can be distinguished from the northern islands based on generic composition. For instance, *Dictyosphaeria* and cyanophytes were encountered more frequently in southern than northern islands, and differences in RAM among sites were more pronounced in southern islands, a pattern that may result from localized anthropogenic activity in southern islands such as Guam (e.g. eutrophication, pollution; Thacker *et al.* 2001; see Table 2 for human population densities across the archipelago). Cyanophytes and the genus *Dictyosphaeria* are often abundant in eutrophic and heavily fished reef areas (Adey 1998; Larned 1998; LeBris *et al.* 1998; Stimson *et al.* 2001). In contrast, the frequency of the phaeophyte *Lobophora* in the northern islands may be related to cooler sea surface temperatures found in northern is-

lands (Fig. 2), especially during winter months. A similar trend has been observed in the subtropical Northwestern Hawaiian Islands (Vroom & Page 2006), and brown algae are known to predominate over other algal lineages in cool, temperate environments (Cheney 1977).

In addition to anthropogenic activities and oceanographic conditions discussed above, feral animals, weather conditions (e.g. storms, typhoons), and volcanic eruptions can also influence spatial variability observed across the archipelago. In the past four years, the southern islands were affected by more typhoons than the northern islands (Table 1), although Alamagan, Pagan, and Agrihan also experienced severe storm activity. Such weather conditions may be responsible for the high variability in RAM between sites at the latter three islands (Vroom *et al.* 2005b). On islands experiencing volcanic activity, reefs are heavily impacted. The northern side of Anatahan Island was surveyed four months after its violent eruption on 10 May 2003 (Wiens *et al.* 2004), and the reefs were found buried in silt-like ash, reducing the visibility to less than 0.5 m. By contrast, southern and western reefs of Anatahan were clearer, probably because of lighter ash fall and higher wave energy, clearing away ash deposits. Surveys conducted at Anatahan found algal populations to have suffered as a result of the eruption. For instance, substantially fewer macroscopic algal genera occurred on Anatahan (seven genera and three functional groups) than on geographically close islands (Sarigan and Saipan with 13 to 25 genera and five functional groups), and populations of algae present were much smaller. These differences were reflected by the placement of Anatahan away from geographically close islands in the nMDS plot but fairly close to Uracas. Uracas is the smallest and newest island in the Mariana Archipelago (Bearden *et al.* 2005) and has erupted at least 16 times in the past 150 years (Uracas 2006). It is hypothesized that the low macroalgal diversity (nine genera plus two functional groups) recorded at Uracas during our expeditions is due to its continually developing reef systems.

Temporal variability

Storm, anthropogenic, and volcanic activities not only influenced the spatial variability of RAM but also likely accounted for some temporal changes observed in the Mariana Archipelago between the 2003 to 2005 surveys. Between our two research expeditions, five typhoons swept over various islands in Guam and CNMI. Recent research on the effects of severe storms on algal populations (Vroom *et al.* 2005b) found that substrata can be scoured clean by severe wave energy and that certain genera fare better than others at re-establishing populations (McManus & Polsenberg 2004). Therefore, it is not surprising that the islands situated closest to the path of the storms (Guam, Rota, Tinian, Saipan, Santa Rosa, Agrihan, and Sarigan) exhibited the highest degree of temporal difference in RAM. Sarigan, the island exhibiting the highest degree of

temporal change in our study, might also have been affected by the volcanic eruptions of Anatahan in 2003 and 2005. Surveys at Sarigan (the closest neighbor to Anatahan) in 2003 revealed a thin layer of ash over large areas of reef that was absent at other islands (Bearden *et al.* 2005).

