Four decades of macroalgal stasis and change on an urban coral reef

Robert A. Kinzie III

Zoology Department, 2538 The Mall, and Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Honolulu, Hawai'i

Abstract— Cover and biomass estimates of the macroalgal assemblage on a coral reef off Waikīkī Beach, Hawai'i were analyzed to determine changes through time. Biomass data spanned 39 years (1966–2005) while data for cover were taken from 1975 to 2005. Data for the 1975–2005 period were collected as part of a regularly scheduled class exercise. Mean biomass in 2005 was the same as in 1966, however during the 1980's biomass was substantially lower. Much of this decline in total algal biomass was due to the low biomass of *Sargassum* spp. during those years. In the 1960's total biomass was essentially constant from the shore to 200m off shore, while in later years there was a decline in biomass with distance from shore. The invasive Rhodophyte, *Gracilaria salicornia*, was a major contributor to biomass starting in 1990. Even with this new dominant species, diversity, based on the 15 most common species, showed little change through time. Cover also remained consistent from 1975 to 2005 with macroalgae generally covering more than 50% of the bottom and living coral less than 5%. As with biomass, macroalgal cover declined with distance from shore. Student projects and class exercises can be used to generate valuable long-term data sets when appropriate quality control is maintained.

Introduction

Macroalgae are an integral component of coral reef communities both structurally and functionally (Odum and Odum 1955; Littler and Littler 1984; Berner 1990, Huisman et al. 2007). While coral reef scientists often emphasize coralline algae due to their contribution to framework construction and consolidation (Littler 1976; Steneck 1997), frondose and turf algae are also of importance in primary production, materials processing and their contribution to the base of reef food webs (Womersley and Bailey 1969; Littler 1973; Hay 1981; Larkum 1983; Charpy-Roubaud and Sournia 1990). Recently macroalgae have been implicated in instances of degradation on coral reefs impacted by human activities (Done 1992; McCook et al. 1997; Lapointe 1997; Lirman 2001; Szmant 2001; Conklin & Smith 2005). In most instances it is not clear whether the algae are themselves part of the causal mechanism of the decline in corals, or are only part of a general shift in community composition. However, it must be remembered that many reefs with no history of direct anthropogenic impact are

characterized by high biomass and diversity of macroalgae (Friedlander et al. 2004; Vroom et al. 2005, 2006).

While scleractinian corals and large 'hermatypic' octocorals can live for decades to centuries, frondose macroalgae turnover at much higher rates (Menge et al. 2005). Many macroalgae are ephemeral or seasonal (Glenn et al. 1990, Lirman and Biber 2000). Even perennial species are more easily removed or damaged by storm events than are corals. Also macroalgae can respond to changes in conditions, e.g. nutrient additions, change in grazer abundance or species composition, high light and temperature events much more quickly than can corals (Tanner 1995; Stimson et al. 1996; McCook 1999; Smith et al. 2001). Furthermore, macroalgae can recover (either by regrowth of existing thalli or appearance of new colonizers) more rapidly than can corals. Because of these differences, temporal changes in the macroalgal assemblage on a reef can give a more detailed and time-nuanced picture of changes through time.

Monitoring studies are often held not to be 'real science' but simply descriptive exercises with no testable hypotheses, nor *a priori* questions (but see Hughes 1992; Rogers et al. 2001, Lovett et al. 2007). Further, funding for monitoring projects is often scarce because the value of monitoring studies in the early stages of a long-term program is perceived to be low. Initially they are simply one-time descriptions of a site. The true value of monitoring programs is in the long term, when ecologically relevant timescales have been achieved, and responses of the study system across an array of changes on several scales can be identified (Hughes 1994; Connell et al. 1997). The unfortunate paradox is that managers, journals and funding bodies, while happy to acknowledge the importance of long-term studies, once they have been in place for an extended period, are much less interested at the outset (Lovett et al. 2007).

Here I report on changes in macroalgal biomass, cover and community composition over a 39-year time span on a coral reef that has been heavily impacted by a range of human and natural forces. The last 30 years of data in this time series were taken by students as part of a regularly scheduled laboratory course.

Materials and Methods

SITE DESCRIPTION AND HISTORY

The south shore of O'ahu is bordered by an extensive fringing reef that ranges from about 100 to 800 m from the shoreline (Aecos 1981). This reef is broken naturally or artificially at the mouths of several harbors but is otherwise almost continuous. Today, shorelines are rocky or sandy, most notably the broad Waikīkī beach. In 1927, a concrete structure with a vertical seawall 117 m wide was constructed on what had previously been a sandy beach, thus hardening that portion of the shoreline. This structure, the Waikīkī Natatorium War Memorial, extends about 80 m seaward from the old shoreline. Offshore of the Natatorium

wall the reef flat extends an additional 200-240 m to the reef crest. Depths on the reef flat range from less than 1 m to approximately 2 m depending on the tide.

The nearest point source of terrestrial runoff is the mouth of the Ala Wai Canal about 2.8 km to the west of the Natatorium. This drainage was constructed in the 1920's. It receives water from the Mānoa, Makiki and Palolo watersheds. Water in this drainage comes from stream flow and surface runoff collected in storm drains. Until 1978 the City of Honolulu discharged untreated sewage into shallow water at a point approximately 10 km northwest of the Natatorium. In 1978 a secondary treatment plant was completed and discharge from this facility is now released at a depth of 70 m. As part of the permitting for this discharge, the area near the outlet has been monitored (Swartz et al. 2001; Bailey-Brock et al. 2002). Results from this ongoing monitoring study indicate that there is no impact of the discharge on bottom communities to the east - the direction of the Natatorium (Bailey-Brock et al. 2002). These reports also indicate that bottom currents generally move to the west - away from the Natatorium.

The Hawai'i State Department of Health (DOH) has at various times monitored nutrients at two sites just offshore of Waikīkī Beach: Gray's Beach 1.5 km to the west of the Natatorium; and Public Baths 350 m to the west of the Natatorium (Aecos 1981, Clark 2005). While much of the DOH water quality monitoring program focuses on enteric bacteria, there are some nutrient data for these two sites from the 1970's (Jan 1973 - Oct 1975) and again in the late 1980's and 1990's (Oct. 1989 – Aug. 1997). These data can be found on EPA's STORET web site at http://www.epa.gov/storpubl/dbtop.html. Additionally, the Waikīkī Aquarium has been collecting water quality data at two points very close to our Natatorium study site since 1999. The samples for the Aquarium are generally taken in June so are mostly useful for discerning secular trends, not seasonal differences. For total phosphorus there was no significant difference at the two DOH stations in the 1970's compared with the 1980-1990 period, nor do either of these Waikīkī sites differ from the Waikīkī Aquarium samples (all P > 0.05). There was also no difference in total nitrogen between the two periods at either of the DOH sites to the west of the Natatorium. However, total nitrogen was higher at Gray's Beach to the west than at Public Baths and the Aquarium site, which did not differ from each other. Ammonium was not measured in the 1970's at the two Waikīkī stations. In the 1980's-1990's ammonium was significantly lower at the Aquarium stations than at either of the two DOH sites (P < 0.05). While these nutrient data are not continuous through time, they suggest that at least for the times data were recorded there have been no marked changes in these nutrients since the 1970's, and that nutrient concentrations in the vicinity of the Natatorium are no higher than along Waikīkī beach.

