Abundance and Spread of the Invasive Red Algae, Kappaphycus spp., in Kane'ohe Bay, Hawai'i and an Experimental Assessment of Management Options

Article *in* Biological Invasions · November 2005

DOI: 10.1007/s10530-004-3125-x

Jennifer E Smith
University of California, San Diego

Biological Invasions (2005) 7: 1029–1039
DOI 10.1007/s10530-004-3125-x

Abundance and spread of the invasive red algae, *Kappaphycus* spp., in Kane'ohe Bay, Hawai'i and an experimental assessment of management options

Eric J. Conklin[1,2,3,*] & Jennifer E. Smith[2,4]
[1]*Hawai'i Institute of Marine Biology, P.O. Box 1346, Kane'ohe, HI 96744 USA;* [2]*Waikiki Aquarium, University of Hawai'i, 2777 Kalakaua Ave., Honolulu, HI 96815, USA;* [3]*Department of Zoology, University of Hawai'i, McCarthy Mall, Honolulu, HI 96822, USA;* [4]*Department of Botany, University of Hawai'i 3190, Maile Way, Honolulu, HI 96822, USA;* **Author for correspondence (e-mail: econklin@hawaii.edu; fax: +1-808-236-7443)*

Received 7 July 2003; accepted in revised form 29 April 2004

Key words: algal blooms, biocontrol, carrageenan, coral reefs, *Eucheuma*, introduced species, invasive macroalgae, *Kappaphycus*, nonindigenous species, *Tripneustes gratilla*

Abstract

Several species of *Kappaphycus* were intentionally introduced into Kane'ohe Bay, Hawai'i in the 1970s. Subsequent research has demonstrated that these algae have spread rapidly throughout the bay and can be found in a variety of reef habitats overgrowing and killing corals. This study was conducted to (a) quantify *Kappaphycus* spp. abundance both spatially and temporally, and (b) investigate control options including manual removal and the use of biocontrol agents. *Kappaphycus* spp. distribution has increased in the bay over the period between surveys conducted in 1999 and 2002, with variation among reefs. The biomass of *Kappaphycus* spp. removed, and the amount of time required to manually remove them from the reef varied with habitat type, but in all cases amounted to at least 10 kg/m^2 requiring almost 2 person-hours to clear 1 m^2. Re-growth of the algae following their removal was rapid at most sites, likely due to the experimentally demonstrated ability of the algae to re-grow from minute attachment points and the low palatability of the algae to native herbivorous fishes. The native sea urchin, *Tripneustes gratilla*, reduced the biomass of *Kappaphycus* spp. in small experimental enclosures and may be a useful biocontrol agent. Because *Kappaphycus* spp. are still spreading in Kane'ohe Bay and can overgrow over 50% cover on some reefs, we recommend that rapid management action be taken to prevent further damage and spread to other Hawaiian coral reefs.

Introduction

Over the last several decades a number of species of tropical carrageenophytes have been intentionally introduced to tropical reef regions around the world, with *Kappaphycus* and *Eucheuma* being the most widely cultivated genera. While several species of either genus occur naturally throughout the Indo-Pacific from eastern Africa to Guam, Philippine-derived *Kappaphycus* spp. and *E. denticulatum* are the most commonly cultivated species (Ask and Azanza 2002). Presently, *Kappaphycus* spp. have been introduced in 19 countries while *Eucheuma* spp. have been introduced in 13 (Zemke-White in press). Annual production of commercially cultivated *Eucheuma* species worldwide (primarily in the Philippines and Indonesia) has increased from less than 1000 tons (dry weight biomass) in 1971 to over 100,000 tons in 2002 with a value of US$ 270 million (Zemke-White and Ohno 1999; Ask and Azanza 2002; McHugh 2002).

New introductions continue to occur with recent farm development and expansion occurring in the Marshall Islands, Kiribati (Teitelbaum 2002) and Eastern Africa (Ronnback et al. 2002). At present, there are no risk assessment or environmental impact procedures in place for intentional introduction of *Kappaphycus* or *Eucheuma*, and in only a few occasions have scientists examined areas adjacent to farms to determine if the populations have established on the benthos. Because nonindigenous marine algae such as *Caulerpa taxifolia* (Bellan-Santini et al. 1996; Boudouresque and Verlaque 2002; Meinesz 1999; Ceccherelli 2002; Meinesz et al. 2001), *Codium fragile* subsp. *tomentosoides* (Carlton and Scanlon 1985; Trowbridge 1995, 1998; Mathieson et al. 2003), *Grateloupia turuturu* (Villalard-Bohnsack and Harlin 2001), *Sargassum muticum* (Critchley 1983; Rueness 1989; Critchley et al. 1997; Viejo 1997), *Undaria pinnatifida* (Campbell and Burridge 1998; Curiel et al. 1998, 2000; Forrest et al. 2000) have displaced many native species in temperate marine ecosystems throughout the world (Ribera 1995; Walker and Kendrick 1998), it is probable that similar losses are occurring in the tropics as a result of both intentional and accidental aquaculture introductions (Naylor et al. 2001).

The most well documented case of the impacts of nonindigenous marine algae in the tropics is from Hawai'i. *Eucheuma striatum* (this species was later split into *Kappaphycus striatum* and *K. alvarezii*) and *E. denticulatum* were intentionally introduced into the fringing reef surrounding the Hawai'i Institute of Marine Biology (HIMB) at Coconut Island (Moku o Lo'e), Kane'ohe Bay, O'ahu, Hawaiian Islands throughout the 1970s, for experimental research and cultivation (Doty 1978; Russell 1983, 1992). Due to the morphological plasticity of all of these species and the lack of sexually mature individuals (which are required for definitive identification) in Hawai'i, we will refer to this species complex as *Kappaphycus* spp. Vegetative propagules were transplanted to open reef cultures on nets and in wire holding pens. Because of the rapid establishment of *Kappaphycus* spp. in areas around the experimental pens, and the concern raised by the public and other scientists, Russell (1983) conducted a number of studies to determine the potential for spread and the impacts of *Eucheuma striatum* (*Kappaphycus* spp.) on the native reef community. From these studies it was concluded that *Kappaphycus* spp. were unlikely to pose a threat to reefs in the bay because (1) vegetative propagules were the primary means of reproduction (sexual reproduction has not been observed in Hawai'i) and these propagules would not be able to establish on adjacent patch reefs because they could not travel over deep water, (2) propagules could not form holdfasts to attach to the reef, (3) fishes appeared to control the biomass to some degree with an estimated grazing rate of 10–20 tons/month (reef area was not specified), and (4) the habitat invaded by *Kappaphycus* spp. was barren, sand-covered grooves on the reef which were not inhabited by native algae or corals. While the above conclusions were made two years following the introduction of *Kappaphycus* spp. the situation some 25 years later is quite different.