Temporal variability in RAM at southern islands may also be related to the intensity and nature of human activities (see Table 2 for human population densities across the archipelago). Although Abraham *et al.* (2004) reported little change in coral and macroinvertebrate communities in CNMI between 2002 and 2004, he suggested that polluted runoff from areas of high population density and increases in fishing pressure in Guam are increasingly degrading coral reef ecosystems and slowing reef recovery after natural disturbances such as typhoons. Therefore, it is not surprising that the unpopulated island of Aguijan (Table 4) was the only southern carbonate island not to exhibit temporal changes in RAM, even though it experienced typhoon and storm activity similar to Rota and Guam. Because of less anthropogenic disturbance, Aguijan also continues to exhibit extensive coral growth (Abraham *et al.* 2004). Based on our analyses, anthropogenic impacts (including fishing, sedimentation, and eutrophication), combined with storm damage, appear to be a major factor affecting RAM on tropical reefs located at the southern end of the archipelago. This lends further support to Hallock's (2005) suggestion that hurricane impacts on coastal ecosystems are exacerbated by deforestation, agriculture, and coastal development. On the northern islands experiencing volcanic activity, reefs are constantly being rebuilt. Surveys conducted at southern and western sites of Anatahan found algal populations to have suffered as a result of the May 2003 eruption (Bearden *et al.* 2005), with existing algal turf communities trapping ash, leading to subsequent decreased light-absorbing and nutrient-uptake capabilities by these turf algal communities (Irving & Connell 2002). Thus, turf communities were reduced up to 50% when compared to neighboring islands (personal observation). Anatahan provides a unique opportunity to observe recovery and development of reef communities including macroalgae over the next several decades.

Comparisons to the Northwestern Hawaiian Islands

An analysis similar to our study of the Mariana Archipelago was recently completed for the Northwestern Hawaiian Islands (NWHI; Vroom & Page 2006) and reveals enlightening differences between the two archipelagoes. Temporal variability of RAM across the NWHI as a whole was not significant despite known temperature variations over latitudes (Bearden *et al.* 2005) but was moderately significant in the Mariana Archipelago, where temperature variations are relatively small. It is hypothesized that differences between these two Pacific archipelagoes are attributable primarily to natural environmental pressures (severe typhoon damage and volcanic activity) coupled with higher anthropogenic activities in the Mariana Archipelago and limited environmental pressures or human activities in the mostly unpopulated NWHI. Despite the relatively pristine nature of the NWHI, moderate temporal variability was seen in the three northernmost atolls of NWHI when they are considered separately from the entire archipelago because of two mass coral-bleaching events in 2002 and 2004 (Vroom & Page 2006). Increasing substratum availabil-

ity affects algal functional community dynamics by clearing space for opportunistic species to settle and grow (McManus & Polsenberg 2004).

When spatial variability of RAM was considered, the NWHI and Mariana archipelagoes exhibited opposite trends. In the NWHI, most island comparisons yielded negative r values, whereas island comparisons in the Mariana Archipelago exhibited positive r values. This indicates that, in the NWHI, more variability exists within reef ecosystems surrounding each island than among islands as a whole (Vroom & Page 2006). In the Mariana Archipelago, positive r values among sites revealed a relative homogeneity within each island ecosystem surveyed. These differences likely occur because the NWHI are estimated to be 75 million years (myr) old (Clague & Dalrymple 1987; Kim *et al.* 1998) and are the remains of larger islands that have slowly sunk over time, allowing myriad habitat types to have evolved within the geologically complex reef shelves found at each atoll or island. In comparison, the Mariana Archipelago is as young as 55 to 20 myr (Meijer *et al.* 1983; Stafford *et al.* 2005), with many islands still consisting of active volcanoes whose eruptions limit habitat variability and continue to dramatically impact the reef environment. The northernmost Mariana Islands slope steeply to great depths with little room for complex reef development and accordingly contain young reefs with relatively low algal diversity compared to older ecosystems. Additionally, the NWHI chain is much longer (2600 km) than the Mariana Archipelago (750 km) and experiences higher annual fluctuations in sea surface temperature (Bearden *et al.* 2005; Friedlander *et al.* 2005). Such temperature variations play an important role in algal diversity, abundance, and distribution (Cheney 1977; Adey 1998; Thacker *et al.* 2001).