On July 1, 1978 the Hawaii State Division of Aquatic Resources (DAR) initiated the Waikīkī-Diamond Head Fishery Management Area (FMA) that includes the reef seaward of the Natatorium (Williams et al. 2006). Originally this management plan consisted of a four-year cycle; two years (1978-1979) no-take, one-year (1980) octopus and hook and line fishing only, and one year

(1981) open to all fishing (including gill netting and spear fishing). In no-take years collection of macroalgae was also prohibited. This four-year cycle was intended to repeat, so on June 30, 1982, the area was again closed to all fishing. The DAR management rules were revised on Jan 1, 1989 when the FMA was closed to all fishing and algal collection. From then on, even years were open (to all fishing and gathering of algae), and odd years were closed (to any removal). DAR has monitored fish numbers and biomass in the FMA since 1979, mostly in the inshore part of the reef flat (Williams Pers. Comm.). This program is still in operation. Williams et al. (2006) reported that while the closed periods may have caused small, short-term increases in fish biomass, overall, fish biomass declined by about two thirds from 1979 to 2002. They speculated that the decline in fish biomass and numbers beginning about 1990 may have been associated with the increasing cover of the invasive *Gracilaria salicornia* (C. Agardh) Dawson. However, they also noted marked declines in biomass of the herbivorous acanthurids and scarids and the carnivorous carangids from the very beginning of their study in 1979, prior to the establishment of this invasive alga.

From January 8 to 10, 1980 the Hawaiian Islands were hit by a severe 'Kona' or southerly winter storm. Torrential rains, high winds and short period storm waves impacted the islands (Haraguchi 1980, Walsh 1983). Unlike the two tropical storms discussed below, this winter storm had very strong effects on the southern shores of O'ahu. When it occurred, this storm was the most destructive Kona storm in at least 20 years (Haraguchi 1980) and there has not been a Kona storm of that magnitude since. Waves as high as 7 m directly impacted the west coast of Hawai'i Island (Dollar 1982). The same storm hit the south shore of O'ahu including Waikīkī. The National Oceanographic Data Center (NODC) maintains records of wave heights at Waikīkī in the Goddard-Caldwell O'ahu Surf Observation Database. On January 8, 1980 the wave index for Waikīkī was 5 (NODC accession No. 001754) which translates into wave heights of greater than 3 m (Caldwell 2005). For comparison, the mean index for all of 1980 was only 3.03 [1.85 m]. Further, these were short period storm waves (Haraguchi 1980) with a great potential to impact shallow waters over the reef. Ecological effects of this storm included damage to the extensive beds of the pen-shell *Pinna muricata* L. which had occurred in soft bottom habitats at depths of 25-30 m on leeward coasts of O'ahu (Hoover 1998), as well as damage to coral reef communities (Walsh et al. 2004).

On November 30 1982, Hurricane Iwa caused some reef damage to the Waikīkī reefs, but there were no thorough post-storm surveys made. Hurricane Iniki struck O'ahu on Sept. 11, 1992 (Dreyer et al 2005). Unlike the winter storm of 1980, these two tropical storms mostly affected the west side of O'ahu rather than the south shore (http://www.prh.noaa.gov/cphc/summaries/).

MACROALGAL STUDIES ON THE NATATORIUM REEF

The Early studies of the reefs of Waikīkī were qualitative, but provide important information on reef structure (Pollock 1928) and algal species

composition and ecology (Neal 1930). In 1966 Prof. Maxwell Doty of the Botany Department, University of Hawaiʻi initiated a project to quantify macroalgal abundance on the Natatorium reef flat (Doty 1969). Doty reported on 7 sampling events at approximately 3-4 month intervals from Dec. 1966 to April 1968. Doty's study was extensive in that the sampled area was 140 m wide, including the entire width of the Natatorium, and extended to 230 m offshore for a total area of 32,200 m^2. It was also intensive in that each of the 7 sampling events consisted of 120 collections, each with an area of 0.159 m^2. Thus, for each period, the samples came from a total area of 19.08 m^2 or 0.06% of the total study area. Samples were sorted to species and wet and dry masses were reported in addition to several other parameters. Doty divided the area into two sectors - north and south. His results were presented for each sector separately as well as the mean of the two. This paper uses his mean values for the total area (both sectors) and his wet biomass values. It should also be noted that Doty was one of the foremost phycologists of his day and his species identifications were probably highly reliable.

From 1971 to 1973 macroalgal standing crop was again estimated in front of the Natatorium (Glenn et al. 1990). The intent of this study was to investigate seasonal changes in macroalgal biomass. Unlike Doty's earlier study, the survey in the 1970's did not specify location on the reef flat, nor did it report data for the 22 individual monthly collections, so only mean wet biomass values for the entire study period and area are used here. In 2002 a study was made of the ecology of the invasive *Gracilaria salicornia* on the reef flat off Waikīkī Aquarium documenting biomass, herbivory, beach wash and growth rates. (Smith et al. 2004).

Starting in November 1975 the Laboratory in Ecology class of the Zoology Department at the University of Hawaiʻi at Manoa (Zoology 439L) began a regular macroalgal sampling exercise on the reef flat off the Natatorium. Samples have been taken at roughly two-year intervals since that time, usually in October or November. Unlike the extensive sampling in Doty's study, all the class collections were made along a single transect extending from the center of the Natatorium wall seaward for 200 m unless rough water conditions necessitated a shorter transect. Samples and data were collected at regular intervals (every 10 or 20 m) along the transect line. In most years both cover estimates and biomass collections were made. Cover was estimated using a 1x1 m square frame with regularly spaced points marked out by strings across the frame at 10 cm intervals. At least 25 points were used for the cover estimates. The frame was set on the reef at the designated distance, and the bottom cover beneath each point (macroalgae, coral rubble, sand) was recorded. When possible, algae were recorded to species, if not, voucher specimens were taken for subsequent identification. When several layers of algae were found, only the uppermost was recorded. At each designated distance a smaller frame was haphazardly tossed near the point-count frame and all macroalgae within the small frame were collected. These collections were returned to the lab, sorted to species when

possible, and the mass of each species in each sample taken. In some years both wet and dry mass (3-5 days at 60ºC) were recorded, but only wet mass data are reported here.

