Reduction in Cover of Two Introduced Invasive Macroalgae by Herbivores on Coral Reefs of Kāneʻohe Bay, Hawaiʻi[1]

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Abstract: Two introduced invasive red macroalgae, *Eucheuma denticulatum* (Burman) Collins & Hervey and *Gracilaria salicornia* C. Ag., progressively declined in abundance in Kāneʻohe Bay, Hawaiʻi, following ~30 years of increase since their introduction in the mid-1970s. The declines were not the result of biological control or mechanical control efforts, but instead were the result of grazing by native herbivores, probably fishes, as demonstrated by field experiments conducted in 2014 with algal thalli exposed to, and protected from grazing. Two long-term time-series of the abundance of herbivorous fishes at Kāneʻohe Bay patch and fringing reef sites indicated that the abundance of herbivorous fishes increased from 2007 through 2014 over the period when these macroalgae declined in cover. Analyses of data of algal cover from surveys of Kāneʻohe Bay reefs carried out between 1996 and 2018 indicate that the declines in *E. denticulatum* and *G. salicornia* began in approximately 2008, several years before control programs commenced on some of the reefs in the bay. In addition to intense herbivory, high summer water temperatures in 2014 and 2015 may have contributed to the decline in *E. denticulatum*. Naturally occurring declines in the abundance of alien invasive marine algal species have rarely been reported in the literature. These reductions in macroalgal abundance are the second instance of decline in invasive macroalgae in Kāneʻohe Bay since 2006, and have reduced competition between macroalgae and corals on reef flats and reef slopes across the bay.

Keywords: control, alien, invasive, coral, reef, macroalgae

HAWAIʻI HAS AN EXTENSIVE RECORD of establishment of introduced macroalgal species on coral reefs. As many as 19 marine macroalgal species have been introduced to Hawaiʻi

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(Smith et al. 2002) and additional cryptic species have been reported (Conklin et al. 2014). Some of the introduced macroalgae in Hawaiʻi have been labeled as invasive because of negative ecological impacts, such as competition for space with native corals (Smith et al. 2002, Williams and Smith 2007). Two invasive introduced macroalgae, the rhodophytes, *Eucheuma denticulatum* (Burman) Collins & Hervey and *Gracilaria salicornia* C. Ag., were brought to Hawaiʻi in the 1970s and began to compete with reef-building corals in Kāneʻohe Bay, Oʻahu, and Hawaiʻi (Woo 2000, Conklin and Smith 2005, Stimson 2013). As of the spring of 2014, one or both of these species were present on 35 of 41 reefs surveyed in the bay, and their percent cover exceeded 10% on seven of the 35 reefs (Neilson et al. 2014). Multiple control measures intended to reduce the distribution

and abundance of *E denticulatum* and *G. salicornia* have been tested in the bay (Conklin and Smith 2005, Stimson et al. 2007, Neilson et al. 2018); the measures involved either manual or mechanical removal, or the enhancement of native grazer populations. These measures have had some success (Neilson et al. 2018), but the rapid regrowth rates of the macroalgae and their habit of anchoring in the interstices of coral heads makes removal difficult (Stimson and Conklin 2008, Stimson 2013).

Natural (i.e., without human intervention) control of invasive marine algae by native herbivores has been reported in the Caribbean (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006, Idjadi et al. 2006, Myhre and Acevedo-Gutierrez 2007), and there are numerous reports of native herbivores consuming introduced macroalgae (Schaffelke et al. 1995, Levin et al. 2002, Britton-Simmons 2004, Sumi and Scheibling 2005, Gollan and Wright 2006, Ruitton et al. 2006, Vermeij et al. 2009, Cebrian et al. 2011, Bahr et al. 2018). However, the control of alien invasive algae by native herbivores has not been documented (Anderson 2007, Williams and Smith 2007), except for the elimination of introduced *Codium fragile* (Suringar) Hariot by a sacoglossan in Scotland (Trowbridge 2002). There are also examples of alien invasive macroalgae that have undergone declines in abundance, but no agent responsible for the decline was identified (Trowbridge et al. 2013).

In this study, we report the recent declines in abundance of two alien invasive macroalgae, *E denticulatum* and *G. salicornia* in Kāne'ohe Bay, and provide evidence that those declines were due to natural control mechanisms including grazing by native herbivores. We use a time-series of quantitative field surveys to reconstruct changes in the abundance of *E. denticulatum* and *G. salicornia* in Kāne'ohe Bay; then we examine experimentally the effects of two potential natural control agents, grazing by native herbivores and a period of elevated sea water temperatures.

BACKGROUND

From 1970 to 1976, thalli from the putative species *Eucheuma denticulatum*, *Kappaphycus striatum* (F. Schmitz) L. M. Liao (formerly *Eucheuma striatum*) and *Kappaphycus alvarezii* (Doty) L. M. Liao were introduced from the Philippines and Pohnpei to southern Kāne'ohe Bay for aquaculture trials (Russell 1983, Russell and Balazs 2009). The main site of the trials was on the fringing reef flat of Moku o Lo'e in the southern bay (Figure 1), where unattached thalli of both species were grown in mesh pens. Visual surveys carried out between 1976 and 2002 documented the subsequent expansions of the *Eucheuma* and *Kappaphycus* ranges in Kāne'ohe Bay. Results of the first survey in 1976 indicated that *Kappaphycus striatum* (as "*Eucheuma striatum*") thalli had drifted down the lee reef-slope of Moku o Lo'e to the bay bottom, but not across deep water to shallow habitats on other patch and fringing reefs (Russell 1983). In the early 1980s, thalli identified as *Eucheuma spinosum* J. Agardh (possibly was *E. denticulatum*) were observed on a reef flat adjacent to Moku o Lo'e (Morrissey 1985). In 1996, taxa identified as *Kappaphycus striatum* and *Kappaphycus alvarezii* were observed on most patch and fringing reef flats in the south and central portions of Kāne'ohe Bay, up to 6 km from Moku o Lo'e (Rodgers and Cox 1999, Woo 2000). In repeated surveys in 1999 and 2002, *Eucheuma* and *Kappaphycus* (as "*Kappaphycus* spp.") were observed on reef flats throughout Kāne'ohe Bay, including the northern-most fringing reef that extends out of the bay to the outer coast (Conklin and Smith 2005). In a 2001 survey of 15 reef flats, *Eucheuma/Kappaphycus* was observed on nine reef flats, and the cover of all introduced algae at the 15 sites averaged 40% (Smith et al. 2002).

