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REPORT

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Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii

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Abstract Since the 1960s, and possibly earlier, the macroalga *Dictyosphaeria cavernosa* has overgrown and displaced corals on reef slopes and outer reef flats in Kaneohe Bay, Oahu. This shift in reef community composition is generally attributed to nutrient enrichment resulting from sewage discharge. Following the diversion of most of the sewage effluent in 1977–1978, it was expected that *D. cavernosa* growth would become nutrient-limited and its abundance would consequently decline, but the alga remains abundant in much of the bay. One explanation for its persistence is that nutrients are once again high enough to support the alga's growth. An alternative explanation is that there has been a reduction in grazing intensity in the bay. In this study we resurveyed the distribution and abundance of *D. cavernosa* at 120 reef slope sites originally surveyed in 1969. We conducted additional surveys to estimate the biomass of herbivores and the areal coverage of *D. cavernosa* and other macroalgae on reef slopes and flats. Field experiments were used to determine spatial and temporal patterns of grazing intensity on and growth rates of *D. cavernosa* and the introduced macroalga *Acanthophora spicifera*. Laboratory experiments were used to examine preferences among herbivores for some of the most abundant macroalgae on Kaneohe Bay reefs. Twenty years after sewage diversion, *D. cavernosa* cover on reef slopes has decreased substantially in southern Kaneohe Bay, the site of most of the historical sewage discharge. *D. cavernosa* cover has changed less in other regions, remaining high in the central bay and low in the north bay. *D. cavernosa* thalli protected by grazer exclusion cages sustained positive growth rates on reef slopes and flats throughout the bay. Reduced nutrient concentrations may have caused a reduction in *D. cavernosa* growth rates, and a consequent reduction in *D. cavernosa* abundance in the south bay shortly after sewage diversion. Measurements of grazing intensity and surveys of herbivorous fish abundance suggest that the continued abundance of *D. cavernosa* is the result of a reduction in grazing intensity. Reduced grazing intensity on *D. cavernosa* may in turn be the result of a historical reduction in herbivore biomass or the establishment of several introduced macroalgae on reef flats. The introduced species are preferred by herbivorous fishes over *D. cavernosa*, as indicated by preference tests. The hypothesis that reduced grazing pressure on *D. cavernosa* is related to the establishment of introduced species is supported by the observation that *D. cavernosa* cover is highest on reef slopes where the cover of preferred introduced macroalgae on the adjacent outer reef flat is also high. Conversely, *D. cavernosa* cover is low or zero on reef slopes where the cover of introduced macroalgae on the adjacent reef flat is low or zero.

Key words Coral reef · *Dictyosphaeria cavernosa* · Herbivory · Macroalgae · Nutrients · Non-native · Phase shift

Introduction

On many coral reefs near large human populations, benthic community composition has shifted in recent decades from coral dominance to macroalgal dominance. Such increases in the relative abundance of macroalgae, or "phase shifts", have been observed on Caribbean, western Atlantic, western and central Pacific, and Indian Ocean reefs (Done 1992; Littler et al. 1992; Naim 1993; Hughes 1994; Hunter and Evans 1995; Lapointe 1997; McClanahan et al. 1999). Phase shifts have been attributed to increased anthropogenic nutrient input (Cuet et al. 1988; Littler et al. 1992; Lapointe 1997), and to

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reductions in the abundance of herbivores (Hay 1984; Hughes 1994). These causes have been considered mutually exclusive (Lapointe 1997; Hughes et al. 1999), but both conditions can exist at reefs subject to the effects of human habitation, and their effects may be simultaneous.

The first well-studied phase shift occurred in Kaneohe Bay, Hawaii, where corals on the reef slopes and outer reef flats were overgrown by the green macroalga *Dictyosphaeria cavernosa*. The alga uses living corals and limestone outcrops as an anchorage and then proceeds to cover them and to kill the corals. Reduced coral cover and increased *D. cavernosa* cover were first reported in the early 1970s (Banner and Bailey 1970; Maragos 1972), but rapid population growth and development in the Kaneohe Bay watershed began in the 1920s, and the phase shift on the bay's reefs may have begun before the 1960s.

The initial expansion of *D. cavernosa* and its persistence on Kaneohe Bay reefs has been attributed to nutrient-rich sewage discharge in the bay (Pastorok and Bilyard 1985; Done 1992; Laws 1993). Six years after the 1977–1978 cessation of discharge (and 12 years after the previous survey) there had been a significant reduction in *D. cavernosa* cover on a bay-wide basis, from 13.2 to 3.1% (Hunter and Evans 1995). This reduction provided circumstantial evidence that high *D. cavernosa* cover had previously been sustained, at least in part, by sewage-derived nutrient enrichment, and led to the prediction that further improvement in water quality in Kaneohe Bay would result in further reductions in *D. cavernosa* cover. However, a comparison of the results of surveys conducted in 1983 and 1990 indicated that *D. cavernosa* cover had increased significantly from 3.1 to 7.9%, despite reductions in water column nutrient concentrations (Hunter and Evans 1995). Although measurements of herbivore abundance or activity are lacking for the years before, during or after the sewage-input period, it is possible that changing herbivore abundance or grazing intensity contributed to the decrease and the subsequent increase in *D. cavernosa* cover.

A number of published reports support the view that spatial and temporal variability in the abundance of macroalgae on reefs is related to herbivory. Herbivore exclusion studies have demonstrated that potential growth (i.e., growth or increase in cover in the absence of herbivory) of coral reef macroalgae is generally high (e.g., Lewis 1986; Morrison 1988; McCook 1997). Large-scale reductions of herbivores due to experimental manipulation (Sammarco 1982; Hay and Taylor 1985), disease (Carpenter 1988, 1990), or fishing pressure (Hay 1984; Hughes 1994), have resulted in significant increases in macroalgal biomass. At sites where roving herbivores are abundant, macroalgal biomass is uniformly low over large areas (Randall 1961; Lewis 1986; Morrison 1988; McCook 1997). When the dominant herbivores are fishes or invertebrates with limited foraging ranges (e.g., pomacentrids, juvenile scarids, echinoids, amphipods), macroalgal biomass is often spatially patchy, with zones of little or no algae corresponding to areas of intense grazing (Randall 1961; Ogden et al. 1973; Carpenter 1986). Herbivores often concentrate their foraging on reef slopes where branching corals provide shelter from predators; the amount of time fish spend foraging on the reef flat decreases with distance onto the reef flat, possibly because of the distance from shelter (Hay 1981, 1985; Lewis and Wainwright 1985; Lewis 1986). Reduced grazing intensity may make reef flats spatial refuges for macroalgae, but the degree of protection from herbivores is likely to vary with the abundance and palatability of macroalgae on both reef slopes and flats, and with predation pressure on herbivores.

In debates over the importance of nutrients and herbivory, one of these factors is often treated as the sole cause of phase shifts (Lapointe 1997; Hughes et al. 1999). This may be a false dichotomy, however. The two factors can interact with compensatory or synergistic effects (Szmant 1997). For example, under conditions of nutrient enrichment and intense herbivory, productivity may be high while biomass remains low (Hatcher and Larkum 1983). Furthermore, high biomass may be achieved, albeit slowly, under conditions of low, nutrient-limited productivity when grazing intensity is also low (Lewis 1986; Stimson et al. 1996).

In this study we related temporal changes in the areal coverage of *D. cavernosa*, and its present distribution pattern, to nutrient levels and herbivore activity. Transect surveys of herbivorous fishes were conducted to determine whether differences in *D. cavernosa* cover within or among individual reefs were correlated with herbivore biomass. Herbivore exclusion experiments were conducted on reef slopes and reef flats across Kaneohe Bay to determine the effects of spatial variability in grazing intensity and potential growth on the distribution of *D. cavernosa* and the non-native macroalga *Acanthophora spicifera*. Laboratory preference tests were conducted to establish preference ranks among the common macroalgal species grazed by herbivorous fishes. The results of these surveys and experiments have led to the development of a hypothesis to explain the distribution and persistence of *D. cavernosa*: the establishment of introduced macroalgae on reef flats in the bay has created an alternative food source for herbivores, and this has resulted in a reduction of grazing on *D. cavernosa* and hence its persistence on adjacent reef slopes.

The Kaneohe Bay environment

Kaneohe Bay is a partially enclosed embayment, 46 km^2 in area, on the windward side of the island of Oahu, Hawaii (Fig. 1). A peninsula and a 5-km-long barrier reef (a lithified dune system) along the northeast margin protects much of the bay from the prevailing oceanic swell. Within the bay, there are approximately 70 patch reefs, and a fringing reef borders the landward shore. The profiles of the patch, barrier and fringing reefs in the bay are all similar. Reef slopes rise from a maximum depth of 15 m. There is generally an abrupt change from reef slope to reef flat, referred to here as the reef crest.