Species diversity is an important component of community structure. It is possible that biomass and percent cover by macroalgae did not change through time while the species composition of the community did. This is especially true since several invasive species have appeared on the Natatorium reef including *Acanthophora spicifera* (Vahl) Børgesen, *Gracilaria salicornia*, and *Hypnea musciformis* (Wulfen in Jacquin) Lamouroux (Smith et al. 2004; http://www2. bishopmuseum.org/algae/results5.asp?search=Waikiki_Natatorium).   Diversity was determined using the Shannon Wiener information function (Krebs 1985) using the biomass data.

It is important to note that the class data come from a single transect with permanently fixed sampling sites. While this allows for strongly supported year to year comparisons, the data cannot be statistically generalized to the whole reef flat as can Doty's randomized sampling scheme, though as will be shown below, the actual biomass and diversity values are quite similar between the two studies. For this reason statistical comparisons between the two data sets are not made in this paper; rather, qualitative statements of similarity or difference are used. However within-dataset statistics are used to point out trends. The class data differ from Doty's not only in the area sampled and the intensity of sampling, but also in the level of taxonomic expertise. Because of this, most of the class data are grouped to genus. Further, most of the data presented here are for the most common taxa. The 15 most frequently recorded taxa were used in calculating the biomass species diversity indices (*Acanthophora spicifera*, *Codium* spp. *Dictyopteris* spp. *Dictyosphaeria* spp., *Galaxaura* spp., *Gracilaria* spp. [but almost entirely *G. salicornia*], *Halimeda* spp., *Hypnea* spp., *Microdictyon* spp. *Padina* spp., *Sargassum* spp., *Turbinaria ornata* (Turner) J. Agardh, *Ulva reticulata* Forskål, and *Ventricaria ventricosa* (J. Agardh) Olsen et West). This loss in taxonomic precision is balanced by the fact that the students could easily identify these common genera. Further, all but two of these genera are only represented by two species (*Hypnea* and *Padina* have three species each) on the Waikīkī reef (Abbott 1999; Abbott and Huisman 2004). If changes in species diversity were due to the loss of uncommon groups, the diversity index based on these 15 groups would not detect the changes. However in the class studies these 15 groups accounted, on average, for 86.59% (range 51.57%–99.35%) of the total biomass of all groups recorded. In Doty's data these 15 groups accounted for an average of 92.63% (range 83.29%–97.15%) of his much more inclusive species enumerations.
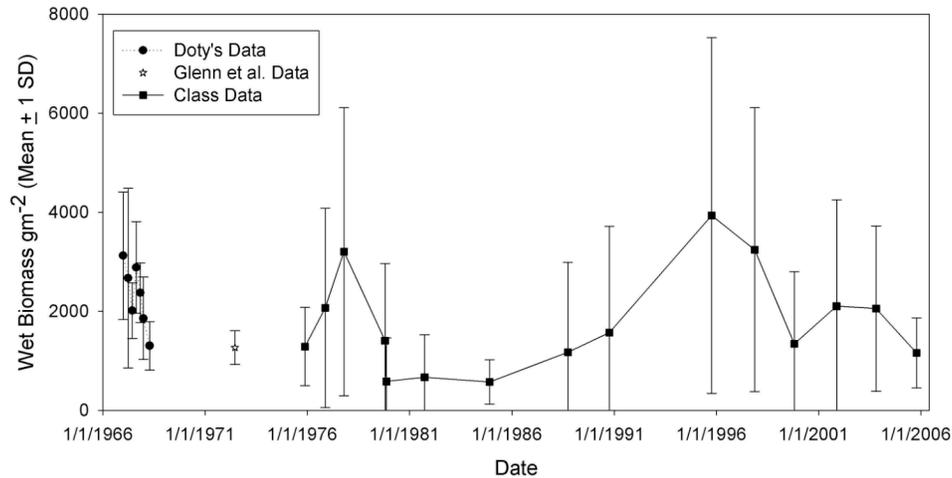
Figure 1. Mean ($\pm$ 1SD) total macroalgal biomass (wet weight) on the Natatorium reef flat from December 1966 to October 2005.

Results

MACROALGAL BIOMASS

Total Biomass

Figure 1 shows data from all the Natatorium surveys in terms of biomass of all macroalgae in a sampling event taken together. The data from Doty's 1966 to 1968 study show a general decline in biomass ($P = 0.02$ $r^2 = 0.62$) as noted by Glenn et al. (1990). The final survey in Doty's study in April 1968 had a mean biomass for all species of 1303 ± 489 g m^{-2} (mean $\pm$ 1 SD). Mean biomass for the 22 months in 1971–1973 reported by Glenn et al. (1990) was 1265 ± 342 g m^{-2}, very similar to Doty's April 1968 sample. The first of the Zoology 439L transects was run on Nov. 22, 1976 when mean biomass was 1288 ± 790 g m^{-2}, very similar to both Doty's last sample and the overall mean biomass from Glenn's 1970's study, even though the methods and data reporting in the three studies were quite different. The next two class estimates were higher, but the Oct. 21, 1979 class estimate was again similar to Doty's last estimate. However, for the next two class samples (Aug. 27, 1981 and Nov. 25, 1984) mean total biomass estimates were both very low—less than 600 g m^{-2}. None of Doty's (1969) mean biomass values in any season fell below 1000 g m^{-2}, nor any August through November samples reported by Glenn et al. (1990). By 1988 the biomass estimates were just over 1000 g m^{-2}, with values continuing to rise to over 3932 g m^{-2} by 1995. In 2002 Smith et al. (2004) reported that biomass of *Gracilaria salicornia* was 5193 ± 6360 g m^{-2} in their intensive removal project, but their collections were meant to totally eradicate this species if possible, so their collection effort was much more intensive than Doty's study or the class projects.

The 2005 class collection produced a mean total biomass of 1160 $\pm$ 708 g m^{-2}. Thus, while there has been year to year variation, the overall macroalgal biomass off the Waikīkī Natatorium in late summer and fall has generally remained between 1 and 3 kg m^{-2} for the last 39 years except for the period 1981–1984 when it fell below 600 g m^{-2}.

There is a slight decline in total biomass over the 39 year period (0.015   g m^{-2} yr^{-1}). Mean macroalgal biomass was greater for all Doty's samples taken together (2318 $\pm$ 636 g m^{-2}) compared with pooled class transect data sets (1841 $\pm$ 1003 g m^{-2}). The class overall biomass estimate is also similar to the Glenn et al. (1990) mean for their entire study period (1265 $\pm$ 342 g m^{-2}). Given the differences in methodology, and the fact that the class samples are all taken in the fall while the other two studies sampled throughout the year, these similarities, except for the low biomasses recorded in the early 1980's, are striking.