As indicated by the shifting nomenclature used in the surveys cited above, the taxonomic identities of *Eucheuma* and *Kappaphycus* species in Hawai'i have changed several times in the last 40 years, partly due to the morphological plasticity and rarity of reproductive thalli of these taxa. Genetic analyses have since confirmed the presence of two taxa in Kāne'ohe Bay, *Eucheuma* clade E (i.e., *E. denticulatum*) and *Kappaphycus* clade B (Conklin et al. 2009). The *Eucheuma* taxon used for experiments in the current study corresponds to *E. denticulatum*. The current study also includes assessments of survey data collected
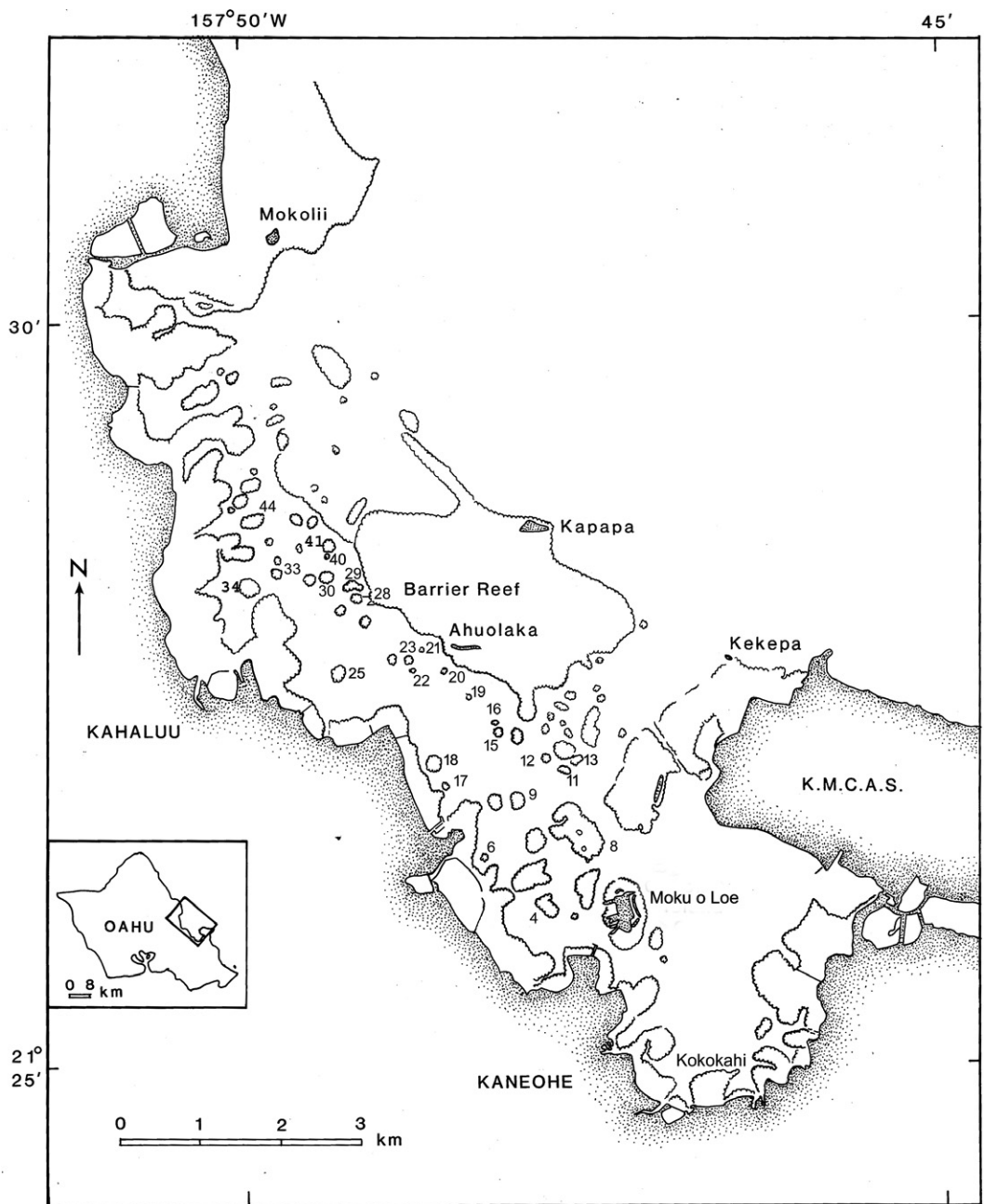
FIGURE 1. Map of Kāneʻohe Bay, its fringing, patch and barrier reefs. Patch reefs are numbered according to the system of Roy (1970).

by multiple researchers prior to and after publication of the genetic analyses (Conklin et al. 2009). For consistency, we refer to the taxa in all pre-2014 studies as *Eucheuma/ Kappaphycus*. The taxon in post-2014 surveys and field and laboratory experiments is referred to as *E. denticulatum*.

Fertile *E. denticulatum* thalli have been reported from Kāneʻohe Bay (Conklin et al. 2009), but propagation and dispersal appear to be dominated by vegetative fragments (Smith et al. 2002). These fragments settle and grow to form interwoven mats of branched thalli. *Eucheuma denticulatum* has been found on reef flats over a wide exposure range in Kāneʻohe Bay, from the high-energy barrier reef and northern fringing reef to low-energy reefs in the lee of the barrier reef. Persistence on high-energy reef flats was facilitated by branch growth into coral interstices and attachment to coral and limestone substrata (Conklin and Smith 2005). On low-energy reefs, detached thalli also sank and accumulated in gaps between coral heads, in sand pockets between corals, and on reef slopes (Conklin and Smith 2005, Stimson 2013). The propensity of *E. denticulatum* to overgrow and kill live corals on Kāneʻohe Bay reef flats (Woo 2000) led to the initiation of a control program in 2005. The control program, carried out by the Hawaii Division of Aquatic Resources (HDAR) and The Nature Conservancy, initially focused on mechanical removal of *E. denticulatum* from selected reefs (Reefs: 6, 10, 14, 15, 16, 19, 20, 24, 26, 27, 28, 29, 30, 31, 38, 40, 41, 43, 44; Figure 1) and was initiated in various years from 2011 to 2017; mechanical removal was combined with biological control based on hatchery-raised sea urchins (Westbrook et al. 2015, Neilson et al. 2018). *Tripneustes gratilla* were initially outplanted on two reefs in the bay (Reef 26 in 2011 and Reef 27 in 2012) with particularly high cover of invasive algae; these steps reduced macroalgal cover on the experimental reefs by 85% (Neilson et al. 2018).

Gracilaria salicornia was first introduced to Kāneʻohe Bay for aquaculture trials in 1978; the point of introduction was a fringing reef on Moku o Loʻe (Rodgers and Cox 1999). In contrast to *E. denticulatum*, field identifications of *G. salicornia* are reliable and the taxonomy has been stable throughout its history in Kāneʻohe Bay (Abbott 1985, Sherwood et al. 2010). Visual surveys of *G. salicornia* on Kāneʻohe Bay reefs did not commence until 1996. At that time, *G. salicornia* was present on most of the fringing and patch reef flats in the southern bay, and on several reef flats in the central bay (Rodgers and Cox 1999). By 1999, the *G. salicornia* range had expanded in the central bay, and in 2002, *G. salicornia* was observed in the northern bay (Conklin and Smith 2005). By 2009, *G. salicornia* was present on low-energy reef flats, including intertidal zones, over the entire length of Kāneʻohe Bay (Hawaiʻi State Division of Aquatic Resources (HDAR), unpublished survey data). Reproduction of *G. salicornia* in Hawaiʻi appears to be mostly limited to vegetative fragmentation (Nishimura 2000, Smith et al. 2002). Fragments settle and attach to limestone substrata on reef flats with small holdfasts, then grow to form mats of densely interwoven thalli; mats can exceed 1 m diameter and can overgrow and kill corals (Martinez et al. 2012, Stimson 2013). Large thalli are often detached from anchoring substratum, transported across reef flats by wind-driven currents, and deposited on leeward reef slopes (Stimson 2013).

Grazing preference experiments with common herbivorous fish and urchins from Kāneʻohe Bay indicate that dietary preferences for both *Eucheuma/Kappaphycus* and *G. salicornia* are moderate to low (Stimson et al. 2001, Smith et al. 2004, Stimson et al. 2007, Westbrook et al. 2015). Field bioassays and surveys of herbivorous fish in Kāneʻohe Bay indicate that herbivore abundance (Stamoulis et al. 2017) and grazing pressure (Stimson et al. 2001) both decline with distance across reefs from crest to interior. The relatively low grazing pressure, moderate to low dietary preference, and limited herbivore abundance may partially explain the high standing crops and persistence of *Eucheuma/ Kappaphycus* and *G. salicornia* on inner reef flats prior to the current study.