Surveys conducted by Rodgers and Cox (1999) in 1996 determined that *Kappaphycus* spp. had indeed spread from the initial sites of introduction at HIMB to reefs as far as 6 km away at an estimated rate of 250 m per year. *Kappaphycus* spp. were most common on patch reefs in waters: <1 m deep with maximum abundance of 4.59 percent cover (± 2.06 SE). In 1999, Woo (2000) found an average 40 (± 5 SE) percent cover of *Kappaphycus* spp. in a back reef site and demonstrated using time series photography that the algae were overgrowing live coral. Woo (2000) suggested that grazing intensity and water motion may influence the ability of *Kappaphycus* spp. to spread in Kane'ohe Bay. Smith et al. (2002) conducted surveys assessing the distribution of nonindigenous marine algae throughout the main Hawaiian Islands and found that *Kappaphycus* spp. had still not spread outside of Kane'ohe Bay but had continued to spread northward in the bay since the Rodgers and Cox (1999) study.

While the rate of spread of these algae is slow in comparison to other nonindigenous marine algae (*Caulerpa taxifolia* in the Mediterranean Sea: 11.94 km/yr (calculated from Meinesz et al.

2001), *Codium fragile* subsp. *tomentosoides* on the Atlantic coast of North America: 50–100 km/yr (calculated from Trowbridge 1998, Hubbard and Garbary 2002, Mathieson et al. 2003), it is clear that *Kappaphycus* spp. have successfully established on Hawaii's reefs and continue to spread each year. Without intervention it is likely that these algae will eventually establish outside of Kane'ohe Bay and perhaps on adjacent islands in the Hawaiian archipelago. Because of their limited distribution in Hawai'i, control and/or eradication may still be possible and management strategies need to be examined.

The goals of this study were to (1) quantify *Kappaphycus* spp. abundance both spatially and temporally in Kane'ohe Bay, (2) evaluate manual removal as a method for reducing algal biomass on reefs, and (3) investigate the potential for biocontrol by native sea urchins.

Materials and methods

Distributional surveys

In order to determine the current extent of *Kappaphycus* spp. throughout Kane'ohe Bay and to measure temporal changes in *Kappaphycus* spp. abundance, quantitative surveys were conducted in 1999 and repeated in 2002. In December 1999, 15 sites throughout Kane'ohe Bay were randomly selected to cover a large spatial extent of the bay and to ensure that several different reef types (back, patch, and fringing) were sampled (Figure 1). At each of these sites, two parallel transects were positioned at the reef crest approximately 15 m apart, running 30 m onto the reef flat (0.5–2 m deep). The percent cover of all benthic organisms was estimated within ten 0.25 m^2 quadrats randomly placed along each transect. In January 2002, these same sites, as closely as could be determined with GPS coordinates taken during the original surveys, were re-surveyed using the same methods.

Manual removal

To quantify the efficiency and effectiveness of manual removal of *Kappaphycus* spp. as a control option, three 28 m transects were established on the reef flats (0.5–2 m deep) of each of three reefs: Mark's Reef, Reef 29, and Reef 44 in April 2002 (Figure 1). Eight 0.25 m^2 plots were established on each transect roughly every 4 m, with the corners of each plot permanently marked with rebar stakes. Plots were subjectively classified as being dominated by live coral, crustose coralline pavement, or unconsolidated rubble. The percent cover of all benthic organisms within each plot was estimated by the point intercept method using a double-strung 0.5×0.5 m quadrat with 6 lines every 7 cm for a total of 36 intersections. One snorkeler then manually removed all *Kappaphycus* spp. within each plot, using forceps to remove algal attachment points, while a second snorkeler used a hand-net to capture any algal fragments in the water column that were left during the removal activity. For each plot, the time required to clear the *Kappaphycus* spp. was recorded, and all *Kappaphycus* spp. removed were collected, spun 10 times in a mesh bag to remove excess water, and weighed to the nearest 0.25 kg.

While seven of the eight plots on each transect were assigned to treatments for an experiment described elsewhere (Smith and Conklin, in preparation), one plot from each transect was used to monitor the rate at which *Kappaphycus* spp. re-grew from any residual algal material that was left behind after the careful manual removal. These plots were left undisturbed except to remove any drifting algal fragments that settled out into the plots. The percent cover of benthic organisms within plots was estimated at approximately 6-week intervals over the following 12 months.