While methods differed, Doty's 1960's data and the class data sets allow estimates of algal biomass at a range of distances offshore of the Natatorium. This spatial characteristic of the area is of interest because exposure to wave energy changes across the reef which will affect different algal species differently. The cross-reef distribution of biomass from Doty's study (Figure 2) remains constant from the Natatorium wall to 190 m offshore. Beyond 190 m his biomasses were higher than inshore, and were dominated by *Sargassum echinocarpum* J. Agardh and *S. polyphyllum* J. Agardh. In contrast to Doty's results for total biomass across the reef, the class data show a marked decline in
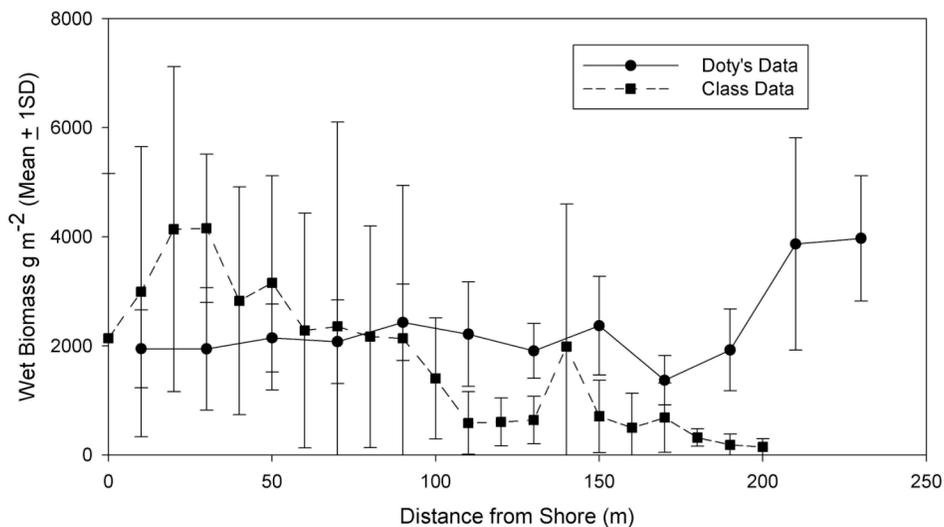

Figure 2. Mean ($\pm$ 1SD) total macroalgal biomass (wet weight) across the Natatorium reef flat for all Doty's data taken together (circles) (Doty 1969) and all the class data taken together (squares). Distances are seaward from the Natatorium wall.

biomass from near shore to about 100 m. Beyond 100 m, biomass is generally low. This trend was consistent across years. However, the class transects never extended beyond 200 m, so the high densities that Doty recorded beyond 200 m would have been missed by the class groups.

Even though the variability is great, there are differences in cross-reef biomass between the two data sets. Figure 2 suggests the difference between Doty's results and those from the class transect is due both to greater inshore biomass and reduced offshore biomass (switching at about 80 offshore) in the class data set. Mean biomass in this area in the 1960's (1927 ± 1821 g m^{-2}) was greater than the biomass found there by the class (mean 866 ± 1427 g m^{-2}). This offshore decline in algal biomass in the class data set was also reflected in estimated algal cover (see below).

Species Contribution to Biomass

Until the early 1980's *Sargassum* spp. generally made the greatest contribution, accounting for 52 to 88% of the total macroalgal biomass (Figure 3). However, from 1981 to 1988 the dominant groups, in terms of percent contribution to biomass were *Turbinaria ornata*, *Codium* spp. and *Dictyota* spp. In these years other genera, e.g. *Halimeda*, *Padina* and *Dictyosphaeria*, which were not important in other years, also comprised substantial percentages of the total algal biomass. In 1981 *Sargassum* spp. was only the eighth most important contributor to macroalgal biomass contributing less than 1%. While the Glenn et al. report (1990) did not give monthly values, the lowest that *Sargassum* spp. fell to in that study was about 27% of the total biomass.

In 1984 and 1988 *Sargassum* spp. was third, then second most abundant respectively. By 1990, *Sargassum* spp. again dominated, contributing more than
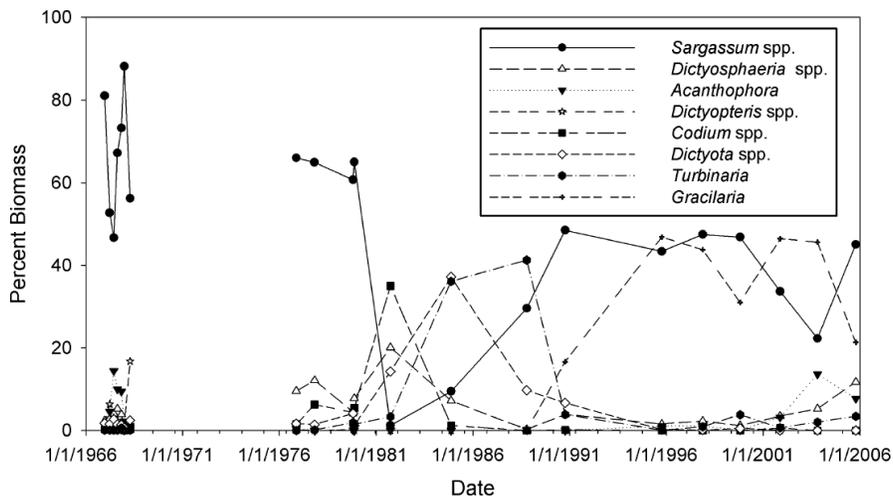

Figure 3. Percent contribution of the eight most important macroalgal groups in terms of biomass to the total macroalgal biomass on the Natatorium reef flat from 1966 to 2005.

50% of the total algal biomass. *Gracilaria* spp., which had been one of the least abundant contributors to macroalgal biomass in Doty's samples, and through 1988, jumped from the 13th position in 1988 to second place in 1990 when it contributed 17% of the total algal biomass, and by 1995 was the most important contributor with 47% of the total biomass. By this time the invasive *Gracilaria salicornia* was essentially the only species recorded for this genus. From 1990 to 2005, *Gracilaria* spp. and *Sargassum* spp were by far the dominant groups, together accounting for 65 to 91% of the total macroalgal biomass.

Figure 4 illustrates an important point. The apparent dominance of groups such as *Codium* spp., *Turbinaria ornata* and *Dictyota* spp. seen in Figure 3 is really a reflection of the dramatic drop in total biomass, mostly the very low biomass of *Sargassum*, not a real increase in the biomass of these less abundant groups.