This study suggests that RAM has high potential as a tool to rapidly assess changes in coral reef communities, both spatially and temporally. In the Mariana Archipelago, geomorphology is likely to be the principal factor that affects RAM spatially, although anthropogenic, storm, and volcanic activities likely play secondary roles in structuring algal communities. The degree of temporal variability observed across the archipelago within a two-year period was surprising because both assessments occurred during the same seasonal time frame. We hypothesize that temporal variation in algal communities, like patterns of spatial variability, occurred because of the combined effects of typhoon intensity and frequency, volcanic eruptions, and human activities. The degree of temporal variation observed in the Mariana Archipelago differed from the NWHI, where RAM varied more spatially than temporally. Differences between the two archipelagoes include less human pressure, larger and more complex islands, increased age of the archipelago, as well as greater fluctuation of oceanographic conditions (such as sea surface temperature) in the NWHI than in the Mariana Archipelago. The continued use of the Preskitt method (Preskitt *et al.* 2004) to rank macroalgal genera in island systems around the Pacific (Vroom *et al.* 2005a, 2006; Vroom & Page 2006) will provide complementary data on macroalgal diversity, abundance, and distribution from other island systems. Additionally, long-term surveys using the technique discussed here, combined with future detailed species-level analyses, are necessary in order to confirm the trends observed over a two-year period and to sort out which environmental factors or anthropogenic activ-

ities influence RAM most heavily. Such surveys will allow better management of coral reefs, especially those impacted by human activities.

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Appendix 1. GPS coordinates, dates visited, and depths of sites where RAM was collected. Rows in bold indicate sites sampled in both 2003 and 2005. GPS coordinates and maximum depths for sites surveyed in both years were collected during initial assessments in 2003. SAI, Saipan; TIN, Tinian; SAR, Sarigan; PAG, Pagan; AGR, Agrihan; URA, Uracas (Farallon de Pajaros); MAU, Maug; ASU, Asuncion; ANA, Anatahan; GUG, Guguan; ALA, Alamagan; AGU, Aguijan (Goat Island); ROT, Rota; GUA, Guam; SAN, Santa Rosa Reef; PAT, Pathfinder Bank; ARA, Arakane Reef.