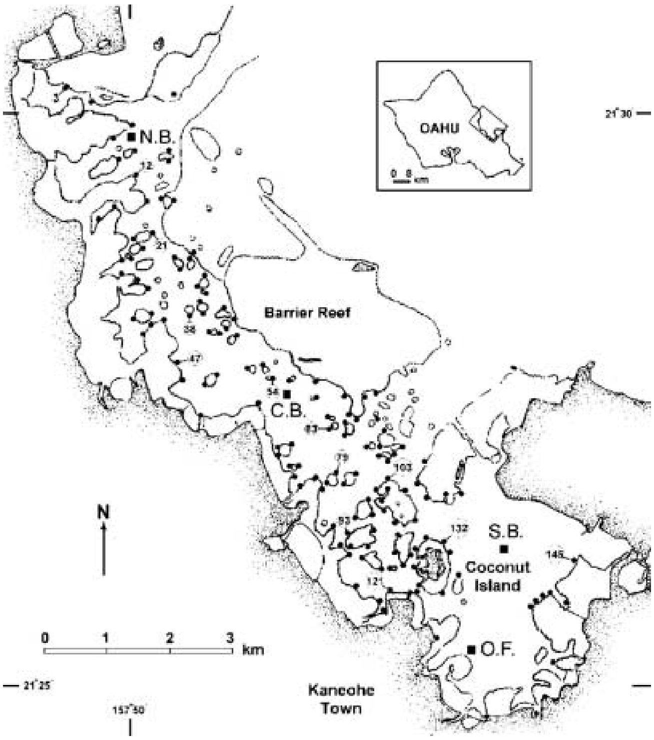

Fig. 1 Map of sites in Kaneohe Bay surveyed by Banner and Bailey (1970) in 1969. Stations are indicated by *black dots* adjacent to reef margins. Identification numbers are shown for some stations to illustrate arrangement of station numbers down length of bay. Sites labeled *NB*, *CB*, *SB* and *OF* indicate locations of monitoring stations where water column nutrient samples were collected

Reef flats are slightly above MLLW (mean level low water). The annual average tidal amplitude is about 1 m. The substrata on reef flats consist of carbonate sand and rubble, limestone reef rock, live coral and coralline, fleshy and turf algae. Live corals are most abundant on the outer edges of reef flats, near the crest. Macroalgae are broadly distributed across reef flats but generally decrease in abundance near the reef crest. Reef slopes are a mixture of live coral, reef rock, silt, sand, rubble and *D. cavernosa*. Live coral and *D. cavernosa* cover on reef slopes decrease with depth and both are scarce at depths >10 m (Hunter and Evans 1995).

Kaneohe Bay may be divided into three regions (north-west, central and south-east) on the basis of watershed land-use and hydrology, and circulation patterns within the bay (Smith et al. 1981). The south bay is adjacent to an urbanized watershed in which the town of Kaneohe and suburbs are located (Fig. 1). The watersheds bordering the north and central bays are rural and suburban. Approximately 70% of the stream runoff reaching Kaneohe Bay enters the north and central bays, and 30% enters the south bay (Smith et al. 1981).

Nutrient input

The recent history of anthropogenic nutrient input to Kaneohe Bay was described by Smith et al. (1981). At its peak in 1977, sewage discharge to the bay was approximately 1.9×10^4 m^3 day^{-1}; the south bay outfalls accounted for almost 95% of this discharge. The discharged effluent included approximately 3.6×10^4 mol day^{-1} of dissolved and particulate nitrogen, and 3.8×10^3 mol day^{-1} of dissolved and particulate phosphorus. Effluent discharged into the south bay and the north bay was diverted to deep ocean outfalls in 1977–1978 and in 1986, respectively (Smith et al. 1981; Hunter and Evans 1995). Prior to the effluent diversion from the municipal plant, sewage was the source of approximately 75% of the nitrogen and phosphorus entering the bay; stream discharge and non-point sources accounted for most of the remainder (Smith et al. 1981).

Changes in water column nutrient levels

Four water quality monitoring stations were established in Kaneohe Bay by Smith et al. (1981). One station was located in each of the three regions of the bay (north, central and south), and the fourth station was located near the site of the municipal outfall in the southeast corner of the south bay. During the prediversion period, the bay-wide means for dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) concentrations were 1.08 and 0.33 μM, respectively. During the post-diversion period, bay-wide DIN and SRP concentrations decreased to 0.80 and 0.11 μM, respectively (Smith et al. 1981). The greatest changes in both DIN and SRP were at the outfall and south bay stations, and the smallest changes were at the north bay station. Results of a survey conducted from October 1989 to June 1992 indicated that bay-wide mean concentrations of DIN and SRP had decreased further, to 0.21 and 0.04 μM, respectively (Laws and Allen 1996). These values represent a 74% decrease in DIN and a 64% decrease in SRP from the post-diversion levels reported by Smith et al. (1981). As in the Smith et al. (1981) study, the greatest reductions in both DIN and SRP concentrations during the Laws and Allen study were at the outfall and south bay stations. Following the Laws and Allen study, the south bay station was monitored in 1996 and 1997 (Stimson and Larned 2000), and the outfall station was monitored in 1997 and 1998 (Cox and Larned, unpublished). During these short-term monitoring programs, ammonium and SRP concentrations were higher than in 1989–1992, but nitrate concentrations were lower. All of the studies carried out between 1989 and 1998 reported lower DIN and SRP concentrations at all stations compared with the immediate post-diversion period.

Herbivores

No long-term records of herbivorous fish populations in Kaneohe Bay have been published, but there are commercial fishery data for the state which suggest that the catch and catch per unit effort of herbivorous fishes have declined in recent years (Smith 1993). Sea urchins are not a major component of the herbivore community in the bay. Their distribution is restricted to areas adjacent to the two major channels that connect the bay and the ocean (Hinegardner 1961; personal observations).

Macroalgae

D. cavernosa thalli are described in Stimson et al. (1996). The morphology of the thalli is unusual in that they can span large areas and create large subthallus chambers. Biomass (dry) per unit area can attain values of 1004 g/m^2 (Larned and Atkinson 1997). In addition to *D. cavernosa*, several introduced red macroalgae are abundant on reefs in Kaneohe Bay: *Acanthophora spicifera*, *Gracilaria salicornia*, *Hypnea musciformis*, *Kappaphycus alvarezii* and *K. striatum* (Russell 1983, 1992). All of these species can disperse rapidly through fragmentation. Surveys carried out in 1996 indicated that, since their introduction in the last 30 to 40 years, *G. salicornia*, *K. alvarezii* and *K. striatum* have spread through Kaneohe Bay at an average rate of 250 m/year (Rodgers and Cox 1999). All five introduced species are currently abundant in the south and central bays, and are present at lower levels in the north bay. *A. spicifera* and *H. musciformis* are largely restricted to reef flats; *G. salicornia*, *K. alvarezii* and *K. striatum* occur primarily on reef flats, but at some sites their distribution extends onto the upper reef slope. *D. cavernosa* cover is greatest on reef slopes, where it is the most common macroalga, but it also occurs on the outer reef flats.

Methods

Changes in reef communities in Kaneohe Bay between 1969 and 1996–1997

In 1969, Banner and Bailey (1970) surveyed 155 sites on patch and fringing reefs and the landward side of the barrier reef to assess the distribution of *D. cavernosa* in Kaneohe Bay and its impact on corals. The sites used for the Banner and Bailey (1970) survey were numbered 1 through 155, and arranged in a roughly sequential pattern along the length of the bay from northwest to southeast (Fig. 1). At each site, Banner and Bailey examined approximately 50 m of the reef slope, then categorized each site on a 7-point scale with regard to the level of *D. cavernosa* cover (see caption of Fig. 3A).

In the summer of 1996 and the winter of 1997, 120 sites from the Banner and Bailey (1970) study were resurveyed. The exact locations of each of the original sites could not be determined from the map in the Banner and Bailey report, but the mapped positions often coincided with reef features or the presence of man-made objects (e.g. posts), so these were adopted as indicators of the position of the original sampling sites. At each of the resurveyed sites, visual estimates of *D. cavernosa* and live coral cover were made in three quadrats 10 m apart. The quadrats were large (3 m wide and 4 m down the reef slope from the crest) and extended deep enough to include more than half of the *D. cavernosa* depth distribution (Hunter and Evans 1995). One person made all the estimates of cover. Introduced algae were not abundant on reef slopes and their percent cover was small relative to the other categories. Thirty-five stations established by Banner and Bailey (1970) were not resurveyed; these were located on the barrier reef, in the channels bordering the barrier reef, and in the northwestern corner of the bay and are generally subject to swells and wave action. At the time of the Banner and Bailey survey (1970) these were recognized as being less likely to be subject to *D. cavernosa* infestation.

Distribution of macroalgae on reef slopes and reef flats

A quadrat survey was conducted in 1992 and 1993 to examine patterns of *D. cavernosa* and coral distribution around the perimeters of individual patch reefs. The same large 3 × 4-m quadrats used in the resurvey described above were placed every 10 m around the perimeters of six small reefs (< 200 m circumference) and every 20 m around 26 large reefs (> 200 m circumference), and the percent cover of *D. cavernosa* and coral in the quadrats was visually estimated. Estimates were made by two or three workers, and each estimate was considered a replicate. In contrast to the 1996–1997 resurveys described above, these patch reef surveys were used to examine finer-scaled (tens to hundreds of meters) variation in *D. cavernosa* cover and to determine the locations of the highest *D. cavernosa* cover around the perimeters of individual reefs.