For all seven of Doty's samples taken together *Sargassum* spp. comprised a mean of 1560 ± 607 g m^{-2}, while it contributed only an average of 844 ± 668 g m^{-2} in the class transects. In terms of percent biomass contribution, *Sargassum* spp. comprised 72.3% of Doty's collections and only 44.5% in the class data set. This is at least partly due to the abundance of *Sargassum* spp. on the reef flat beyond 200 m in Doty's data, and the fact that the class did not sample that far offshore. If biomass for *Sargassum* spp. in Doty's study calculated to 190 m offshore the mean drops to 1200 ± 658 g m^{-2} and the percentage contribution to total biomass is 62.5% (± 19). In the Glenn et al. study, over all their samples, *Sargassum* spp. contributed 961 g m^{-2}, or 76% of the total wet macroalgal biomass more similar
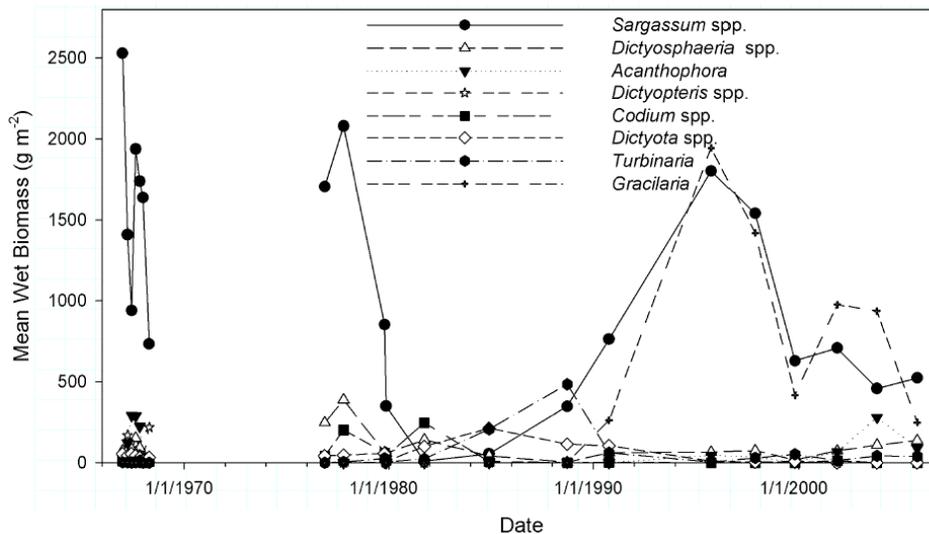

Figure 4. Mean macroalgal biomass (wet weight) of the eight most important macroalgal groups on the Natatorium reef flat from 1966 to 2005. Error estimates are not shown for clarity.

to the class data. However, the data they present are for all seasons combined. Even until the early 1980's *Sargassum* spp. generally made the greatest contribution, accounting for 52 to 88% of the total macroalgal biomass (Figure 3). However, from 1981 to 1988 the dominant groups, in terms of percent contribution to biomass were *Turbinaria ornata*, *Codium* spp. and *Dictyota* spp. In these years other genera, e.g. *Halimeda*, *Padina* and *Dictyosphaeria*, which were not important in other years, also comprised substantial percentages of the total algal biomass. In 1981 *Sargassum* spp. was only the eighth most important contributor to macroalgal biomass contributing less than 1%. While the Glenn et al. report (1990) did not give monthly values, the lowest that *Sargassum* spp. fell to in that study was about 27% of the total biomass.

Biomass Diversity

Mean diversity based on biomass of the 15 most important taxonomic groups across all years was 1.15 + 0.41 for Doty's samples and 1.34 + 0.19 for the class data set. The macroalgal diversity in 1971–1973 (Glenn et al. 1990) was only 0.85. Like the earlier study by Doty, the data reported by Glenn et al. are from all seasons. The highest biomass diversity occurred in the 1981 sample when *Sargassum* biomass had crashed. The two lowest diversity indices occur in Doty's samples taken in December, and the next lowest was for all months together in the Glenn et al. (1990) data set. However, a regression of diversity on time of year for Doty's data set was not significant (P = 0.11). There is no apparent trend in species diversity over the entire 39-year sample period (Figure 5). Further, there were also no cross reef trends in diversity for Doty's 1960's data or the class data.
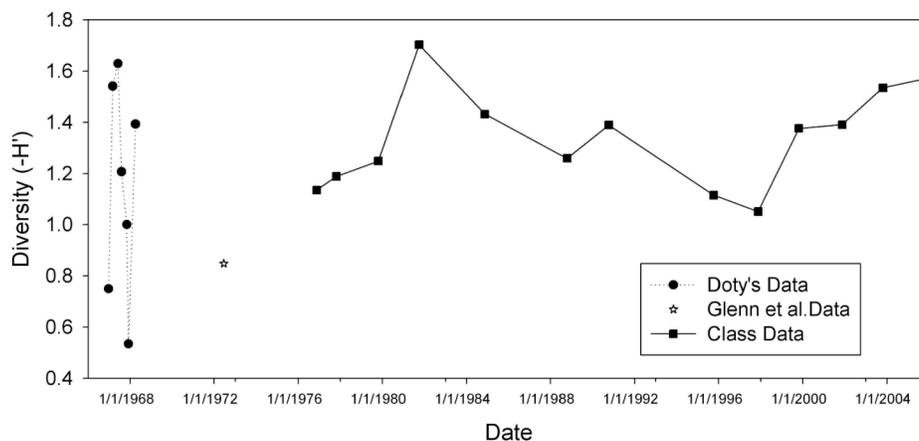

Figure 5. Species diversity (-H') based on the biomass for the 15 most common groups (see text for listing) on the Natatorium reef flat from 1966 to 2005. Diversity is calculated from the entire collection on each date.
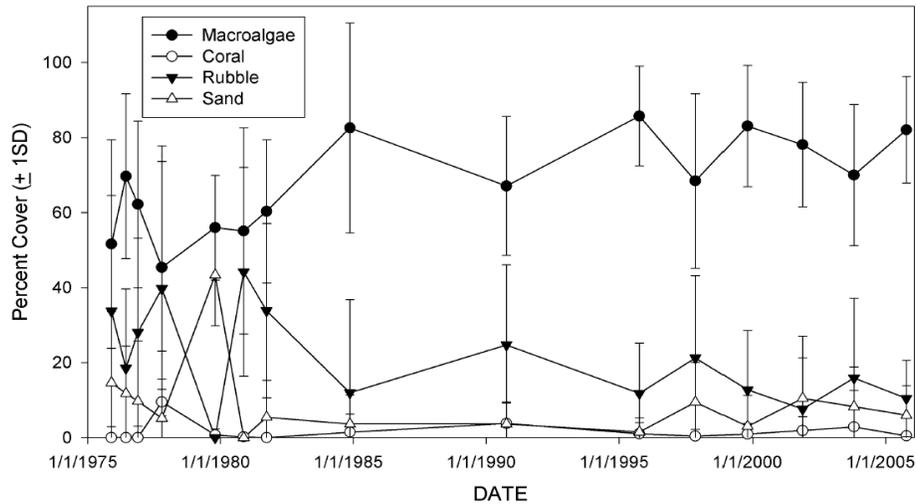
Figure 6. Mean (± 1SD) percent cover for the four bottom types from 1975 to 2005.