| Site no. | Date | Latitude | Longitude | Max depth (m) | Habitat |
|-------------|---------------------|-------------------|--------------------|---------------|-----------------|
| SAI1 | 22 Aug. 2003 | N15 15.542 | E145 48.872 | 7.9 | Forereef |
| | 4 Sep. 2005 | | | | |
| SAI2 | 22 Aug. 2003 | N15 10.561 | E145 47.257 | 13.1 | Forereef |
| | 4 Sep. 2005 | | | | |
| SAI3 | 4 Sep. 2005 | N15 09.424 | E145 46.105 | 13.4 | Forereef |
| SAI4 | 22 Aug. 2003 | N15 09.350 | E145 46.186 | 9.8 | Forereef |
| | 22 Sep. 2005 | | | | |
| SAI5 | 21 Sep. 2005 | N15 05.917 | E145 44.679 | 13.1 | Forereef |
| SAI6 | 22 Sep. 2005 | N15 09.386 | E145 41.417 | 13.4 | Forereef |
| SAI7 | 21 Sep. 2005 | N15 06.483 | E145 42.376 | 14.6 | Forereef |
| SAI8 | 22 Sep. 2005 | N15 16.412 | E145 47.423 | 14.6 | Forereef |
| TIN1 | 23 Aug. 2003 | N15 02.083 | E145 39.055 | 15.8 | Forereef |
| | 26 Sep. 2005 | | | | |
| TIN2 | 23 Aug. 2003 | N14 56.401 | E145 37.651 | 13.7 | Forereef |
| | 26 Sep. 2005 | | | | |
| TIN3 | 23 Aug. 2003 | N14 59.426 | E145 36.182 | 12.2 | Forereef |
| | 27 Sep. 2005 | | | | |
| TIN4 | 26 Sep. 2005 | N14 56.870 | E145 39.783 | 13.4 | Forereef |
| TIN5 | 27 Sep. 2005 | N14 57.342 | E145 37.713 | 7.9 | Lagoon |
| TIN6 | 27 Sep. 2005 | N15 04.816 | E145 37.279 | 11.6 | Forereef |
| SAR1 | 24 Aug. 2003 | N16 41.943 | E145 46.287 | 10.7 | Forereef |
| | 18 Sep. 2005 | | | | |
| SAR2 | 24 Aug. 2003 | N16 42.978 | E145 46.496 | 12.2 | Forereef |
| | 18 Sep. 2005 | | | | |
| SAR3 | 24 Aug. 2003 | N16 42.649 | E145 46.080 | 14.0 | Forereef |
| SAR4 | 18 Sep. 2005 | N16 41.916 | E145 47.316 | 18.3 | Forereef |
| PAG1 | 26 Aug. 2003 | N18 06.435 | E145 47.146 | 12.2 | Forereef |
| | 8 Sep. 2005 | | | | |
| PAG3 | 7 Sep. 2003 | N18 10.097 | E145 47.268 | 13.7 | Forereef |
| | 7 Sep. 2005 | | | | |
| PAG4 | 7 Sep. 2003 | N18 08.463 | E145 45.518 | 11.6 | Forereef |
| PAG5 | 7 Sep. 2003 | N18 07.182 | E145 45.339 | 12.2 | Forereef |
| | 7 Sep. 2005 | | | | |

Appendix 1. Continued.