A transect survey was conducted on the reef flats of six patch reefs in 1996–1997 to examine the distribution of reef flat macroalgae (Fig. 2). At each reef, three transects were established on the reef flat at each of two types of sites, a site with high *D. cavernosa* cover on the adjacent reef slope, and a site with low *D. cavernosa* cover on the reef slope. The length of the section of reef slope characterized by high or low cover of *D. cavernosa* exceeded 50 m on each reef. The two sites on each reef had similar exposure to wind and waves. The three transects at each site were perpendicular to the crest, 5 m apart, and extended 40 m onto the reef flat and 10 m down the reef slope. The percent cover of macroalgal species and corals was determined using a line intercept method. The transects were surveyed five times at 3-month intervals between September 1996 and September 1997. The high and low *D. cavernosa*-cover sites chosen for the reef flat transects were also used for the herbivory experiments and herbivore surveys described below.

Water column nutrient levels

Dissolved nutrient concentrations in the water column were measured bimonthly from November 1998 to November 1999 at three of the stations (NB, CB, SB) established by Smith et al. (1981; Fig. 1). Water samples were collected just below the surface with acid-washed (10% HCl) and sample-rinsed 60-ml syringes, filtered through GF/F filters into acid-washed, sample-rinsed Nalgene bottles, then frozen until analysis. Ammonium, nitrate + nitrite, SRP, silicate and total dissolved nitrogen and phosphorus concentrations were measured with a Technicon Autoanalyser II at Analytical Services, University of Hawaii. Dissolved organic nitrogen (DON) and phosphorus (DOP) concentrations were calculated by subtracting inorganic nitrogen and phosphorus concentrations from totals.

Bay-wide patterns of potential growth and herbivore consumption of *D. cavernosa*

This experiment had two objectives: to determine whether *D. cavernosa* can grow in the absence of herbivory (potential growth) on reef slopes throughout Kaneohe Bay, and to assess spatial and seasonal patterns of grazing intensity on *D. cavernosa*. The experiment was carried out at the high and low *D. cavernosa*-cover sites on the six patch reefs described above (Fig. 2).

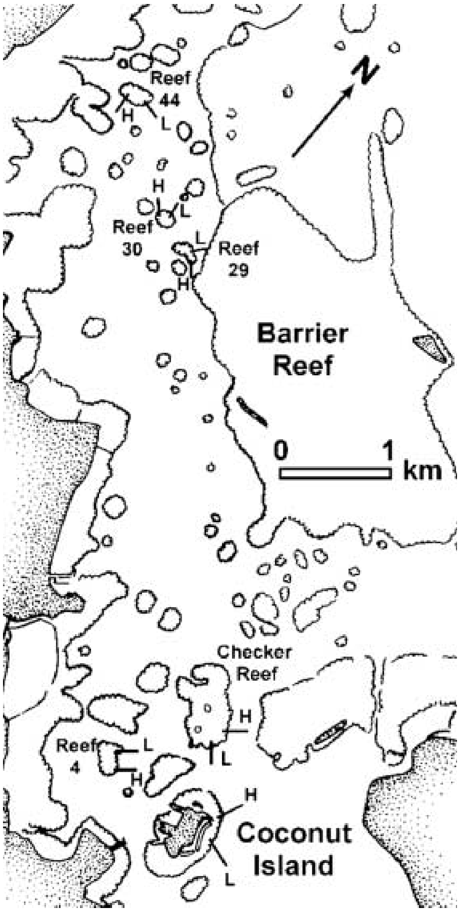

Fig. 2 Map of portion of Kaneohe Bay showing location of the six reefs used in studies of algal growth rates, grazing intensity, algal distribution and biomass of grazing fishes. Reefs are Checker Reef, Coconut Island, Reef 4, Reef 29, Reef 30 and Reef 44. *H* and *L* refer to reef slope sites that had either high or low *Dictyosphaeria cavernosa* cover

Potential growth rates and grazing intensity were measured using caged and uncaged *D. cavernosa* thalli. Detailed methods for thallus collection and preparation are given in Stimson et al. (1996). Preweighed thalli (120 to 130 g fresh weight) were assigned at random to pairs, and each pair was attached to a plastic-coated wire-mesh platform. A cage made of plastic mesh (0.4 cm^2 mesh openings) with a monofilament mesh top was attached over one thallus on each platform while the other thallus remained uncaged. Grazing kept the mesh relatively unfouled; irradiance measurements made in the cages after their use in the field indicated that the cages transmitted ≥95% of the photosynthetically active radiation measured outside the cages. Six replicate pairs of caged and uncaged thalli were placed on sand/rubble substratum on the reef slope at each site, at 2 to 3 m depth. The experimental thalli were recovered after 29 to 35 days and reweighed, and specific growth rates were calculated from the weight changes and elapsed time. Grazing intensity was measured as the difference between the specific growth rates (grams per gram per day) of caged and uncaged thalli. Specific growth rates of the caged thalli were used as a measure of potential growth, although it is possible that small herbivores removed tissue from these thalli. The potential growth rate of *D. cavernosa* and the intensity of grazing on this alga were measured five times at 3-month intervals from August 1996 to August 1997 to assess seasonality in these measures. Effects of reef location, season and reef slope-*D. cavernosa* cover on potential growth and grazing intensity were analyzed with factorial analyses of variance.

Patterns of herbivory and potential growth of macroalgae on reef flats

A second herbivory experiment was carried out to determine whether grazing intensity and the potential growth of macroalgae on reef flats in Kaneohe Bay vary with distance from the reef crest. Rates of grazing intensity and potential growth were measured using *Acanthophora spicifera* and *D. cavernosa* thalli. A total of four runs using *A. spicifera* were conducted on Checker Reef (one run) and Coconut Island reef (three runs) (Fig. 2) between August 1997 and August 1998. Due to rapid consumption of uncaged *A. spicifera* thalli, the runs were only 3 to 24 h in duration. Starting fresh weights of *A. spicifera* thalli were small, approximately 1 g, because larger pieces fragmented during attachment and transport. Two runs were conducted using *D. cavernosa* (120 to 130 g starting fresh weight) on Checker Reef, Reef 29 and Reef 44, in January and February 1997 (31 days' duration), and in June and July 1997 (29 days' duration). In both the *A. spicifera* and *D. cavernosa* runs, preweighed caged and uncaged thalli were attached to wire-mesh platforms. At each reef, the platforms were placed along the three 40-m reef flat transects described above, at the high and low *D. cavernosa*-cover sites. Platforms were placed at 10-m intervals, starting at the reef crest. Grazing intensity and potential growth rates were calculated as in the preceding reef slope experiment. The effects of reef location, distance from the reef crest, reef slope *D. cavernosa* cover and date were analyzed with factorial analyses of variance.

Abundance and biomass of herbivorous fishes

The abundance and biomass of herbivorous fishes were visually estimated at the sites with high and low *D. cavernosa* cover on the six patch reefs described above (Fig. 2). The estimates were made between 09:00 and 15:00 h during periods of neap tides. Fishes were counted along a 40-m transect extending along the reef crest. The transect area extended 5 m down the reef slope and 3 m across the outer reef flat. Visual estimates were made when visibility was ≥6 m. As the fish were counted, their total lengths were estimated to the nearest centimeter. The sizes and numbers of juvenile scarids in large schools were estimated by first estimating school size, then estimating the proportion of individuals in 1-cm size classes. Most fishes were < 15 cm in total length. The accuracy of these length estimates was checked using the method described in Stimson (1990). The principal grazers in the bay are five species of acanthurids and a number of species of juvenile scarids. No attempt was made to identify juvenile scarids to species. One to three fish species were counted on each pass along the length of a transect, so each transect was swum several times to count and estimate lengths of all grazing species present. Counts at all six study reefs were completed in 1 or 2 days to minimize the risk of changes in weather or visibility. Counts were made 11 times at each site during five census periods from September 1996 to September 1997. These counts provided a measure of the relative abundance of herbivores, but underestimated actual abundances. The counts are estimated to be approximately 60% of the actual abundance (Brock 1982), because some fraction of the fishes are hidden from view in shelter sites during a survey.

Size-frequency distributions of each fish species observed on the transects were converted to biomass estimates using regression equations for the fishes in Kaneohe Bay (acanthurids: weight in grams = 5.52×10^{-6} (length in mm)$^{3.45}$, scarids: weight in grams = 8.63×10^{-6} (length in mm)$^{3.31}$). Regression equations were provided by R. Brock, University of Hawaii (personal communication). Biomass estimates for the transects were very variable due to the occasional appearance of large individual scarids, schools of large acanthurids, or very large schools of juvenile scarids. Due to the skewed distribution of biomass values, the biomass estimates were natural-log transformed. Biomass was used to measure grazer abundance rather than numbers of fish because of the large range of sizes (total length) which occurred in all grazing species, 3 to 50 cm.

Macroalgal food preferences among herbivores

The preferences of five common herbivorous fishes, the acanthurids *Acanthurus triostegus*, *Acanthurus blochii*, *Ctenochaetus strigosus* and *Zebrasoma favescens* and juvenile scarids *Scarus* spp., were examined in this experiment. Fishes were between 6 and 15 cm in total length. Fishes were offered two to five species of macroalgae for 24-h periods in 54-L aquaria supplied with flowing unfiltered seawater. The macroalgae used in the experiments were *D. cavernosa*, the native brown alga *Padina japonica*, and the introduced red algae *Gracilaria salicornia*, *Kappaphycus striatum* and *Acanthophora spicifera*. Fresh, preweighed algal thalli were offered to each fish. At the end of each 24-h run, the uneaten algae were removed and reweighed. In experiments where fish were offered two or three species of algae at a time, all the possible pairs or triplets of algal species were offered to each fish in a random sequence over the course of a number of days; the number of combinations is given by the combinatorial:

$$\left(\frac{\text{Total number of species tested}}{\text{Number of species per run}}\right)$$

In other experiments up to five species of algae were offered simultaneously. Approximately equal weights of each species were offered, and at the end of most runs, at least 50% of the most preferred algae remained. If any algal species was entirely consumed during a run, the results from that run were not used in subsequent analyses. Additional thalli of each species were placed in aquaria without fishes during each run. Changes in weight of the grazed thalli were corrected using the growth rates of these control thalli. The corrected grazing rates (grams per day) of each fish on each algal species were converted to ranks for each macroalgal species. No statistical analyses were performed on these rankings because the number of algal species offered simultaneously differed among experiments.