Study Site

Kāneʻohe Bay is a partially enclosed, 46 km^2 embayment on the northeast coast of Oʻahu (Figure 1). The bay is subdivided into northern, central, and southern sectors based on circulation patterns (Smith et al. 1981). A peninsula and a 5-km-long barrier reef protect the south and central sectors from oceanic swells. Within the bay there are approximately 60 individual patch reefs (30 to >200 m diameter at the level of the reef flat), and a fringing reef borders the landward shore. The identification numbers for patch reefs used here follow Roy (1970). Patch reefs in the southern and central sectors generally have shallow sand-dominated inner reef flats and shallow coral- and limestone-dominated outer reef flats. Reef flats of patch reefs in the northern bay have lower sand cover and higher coral and limestone cover. Reef slope substrata are a mixture of live coral, toppled coral heads, fine sediment, and rubble. Live coral cover decreases with depth from reef crests to the bay bottom at ~15 m depth (Hunter and Evans 1995).

Surveys of Algal Cover

Data from four multi-year surveys with different starting dates (designated Surveys A, B, C, and D) were used to assess changes in *Kappaphycus/Eucheuma* and *G. salicornia* cover on sets of patch reefs in Kāneʻohe Bay. Surveys A and B were initially designed to investigate the distribution and cover of corals and the invasive native green alga, *Dictyosphaeria cavernosa* (Forsskål) Børgesen (Stimson et al. 2001). Both these surveys also included observations on the cover of *Kappaphycus/Eucheuma* and *G. salicornia*, but those data have not previously been assembled and analyzed. Survey C was initiated for the purpose of monitoring the cover of *Kappaphycu/Eucheuma* and *G. salicornia* over time, and Survey D was initiated to compare cover of these algae on reef slopes versus reef flats. Survey A commenced in 1996 and was repeated in 1997, 2006, 2008, 2009, 2013, 2014, and 2017. This survey consisted of triplicate transects spaced 5 m apart, at two sites on each of five patch reefs (Patch reefs 4, 8, 29, 30, and 44) and on the fringing reef of Moku o Loʻe (Figure 1). The transects extended 40 m onto the reef flat from the crest of the patch or fringing reef, and 5 m down the reef slope. The organisms or substrata under the transects were recorded at 20 cm intervals along the length of the transects, and percentage cover estimates were based on these data. Detailed methods for Survey A are in Stimson et al. (2001). Starting in 2012, the data for Reef 29 were separated from that of the other reefs, because mechanical, and a year later, biological control of these alien red macroalgae was initiated on this reef by HDAR and The Nature Conservancy.

Survey B commenced in 2006 on three patch reefs in central Kāneʻohe Bay (Reefs 19, 20, and 21) and was repeated approximately three times per year since then. This survey consisted of one or two transects per reef on each date; each transect extended approximately 30 m across the center of the almost circular reef flat and 5 m down slope at each end of the 30-m section. Cover estimates were derived as in Survey A. Detailed methods for Survey B are in Stimson and Conklin (2008). Starting in 2013, biological control (addition of urchins) and mechanical removal of the alien red macroalgae was initiated on these reefs by HDAR and The Nature Conservancy; biological control began on Reef 20 in 2013, then in 2014 biological control was initiated on Reef 19, and mechanical removal on Reef 20.

A third set of macroalgal cover surveys (Survey C) on Kāneʻohe Bay reefs was initiated in the summer and fall of 2014 and repeated in 2018. In Survey C, 25-m transects were used to estimate the cover of macroalgae, coral, and other substrata on the reef flats and upper reef slopes of the following reefs: 7, 8, 9, 11, 12, 13, 17, 18, 22, 25, 34, and 41. These were reefs which were not subject to manipulation for algal control in the 2014 to 2018 period. At each of the Survey C reefs, three to nine transects were surveyed on the reef flat, and three to six transects were surveyed on the reef slope at a depth approximately 2 m below

the crest; the number of transects varied with reef area. The organism or substratum type was scored beneath each 20 cm interval along each line to obtain a % cover value. This survey was repeated in 2018. Comparison of the average macroalgal cover on the reefs at the two times was by Wilcoxon's signed rank test because of the variability in the data and the small sample size.

A fourth set of reefs with a range in percent cover of *E. denticulatum* were selected in 2014 in order to compare the cover of this alga on upper reef slopes with that on reef flats (Survey D). Subsequently, these reefs were used in 2014 for the study of the growth rate of *E. denticulatum* in caged versus uncaged treatments (described below) on the reef flat and the reef slope. The reefs in this fourth set were: 6, 9, 12, 15, 16, 17, 19, 22, 23, 28, 33, and 40. Comparison of the average cover values on reef slope versus reef flat of these reefs were performed with Wilcoxon's signed rank test because of the variability in the data and the small sample size.

Growth of Caged and Uncaged Eucheuma denticulatum *on Reef Flats and Slopes*

Eucheuma denticulatum thallus growth rates and grazing intensity were measured in a field experiment conducted on 13 reefs on 13 dates in the summer, autumn, and winter of 2014. Twelve trials of the experiment were carried out on 12 patch reefs of the Survey D set from August to October 2014 (Reefs: 6, 9, 12, 15 (3 years after urchin introduction), 16, 17, 19, 22, 23, 28, 33, and 40), and eight additional trials were carried out on the NE fringing reef of Moku o Loʻe from June to December 2014. *E. denticulatum* thalli for the experiment were collected from sites of high abundance on reef flats and then held overnight in outdoor tanks with flowing, unfiltered seawater. Thalli were divided into experimental units (approximately 30 g wet weight), shaken to remove excess water, and weighed on an analytical balance to 0.1 g. Two thalli were attached to vinyl-coated wire mesh platforms (15 × 30 cm) using fine plastic-coated wire, and one of the thalli was enclosed in a plastic-mesh cage

($12 \times 12 \times 12$ cm, 6-mm mesh, mesh diameter ~0.5 mm) to exclude herbivorous fishes and green turtles. The platforms with paired caged and uncaged *E. denticulatum* thalli were transported by boat to the reef where they were to be deployed; thalli were shaded and sprayed with seawater during transport. At each reef, approximately 20 platforms were positioned on the reef slope and 30 platforms were positioned on the reef flat. The reef slope platforms were evenly spaced around the reef perimeter at 2 m depth, and the reef flat platforms were arranged in a regular grid across the entire flat. Platforms were retrieved after 2 days and the thalli were reweighed. Specific growth and loss rates were calculated as weight change per initial weight per day ($g \, g^{-1} \, d^{-1}$). Data used in the analysis were the means for each treatment (caged vs uncaged) for each reef or for each trial of the experiment performed at Moku o Loʻe. A factorial GLM analysis (Minitab Statistical Software) was performed on the untransformed data; caging and habitat were the two factors, the trials from Moku o Loʻe and the numbered reefs were treated as two blocks. The net effect of simultaneous thallus growth and grazing loss was measured as grazing intensity (Stimson et al. 2001). Grazing intensity for each platform was calculated as the specific growth rate of the caged thallus minus the specific growth rate of uncaged thallus.