Benthic Cover through Time

Neither the Doty nor the Glenn data sets had information on cover, so benthic cover data are only available from 1975 when the classes began taking point counts of the substratum. Macroalgae were always the dominant cover, never falling much below 50% (Figure 6). In November 1980 cover estimates were made, but not biomass collections. There was no marked decrease in proportion of macroalgal cover in the 1980 - 1984 samples when total biomass was low. However, in the 1980 sample, taken 10 months after the severe Kona storm, sand cover was 0% whereas the mean sand cover for the 30-year period was 7.1%. From 1984 to the present, percent contribution of the four bottom cover types has shown little year-to-year change.

Cover Across Zones

Figure 7 shows the change in bottom cover from the Natatorium wall to 200 m offshore. Means are across all 30 sampling years so the large error bars represent among-year variability. In the first 100 m, macroalgal cover is never less than 60%. The cross-reef decline in macroalgal contribution to benthic cover is significant (r^2 0.21 P = 0.025), consistent with the biomass data (Figure 2). Living coral cover never reached 5% in any year.

Species contribution to cover

Figure 8 shows the relative contribution the 8 dominant groups to the total macroalgal cover from 1975–2005. The most striking change in species importance over the study period is the apparent rise to dominance of *Dictyota* spp. Beginning in November 1980 and ending in November 1993. Outside that
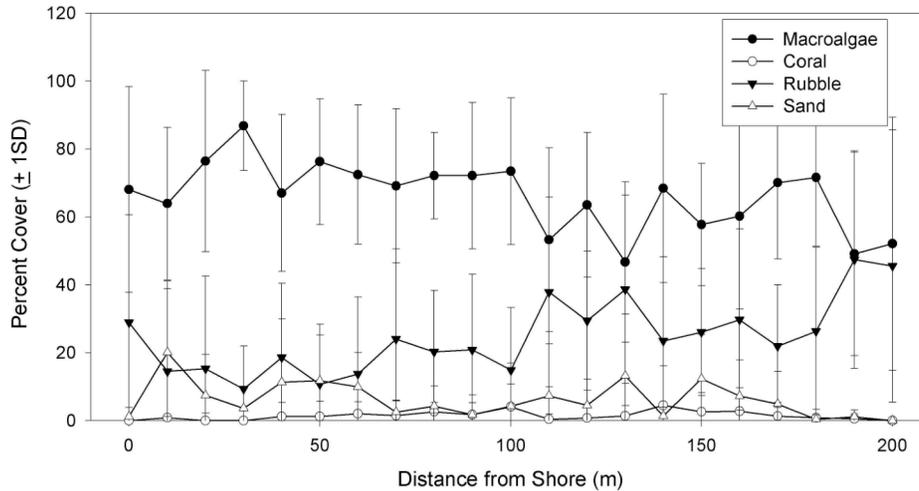
Figure 7. Mean (± 1SD) percent cover for the four bottom types across the Natatorium reef flat from 1975 to 2005. Distances are seaward from the natatorium wall.

period *Dictyota* spp. never contributed more than 8 percent to total cover. In 1995 when the contribution of *Dictyota* began to decline, *Padina* spp. contribution increased to over 30 % before it too declined. As discussed above, the percent importance of these groups might simply reflect the very low *Sargassum* spp. abundance in the 1980's. However in terms of cover, *Sargassum* spp. never contributed more than 30% even when it was contributing up to 65% of the total algal biomass. *Gracilaria salicornia*, though it dominated the later biomass samples, usually contributed less than 20% to algal cover.