| Site no. | Date | Latitude | Longitude | Max depth (m) | Habitat |
|--------------|---------------------|-------------------|--------------------|---------------|-----------------|
| PAG6 | 8 Sep. 2003 | N18 05.573 | E145 44.646 | 15.2 | Forereef |
| | 6 Sep. 2005 | | | | |
| PAG7 | 8 Sep. 2003 | N18 04.242 | E145 42.816 | 11.0 | Forereef |
| PAG8 | 8 Sep. 2003 | N18 03.640 | E145 44.509 | 12.2 | Forereef |
| | 8 Sep. 2005 | | | | |
| PAG9 | 6 Sep. 2005 | N18 04.243 | E145 42.809 | 14.6 | Forereef |
| PAG11 | 13 Sep. 2003 | N18 05.155 | E145 43.792 | 14.0 | Forereef |
| | 6 Sep. 2005 | | | | |
| PAG12 | 7 Sep. 2005 | N18 09.994 | E145 45.988 | 15.2 | Forereef |
| PAG13 | 8 Sep. 2004 | N18 05.796 | E145 45.988 | 11.9 | Forereef |
| AGR1 | 27 Aug. 2003 | N18 44.897 | E145 41.648 | 13.7 | Forereef |
| AGR2 | 27 Aug. 2003 | N18 43.610 | E145 39.806 | 14.3 | Forereef |
| | 13 Sep. 2005 | | | | |
| AGR3 | 27 Aug. 2003 | N18 43.947 | E145 39.121 | 12.5 | Forereef |
| AGR4 | 6 Sep. 2003 | N18 48.431 | E145 38.938 | 14.6 | Forereef |
| | 15 Sep. 2005 | | | | |
| AGR5 | 6 Sep. 2003 | N18 47.542 | E145 38.398 | 12.5 | Forereef |
| AGR6 | 6 Sep. 2003 | N18 45.454 | E145 38.425 | 14.3 | Forereef |
| | 14 Sep. 2005 | | | | |
| URA1 | 30 Aug. 2003 | N20 32.758 | E144 53.144 | 15.8 | Forereef |
| | 10 Sep. 2005 | | | | |
| URA2 | 31 Aug. 2003 | N20 32.267 | E144 53.950 | 14.3 | Forereef |
| | 10 Sep. 2005 | | | | |
| URA3 | 31 Aug. 2003 | N20 33.020 | E144 53.886 | 10.1 | Forereef |
| URA4 | 31 Aug. 2003 | N20 33.189 | E144 53.437 | 10.1 | Forereef |
| | 10 Sep. 2005 | | | | |
| MAU1 | 2 Sep. 2003 | N20 01.409 | E145 12.474 | 16.8 | Forereef |
| | 13 Sep. 2005 | | | | |
| MAU2 | 2 Sep. 2003 | N20 01.352 | E145 13.796 | 16.2 | Lagoon |
| | 11 Sep. 2005 | | | | |
| MAU3 | 2 Sep. 2003 | N20 00.828 | E145 13.663 | 15.5 | |
| MAU4 | 3 Sep. 2003 | N20 00.866 | E145 14.052 | 14.0 | Forereef |
| | 11 Sep. 2005 | | | | |
| MAU5 | 3 Sep. 2003 | N20 02.117 | E145 13.472 | 14.0 | Forereef |
| | 11 Sep. 2005 | | | | |
| MAU6 | 3 Sep. 2003 | N20 01.847 | E145 13.655 | 13.7 | Lagoon |
| | 13 Sep. 2005 | | | | |
| MAU8 | 13 Sep. 2005 | N20 01.333 | E145 13.243 | 20.4 | Lagoon |
| MAU9 | 12 Sep. 2005 | N20 01.734 | E145 12.477 | 16.2 | Forereef |
| MAU10 | 4 Sep. 2003 | N20 01.049 | E145 12.751 | 11.6 | Lagoon |
| | 12 Sep. 2005 | | | | |
| MAU11 | 4 Sep. 2003 | N20 00.815 | E145 12.535 | 14.9 | Forereef |
| | 12 Sep. 2005 | | | | |
| ASU1 | 5 Sep. 2003 | N19 41.986 | E145 25.044 | 13.1 | Forereef |
| | 9 Sep. 2005 | | | | |
| ASU2 | 5 Sep. 2003 | N19 40.847 | E145 23.523 | 12.2 | Forereef |
| | 9 Sep. 2005 | | | | |
| ASU3 | 5 Sep. 2003 | N19 42.121 | E145 23.627 | 12.5 | Forereef |
| | 9 Sep. 2005 | | | | |
| ANA3 | 10 Sep. 2003 | N16 20.054 | E145 38.700 | 13.1 | Forereef |
| ANA4 | 18 Sep. 2003 | N16 20.440 | E145 43.091 | 12.8 | Forereef |
| ANA5 | 18 Sep. 2003 | N16 19.997 | E145 42.260 | 13.7 | Forereef |
| ANA6 | 18 Sep. 2003 | N16 20.003 | E145 39.182 | 13.7 | Forereef |
| GUG1 | 11 Sep. 2003 | N17 18.365 | E145 51.069 | 12.2 | Forereef |
| GUG2 | 11 Sep. 2003 | N17 18.016 | E145 50.098 | 12.2 | Forereef |
| GUG3 | 11 Sep. 2003 | N17 19.012 | E145 49.940 | 14.9 | Forereef |
| GUG4 | 5 Sep. 2005 | N17 18.546 | E145 49.855 | 13.1 | Forereef |
| ALA1 | 12 Sep. 2003 | N17 36.844 | E145 50.575 | 12.5 | Forereef |
| | 16 Sep. 2005 | | | | |
| ALA2 | 12 Sep. 2003 | N17 36.448 | E145 48.914 | 13.1 | Forereef |
| | 16 Sep. 2005 | | | | |
| ALA3 | 2 Sep. 2003 | N17 35.225 | E145 49.084 | 10.1 | Forereef |
| | 16 Sep. 2005 | | | | |
| AGU1 | 17 Sep. 2003 | N14 50.947 | E145 34.319 | 14.9 | Forereef |
| | 28 Sep. 2005 | | | | |
| AGU2 | 17 Sep. 2003 | N14 50.844 | E145 32.182 | 14.0 | Forereef |
| | 28 Sep. 2005 | | | | |
| AGU3 | 28 Sep. 2005 | N14 51.585 | E145 33.334 | 13.7 | Forereef |