Effects of Water Temperature on the Growth of Eucheuma denticulatum *and* Gracilaria salicornia

Water temperatures of ~30 °C were measured in shallow waters in Kāneʻohe Bay in the late summers of 2014 and 2015 (www.pacioos. hawaii.edu) in association with coral bleaching events both years (Bahr et al. 2015, 2017). Outdoor laboratory experiments were conducted in October and November 2016 to examine the effect of high temperatures on the growth of *E. denticulatum* and *G. salicornia*. Small *E. denticulatum* and *G. salicornia* thalli were maintained in an outdoor tank for use in the experiment. At the start of each trial of the experiment, sets of three *E. denticulatum* thalli

(2–4 g wet weight) were drawn from this tank, shaken to remove excess water, weighed, and transferred to each of six 6.4 l glass tanks at a depth of 7 cm. Each tank was supplied with unfiltered seawater at a rate of 300 ml min^{-1}. Aeration was used to increase water motion in the tanks. The water in two tanks was heated with aquarium heaters, the water in one tank was cooled with a small aquarium chiller, and the water in the remaining three tanks was maintained at the temperature of the laboratory seawater system. Temperatures were recorded in the tanks using Hobo temperature loggers; the treatments produced a range of mean temperatures from 24 to 31 °C. The tanks were covered with one layer of window screen to reduce irradiance by ~40% (measured with a Biospherical Instruments QSI-140 meter and 4-π sensor). The thalli were reweighed after 48 h and specific growth rates of the three thalli in each tank were averaged, then this growth rate was plotted against the average temperature in the tank for the period of the trial. Eight experimental trials (statistical blocks) were carried out in October 2016; all six treatments were included in each trial, but results from six of the 48 replicates were excluded from analysis because of aeration or water supply problems. The mean temperature in each tank over the 48-h growth period was used in a regression analysis to quantify the relationship between *E. denticulatum* growth rate and water temperature. Effects of water temperature on *G. salicornia* growth were measured using the same methods used for *E. denticulatum*, with the following modifications. Starting weights of *G. salicornia* thalli were 2–3 g. Three 2-day experimental trials (statistical blocks) were carried out from 1 November 2016 to 7 November 2016. Six tanks were used in each trial, two heated, one cooled, and three with ambient water temperature, treatment temperatures ranged from 24.5 to 30 °C.

Herbivorous Fish Abundance and Biomass

The abundance of herbivorous fishes has been visually estimated on a set of Kāneʻohe Bay reefs in two multi-year surveys that were extended for the current study. The first survey consisted of counts of herbivorous surgeonfishes (Acanthuridae) around the perimeters of four small patch reefs (~30 m in diameter) in the central bay (Reefs 19, 20, 21, 23). The width of the survey transect was 8 m, the outer 3 m of the reef flat and the upper 5 m of the reef slope. Surveys were carried out 112 times from early 2007 to mid 2014. Each fish was assigned to one of three size classes, but these counts were not converted to biomass. Total length of acanthurid individuals on these reefs is generally less than 14 cm. Detailed methods for the first fish survey are in Stimson (2005). The second survey consisted of counts and estimated lengths of herbivorous surgeonfishes and parrotfishes (Scaridae) along 50 m long belt transects located on a 750-m long section of the windward (NE facing) reef of Moku o Loʻe (Figure 1). The transect belt extended from the crest of the patch reef to 3 m onto the reef flat and 5 m down the reef slope. The total length of each fish was estimated to the nearest cm; fish were generally less than 15 cm total length. Length estimates were converted to biomass estimates using the conversion factors in Stimson et al. (2001). The individual biomass values were multiplied by the number of individuals in a size class in a species, then these products were summed across the size classes and species in a survey. The analysis presented here used the natural log of the biomass value of each survey. Detailed methods for the second fish survey are in Stimson et al. (2001). A total of 107 Moku o Loʻe surveys were carried out from early 2007 to mid 2014. Grazing sea urchins are uncommon in Kāneʻohe Bay (Hinegardner 1961).

RESULTS

Multi-Year Surveys of Algal Cover

In Survey A (commencing in 1996), mean *Kappaphycus/Eucheuma* cover increased from 1996 to 2008–2009 on reef flats, then declined by 2013 (Figure 2A, un-manipulated reefs). In 2012, manual removal of *Kappaphycus/ Eucheuma* commenced on Reef 29; the cover
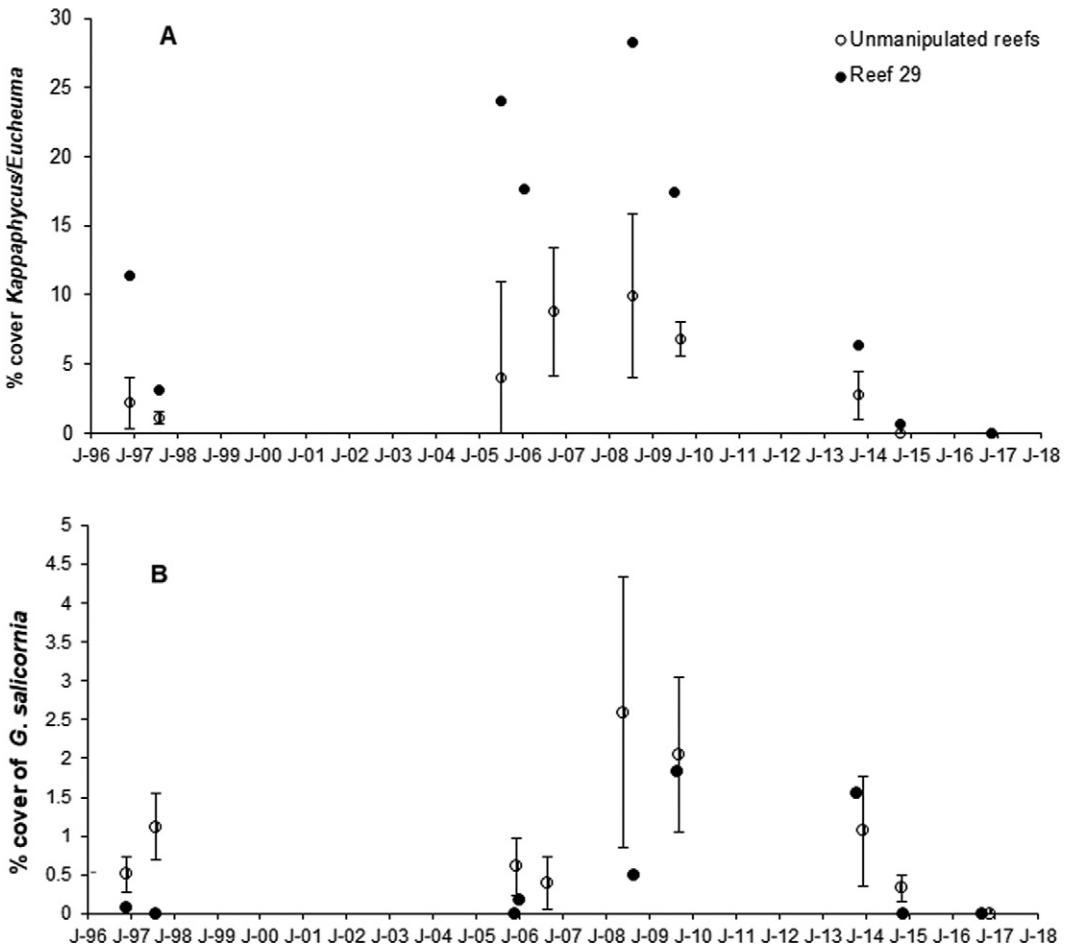
FIGURE 2. (*A*) Change in *Kappaphycus/Eucheuma* cover on the reef flats and upper slopes of six reefs in Survey A. Manual removal of *Kappaphycus/Eucheuma* on Reef 29 began in 2012, urchin addition began in 2013. Points corresponding to "Unmanipulated reefs," those not subject to manual removal or urchin addition, are means ± 1 standard error for all six reefs until 2012, and thereafter the points represent the values from the five unmanipulated reefs. (*B*) Changes in *Gracilaria salicornia* cover on the reef flats and upper slopes of six reefs in Survey A. Manual removal did not target *G. salicornia*.