Species Contribution Across the Reef Flat

Figure 9 illustrates how algal cover changes across the reef. Because three of the five groups (*Dictyota*, *Padina* and *Gracilaria*) were dominant in some years and absent in others the variability at any point was very high so error bars are not shown in the figure. While *Ulva* spp. (almost entirely *U. reticulata*) is found at all sites along the transect, it dominates at the Natatorium wall. *Sargassum* spp. dominates from 10 m to about 100 m where it declines. Recall the drop in total biomass at about 100 m. After 1990 when it first became common, *Gracilaria salicornia* was also restricted to the inshore 100 m of the transect. Beyond 100 m there is no clear dominant in terms of cover. At the more offshore sites, *Ulva* was typically entwined with attached algae, not growing from the bottom. These values are shown as percent contribution to total macroalgal cover. Because total macroalgal cover declines offshore, the total cover by these species also declines. The decline in cover was slight (1% m^{-1}) but significant (P = 0.008 adj. r^2 = 0.28).
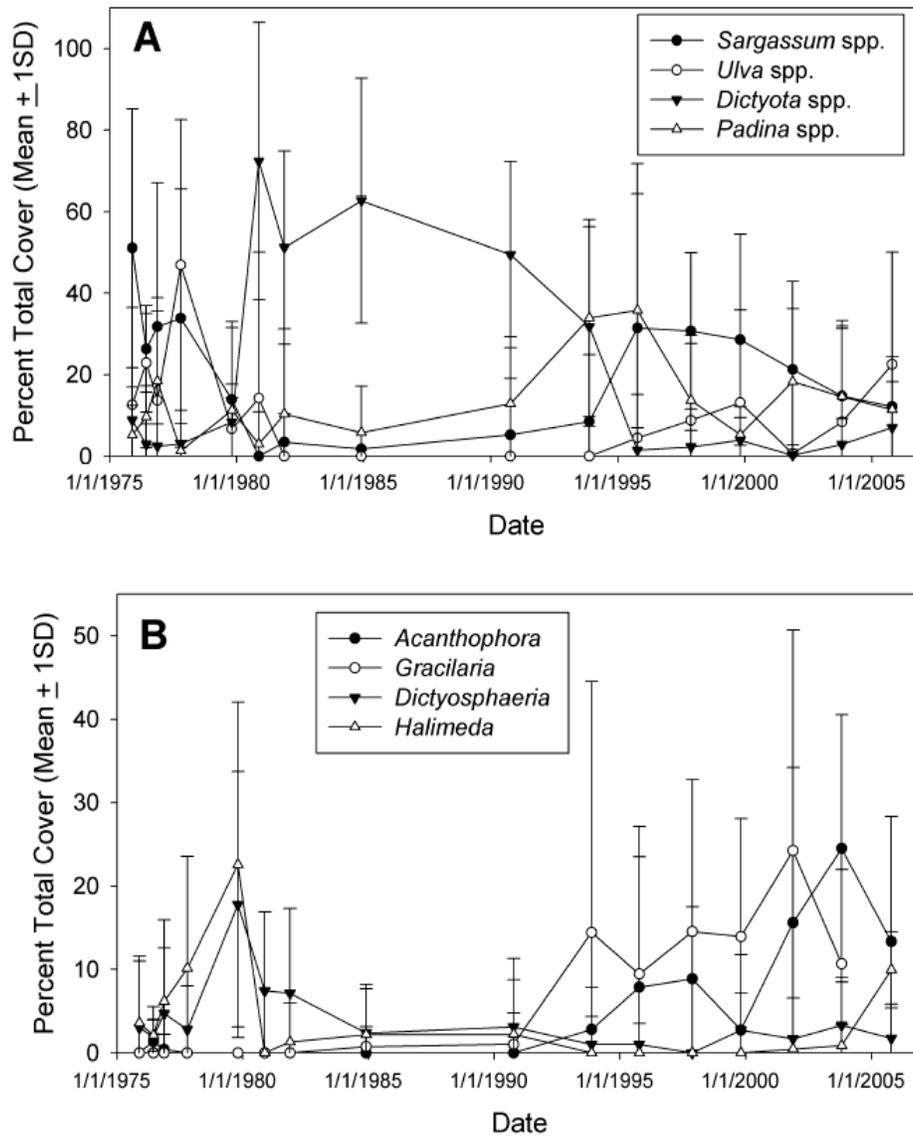
Figure 8. Mean (± 1SD) percent cover for the eight most important macroalgal groups on the Natatorium reef flat from 1975 to 2005. Panel A shows genera that at some time had more than 30% cover. Panel B shows the four next most common genera.
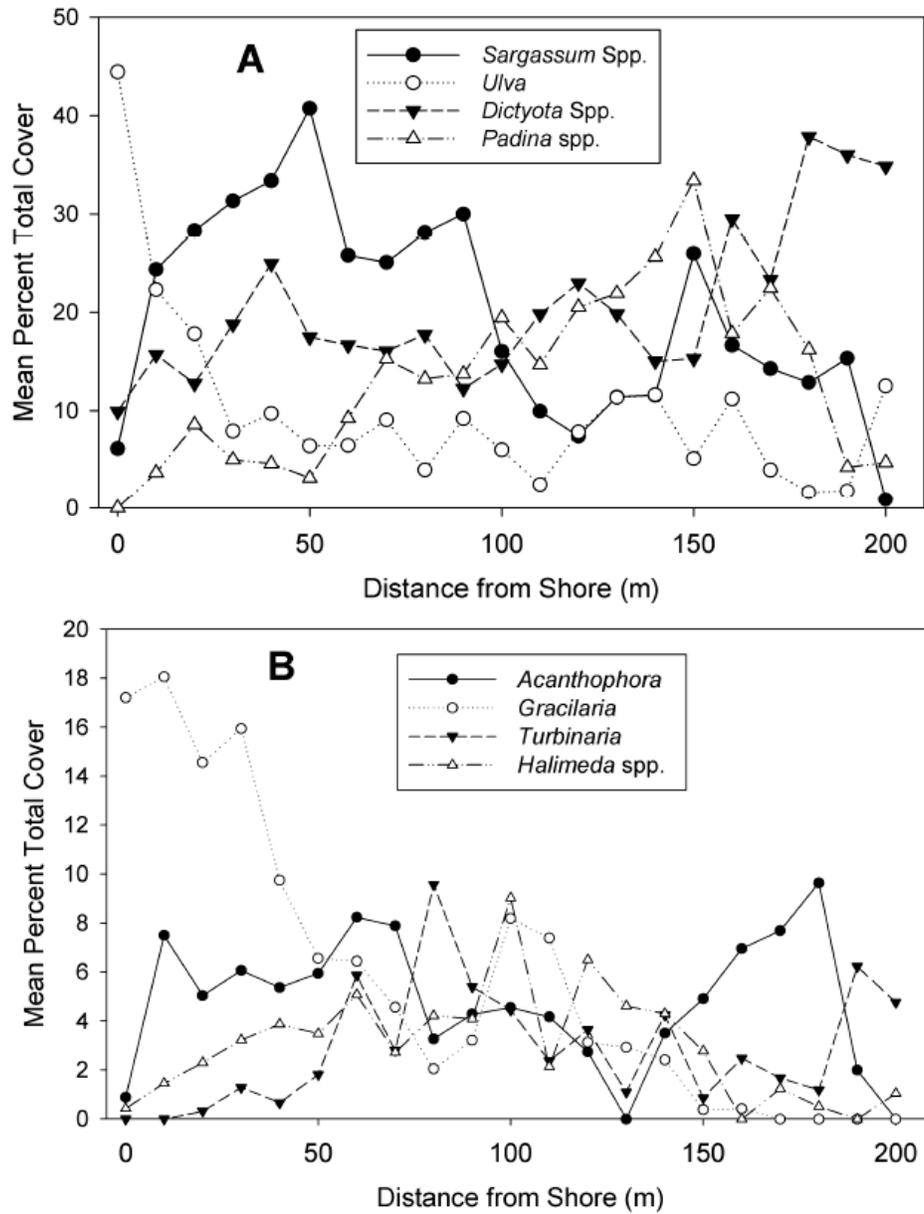
Figure 9. Mean percent cover for the eight most important macroalgal groups across the Natatorium reef from 1975 to 2005. Error estimates are not shown for clarity. Distances are seaward of the Natatorium wall. Panel A shows genera that at some time had more than 30% cover. Panel B shows the four next most common genera.

Discussion

Two dramatic changes have taken place on this reef in the past four decades; the decline and recovery of *Sargassum* spp., and the invasion of *Gracilaria salicornia*. The decrease in total biomass seen in the class collections from the early 1980's is striking. There were fluctuations in total biomass from 1968 to 1990 that may have been due to seasonal differences. Glenn et al. (1990) showed that algal biomass shows strong seasonal changes on this reef flat. However, in their study the months with low biomass were Feb. - May and the months with high biomass were Oct – Jan, with summer months intermediate. Since the class collections were generally made from October to November, seasonal effects may not be the main cause of this oscillation over the 39 years of record.

This decline in total algal biomass in the 1980's is mainly due to the decline in *Sargassum* spp. in those years (Figures 3 and 4). In the class samples from Aug. 1981 until Oct. 1995, the mean biomass recorded for *Sargassum* spp. never rose above 800 g m^{-2}. In the Aug. 27, 1981 sample, *Sargassum* spp. only contributed 8.6 g m^{-2}. While it is possible that this decline could be due to errors made by the class in collecting the biomass samples, cover of *Sargassum* in the 1981 class data set was only 2.5%, supporting the suggestion that this group was essentially absent from the Natatorium reef flat at that time. This drop in dominance of *Sargassum* resulted in an increase in relative dominance of other algal groups including *Codium* spp., *Dictyota* spp. and *Turbinaria ornata* (Figure 3). However the biomass of those groups did not show any substantial increase in that period.