Attachment-point re-growth

While every effort was made to remove all algal material during manual removal, some tissue remained on the substratum at the point at which the thalli was attached to the substratum. To assess the ability of *Kappaphycus* spp. to re-grow from the tissue remaining at these attachment points, 13 pieces of rubble (dead *Porites compressa*) with *Kappaphycus* spp. attached, were brought to the water tables of HIMB. The number of *Kappaphycus* spp. plants attached to each piece of rubble was counted, and then each was

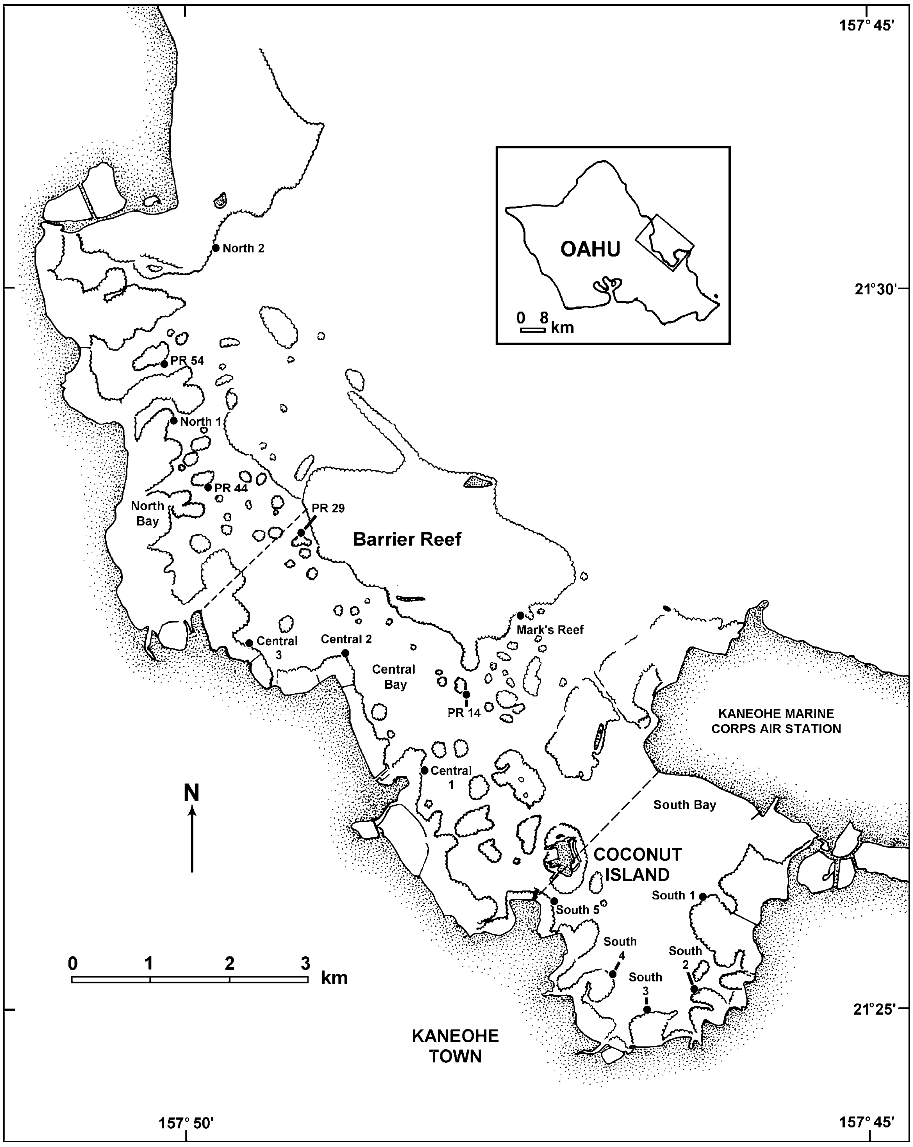

Figure 1. Map of Kane'ohe Bay, Oahu showing survey sites. North bay survey sites are North 1–2 and Patch Reefs 44 and 54; central bay sites are Central 1–3, Mark's Reef, and Patch Reefs 29 and 14; south bay sites are South 1–5. Mark's Reef and Patch Reefs 29 and 44 were also sites of manual removal and urchin addition experiments. Dashed lines delineate north, central, and south regions of the bay. Coconut Island was the original site of introduction of *Kappaphycus* spp. in 1970s.

scraped off by hand, removing all visible tissue at the attachment points. The pieces of rubble were then placed in outdoor, flow-through seawater tanks with natural lighting. After two months, the pieces of rubble were examined and the number of emergent *Kappaphycus* spp. branches growing on each rock was enumerated. Due to the lack of sexual reproduction in these species, all algal growth observed can be attributed to growth of existing tissue as opposed to settlement of new algal spores.

Sea urchins as biocontrol agents

The ability of the native sea urchin, *Tripneustes gratilla*, to reduce Kappaphycus spp. biomass was tested by placing urchins within enclosures on the reef in areas where *Kappaphycus* spp. were abundant. In July 2002, plastic coated chicken-wire fences were constructed around three 0.25 m^2 plots on each of three reefs, (Mark's Reef, Reef 29, and Reef 44, Figure 1). Digital photographs were taken of each enclosure using a photoquadrat (Preskitt et al. 2004) and the percent cover of benthic organisms measured by tracing the total area within each photograph occupied by each benthic species using Image-J software. Once initial *Kappaphycus* spp. abundance was quantified, one urchin was placed inside each fence. Photographs were taken approximately every 6 weeks until November 2002, to measure changes in *Kappaphycus* spp. abundance over time.

Results

Distributional surveys

Results of surveys conducted in 1999 and 2002 showed that *Kappaphycus* spp., reef building coral (primarily *Porites compressa* and *Montipora capitata*), the green alga *Dictyosphaeria cavernosa* and another introduced red alga, *Gracilaria salicornia,* were the most abundant benthic organisms on reef flats in Kane'ohe Bay. The bay can be divided into three regions based on watershed land-use, hydrology, and circulation patterns – south, central and north bay (Smith et al. 1981; Figure 1). *Kappaphycus* spp. was most abundant in the central bay, *D. cavernosa* was most abundant in the north bay, *G. salicornia* was most abundant in the south bay, and coral abundance is variable. Individual reefs showed mixed results as to whether established populations of *Kappaphycus* spp. increased or decreased in abundance over time (Figure 2). Coral cover across the bay was variable and appeared to be increasing at some of the sites while decreasing at others. *D. cavernosa* and *G. salicornia* decreased in abundance at some sites but overall remained relatively constant.