Results

Changes in reef communities in Kaneohe Bay between 1969 and 1996–1997

Although the scales expressing *D. cavernosa* cover in the Banner and Bailey (1970) survey and the 1996–1997 resurvey are different, patterns of *D. cavernosa* cover during the two studies can be compared (Fig. 3). The 1969 survey indicated that *D. cavernosa* cover increased from the northwest end of Kaneohe Bay to site 50 (the approximate boundary between the north and central bays), and remained high from site 50 to the southeast end of the bay (Fig. 3A). Sites with little or no *D. cavernosa* generally had high coral cover. In the 1996–1997 resurvey, *D. cavernosa* cover also increased from the northwest end of the bay to site 50, but then declined from site 50 toward site 145 in the south bay. The greatest decreases in *D. cavernosa* cover since 1969 were in the south bay (sites 100 to 145) (Fig. 3B).

Distribution of macroalgae on reef slopes and reef flats

D. cavernosa covered approximately 30% of the reef slope area on the 34 patch reefs surveyed in 1992–1993 (Table 1). There was no indication that sections of reef perimeter with high *D. cavernosa* cover corresponded to the direction of prevailing winds and waves. However, the surveys did reveal alternating areas of high and low *D. cavernosa* cover. This pattern is most dramatically illustrated on the large patch reefs in the south bay such as the slope of Checker Reef (Fig. 4). On smaller reefs there were fewer areas of high and low cover, but the alternation of high and low cover areas was still apparent.

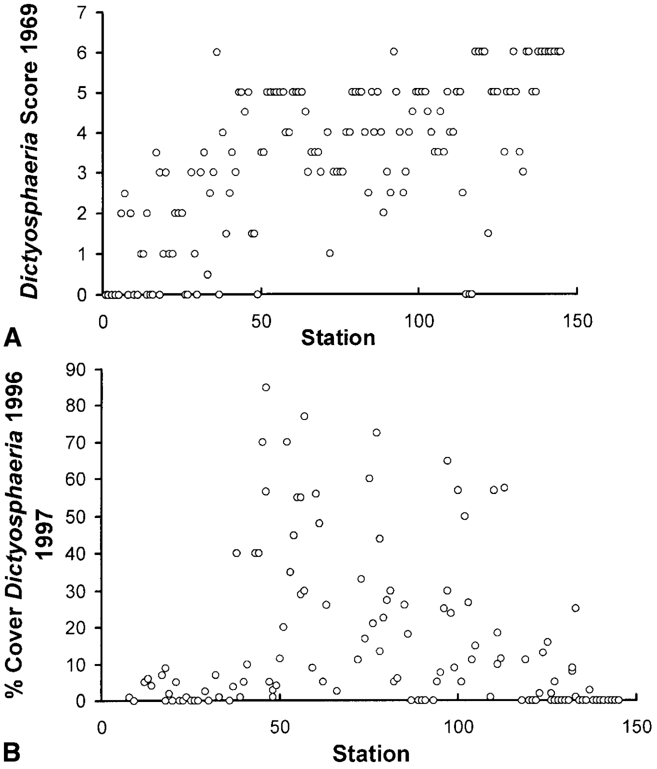

Fig. 3 Patterns of abundance of *Dictyosphaeria cavernosa* in Kaneohe Bay. **A** Pattern reported by Banner and Bailey (1970). Descriptions of conditions and associated scores are as follows: *0* no *D. cavernosa*, normal coral growth; *1* slight *D. cavernosa* growth, no interference with coral; *2* some invasion of coral heads by *D. cavernosa*; *3* heavy invasion of some or much of the coral, coral tips emergent (from *D. cavernosa* thalli); *4* most coral gone, remaining coral heavily invaded; *5* bottom either completely covered with alga or at most with only scattered heads of coral remaining; *6* neither living coral nor *D. cavernosa*, *D. cavernosa* replaced by mats of several other genera of algae. **B** Percent cover estimates made in 1996–1997 resurvey. Low-numbered sites are in north bay, high-numbered sites in south bay

Table 1 Estimates of percent cover of *Dictyosphaeria cavernosa* on a bay-wide basis in the 1990s. The 1992–1993 survey was limited to patch reefs but sampled the entire perimeter of each of 34 patch reefs. The 1996–1997 survey sampled 123 sites previously surveyed by Banner and Bailey (1970), and included sites on the lee side of barrier reef and on the fringing reef

Survey	*Dictyosphaeria cavernosa*	Live coral	Limestone	Sand and rubble
1992–1993	32	32	15	22
1996–1997	16	51	9	21

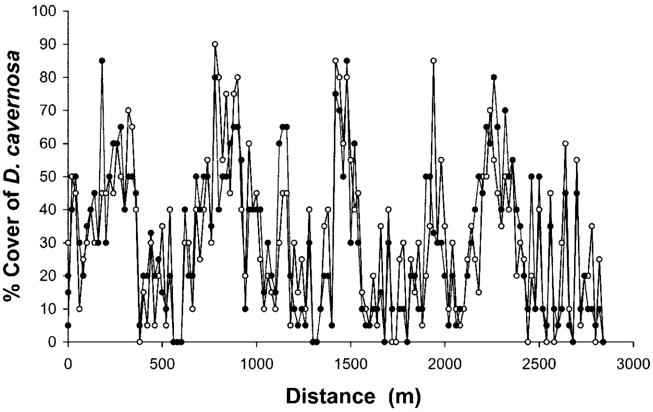

Fig. 4 Distribution of *Dictyosphaeria cavernosa* along reef slopes of a large patch reef, Checker Reef (points are estimates made by two individuals). 0-m point is northernmost point on perimeter of patch reef

Areas of both high and low *D. cavernosa* cover extended for distances of 10 to several 100 m along reef slopes. On six reefs, a section of reef slope with high percent cover of *D. cavernosa* and a section with low cover were selected for subsequent experiments. Percent cover of *D. cavernosa* at each high-cover site was at least twice as high as that of the low-cover site on the same reef, but the high cover sites on some reefs had lower cover than the low cover sites on other reefs. Low cover values ranged from 0 to 16%, high cover values ranged from 10 to 39%.

The dominant macroalgal species on the patch reef flat transects were *Gracilaria salicornia*, *Kappaphycus striatum*, *Acanthophora spicifera* and *Padina japonica*. The percent cover of these species was generally low (< 10%) within 10 to 20 m of reef crests, and increased with distance toward the centers of reef flats (Fig. 5). Each of the dominant species had a distinct pattern of distribution across reef flats in terms of the distance from the reef crest where each species began to increase in cover, and the distance at which cover reached a maximum. The species closest to the reef crest was *K. striatum*, followed by *G. salicornia*, then *A. spicifera* and *P. japonica*. *D. cavernosa* cover was highest on reef slope and decreased across the reef flats.

There was a positive relationship between the cover of *D. cavernosa* on reef slopes and the abundance of macroalgae on adjacent reef flats (Fig. 6). On reef flats adjacent to slopes with high *D. cavernosa* cover, the mean percent cover of macroalgae (all species except *Kappaphycus striatum* and *D. cavernosa*) was 17%. On flats adjacent to slopes with low *D. cavernosa* cover, the mean percent cover of macroalgae (all species except *K. striatum* and *D. cavernosa*) was 7%. The contribution of *K. striatum* and *D. cavernosa* to the cover of macroalgae on reef flats was excluded from Fig. 6 because these species ranked low in herbivore preference tests, and because their cover was high on only two reefs, Reef 29 and Reef 44. The difference between macroalgal cover on the two types of reef flats was significant (one-way ANOVA, $F = 6.05$, df = 1 and 46, $P = 0.018$). Reef flat macroalgae extended closer to the reef crest at the sites with high reef slope *D. cavernosa* cover than at the low *D. cavernosa*-cover sites (Fig. 6).