of *Kappaphycus/Eucheuma* on this reef has been plotted separately in Figure 2*A*. By 2014, no *Kappaphycus/Eucheuma* cover was observed on the un-manipulated reefs and very little was detected on Reef 29. The pattern of temporal variation in *G. salicornia* cover on the six reefs used for Survey A was similar to that of *Kappaphycus/Eucheuma*; cover declined after 2008/2009 on the un-manipulated reefs and virtually disappeared from all six reefs by 2014, even though this species was not targeted for manual removal (Figure 2*B*).

The mean % cover values are low on these reefs because the 40-m survey transects on some reefs crossed large areas of sand substratum on the reef flat, with few coral outcrops and little rubble to which macroalgal thalli could attach. All other macroalgal species constitute less than 1% of the cover on these reef flats and slopes.

In Survey B (commencing in 2006), *Eucheuma/Kappaphycus* reached its maximum cover on Reef 19 by 2010 (Figure 3*A*), apparently remained at that level until 2014,
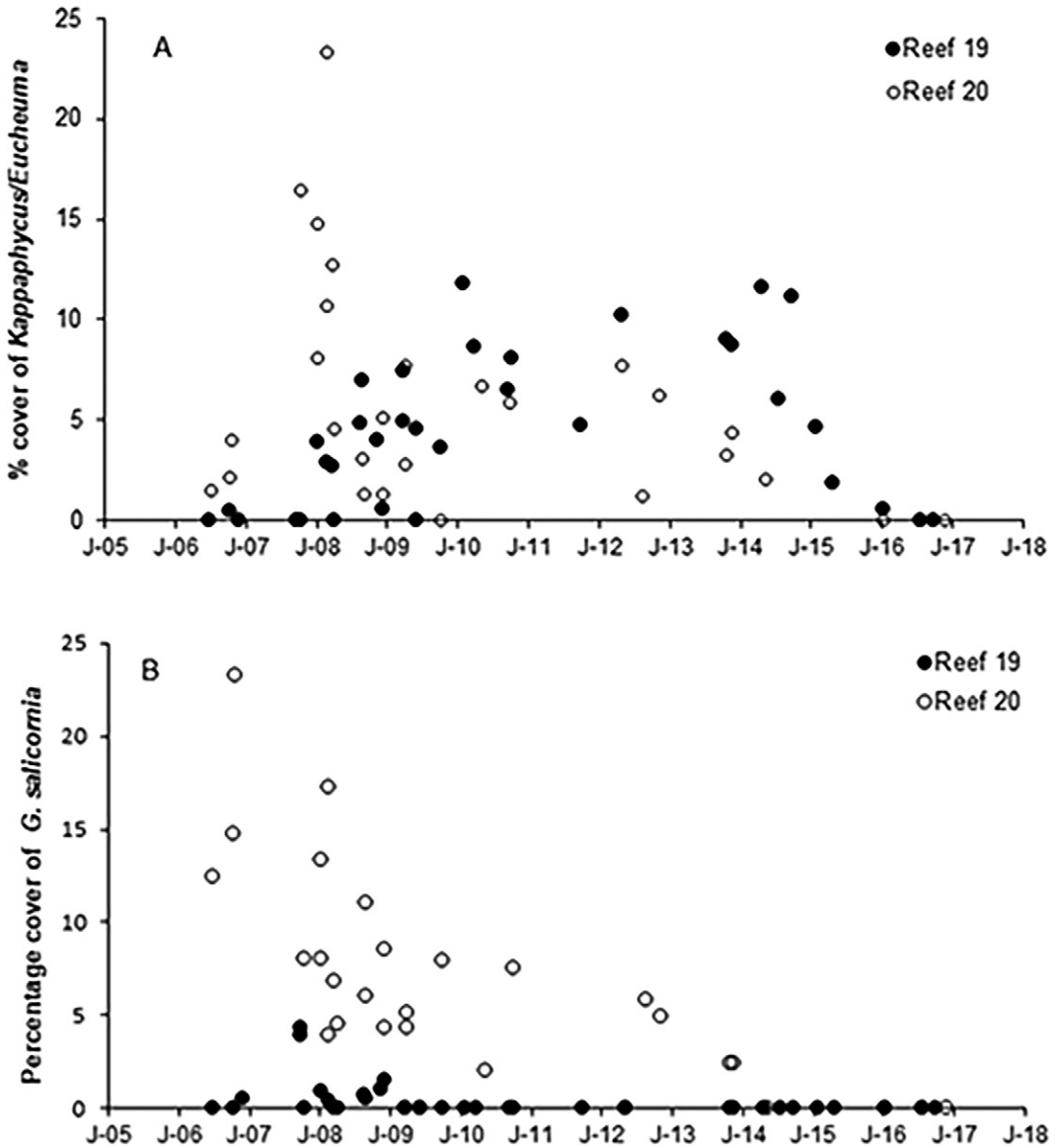
FIGURE 3. Changes in (*A*) *Kappaphycus/Eucheuma* cover and (*B*) *Gracilaria salicornia* cover on the reef flats and upper slopes of two reefs in Survey B. Large numbers of urchins (*Tripneustes gratilla*) were outplanted on Reef 19 in 2014 and to Reef 20 in 2013 to consume macroalga as part of a biological control program.

then declined coincident with both herbivorous urchin stocking in the HDAR control program (October 2014) and elevated water temperatures in 2014. *Eucheuma/Kappaphycus* reached its maximum cover on Reef 20 in 2008, then declined sharply within about a year. The cover showed further decline following the addition of sea urchins to this reef in September 2013 and the institution of mechanical removal in 2014. By 2016 the algae had virtually been eliminated from these reefs, but cover level had either declined or shown no further increase between 2010 and 2013 when biological or mechanical control

were instituted. *Gracilaria salicornia* cover peaked on Reefs 19 and 20 in 2007/2008, then disappeared from Reef 19 by 2009, and persisted on Reef 20 until the time of the urchin stocking in September 2013 (Figure 3*B*). Neither species of algae established on Reef 21 during the study.

Between 2014 and 2018 the cover of *E. denticulatum* on unmanipulated reef flats in Survey C declined significantly from 1.36% cover to 0.29 % (Table 1). The cover of *G. salicornia* also declined significantly. The percent cover values on these reefs are low partly because these are reefs, which were not selected for control efforts: control efforts by HDAR and the Nature Conservancy were concentrated on reefs with high cover. Comparison of the cover of *E. denticulatum* on reef flats with that on reef slopes on 10 unmanipulated reefs in the summer of 2014 (Survey D) showed that reef flats had significantly higher cover by Wilcoxon's signed rank test ($P < .05$, Table 2). The cover of *E. denticulatum* was about 6% on the reef flats of unmanipulated reefs and 0.9% on reef slopes. *Gracilaria salicornia* only occurred on the reef flats of two of the 10 reefs in 2014 (5% and 15%).