When the sites were combined with the three regional categories (south, central and north bay), *Kappaphycus* spp. abundance was low and constant in the south bay, high and constant in

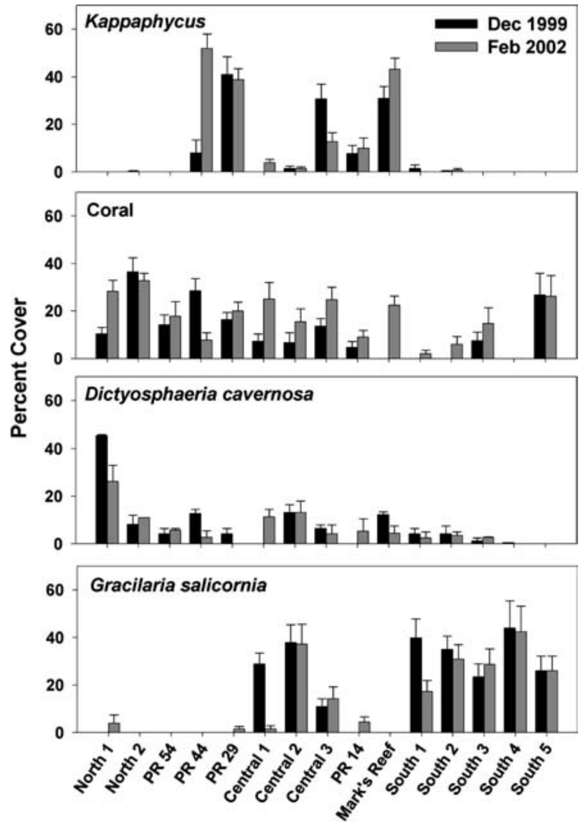

Figure 2. Results of surveys conducted in Kane'ohe Bay in both 1999 and 2002 showing the four most abundant benthic organisms (data are means ± 1 SE).

the central bay and had increased substantially in the north bay (Figure 3). The increase in *Kappaphycus* spp. abundance in the north bay is largely due to the roughly 5-fold increase observed at Reef 44 over the two-year period between the surveys, demonstrating that *Kappaphycus* spp. are capable of exhibiting rapid increases in abundance.

While *Kappaphycus* spp. were not found on transects at some of the sites in 2002 where they had been found in 1999, broader, qualitative surveys conducted concurrently with our 2002 surveys found that *Kappaphycus* spp. were indeed present at these sites in 2002 despite not appearing on the transects. In addition, subsequent surveys conducted in 2003 have found *Kappaphycus* spp. to be present at the two northern sites where it was not found in either 1999 or 2002 (Smith and Conklin, unpublished data).

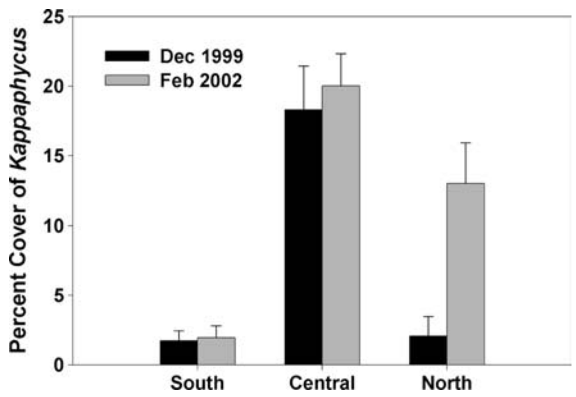

Figure 3. Abundance of *Kappaphycus* spp. pooled for the three regions (south, central and north) of Kane'ohe Bay (data are means ±1 SE).

Manual removal

The biomass of *Kappaphycus* spp. removed from the seventy-two 0.25 m^2 plots varied with habitat type (Figure 4a). A one-way ANOVA found significant differences between the three habitats ($F_{2,69} = 12.57$, $P < 0.001$), and Tukey's multiple comparisons found that the rubble habitat contained significantly less biomass than the other two habitats (rubble less than coral or pavement, $P < 0.05$ for both tests). Even the rubble habitat, however, had on an average almost 15 kg/m^2 of wet weight *Kappaphycus* spp.

The time required to remove all *Kappaphycus* spp. from 0.25 m^2 plots varied with habitat type as well (Figure 4b). A one-way ANOVA found significant differences in the time required to clear these plots ($F_{2,69} = 10.79$, $P < 0.001$), and Tukey's multiple comparisons showed that the pavement habitat required significantly less time to clear than the other two habitats (coral or rubble, $P < 0.05$). The pavement habitat, however, still required on average almost 120 person-minutes to clear of *Kappaphycus* spp.

Following a subset of these removal plots ($n = 3$ for each reef) over time, showed that *Kappaphycus* spp. can re-grow rapidly after removal (Figure 5). Percent cover of *Kappaphycus* spp. was reduced from an overall mean of 56.2% (±6.65 SE) in the plots to 0% effectively by manual removal in May 2002. In the subsequent 12 months, all three reefs showed substantial

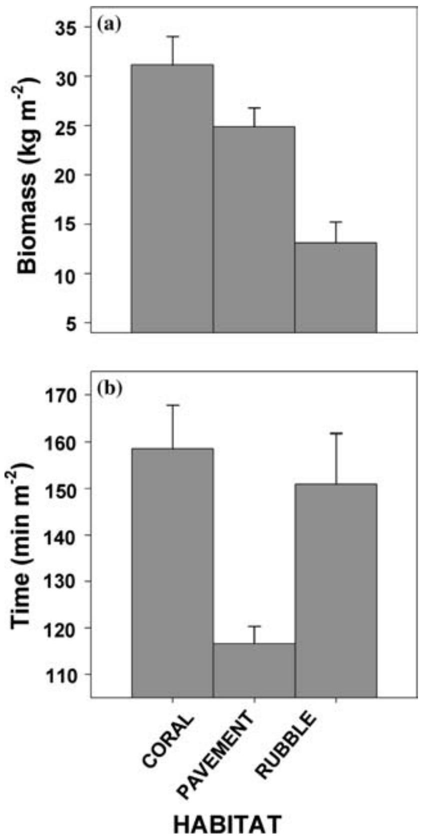

Figure 4. Data from manually cleared plots on (a) biomass (mean wet weight, ±1 SE, $n = 72$) of *Kappaphycus* spp. per m^2 in the three different habitat types (coral, pavement and rubble) and (b) length of time in person-hours (mean number of minutes, ±1 SE, $n = 72$) to manually remove all *Kappaphycus* spp. tissue per m^2 in each of the three habitat types (coral, pavement and rubble).

re-growth of the algae from tissue remaining following manual removal. Abundance of *Kappaphycus* spp. in May of 2003, one year after initial removal was 38.89% cover (±10.02 SE), 57.41% cover (±22.76 SE) and 88.89 % cover (±22.76 SE) at Mark's Reef, Reef 29 and Reef 44, respectively. The abundance of the algae appears to be increasing on all three reefs, and has even surpassed pre-removal abundance on Reef 44.