Water column nutrient levels

Mean ammonium, SRP, DON and DOP concentrations measured from October 1998 to January 1999 at the north, central and south bay stations were very similar; the largest differences between the means of these

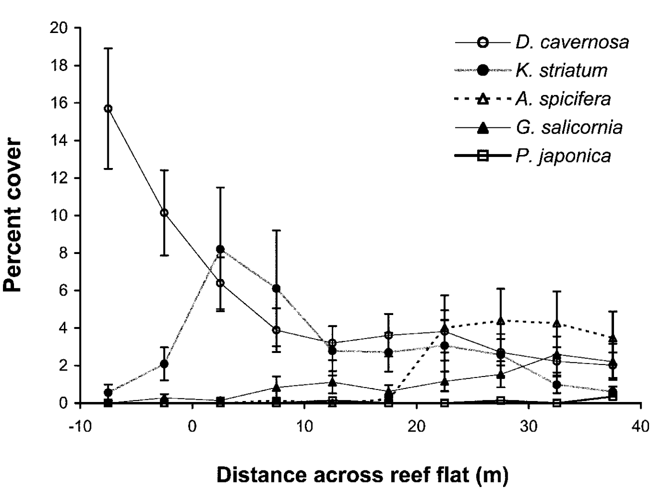

Fig. 5 Percent cover of dominant macroalgal species across outer reef flats. Values are means ± 1 SE from six transect surveys conducted in March 1997 on each of the six study reefs indicated in Fig. 2. Negative values on abscissa refer to distance down reef slope

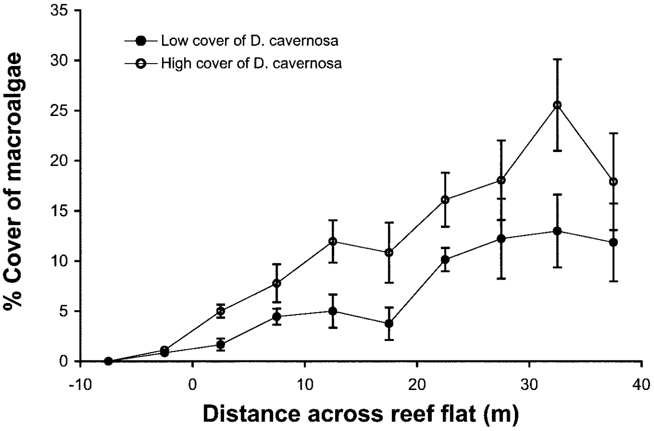

Fig. 6 Percent cover of dominant macroalgae across outer reef flats at sites with high and low *Dictyosphaeria cavernosa* cover on adjacent reef slope. Values (means ± 1SE) shown are pooled across algal species and across the six study reefs. Transect surveys were conducted in March 1997. Cover of *D. cavernosa* and *Kappaphycus alvarezii* were excluded because of low preference shown by grazing fishes for these species. Negative values on abscissa refer to distance down reef slope

Table 2 Nutrient concentrations (µM) at three stations in Kaneohe Bay for period October 1998 to January 2000. Values are means ±1 SD. Sample sizes in parentheses

Station	PO_4 (33)	NO_3+NO_2 (33)	NH_4 (33)	DOP (19)	DON (19)	Si (33)
North bay	0.08±0.04	0.40±0.42	0.20±0.11	0.26±0.05	6.68±1.27	7.02±1.87
Central bay	0.08±0.05	0.17±0.39	0.21±0.20	0.27±0.06	6.66±1.14	4.93±2.60
South bay	0.08±0.03	0.08±0.18	0.15±0.10	0.28±0.03	7.22±1.02	6.80±2.02

stations for these nutrients were ~25% (Table 2), and there were no significant differences among the three stations. Nitrate + nitrite concentrations were higher at the north bay station than at the central or south bay stations [one-way ANOVA of ln(NO_3 concentration + 1): $F=15.08$, df = 2 and 64, $P<0.001$, Tukey tests: $P<0.01$ for both comparisons]. High nitrate concentrations may have resulted from high stream discharge into the north bay. Silicate concentrations, which are generally indicative of fresh-water runoff, were also slightly but significantly higher at the north bay station than at the central and south bay stations (Table 2, one-way ANOVA, $F=15.05$, df = 2 and 64, $P<0.001$, Tukey tests: $P<0.05$ for both comparisons).

Bay-wide patterns of potential growth and herbivory on *D. cavernosa*

There were significant differences among reefs and among dates in the potential growth rates of *D. cavernosa* thalli on reef slopes, but there was no significant difference between areas of high and low *D. cavernosa* cover, and no significant interactions (Table 3). Results of this experiment indicated that *D. cavernosa* can sustain long-term growth on reef slopes throughout Kaneohe Bay (Fig. 7A). The potential growth rates of thalli on Reef 44 were significantly higher than those on four of the other reefs, and the potential growth rates on Reef 30 and Checker Reef were greater than on Reef 4 (Table 3). Significant differences among dates were due to higher growth rates at all sites in November 1996.

Table 3 Analysis of potential growth rates of *Dictyosphaeria cavernosa* thalli on patch reef slopes. Cover refers to sites of high and low *D. cavernosa* cover on reef slope

Factorial analysis of variance				
Source	df	MS	*F*	*P*
Reef	5	0.00015	9.47	<0.0001
Date	4	0.00087	54.44	<0.0001
Cover	1	0.00006	3.59	0.0591
Date × reef	20	0.00002	1.16	0.2857
Reef × cover	5	0.00003	1.95	0.0865
Date × cover	4	0.000003	0.22	0.9249
Reef × date × cover	20	0.00002	1.03	0.4282
Error	300	0.00002		
Total	359			

Tukey test results: Reefs and dates are shown in descending order of mean growth rate. Reefs and dates with the same superscript letter are not significantly different ($P>0.05$)

Reefs: Reef 44^{a} > Reef 30^{ab} > $Checker^{b}$ > $Coconut^{bc}$ > Reef 29^{bc} > Reef 4^{c}

Dates: Nov 1996^{a} > Aug 1996^{b} > Feb 1997^{b} > May 1996^{b} > Aug 1997^{b}

There were significant differences in grazing intensity on *D. cavernosa* among reefs, among dates and between areas of high and low *D. cavernosa* cover, and three of the interactions among the main effects were significant (Table 4, Fig. 7B). Grazing intensity was significantly higher on reef slopes with low *D. cavernosa* cover than on slopes with high *D. cavernosa* cover (Table 4). Grazing intensity varied about four-fold among reefs (pooling across dates), and Tukey post-hoc test comparisons indicated that grazing intensity was highest at the northernmost reef, Reef 44 (Table 4), and generally higher in the northern end of the bay. Similarly, Tukey test comparisons identified several significant differences among dates, but there was no marked seasonal pattern

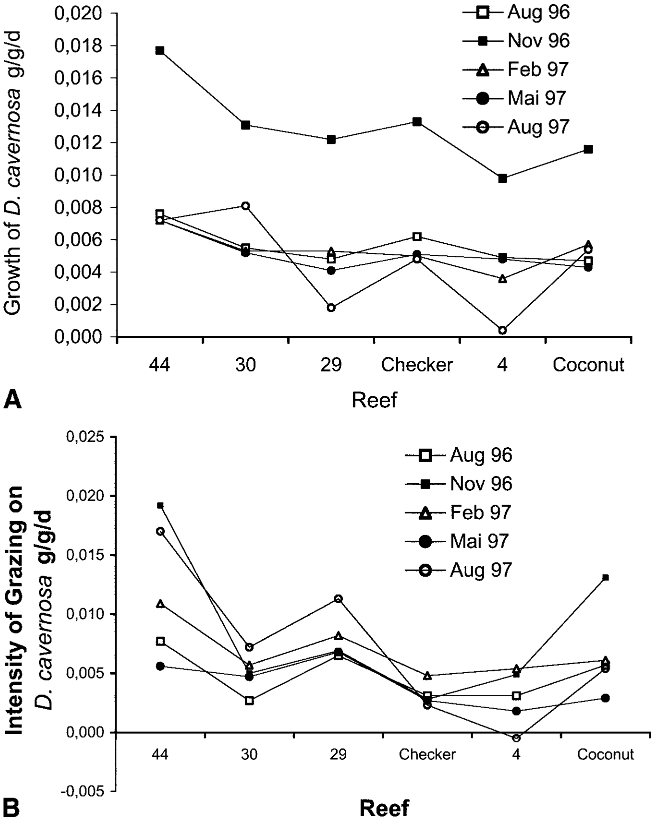

Fig. 7 Growth and grazing intensity on *Dictyosphaeria cavernosa* on reef slopes with high and low *D. cavernosa* abundance. Values are means of six replicates on each reef on each date. Reefs are arranged in approximate order down length of bay from north-west to south-east. Statistical analyses are reported in Tables 3 and 4. **A** Potential (caged) growth rates of *D. cavernosa* thalli. **B** Grazing intensity on *D. cavernosa* thalli

Table 4 Analysis of grazing intensity on *Dictyosphaeria cavernosa* thalli on patch reef slopes. Cover refers to sites of high and low *D. cavernosa* cover on reef slope

Factorial analysis of variance

Source	df	MS	*F*	*P*
Reef	5	0.00071	19.98	< 0.0001
Date	4	0.00024	6.85	< 0.0001
Cover	1	0.00251	71.20	< 0.0001
Reef × date	20	0.00010	2.84	< 0.0001
Reef × cover	5	0.00038	10.81	< 0.0001
Date × cover	4	0.00007	1.85	0.1185
Reef × date × cover	20	0.00011	2.21	0.0024
Error	301	0.00002		
Total	360			

Tukey test results: Reefs and dates are shown in descending order of mean grazing intensity. Reefs and dates with the same superscript letter are not significantly different ($P > 0.05$)

Reefs: Reef 44^{a} > Reef 29^{b} > Coconut Is.^{b} > Reef 30^{bc} > Checker^{c} > Reef 4c

Dates: Nov 1996^{a} > Aug 1997^{ab} > Feb 1997^{ab} > Aug 1996^{bc} > May 1997^{c}

(Fig. 7B). The significant reef × date interaction was due to high grazing intensity in November 1996 on the Coconut Island reef slope (Fig. 7B).