Growth of Caged and Uncaged *Eucheuma denticulatum* on Reef Flats and Slopes

Caged (ungrazed) *E. denticulatum* thalli sustained net growth on reef flats and reef slopes

TABLE 1

Comparison of the Percentage Cover of *Eucheuma denticulatum* and *G. salicornia* on Unmanipulated Reefs in 2014 with that in 2018

	2014	2018	P
E. denticulatum			
Average cover	1.36	0.29	<.05
Range	0–9.7	0–2.5	
Number of reefs	12	12	
G. salicornia			
Average cover	2.19	0.25	<.01
Range	0–13.1	0–3	
Number of reefs	12	12	

P-value based on Wilcoxon's signed rank test. Cover is different between years by a Wilcoxon's signed rank test, $P < .01$.

TABLE 2

Comparison of the Percentage Cover of *Eucheuma denticulatum* on Reef Flats Versus Reef Slopes in 2014 on Reefs in Survey C

	Reef Flat	Reef Slope	P
Average % cover	5.6	0.1	<.05
Range	0–23.9	0–3.0	
Number of reefs	10	10	

P-value based on Wilcoxon's signed rank test.

during the summer and fall of 2014, while uncaged thalli lost weight in both habitats over the same period (Table 3). The mean specific growth rates of caged thalli on reef flats was 0.021 g g^{-1} d^{-1} and 0.010 g g^{-1} d^{-1} on reef slopes (Table 3). The mean specific growth rates of uncaged thalli were -0.013 g g^{-1} d^{-1} on reef flats, and -0.082 g g^{-1} d^{-1} on reef slopes (Table 3). Results of the GLM analysis showed that growth rates of caged thalli were significantly greater than those of the uncaged thalli and that growth rates on reef flats were significantly higher than those on slopes (Table 3). Seven trials of the growth/grazing experiment were carried out prior to the end of August 2014, when the average daily water temperature at Moku o Loʻe was still below 28 °C. In each of these early trials, mean grazing

TABLE 3

Comparison of Specific Growth (g g^{-1} d^{-1}) of Caged and Uncaged *E. denticulatum* Thalli on Reef Flats and Reef Slopes (Habitat) in Kāneʻohe Bay

Average Growth		
	Inside Cages	Outside Cages
Reef flat	0.021 ± 0.002 (19)	−0.013 ± 0.006 (19)
Reef slope	0.010 ± 0.001 (20)	−0.082 ± 0.021 (20)
GLM Analysis		

Source	df	MS	F	P
Caging	1	0.075	34.49	<.001
Habitat	1	0.028	12.76	<.001
Blocks	1	0.027		
Habitat × Caging	1	0.016	7.18	.009
Error	73	0.002		
Total	77			

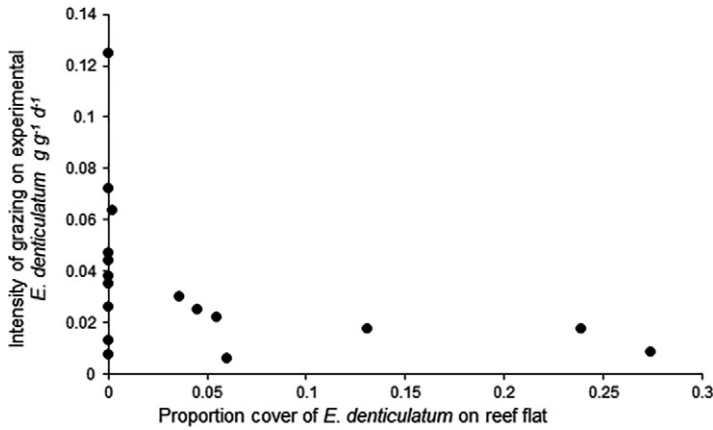Values are means ± 1 SE; sample sizes in parentheses.

FIGURE 4. Grazing intensity on experimental *E. denticulatum* thalli on reef flats in summer, fall, and early winter 2014, plotted against *E. denticulatum* cover on the corresponding reef flats in 2014.

intensity (calculated as the specific growth or loss rates of the caged *E. denticulatum* thallus minus that of the uncaged thallus on each platform) exceeded mean growth on both reef flats and reef slopes. Grazing intensity, was a decreasing function of *E. denticulatum* cover on reef flats (Figure 4).

Effects of Water Temperature on the Growth of Eucheuma denticulatum *and* Gracilaria salicornia

Eucheuma denticulatum growth in outdoor laboratory tanks increased with increasing water temperature from 25 °C to 28 °C, then declined at higher temperatures (Figure 5). A
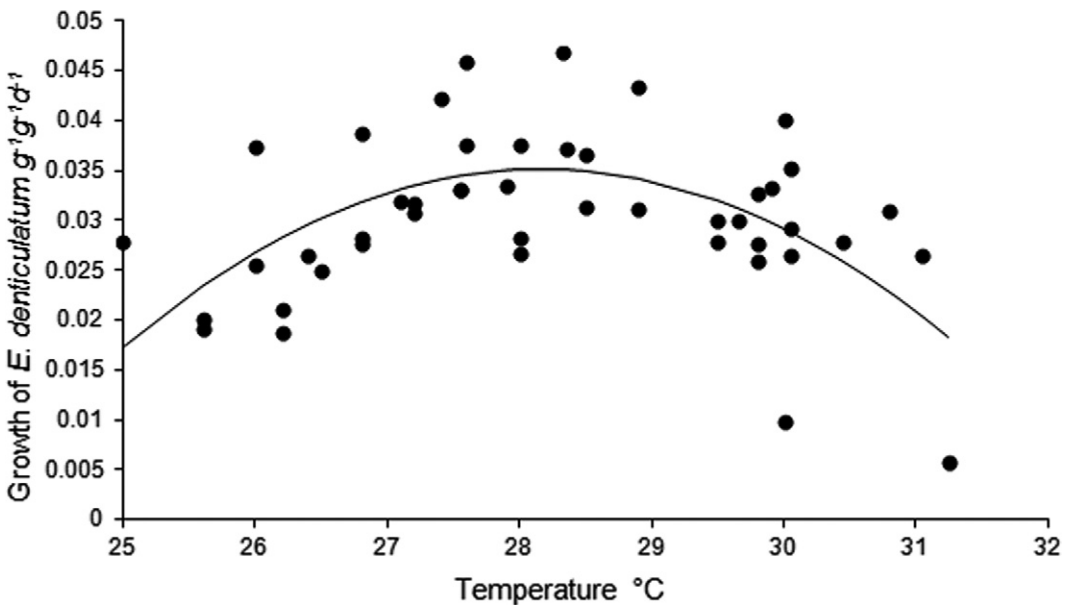

FIGURE 5. Specific growth rates of *E. denticulatum* thalli over a range of seawater temperatures. Each data point represents the average growth of three thalli. Curves represent the fitted quadratic equation: $Y = -1.055 + 0.077X - 0.002X^2$, excluding the two points in the lower right corner.

quadratic polynomial curve fitted to the data was significant and explained 29% of the variation in *E. denticulatum* specific growth rates ($F = 14.25$, df = 1,41, $P < .001$). In contrast, the growth rate of *G. salicornia* was neither a linear ($F = 2.80$, df = 1,18) nor a quadratic ($F = 0.39$, df = 1,18) function of water temperature.