What could be the cause of this dramatic drop in *Sargassum* dominance in both biomass and cover, as well at the total macroalgal biomass (but not cover) in 1981? Hurricane Iwa caused some changes in the Natatorium reef flat, but that event did not occur until November 1982. The January 1980 storm was the most damaging to hit the Islands in terms of monetary damage until Iwa, and in terms of loss of life, the winter storm equaled that of Iniki (Haraguchi 1980). Further, the 1980 winter storm had far greater impacts on the south shore of Oʻahu than the two subsequent tropical storms (Walsh 1983, Walsh et al. 2004, Dreyer et al. 2005). If the storm removed or destroyed holdfasts of *Sargassum*, recovery might have been delayed for some time, perhaps as long as the 9-year low in total *Sargassum* biomass on the Natatorium reef. Because no post-storm macroalgal survey of the Natatorium reef was conducted, this hypothesis of loss of holdfasts cannot be evaluated.

The water quality data available for areas near the Natatorium site only extend back to 1973 and are not continuous from that date to the present. Nevertheless there is no suggestion that there have been clear long-term trends over that time period. So while some unmeasured water quality parameter may have influenced the loss of *Sargassum* spp. in the 1980's there is nothing in the available data to support that hypothesis.

The DAR FMA regulations went into effect in July 1978, but it is difficult to see how these could have caused a decline in *Sargassum* biomass. Data in

Williams et al. (2006) show that total fish biomass on the Natatorium reef flat has declined from at least 1979 to 1995. In that paper they suggest changes in the macroalgal community structure may be the cause rather than an effect of changes in fish biomass and abundance.

Another possibility is that somehow in the surveys in the 1980's the classes missed or skipped the *Sargassum* in the biomass samples. However, the cover estimates taken by different students and using a different method are similar in that cover of *Sargassum* was also lower in those years. Since the two samples were taken independently, the class data support the idea that *Sargassum* was really scarce.

The second major change in algal species composition is the appearance of the invasive alien species *Gracilaria salicornia*, first noted in biomass samples in October 1990 and in cover estimates in November 1993. By October 7, 1995 Gracilaria had surpassed *Sargassum* in terms of biomass. Both have maintained similar biomass levels since that time (Figure 4). It should be noted that cover data for *Gracilaria salicornia* may be underestimates because only the first alga encountered below the sample point is recorded. Often *G. salicornia* covers the bottom in some areas, but epiphytes and algae entangled on it would be the ones recorded for the cover estimates. Consistent with this suggestion is the observation that our October 2003 estimates for cover and biomass of G. salicornia ($8.0 \pm 9.4\%$ and 936 ± 1298 g m^{-2} respectively) were much lower than the November 2002 values reported by Smith et al. (2004) ($48 \pm 24\%$ and $5193 \pm 24,632$ g m^{-2}). In the class samples only the uppermost 'hit' was recorded whereas Smith et al. recorded all understory algae as well. Also the Smith et al. study site was intentionally located in the area where *G. salicornia* had the highest density, and further, an effort was made to remove every trace of *G. salicornia* with the intention of preventing regrowth. Additionally, the class cover and biomass estimates are averaged across the entire reef flat whereas *G. salicornia* does not occur much beyond 100m offshore.

In light of the dramatic decline in *Sargassum* biomass in the 1980's and the influx of *Gracilaria salicornia* in the 1990's the composition of substratum cover over the 30 years where there are cover data is remarkably consistent (Figure 7). There is a slight (0.22% y-1), but significant (P = 0.003) increase in cover by macroalgae coupled with a decrease (-0.17% y^{-1}; P = 0.04) in percent cover by rubble. Neither coral nor sand shows any consistent change in cover over the 30 years of class data, though as noted above, there was no sand recorded in 1980.

Species diversity of the macroalgal assemblage also has not appreciably changed since the 1960's. This suggestion should be viewed with some caution since the index is based on only 15 lumped taxa. There may have been dramatic changes in species which contributed little to the total biomass or comprised the turf assemblage which was not assessed in the class data. These small species could be important as indicators but were not included in the class data set. For example *Hypnea musciformis* is known to be invasive on this reef flat (Smith et al. 2004) yet it never was common in either our biomass or cover data sets.

Further, there may be seasonal changes in diversity that could mask year-to-year trends (Glenn et al. 1990, Lirman and Biber 2000). When total diversity in Doty's data is regressed over the month of collection (from Jun. to Mar.) there is a decline through the year. However the change is not significant (P = 0.11).

There is a third temporal change that, while not as marked, is clear from comparison of two of the data sets. This is the difference in distribution of biomass across the reef. Doty's surveys clearly show an almost uniform distribution of total biomass from the shore to 190 m whereas the results from the class data indicate a clear decline in biomass with distance from shore. Doty's mean total biomass estimates from 100 to 200 m are 2.2 times greater than the class estimates for the same zone. The data do not suggest a reason for this change. It could be hypothesized that somehow the ability of the reef edge to reduce wave energy has declined so that biomass cannot accumulate on the more offshore part of the reef flat. However, there is no independent support for this idea. The invasive *G. salicornia* has its highest cover near shore. The thallus of this species is easily broken (Smith et al. 2002) which may account for its scarcity offshore where water motion is greater.

What can be made of this long-term data set that might be of use to those concerned with changes on reefs today? A snorkeler on the Natatorium reef in the 1960's who returned to Waikīkī in the early years of the 21st century would see the same dominance of *Sargassum*, but with the addition of a new co-dominant *Gracilaria salicornia*. The total biomass of macroalgae would not have changed perceptibly, and the cover of living algae would have remained the same.

However, the 21st century snorkeler would be wrong in assuming that the reef, with the exception of the appearance of the alien species *Gracilaria salicornia*, had not changed in 40 years. The apparent loss of *Sargassum* in the 1980's with the associated shift in relative importance of the remaining species apparently left no trace discernable to the observer in 2005. Even if this snorkeler had access to the cover data from the 30-year period, this shift in community composition would not have been apparent. Without continuous long-term data sets, events that alter community composition, and perhaps function, may occur unnoticed. Confirmation of any predictions about future changes in coral reefs will require good, consistent data before and during any changes in environmental conditions.

Finally, these data indicate the potential for regularly scheduled class projects in colleges and universities to make valuable contributions to our understanding of long term changes. As noted in the introduction long-term monitoring studies are expensive to fund and difficult to maintain over long time periods. If teachers incorporate such monitoring studies in their curriculum, data from class projects can make important contributions. The responsibility for quality control maintenance of the data lie, of course with the instructor, but the credit for the work belongs to the students.

Acknowledgements

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