Patterns of potential growth and herbivory of macroalgae on reef flats

Growth rates of *D. cavernosa* and *Acanthophora spicifera* on outer reef flats were examined to determine whether differences in growth rate could explain the patterns of distribution of these species. There were no significant differences in the potential growth rates of *D. cavernosa* thalli among distances along the 40-m reef flat transects (Table 5, Fig. 8). There were significant differences in potential growth rates of *D. cavernosa* between reefs, between dates and between sites with high and low reef slope *D. cavernosa*, and there was a significant reef × date interaction. Potential growth rates of *A. spicifera* were significantly lower at reef crests (0 m) than at distances of 30 and 40 m onto the reef flat, but no other differences were detected among distance intervals (Table 6, Fig. 9A). There was a significant effect of reef location on potential growth rates of *A. spicifera*. This result was due in part to a single run at Coconut Island with unusually low growth rates.

Grazing intensity on *Acanthophora spicifera* was significantly higher near reef crests and decreased with distance onto reef flats (Table 7, Fig. 9B). Since grazing intensity is greater than specific growth rate at reef flat positions from 0 to 30 m, grazing essentially prevents this species from growing on the outer reef flat/reef crest areas. The mean grazing intensity on *A. spicifera* at the reef crest was about three times higher than at a distance of 40 m from the crest (Fig. 9B). Grazing intensity on *A. spicifera* at sites with low *D. cavernosa* cover was significantly higher than at sites with high *D. cavernosa* cover, and was significantly higher at Coconut Island than at Checker Reef. Grazing intensity on *D. cavernosa* did not vary significantly with distance from reef crests, and no other main effects were significant.

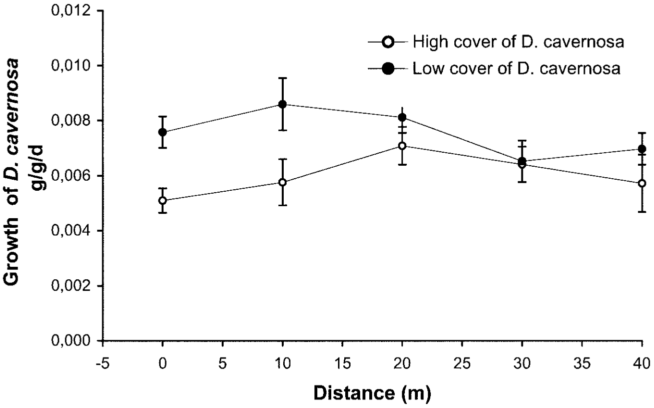

Fig. 8 Potential growth of *Dictyosphaeria cavernosa* thalli with distance on reef flats from reef crests. Growth rates are shown for sites with high and low *D. cavernosa* cover on adjacent reef slope. Values are means ± 1 SE and are based on three transects on three study reefs during 2 months of the year

Biomass and abundance of herbivorous fishes

The log-transformed biomass of herbivorous fishes was highest on patch reefs in the north bay and decreased down the length of Kaneohe Bay (Table 8, Fig. 10). This gradient resulted in part from a higher abundance of large

Table 5 Analysis of potential growth rates of *Dictyosphaeria cavernosa* thalli on patch reef flats.*Cover* refers to sites of high and low *D. cavernosa* cover on adjacent reef slope. *Distance* refers to distance in meters from reef crest

Factorial analysis of variance

Source	df	MS	*F*	*P*
Cover	1	0.000105	12.5	0.001
Reef	2	0.000087	10.34	< 0.001
Distance	4	0.000011	1.33	0.264
Date	1	0.000082	9.76	0.002
Cover × reef	2	0.000002	0.27	0.762
Cover × distance	4	0.000012	1.38	0.247
Cover × date	1	0.000000	0.00	0.978
Reef × distance	8	0.000005	0.58	0.794
Reef × date	2	0.000054	6.47	0.002
Distance × date	4	0.000007	0.84	0.503
Cover × reef × distance	8	0.000007	0.86	0.554
Cover × reef × date	2	0.000024	2.86	0.061
Cover × distance × date	4	0.000003	0.33	0.855
Reef × distance × date	8	0.000012	1.42	0.197
Cover × reef × distance × date	8	0.000004	0.48	0.871
Error	118	0.000084		
Total	177			

Tukey test results: Reefs are shown in descending order of mean growth rate. Reefs with the same superscript letter are not significantly different ($P > 0.05$)

Reefs: Reef 44^{a} > Checker Reef^{b} > Reef 29b

Table 6 Analysis of potential growth rates of *Acanthophora spicifera* on patch reef flats. *Cover* refers to sites of high and low *Dictyosphaeria cavernosa* cover on adjacent reef slope. *Distance* refers to distance in meters from reef crest. Only results from transect distances 0, 10, 20, 30 and 40 m were included in ANOVA

Factorial analysis of variance

Source	df	MS	*F*	*P*
Reef	1	0.0781	15.01	< 0.001
Cover	1	0.0002	0.04	0.838
Distance from crest	4	0.0162	3.12	0.016
Reef × cover	1	0.0001	0.01	0.914
Reef × distance	4	0.0012	0.23	0.919
Cover × distance	4	0.0090	1.73	0.144
Reef × cover × distance	4	0.0096	1.85	0.121
Error	216	0.0052		
Total	235			

Tukey test results: Distances from the reef crest are show in descending order of mean growth rate Distances with the same superscript letter are not significantly different ($P > 0.05$)
Distance: 40 $m^a > 30\ m^a > 10\ m^{ab} > 20\ m^{ab} > 0\ m^b$

Table 7 Analysis of grazing intensity on *Acanthophora spicifera* on patch reef flats. *Cover* refers to sites of high and low *Dictyosphaeria cavernosa* cover on adjacent reef slope. *Distance* refers to distance in meters from reef crest. *Run* refers to three experiments conducted on Coconut Island reef flat in August 1997, and July and August 1998, and to one experiment conducted on reef flat of Checker Reef in July 1998

Factorial analysis of variance

Source	df	MS	*F*	*P*
Run	3	0.869	20.66	< 0.0001
Cover	1	0.315	7.48	0.007
Distance from crest	4	0.860	20.45	< 0.001
Cover × distance	4	0.086	2.06	0.087
Error	222	0.042		
Total	234			

Tukey test results: Distances from the reef crest are show in descending order of mean grazing intensity. Distances with the same superscript letter are not significantly different ($P > 0.05$)
Distance: 0 $m^a > 10\ m^b > 20\ m^{bc} > 30\ m^c > 40\ m^c$

acanthurids on the northern reefs, compared to south and central bay reefs, where small scarids were the dominant herbivores. Large scarids (> 20 cm length) were rarely encountered on any reef. Herbivore biomass at the sites with low *D. cavernosa* cover did not differ significantly from herbivore biomass at the high cover sites (Table 8).

High variability in the estimates of herbivorous fish biomass was due in part to the large range of sizes. Most scarids censused were less than 12 cm in length and occurred in small schools (< 20), so the appearance of single large (20 to 40 cm) scarids greatly increased the estimated biomass in a census, as did occasional large schools (> 100) of small scarids.

Macroalgal food preferences among herbivores

The results of the preference experiments indicated that both acanthurids and scarids prefer the red alga *Acanthophora spicifera* over all other macroalgal species tested (Table 9). The next most highly preferred alga for the scarids was the calcareous brown alga *Padina japonica*, although it was only tested once, while acanthurids showed about equal preference for *Gracilaria salicornia* and *Kappaphycus striatum*. Fishes of both families ranked *D. cavernosa* low, and scarids ranked *K. striatum* even lower than *D. cavernosa*.

Discussion

Changes in *D. cavernosa* cover over time

Our 1996–1997 resurvey of the Banner and Bailey (1970) stations revealed a change in the distribution of *D. cavernosa* on a bay-wide scale (Fig. 3); *D. cavernosa* cover in the south bay has declined substantially, while

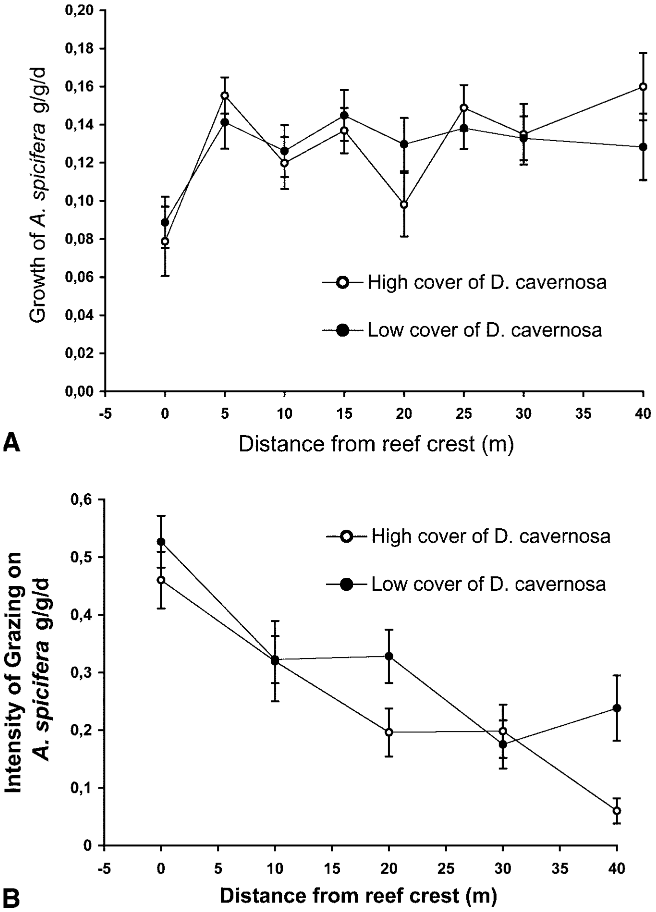

Fig. 9 Growth and grazing intensity on *Acanthophora spicifera* on reef flats with distance from reef crests. Growth rates and rates of grazing intensity are shown for sites with high and low *Dictyosphaeria cavernosa* cover on adjacent reef slope. Values are means ± 1 SE from two study reefs during 3 months of the year. **A** Potential growth rates of *A. spicifera*. Figure includes growth rates at stations 5, 15 and 25 m from reef crest, which were not included on all transects, and were not included in the analysis (Table 7). **B** Grazing intensity on *A. spicifera* at same sites