Attachment-point re-growth

Kappaphycus spp. are capable of re-growing from minute amounts of tissue remaining at

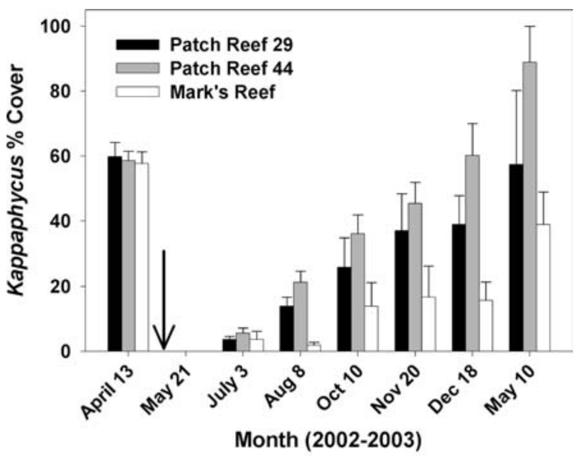

Figure 5. Re-growth of *Kappaphycus* spp. from cleared plots on each of three reefs (data are mean percent cover ± 1 SE, $n = 3$ per reef). The first sampling date represents pre-removal conditions. All algal tissue visible to the naked eye was removed in May 2002 (indicated by the arrow) and the subsequent sampling dates indicate re-growth.

attachment points following manual removal. Rubble used in this experiment had a mean of 7.7 (± 1.1231 SD; $n = 13$ pieces of rubble) plants growing out of attachment points prior to removal. Two months after removing all visible algal tissue (tissue remaining at the attachment point was not visible to the naked eye), there was a mean of 4.7 (± 1.43841 SD, $n = 13$ rocks) branches re-growing from attachment points, a 61% recovery in branch density.

Sea urchins as biocontrol agents

A single *Tripneustes gratilla*, when placed within a 0.25 m^2 enclosure containing large amounts of *Kappaphycus* spp., was able to substantially decrease the abundance of *Kappaphycus* spp. within the enclosure in five months (Figure 6a). Across all three reefs, urchins were able to reduce the percent cover of *Kappaphycus* spp. from an initial mean of 62.49% (± 6.00 SE, $n = 9$) to a final mean of 15.87 % (± 4.62 SE, $n = 9$; Figure 6a). Live coral cover remained similar throughout the study, with abundance ranging from 11.76% cover (± 5.13 SE, $n = 9$) in July 2002, to 14.27% cover (± 6.17 SE, $n = 9$; Figure 6b) in Dec 2002. Sessile invertebrates, fleshy, and calcified algae all increased when *Kappaphycus*

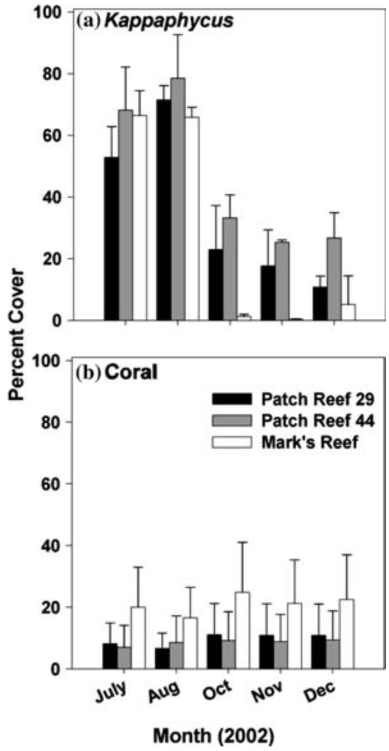

Figure 6. Quantitative results of urchin addition plots showing (a) *Kappaphycus* spp. and (b) coral abundance over time (mean ± 1 SE, $n = 3$ per reef), urchins were added to the plots in July 2002.

spp. decreased. Urchin grazing scars were evident on *Kappaphycus* spp. thalli within enclosures indicating consumption had occurred.

Discussion

Despite predictions that *Kappaphycus* spp. would be incapable of effectively dispersing from the initial site of introduction at HIMB (Russell 1983), several studies have documented the continual spread of these invasive algae to reefs throughout Kane'ohe Bay (Rodgers and Cox 1999; Woo 2000; Smith et al. 2002). This study located *Kappaphycus* spp. at the northernmost site surveyed on a reef contiguous with the outside of the bay and noted *Kappaphycus* spp. presence at a number of sites where they were absent 5 years before (Rodgers and Cox 1999). *Kappaphycus* spp. were also found on reefs near both of the main channels leading out of the bay. While established populations have yet to be documented outside of the bay, their current distribution and dispersal success to date strongly suggest that this will soon happen.

Temporal changes in abundance of *Kappaphycus* spp. varied between reefs, but the number of reefs at which the abundance of *Kappaphycus* spp. remained the same between years, or diminished was surprising. Whether these populations are truly static, or whether the lack of an increase in *Kappaphycus* spp. abundance is due to sampling error is impossible to discern at this point and would require greater sampling effort over time to determine. The almost 40% increase seen on Reef 44 between 1999 and 2002, however, demonstrates that populations of the algae are capable of rapid growth.