Herbivorous Fish Abundance and Biomass

Over the period from 2007 to 2014, during which much of the decline in *Eucheuma/Kappaphycus* and *G. salicornia* took place (Figures 2 and 3), there was a statistically significant positive temporal trend in the density of acanthurids (fish $100 \, \text{m}^{-2}$) on three of the four reefs in the central bay (Reefs 19, 20, 21, Table 4). On the reef slope and outer reef flat of Moku o Lo'e, the estimated total biomass of scarids and acanthurids ($\text{g} \, \text{m}^{-2}$) increased significantly from 2007 to 2014 (linear regression of the natural log of biomass m^{-2} versus days, $Y = 0.00025X - 4.86$, $R^2 = 0.095$, F test of regression slope = 11.00, $P = .00125$, sample size (censuses) =

TABLE 4

Regression Statistics for the Test of the Slopes of the Regressions of the Numbers of Acanthurids Per $100 \, \text{m}^{-2}$ Versus Time (in Days), for Reefs 19, 20, 21 and 23

Reef	Number of Censuses	Slope	S_b	F	P
19	56	0.003	0.0005	40.05	<.001
20	31	0.005	0.002	8.70	<.006
21	41	0.002	0.0004	16.68	<.001
23	11	0.002	0.0015	1.19	ns

107, Figure 6). Predicted values (antilogs) calculated from the regression give an increase from $19.26 \, \text{g} \, \text{m}^{-2}$ in 2007 to $33.28 \, \text{g} \, \text{m}^{-2}$ in 2014.

DISCUSSION

The decline of introduced invasive species through the agency of native species and without some type of human intervention, such as biological control, is an unusual event in terrestrial (Simberloff and Gibbons 2004)
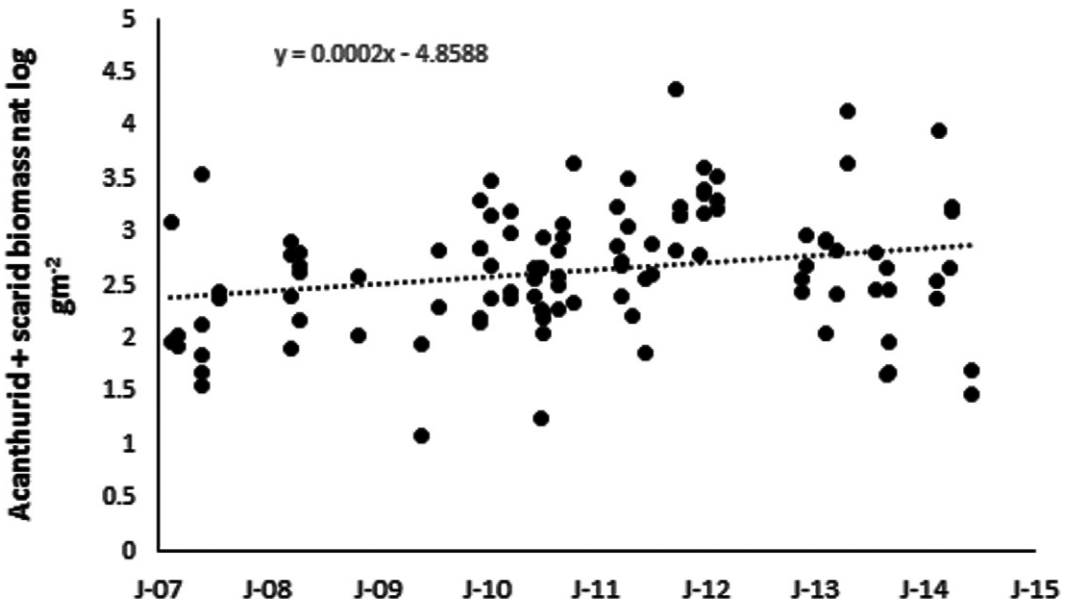

FIGURE 6. Change in the natural log of the biomass per unit area of herbivorous fishes on the windward reef slope and outer reef flat of the fringing reef of Moku o Lo'e in the period during which the decline in cover of *E. denticulata* and *G. salicornia* took place in Kāne'ohe Bay.

and marine (Davis et al. 2005) environments. The examples of the decline in cover or distribution of introduced marine macroalgae are from the temperate zone for four chlorophyte species. Trowbridge (2002) reported the local elimination of *Codium fragile* from an area in Scotland several decades after its introduction; Iveša et al. (2006) reported a decline in *Caulerpa taxifolia* (M. Vahl) C. Agadh about 6 years after its introduction to a site in Croatia; Lapointe et al. (2006) reported the loss of *Caulerpa brachypus* f. *parvifolia* (Harvey) A. B. Cribb from a site on the Florida coast 3 years after its introduction; Trowbridge et al. (2013) reported a decline in *Codium fragile* in Ireland about 70 years after its introduction, and Montefalcone et al. (2015) reported the decline of *Caulerpa taxifolia* along the coast of the Ligurian sea about 26 years after its introduction. In only two of these examples is a cause of the disappearance of the introduced species fairly certain: an herbivorous saco-glossan grazed the herbivorous *C. fragile* in Scotland, and the action of two successive hurricanes in Florida removed the *C. brachypus* f. *parvifolia*. When decrease in range is considered as a measure of control of a species, rather than decrease in cover, Lyons and Scheibling (2009) found no decreases in range in 22 studies of marine algae. The studies covered periods, which averaged approximately 27 years in length. Boudour-esque and Verlaque (2012) speculate that naturally occurring declines in abundance of introduced species in marine environments may be rare.

Boudouresque and Verlaque (2012) describe four phases in the introduction and expansion of alien invasive species: arrival, establishment, increase/expansion, and per-sistence. They present two models of how abundance changes during these phases. In one, the "boom and bust" model, expansion is followed by persistence, but at a low level of abundance. This appears to be the case now with *E. denticulatum* and *G. salicornia* in Kāneʻohe Bay. These two rhodophytes are still present, but 40 years after their introduc-tion to the bay they are now much less abundant and less widespread. Thalli of *E.*

denticulatum are restricted to crevices between corals and their branch tips show signs of grazing, and *G. salicornia* are generally restricted to the innermost parts of sand and rubble reef flats, where herbivorous fishes are uncommon, with the notable exception of *Naso unicornis* (Forsskål) (Bierwagen et al. 2017). Even in these inner reef flat habitats the branches of *G. salicornia* have been blunted by grazing.

The bay-wide reduction in the abundance of these two species may have begun as early as 2008 (Figures 2 and 3), and has continued to 2019. The results of the grazing experiments conducted in 2014 (Table 3) suggest the reduction in distribution and abundance is the result of grazing by native herbivores, and was not the result of human intervention using biological, manual, or mechanical control, although these methods were effective on reefs where they were used (Neilson et al. 2018).

The control of these alien invasive macro-algal species is evidently an example of control by generalist herbivores (Parker et al. 2006, Morrison and Hay 2011). The grazing experiments (Table 3) indicated that rates of *E. denticulatum* consumption by herbivorous fishes in Kāneʻohe Bay exceeded *E. denticu-latum* growth rates on both reef flats and reef slopes in 2014. No field measurements of *G. salicornia* growth and grazing intensity were made in this study, but previous experiments indicate that *G. salicornia* ranks higher in preference for Kāneʻohe Bay herbivores than *E. denticulatum* (Stimson et al. 2001, Westbrook et al. 2015). Therefore, the effect of high grazing pressure on the abundance of *G. salicornia* is likely to be similar to, or greater than, the effect on *E. denticulatum* abundance.