Table 8 Analysis of grazing fish biomass on study reefs over a 1-year period. Date is treated as a block. Variable is natural log of estimated biomass of acanthurids and scarids. *Cover* refers to sites of high and low *Dictyosphaeria cavernosa* cover on reef slope

Source	df	MS	*F*	*P*
Reef	5	2.10	5.59	0.0001
Cover	1	1.02	2.70	0.103
Date	10	6.58	17.49	
Reef × cover	5	0.22	0.57	0.72
Error	108	0.38		
Total	129			

Tukey test results: Reefs are shown in descending order of mean growth rate. Reefs with same superscript letter are not significantly different ($P > 0.05$)

Reefs: Reef 44^{ab} > Reef 30^{ab} > Reef 29^{abc} > Coconut^{bc} > Reef 4^{bc} > Checker^{c}

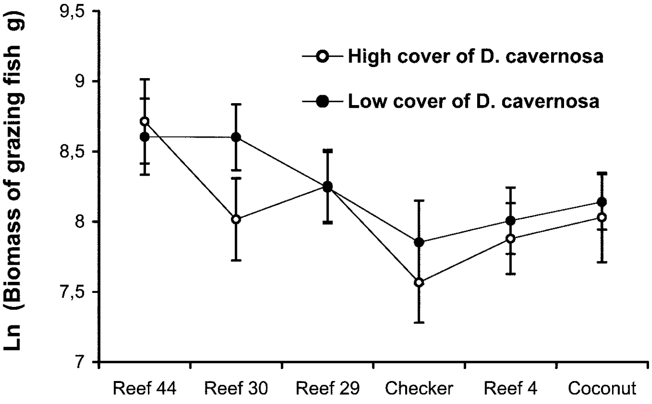

Fig. 10 Biomass of grazing acanthurids and scarids on six reefs distributed down length of Kaneohe Bay. Biomass was assessed in two areas (each 8 × 40 m) along perimeters of each reef, an area with high reef slope *Dictyosphaeria cavernosa*-cover and an area with low *D. cavernosa* cover. Values are means ± 1 SE, based on 15 sampling dates

cover has remained relatively high in the central bay and low in the north bay (Fig. 3). This decline may have been due to a reduction in the concentration of inorganic nitrogen in the south bay, particularly ammonium, following diversion of sewage discharge out of the bay in 1977. Diversion resulted in a greater absolute and relative reduction in water column DIN concentrations in the south bay than in the central and north bays (Fig. 11). Since DIN concentrations in the south bay were much higher before sewage diversion than after (Fig. 11), and given that *D. cavernosa* growth rate increases with increasing DIN concentrations up to 17 μM (Larned and Stimson 1996), growth rates of *D. cavernosa* in the south bay were probably higher prior to sewage diversion. The large decrease in *D. cavernosa* cover between 1969 and 1996–1997 may reflect a substantial decrease in the rate of growth of *D. cavernosa* in the south bay, to the point that present-day growth rates are usually exceeded by losses to herbivores.

Reefs in the central bay currently support high *D. cavernosa* cover, as was the case in 1969 (Fig. 3). The central bay has a very small watershed and relatively low rates of nutrient runoff from the land (Smith et al. 1981), so the high *D. cavernosa* cover we observed there was unexpected. *D. cavernosa* cover in the north bay was low in both the 1969 survey and our resurvey, despite the fact that the north bay receives higher runoff, and, consequently, has higher water column nitrate concentrations than the central or south bays (Table 2).

Causes of the persistence of *D. cavernosa* in Kaneohe Bay and its current spatial distribution

The abundance of *D. cavernosa* on Kaneohe Bay reefs was expected to decline following the diversion of sew-

Table 9 Preference rankings for macroalgae in nine laboratory preference tests. Tests differ in number of algal species offered simultaneously, but all were conducted using fishes in individual aquaria. Summary rankings are not weighted for sample sizes in individual tests

Summary of lab preference test for acanthurids							
Test	1	2	3	4	5	Average rank (out of 5)	Average rank (out of 4)
Number of fish tested	10	5	5	3	1		
Number of algal species offered	5	2	3	5	5		
Acanthophora spicifera	1	1	1	1	1	1	1
Dictyosphaeria cavernosa	4	4	3	4	4	4	4
Gracilaria salicornia	3	2	2	2	3	2.6	2.25
Kappaphycus alvarezii	2	3		4	2	2.6	2.75
Padina japonica	5			4	5	4.7	
Summary of lab preference tests for scarids							
Test	1	2	3	4		Average rank (out of 4)	Average rank (out of 3)
Number of fish tested	6	5	7	3			
Number of algal species offered	5	2	3	2		1	1
Acanthophora spicifera	1	1	1			3	3
Dictyosphaeria cavernosa	4	3	3			2	2
Gracilaria salicornia	3	2	2	2		4	
Kappaphycus alvarezii	5	4					
Padina japonica	2						

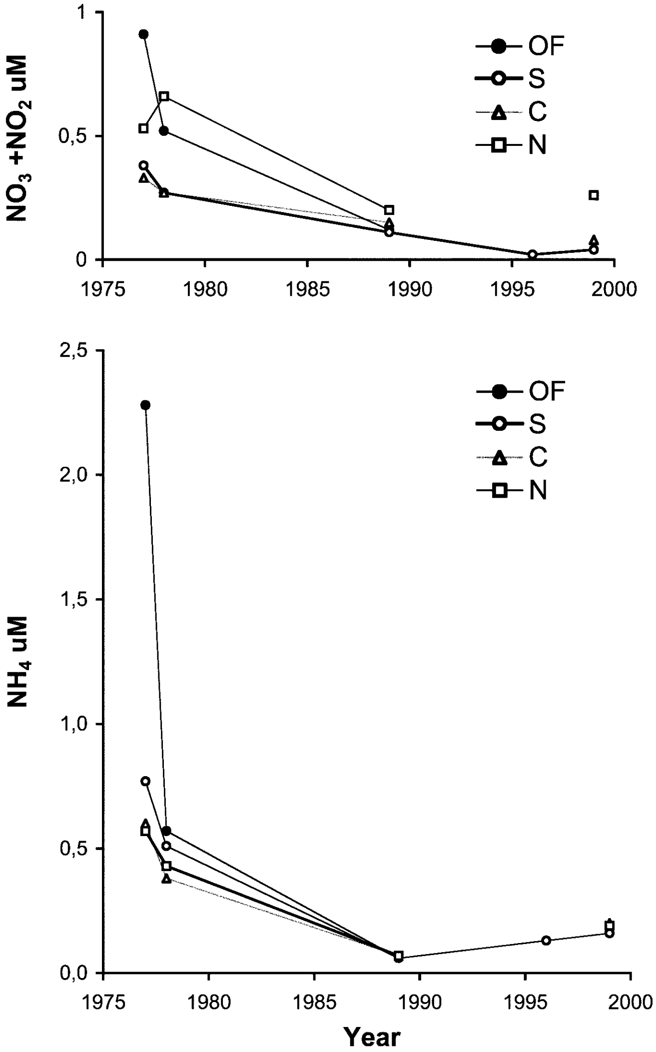

Fig. 11 Changes in DIN concentrations in three regions of Kaneohe Bay since diversion of sewage in 1977–1978. Values for 1977 are prediversion values and for 1978 are post-diversion values, both from Smith et al. (1981). Values for 1989 are from Laws and Allen (1996); values for 1996 are from Larned and Stimson (1996). Only the south bay was sampled in 1996. No samples for the outfall station were available that were contemporaneous with the 1998–1999 samples for the other three stations

age from the bay (Smith et al. 1981). A study by Hunter and Evans (1995) which compared the results of surveys conducted at 15 permanent stations in 1971, 1983 and 1990 revealed a bay-wide decrease in *D. cavernosa* cover (and increased coral cover) between 1971 and 1983; in 1983 *D. cavernosa* cover was approximately 25% of its 1971 level (13.2% cover). However, in the interval from 1983 to 1990, Hunter and Evans (1995) reported a reversal of the trend, as *D. cavernosa* cover doubled on a bay-wide scale. The reason for this temporal change in cover at the permanent stations is not clear. As of 1989–1992, inorganic nutrient concentrations in the Kaneohe Bay water column had reached very low concentrations (Laws and Allen 1996), comparable to the most oligotrophic coral reef ecosystems (D'Elia and Wiebe 1990). The current DIN and SRP concentrations in the Kaneohe Bay water column are well below the thresholds (1 μM DIN, 0.1 μM SRP) proposed by Bell (1992) and Lapointe (1997), above which rapid macroalgal growth is predicted to cause phase shifts on reefs.