Predictions that *Kappaphycus* spp. would not directly compete with native species due to their restriction to sand-covered habitats (Russell 1983) have also proven untrue. While their original distribution within a reef may have been limited, time series photographs show that *Kappaphycus* spp. grow over coral (Woo 2000, although this was not quantified rigorously), and it is common to see the algae growing out of cracks and crevices between coral and growing over the top of the colonies. Removal of the invader generally reveals a continuum of photoacclimated but otherwise healthy coral cover at the edge of the thallus to dead coral overgrown by algae turf near the center of the thallus (personal observation).

As recently as 1997, surveys conducted on many of the same reefs surveyed in this study, found *Kappaphycus* spp. primarily restricted to the outer margins of reef flats, and rarely occurring on reef slopes (Stimson et al. 2001). Today several reefs within the bay have large accumulations of unattached *Kappaphycus* spp. on the reef slope, often resting on top of coral colonies. The continued spread of these algae into new geographic regions (i.e. the north end of the bay) and into new habitats (i.e. reef slopes) taken with their proven ability to rapidly overgrow and kill native corals and algae, highlight the need to develop effective management strategies.

The development of such a strategy will be difficult, however, due both to difficulties in efficiently removing *Kappaphycus* spp. from reefs as well as the ability of these algae to re-grow quickly following removal. While the biomass of *Kappaphycus* spp. was least in habitats composed of rubble, most likely due to the scarcity of stable attachment substrata, all habitat types on the three experimental reefs contained large quantities of the invader (Figure 4a). And while pavement habitats required the least amount of time to clear due to the lack of topographic complexity, all habitats still required prohibitive amounts of time to clear small areas of reef (Figure 4b). At two person-hours per m^2, clearing the tens to hundreds of thousands of square-meters of reef impacted by *Kappaphycus* spp. is a daunting task. As a potential means of increasing the efficiency of removal, partners from The Nature Conservancy have recently purchased a modified dredge capable of removing large quantities of algae via suction that is currently undergoing testing.

Even if efficient means of removal are developed, the rapid re-growth of *Kappaphycus* spp. following removal is still an issue. In our experimental plots on three reefs, extensive re-growth was observed within two months of removing all visible algal biomass (Figure 5). Rates of re-growth were somewhat variable among our three experimental reefs and may be the result of a number of factors including water motion, nutrient levels and the abundance of grazers, all that need further investigation. But perhaps one of the main reasons that *Kappaphycus* spp. can re-grow so rapidly is its ability to re-grow from the residual tissue left at attachment points. Even after removing all algal material visible to the naked eye, *Kappaphycus* spp. was still able to re-grow from the residual tissue.

Another factor that may have contributed to the rapid recovery of *Kappaphycus* spp. following removal is the relatively low preference that native herbivorous fishes have for the algae. Within their native range, the primary grazers upon *Kappaphycus* spp. are siganids (a family of fish not found in Hawai'i) and sea urchins (Doty and Alvarez 1975; E. Ask personal communication), which are not abundant within Kane'ohe Bay. Preliminary preference tests (authors' unpublished data) suggest that *Kappaphycus* spp. is a low-preference food item for native surgeonfish (acanthurids) and parrotfish (scarids), similar in preference ranking to the native alga *Dictyosp-*

haeria cavernosa. *D. cavernosa* has a well-documented history of overgrowing and killing coral (Hunter and Evans 1995; Stimson et al. 1996, 2001), and its success has been attributed in part to the low preference of herbivorous fishes for this native alga which leads to a lack of grazer control of algal populations (Stimson et al. 2001). While we did not explicitly test for it in this study, the low preference of herbivorous fishes for *Kappaphycus* spp. likely contributes to the ability of the algae to re-grow following removal. Whereas a more preferred alga would be heavily grazed and slowed down in its recovery, *Kappaphycus* spp. is largely ignored by herbivores, perhaps allowing it to rapidly regain pre-removal abundances (Figure 5).

This study presents some options that may be useful in controlling *Kappaphycus* spp. and/or slowing down the rates of re-growth following manual removal. The use of native sea urchins, *Tripneustes gratilla*, as biocontrol agents appears quite promising. Unlike herbivorous fish, these urchins appear to prefer *Kappaphycus* spp. over many other species of algae (J. Stimson, personal communication). This study demonstrated that they were highly successful in rapidly removing large amounts of algal biomass (Figure 6a). While we did not see a corresponding increase in coral cover (Figure 6b), this is most likely due to the fact that the coral colonies underneath algal thalli were dead, and the short period of the urchin experiments was too short relative to the settlement and growth of coral species to see recovery. *T. gratilla* is a common component of many Hawaiian reefs but occurs in very low abundance on the reefs in Kane'ohe Bay (J. Stimson, personal communication). It is unclear whether this urchin has been over-fished in the bay, or whether its absence is due to other physical or biological factors or a combination thereof. To further examine their potential use as biocontrol agents, more research would be needed to determine if these grazers can remove *Kappaphycus* spp. from large reef areas, and also to understand other potentially negative effects of enhancing their populations on the bay's reefs.

Other potential means by which *Kappaphycus* may be controlled include methods of killing invasive algae *in situ*. These methods have been tried in several parts of the world as means of controlling and eradicating invasive algal populations in temperate regions and include the use of rock salt, copper sulfate, temperature gradients and chlorine bleach (Uchimura et al. 2000; Meinesz et al. 2001; Millar and Talbot 2002; Thibaut and Meinesz 2002; S.L. Williams, personal communication). The environments in which such treatments have proven successful, however, have been in semi-enclosed sand or mudflats with little habitat complexity and faster growing native species (in comparison to reef building coral species). While preliminary experiments (authors' unpublished data) have found high mortality rates of *Kappaphycus* spp. when subjected to changes in temperature and salinity, as well as the application of chemicals, the living coral reefs that *Kappaphycus* spp. have invaded in Hawai'i present a much more difficult situation, both in terms of the effective delivery of these techniques, as well as the paramount concern of potential collateral damage to native species. Further research on these methods in limited applications is warranted, however, given the success of these methods elsewhere and the apparent susceptibility of *Kappaphycus* spp.