The grazing pressure responsible for the decline in cover of *E. denticulatum* and *G. salicornia* evidently came about because of an increase in the abundance and biomass of herbivorous fishes prior to 2014 (Table 4 and Fig. 6). Native acanthurids and scarids are the grazers most likely to be responsible for the high grazing intensities we observed; these are the most abundant herbivorous fishes in the Bay. Species in both families are generalist herbivores in Kāneʻohe Bay (Stamoulis et al.

2017). Siganids do not occur in Hawai'i; grazing pomacentrids and macroalgae-grazing kyphosids are rare in the bay, and large grazing urchins are generally restricted to areas on and near the barrier reef (Hinegardner 1961). Five common acanthurids in Kāne'ohe Bay have been observed feeding on *E. denticulatum* and *G. salicornia*: *Acanthurus dussmerili* (Valenciennes), *Acanthurus triostegus* (L.), *Naso unicornis* (Forsskål), *Zebrasoma flavescens* (Bennett), and *Zebrasoma velliferum* (Bloch) (Russell 1983, Bierwagen et al. 2017, Stamoulis et al. 2017, authors' observations). In addition to herbivorous fishes, green turtles, *Chelonia mydas* (L.), also generalist herbivores (Russell and Balazs 2009, 2015), may have contributed to the recent declines in *E. denticulatum* and *G. salicornia*. Green turtle populations have been increasing in Hawai'i since protective management was initiated in 1978 (Balazs and Chaloupka 2004) and they are abundant in Kāne'ohe Bay, though no intensive censuses have been carried out there. In the spring of 2017, Bahr et al. (2018) reported that *C. mydas* abundance became so high in south Kāne'ohe Bay that *C. mydas* grazing caused a precipitous decline in the cover of *G. salicornia* in near-shore areas not characteristically used by herbivorous fishes. Both *E. denticulatum* and *G. salicornia* occur in the diets of green sea turtles in the bay (Arthur and Balazs 2008, Russell and Balazs 2009). *Gracilaria salicornia* is a particularly important component of green sea turtle diets and is estimated to comprise >30% of the macroalgae consumed by Kāne'ohe Bay turtles (Russell and Balazs 2009, 2015).

In addition to grazing by herbivorous fishes, elevated water temperatures may have contributed to the control of *E. denticulatum* in Kāne'ohe Bay. The decline in *E. denticulatum* cover observed in early 2016 followed consecutive warm-water events in the summers of 2014 and 2015. These events resulted in coral bleaching in the bay in both years (Bahr et al. 2015, 2017). Water temperatures at 2 m depth at a site on the reef slope of Moku o Lo'e in southern Kāne'ohe Bay reached a peak of 29.8 °C on 20 September 2014 and a peak of 30 °C on 28 August 2015 (www.pacioos.hawaii.edu), and water temperatures at 2–3 m depth at seven other sites in the bay were between 29 and 31.5 °C from late August to early September of 2015 (Bahr et al. 2017). In the previous 10 years, maximum water temperatures at the Moku o Lo'e site remained below 29 °C and averaged 27.8 °C.

The results of the laboratory experiments on growth over a range of water temperatures indicated that *E. denticulatum* growth rates decreased at water temperatures above approximately 28 °C, but there was no apparent growth inhibition in *G. salicornia* over a temperature range from 26 to 30 °C. This suggests that the elevated water temperatures of the late summers of 2014 and 2015 could have contributed to the decline of *E. denticulatum*. Previous assessments of the effects of elevated water temperature on the growth of tropical marine macroalgae have revealed a range of responses; in many species, growth was reduced at temperatures above 25 °C (Pakker et al. 1996, Hwang et al. 2004, Graba-Landry et al. 2020), while Tsai et al. (2005) found increasing growth rate in *Laurencia papillosa* (C. Agardh) Grevilleup to 32.5 °C and up to 30 °C in *Gracilaria coronopifolia* (J. Agardh). Experimentally increased water temperature has been found to decrease the growth of subtropical macroalgae (Graba-Landry et al. 2018).

While high water temperatures (>28 °C) and high grazing pressure may have jointly caused the decline of *E. denticulatum* in Kāne'ohe Bay, grazing alone was sufficient to cause the decline. This conclusion is based on our observations that *E. denticulatum* grazing loss rates exceeded tissue growth rates in seven trials of the field experiment carried out before 30 August 2014, when temperatures were <28 °C, as well as the observations that the cover *of E. denticulatum* and *G. salicornia* were declining before 2014 (Figures 2 and 3). Given that experimentally increased water temperatures did not reduce *G. salicornia* growth, grazing appears to have been the primary cause for the decline in *G. salicornia* cover. In addition to direct effects

of grazing and elevated water temperatures, the high water temperatures in Kāneʻohe Bay in 2014 and 2015 may have indirectly caused grazing rates to increase, by increasing metabolic rates in herbivorous fishes, and perhaps sea turtles, thereby increasing food requirements (Clarke and Johnstone 1999, Smith 2008).

The rapid decline of *E. denticulatum* and *G. salicornia* appears to be the first reported example of natural (i.e., nonexperimental) control of introduced invasive macroalgae by native herbivores on coral reefs. There are reports of proliferations of native coral-reef macroalgae controlled by native herbivores; many of these involve the sea urchin *Diadema antillarum* (Philippi) on Caribbean reefs (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006, Idjadi et al. 2006, Myhre and Acevedo-Gutierrez 2007). In each of these cases, *D. antillarum* populations that had recovered from a large-scale die-off in the 1980s, reduced the abundance of native filamentous and foliose macroalgae, and the sea urchins achieved densities similar to those reported in the Caribbean before the die-off in 1983/1984 (Lessios et al. 1984, Carpenter and Edmunds 2006). Previous reports of herbivorous fish controlling proliferations of native macroalgae on coral reefs are limited to field experiments (Bellwood et al. 2006, Mumby et al. 2006, 2007, Hughes et al. 2007). Native herbivores have been observed consuming introduced marine macroalgae in other tropical (Smith et al. 2004, Vermeij et al. 2009) and temperate (Levin et al. 2002, Sumi and Scheibling 2005, Gollan and Wright 2006, Thomas et al. 2011) locations, but low dietary preference for the introduced macroalgae generally limits grazing intensity.

The reductions in *E. denticulatum* and *G. salicornia* reported here are the second major decline in macroalgae in Kāneʻohe Bay in the last 10 years. The first of these was the abrupt decline in the green alga *Dictyosphaeria cavernosa* cover in 2006, which ended nearly four decades of *D. cavernosa* dominance on reef slopes through most of Kāneʻohe Bay (Stimson and Conklin 2008). The abrupt decline of *D. cavernosa* was attributed to the low irradiance levels and low water temperatures associated with a 42-day period of rain and overcast weather in February and March 2006 (Stimson and Conklin 2008). The decline of this native invasive in Kāneʻohe Bay represents the reversal of a phase shift (Stimson and Conklin 2008). As of 2018, the abundance of *D. cavernosa* in Kāneʻohe Bay remains very low.

The declines of *E. denticulatum* and *G. salicornia* probably should not be regarded as the reversal of a phase shift, because these species are not native to Hawaiʻi. The concepts of phase shift and phase shift reversal have not been developed with introduced nonnative species in mind (Done 1992, Hughes 1994, McManus and Polsenberg 2004). The declines of *E. denticulatum* and *G. salicornia* are rare examples of the observation and documentation of control of introduced invasive species without the introduction of a nonnative biological or chemical control agent. This control may turn out to be temporary (Simberloff and Gibbons 2004), but has lasted for 6 years.

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