This study shows there has been a differential decline in *D. cavernosa* cover in the south bay between 1969 and 1996–1997. This difference in pattern of decline occurred despite the fact that in the 1998–1999 period the three basins had similar, low DIN concentrations (Table 2).

Despite low water column nutrient concentrations, *D. cavernosa* persists on reef slopes in the bay. A possible explanation for its persistence is that *D. cavernosa* (and other macroalgae in the bay) draw on additional sources of nutrients. Previous studies (Larned and Stimson 1996 ; Larned 1998) have shown that *D. cavernosa* cannot sustain long-term growth in laboratory cultures when supplied with flowing, non-enriched seawater from the Kaneohe Bay water column, but that *D. cavernosa* can obtain inorganic nitrogen from the water in chambers which develop beneath the alga as it grows. Nutrient-rich sediments accumulate within the chambers, and the undersides of the thalli and the surfaces of the overgrown corals are colonized by invertebrates (Stimson et al. 1996 ; Larned 1997). As a result of nutrient efflux from the sediments and excretion by invertebrates, the mean DIN concentration in *D. cavernosa* chambers is about 10 times the mean DIN concentration in the adjacent water column (Larned and Stimson 1996). In a field experiment in which *D. cavernosa* thalli were exposed to the water column and either exposed to or isolated from underlying sediments, thalli exposed only to water column nutrients did not grow, while thalli exposed to both the water column and sediments grew (Larned and Stimson 1996). DIN efflux rates from reef slopes with abundant *D. cavernosa* average 610 μmol m^{-2} of reef slope day^{-1} (Stimson and Larned 2000). DIN excretion rates from invertebrates inhabiting *D. cavernosa* thalli average 1000 μmol m^{-2} of thallus day^{-1} (Larned 1997). Sedimentation of particulate organic nitrogen has been measured at a number of sites in the bay and is on the order of 12–61 mg N m^{-2} day^{-1} (Stimson and Larned 2000). It appears that, under present conditions, *D. cavernosa* obtains nutrients required to sustain growth through a combination of sediment efflux, invertebrate excretion, and advection of water column nutrients (Larned and Atkinson 1997), and that its growth rate is independent of the concentration of inorganic nutrients in the overlying water column.

Measurements made at sites in the north, central and south bay suggest that DIN efflux from reef sediments occurs at comparable rates across Kaneohe Bay (Stimson and Larned 2000). *D. cavernosa* thalli collected from sites across the bay have comparable levels of epiphytic invertebrate biomass (Larned 1997). These observations, in combination with the data on growth of caged *D. cavernosa* at the six study reefs in 1996–1997 (Fig. 7A), suggest that *D. cavernosa* is capable of growing throughout the bay, and that spatial variability in its abundance is not a function of nutrient availability, but of grazing intensity.

Grazing and a grazing-related hypothesis to explain the distribution of *Dictyosphaeria*

Most reef slopes in Kaneohe Bay are characterized by alternating areas of high and low *D. cavernosa* cover, yet potential growth rates of *D. cavernosa* at the high and low cover sites on the six study reefs were comparable. The areas of high and low cover occur on scales of tens to hundreds of meters. An example of this pattern is the fringing reef slope of Checker Reef, where regions of very low *D. cavernosa* cover alternate with regions of high cover (Fig. 4).

The patchy distribution of *D. cavernosa* could arise because the abundance of herbivores varies at a similar spatial scale, i.e., herbivore biomass is unevenly distributed around reefs, and is higher at sites of low *D. cavernosa* cover. However, the surveys of herbivore biomass did not reveal significant differences in estimated herbivore biomass at the high and low cover sites (Table 8).

In the absence of evidence directly linking patterns of *D. cavernosa* distribution to herbivore biomass or nutrient availability, we propose that the distribution of this alga is related to the availability of other macroalgal species that occur on reef flats and that are more highly preferred as foods by herbivores. The percent cover of reef flat macroalgae preferred by herbivores increases with distance from the crest (Fig. 5), because of decreased grazing along the same gradient, as illustrated by the preferred species *Acanthophora spicifera* (Fig. 9). In contrast, grazing intensity on the less preferred *D. cavernosa* was uniformly low across the width of the reef flat. Grazing decreases with distance from reef crests either because access to shelter for grazers diminishes with greater distance, or because tidal changes in water depth reduce the time that fish can feed on the inner reef flat. Corals, and the vertical relief they produce, are restricted to the outer 10 m of most reef flats. These observations suggest that highly preferred macroalgae have a refuge from herbivorous fish by inhabiting inner reef flats, while less preferred macroalgae, such as *D. cavernosa*, can occupy habitats with high grazing pressure.

Preference test results (Table 9) bear this out: *Acanthophora spicifera* and *Gracilaria salicornia* were among the most preferred and *D. cavernosa* and *Kappaphycus striatum* among the least preferred algal species for the fishes tested. Similar observations have been made at Caribbean reefs; when macroalgal species collected from habitats with a range of herbivore densities were transplanted into a back reef with abundant herbivores, macroalgae from habitats with high grazing pressure were resistant to herbivory, while macroalgae from habitats with low grazing pressure were susceptible (Lewis 1986).

Based on the results of surveys and field experiments conducted during this study, we propose the following hypothesis to explain the distribution and abundance of *D. cavernosa* on Kaneohe Bay reef slopes. Distribution and abundance of this species are determined primarily by grazing intensity, which is in turn determined by the availability and relative palatability of macroalgae on adjacent reef flats. The introduction of non-native red macroalgae in Kaneohe Bay (Russell 1983, 1992; Rodgers and Cox 1999) has greatly increased the availability of palatable food for herbivorous fishes. We propose that increased availability of these macroalgae on some reef flats has lead to a reduction of grazing intensity on *D. cavernosa* on adjacent reef slopes and, consequently, to the development of areas of high *D. cavernosa* cover. Conversely, the absence or low abundance of preferred macroalgae on some reef flats results in high grazing pressure on *D. cavernosa* and, consequently, to low *D. cavernosa* cover on the adjacent slope. *D. cavernosa* has the lowest growth rate of the ten most common macroalgae in the bay (Larned 1998), but under conditions of very low grazing intensity, *D. cavernosa* may slowly accumulate biomass and achieve high cover. Our hypothesis assumes that herbivore abundance, and, consequently, grazing intensity, are sufficiently low in Kaneohe Bay that preferential grazing results in a proliferation of the most unpalatable macroalgae. Presumably, large increases in grazing intensity would lead to the removal of both the highly preferred and the least preferred macroalgae, as the accessibility and cover of algae decrease (Lewis 1986).

The hypothesis predicts that the pattern of alternating areas of high and low *D. cavernosa* cover on reef slopes is related to the distribution and abundance of macroalgae on adjacent reef flats. Factors influencing the distribution and abundance of these reef flat macroalgae (Figs. 5 and 6) have not been addressed. The patchy distribution of reef flat macroalgae could be determined by the availability of suitable substratum for attachment (Hay 1981), by the narrowness of the reef flat zone and hence the degree to which there is a refuge from herbivory, or by differences in the availability of shelter for herbivores on reef flats.

A critical experiment to test our hypothesis has not yet been carried out. We propose the following: if existing highly preferred macroalgae are removed from reef flat areas, a shift toward higher grazing intensity on *D. cavernosa* should result in decreased *D. cavernosa* abundance. Conversely, if preferred macroalgae are added to a reef flat area where there was previously none, grazing intensity on nearby *D. cavernosa* thalli should decrease and result in increased *D. cavernosa* abundance.

Kaneohe Bay is currently quite oligotrophic (SRP concentration <0.1 μM, DIN concentration <0.4 μM). The water column DIN concentration below which *D. cavernosa* requires a nutrient subsidy to grow is about 0.5 μM (Larned and Stimson 1996). There is a large nutrient reservoir in the bay sediments, however, and DIN efflux rates are high relative to other coral reef ecosystems (Stimson and Larned 2000). *D. cavernosa* relies in part on nutrient efflux and possibly on invertebrate excretion to sustain growth. The fact that substantial nutrient efflux continues long after sewage diversion suggests that *D. cavernosa* growth will be supported by benthic nutrient sources well into the future. The proliferation of

D. cavernosa on Kaneohe Bay reef slopes can be reduced by further reducing anthropogenic nutrient input, by increasing grazing intensity, or by physically removing *D. cavernosa* and/or the non-native macroalgae on reef flats. Given the current level of urbanization in the Kaneohe Bay watershed, substantial reductions in water column or sediment nutrient concentrations are unlikely. Experimental removals of macroalgae have been carried out (McClanahan et al. 1999), but large-scale reductions will be labor intensive and the effects may be short-lived. The most efficacious way to reduce *D. cavernosa* is to increase grazing intensity by increasing herbivore biomass. This may be achieved by reducing fishing pressure on herbivorous fishes, either by restricting fisheries or by better-enforcing existing restrictions.

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