Because *Kappaphycus* spp. has been introduced throughout tropical reef regions around the world for the carrageenan industry, it is critical that the information on the invasiveness of *Kappaphycus* spp. be considered in aquaculture applications. While it is unclear at this point whether *Kappaphycus* spp. have become successful invaders on other coral reefs across the globe, the data presented here suggest that establishment of invasive species in new environments remains unpredictable. Despite a thorough preliminary assessment just two years after the introduction of *Kappaphycus* spp. to Hawai'i, the current situation is quite contrary to initial predictions. *Kappaphycus* spp. have become some of the most abundant benthic organisms in Kane'ohe Bay where they readily overgrow reef-building coral. Shifts such as these from coral to algal domination on reefs have been found elsewhere to be associated with the loss of biodiversity, reduction in the numbers of fish, decrease of the intrinsic value of the reef, and ultimately the erosion of the physical structure of the reef (Done 1992; Hughes 1994; McClanahan et al. 1999). Without the implementation of a management plan, *Kappaphycus* spp. are likely to continue spreading to other reef areas and will likely establish outside the bay in the near future.

The primary challenges faced in developing an effective management strategy will be to: (1) develop an efficient means to remove algal biomass and, (2) prevent or slow the re-growth of the invader following removal. Manual removal is too time-consuming for large-scale removals, and the modified dredge for algal removal is currently undergoing testing as a means of improving efficiency. Careful experiments using salinity and temperature manipulations to kill the algae *in situ* need to be conducted, and the use of the native *T. gratilla* as a biocontrol agent seems promising as a mechanism for controlling algal growth. Efficient means of manual removal in concert with manipulations to prevent re-growth following removal represent an achievable and experimentally supported strategy for managing populations of *Kappaphycus* spp. in Kane'ohe Bay.

In the future, effective control options should be integrated into *Kappaphycus* spp. aquaculture development to prevent similar problems from occurring on other reefs around the world.

Acknowledgements

We would like to thank C.L. Hunter, C.M. Smith and J. Stimson for intellectual support. J. Stimson provided logistical support at HIMB and should be credited with the idea of using *Tripneustes gratilla* as a biocontrol agent for nonindigenous algae. HIMB provided laboratory space. We would like to thank S. Atkinson and E. Co with The Nature Conservancy Hawai'i and D. Gulko with Hawai'i Department of Land and Natural Resources, Division of Aquatic Resources for their continual support in addressing invasive algal issues on Hawaii's coral reefs. A. Taylor provided assistance with experimental design and statistical analysis. K. Ikemoto, R. Most, T. Sauvage, and C. Squair provided invaluable help in the field. This manuscript was much improved by the comments of anonymous reviewers. Funding for this research was provided by the National Oceanic and Atmospheric Administration, Hawai'i Coral Reef Initiative Research Program Grant #NA160A1449 awarded to C.L. Hunter and C.M. Smith.

References

Ask EI and Azanza RV (2002) Advances in cultivation technology of commercial eucheumatoid species: a review with suggestions for future research. Aquaculture 206: 257–277

Bellan-Santini D, Arnaud PM, Bellan G and Verlaque M (1996) The influence of the introduced macroalga *Caulerpa taxifolia* on the biodiversity of the Mediterranean marine biota. Journal of the Marine Biological Association of the United Kingdom 76: 235–237

Boudouresque CF and Verlaque M (2002) Biological pollution of the Mediterranean Sea: invasive *versus* introduced macrophytes. Marine Pollution Bulletin 44: 32–38.

Campbell SJ and Burridge TR (1998) Occurrence of *Undaria pinnatifida* (Phaeophyta: Laminariales) in Port Phillip Bay, Victoria. Australian Journal of Marine and Freshwater Research 49: 379–381

Carlton JT and Scanlon JA (1985) Progression and dispersal of an introduced alga: *Codium fragile* on the Atlantic coast of North America. Botanica Marina 28: 155–165.

Ceccherelli G (2002) The spread of *Caulerpa taxifolia* in the Mediterranean: dispersal strategy, interactions with native species and competitive ability. Proceedings of the International *Caulerpa taxifolia* Conference. San Diego, CA (CD-ROM)

Critchley AT (1983) The establishment and increase of *Sargassum muticum* (Yendo) Fensholt populations within the Solent area of Southern Britain. Botanica Marina 24: 547–552

Critchley AT, Farnham WF and Thoro CH (1997) On the co-occurrence of two exotic, invasive marine organisms: the brown seaweed *Sargassum muticum* and the spirorbid tube worm *Janua brasiliensis* in association with the indigenous eelgrass *Zostera marina* and *Fucus serratus* in the southwest Netherlands and the Channel Islands, Europe. South African Journal of Botany 63: 474–479

Curiel D, Bellemo G and Marzocchi M (1998) Distribution of introduced Japanese macroalgae *Undaria pinnatifida*, *Sargassum muticum* (Phaeophyta) and *Antithamnion pectinatum* (Rhodophyta) in the Lagoon of Venice. Hydrobiologia 385: 17–22

Curiel D, Guidetti P and Bellemo G (2002) The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the lagoon of Venice. Hydrobiologia 477: 209–219.

Done T (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247: 121–132

Doty MS (1978) Eucheuma – current marine agronomy. In: Klauss R (ed) The Marine Plant Biomass of the Pacific, pp 203–214. Oregon State University Press, Corvallis, OR

Doty MS and Alvarez VB (1975) Status, problems, advances and economics of Eucheuma farms. Marine Technology Society Journal 9(4): 30–35

Forrest BM, Brown SN and Taylor MD (2000) The role of natural dispersal mechanisms in the spread of *Undaria pinnatifida* (Laminariales, Phaeophyceae). Phycologia 39: 547–553

Hubbard CB and Garbary DJ (2002) Morphological variation of *Codium fragile* (Chlorophyta) in Eastern Canada. Botanica Marina 45: 476–485

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551

Hunter CL and Evans CW (1995) Coral reefs in Kaneohe Bay: two centuries of western influence and two decades of data. Bulletin of Marine Science 57: 501–515

Mathieson AC, Dawes CJ, Harris LG and Hehre EJ (2003) Expansion of the Asiatic green alga *Codium fragile* subsp. *tomentosoides* in the Gulf of Maine. Rhodora 105(921): 1–53

McClanahan TR, Hendrick V, Rodrigues MJ and Polunin NVC (1999) Varying responses of herbivorous and invertebrate-feeding fish to macroalgal reduction on a coral reef. Coral Reefs 18: 95–203

McHugh DJ (2002) Prospects for seaweed production in developing countries. FAO Fisheries Circular No. 968 FIIU/C968

Meinesz A (1999) Killer Algae. The University of Chicago Press, 360 pp.