Appendix 1. Continued.

| Site no. | Date | Latitude | Longitude | Max depth (m) | Habitat |
|-------------|---------------------|-------------------|--------------------|---------------|-----------------|
| ROT1 | 19 Sep. 2003 | N14 10.526 | E145 17.144 | 11.3 | Forereef |
| | 29 Sep. 2005 | | | | |
| ROT2 | 19 Sep. 2003 | N14 09.232 | E145 15.563 | 12.2 | Forereef |
| | 29 Sep. 2005 | | | | |
| ROT3 | 19 Sep. 2003 | N14 06.848 | E145 10.034 | 13.4 | Forereef |
| | 29 Sep. 2005 | | | | |
| ROT5 | 20 Sep. 2003 | N14 10.957 | E145 12.420 | 12.5 | Forereef |
| | 30 Sep. 2005 | | | | |
| ROT6 | 20 Sep. 2003 | N14 09.494 | E145 09.030 | 14.3 | Forereef |
| | 30 Sep. 2005 | | | | |
| ROT7 | 30 Sep. 2005 | N14 08.202 | E145 08.503 | 8.2 | Forereef |
| GUA1 | 23 Sep. 2003 | N13 25.821 | E144 38.253 | 11.9 | Forereef |
| GUA2 | 23 Sep. 2003 | N13 18.323 | E144 39.181 | 11.0 | Forereef |
| | 8 Oct. 2005 | | | | |
| GUA3 | 8 Oct. 2005 | N13 14.449 | E144 42.228 | 13.7 | Forereef |
| GUA4 | 24 Sep. 2003 | N13 31.019 | E144 47.851 | 12.2 | Forereef |
| | 4 Oct. 2005 | | | | |
| GUA5 | 24 Sep. 2003 | N13 34.727 | E144 49.696 | 11.9 | Forereef |
| GUA6 | 25 Sep. 2003 | N13 19.949 | E144 46.459 | 13.4 | Forereef |
| GUA7 | 25 Sep. 2003 | N13 36.139 | E144 55.615 | 12.8 | Forereef |
| | 5 Oct. 2005 | | | | |
| GUA8 | 26 Sep. 2003 | N13 29.334 | E144 52.668 | 11.9 | Forereef |
| | 5 Oct. 2005 | | | | |
| GUA9 | 26 Sep. 2003 | N13 37.944 | E144 53.579 | 12.5 | Forereef |
| | 4 Oct. 2005 | | | | |
| GUA10 | 3 Oct. 2005 | N13 28.405 | E144 41.608 | 15.2 | Forereef |
| GUA11 | 5 Oct. 2005 | N13 25.689 | E144 48.601 | 12.2 | Forereef |
| SAN1 | 7 Oct. 2005 | N12 48.784 | E144 25.483 | 13.1 | Bank |
| SAN2 | 28 Sep. 2003 | N12 48.678 | E144 25.432 | 12.8 | Bank |
| | 7 Oct. 2005 | | | | |
| PAT1 | 24 Sep. 2005 | N16 30.228 | E143 08.956 | 16.2 | Bank |
| PAT2 | 24 Sep. 2005 | N16 30.145 | E143 08.717 | 20.4 | Bank |
| ARA1 | 25 Sep. 2005 | N15 38.624 | E142 45.529 | 16.5 | Bank |
| ARA2 | 25 Sep. 2005 | N15 38.167 | E142 45.567 | 19.8 | Bank |