Meinesz A, Belsher T, Thibaut T, Antolic B, Mustapha KB, Boudouresque CF, Chiaverini D, Cinelli F, Cottalorda JM, Djellouli A, Abed AE, Orestano C, Grau AM, Ivesa L, Jaklin A, Langar H, Massuti-Pascual E, Peirano A, Tunesi L, De Vaugelas J, Zavodnik N and Zuljevik A (2001) The introduced green alga *Caulerpa taxifolia* continues to spread in the Mediterranean. Biological Invasions 3: 201–210

Millar A and Talbot B (2002) The introduction of *Caulerpa taxifolia* in New South Wales, Australia. Proceedings of the International *Caulerpa taxifolia* Conference. San Diego, CA (CD-ROM)

Naylor RL, Williams SL and Strong DR (2001) Aquaculture – a gateway for exotic species. Science 294: 1655–1656

Preskitt LB, Vroom PS and Smith CM (2004) A rapid ecological assessment (REA) quantitative survey method for benthic algae using photo quadrats with SCUBA. Pacific Science 58: 201–209

Ribera MA (1995) Introduced marine plants with special reference to macroalgae: mechanisms and impact. Progress in Phycological Research 11: 217–268

Rodgers SK and Cox EF (1999) The distributions of the introduced rhodophytes *Kappaphycus alvarezii*, *Kappaphycus striatum* and *Gracilaria salicornia* in relation to various physical and biological factors in Kane'ohe Bay, O'ahu, Hawai'i. Pacific Science 53: 232–241

Ronnback P, Bryceson I and Kautsky N (2002) Coastal Aquaculture development in Eastern Africa and the Western Indian Ocean: prospects and problems for food security and local economies. Ambio 31: 537–542

Rueness J (1989) *Sargassum muticum* and other introduced Japanese macroalgae: Biological pollution of European coasts. Marine Pollution Bulletin 20: 173–176

Russell DJ (1983) Ecology of the red imported seaweed *Kappaphycus striatum* on Coconut Island, Oahu, Hawai'i. Pacific Science 37: 87–107

Russell DJ (1992) The ecological invasion of Hawaiian reefs by two marine ref algae, *Acanthophora spicifera* (Vahl) Boerg, and *Hypnia musciformis* (wulfen) J. Ag., and their association with two native species, *Laurencia nidifica* J. Ag. and *Hypnia cervicornis* J. Ag. ICES Marine Science Symposia 194: 110–125

Smith JE, Hunter CL and Smith CM (2002) Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. Pacific Science 56: 299–315

Smith SV, Kimmerer WJ, Laws EA, Brock RE and Walsh TW (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. Pacific Science 35: 279–395

Stimson J, Larned S and McDermid K (1996) Seasonal growth of the coral reef macroalga *Dictyosphaeria cavernosa* (Forskal) Borgesen and the effects of nutrient availability, temperature and herbivory on growth rate. Journal of Experimental Marine Biology and Ecology 196: 53–67

Stimson J, Larned ST and Conklin EJ (2001) Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive alga *Dictyosphaeria cavernosa* in Kane'ohe Bay, Hawai'i. Coral Reefs 4: 343–357

Teitelbaum A (2002) Seaweed Farming in Kiribati: The 7th Training and Extension Workshop. SPC Fisheries Newsletter, FAO No. 103, pp. 39–40

Thibaut T and Meinesz A (2002) Management successes and failures in the Mediterranean. Proceedings of the International *Caulerpa taxifolia* Conference. San Diego, CA (CD-ROM)

Trowbridge CD (1995) The establishment of the green alga *Codium fragile* on New Zealand rocky shores: current distribution and invertebrate grazers. Ecology 83: 949–965

Trowbridge CD (1998) Ecology of the green macroalga *Codium fragile*: invasive and non-invasive subspecies. Oceanography and Marine Biology: An Annual Review 36: 1–64

Uchimura M, Rival A, Nato A, Sandeaux R, Sandeaux J and Baccou J (2000) Potential use of copper, potassium and sodium for the destruction of *Caulerpa taxifolia*: differential effects on photosynthetic parameters. Journal of Applied Phycology 12: 15–23

Viejo RM (1997) The effects of colonization by *Sargassum muticum* on tidepool macroalgal assemblage. Journal of the Marine Biological Association of the United Kingdom 77: 325–340

Villalard-Bohnsack M and Harlin M (2001) *Grateloupia turuturu* (Halymeniaceae, Rhodophyta) in Rhode Island waters (USA): geographical expansion, morphological variations and associated algae. Phycologia 40: 372–380

Walker DI and Kendrick GA (1998) Threats to macroalgal diversity: marine habitat destruction and fragmentation, pollution and introduced species. Botanica Marina 41: 105–112

Woo M (2000) Ecological impacts and interactions of the introduced red alga *Kappaphycus striatum* in Kane'ohe Bay, O'ahu. Master's thesis, Department of Botany, University of Hawai'i, Honolulu, HI

Zemke-White WL and Ohno M (1999) World seaweed utilization: an end of the century summary. Journal of Applied Phycology 11: 369–376

Zemke-White WL (in press) Assessment of the current knowledge on the environmental impacts of seaweed farming in the tropics. Proceedings of the Asia–Pacific Conference on Marine Science and Technology, 12–16 May 2002, Kuala Lumpur, Malaysia