

## Observations of a rapid decline in invasive macroalgal cover linked to green turtle grazing in a Hawaiian marine reserve\*

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**Abstract**— The persistent, non-native invasive alga *Gracilaria salicornia* has dominated the protected waters surrounding Moku o Lo‘e, Kāne‘ohe Bay since its introduction in 1978; however, a sudden decline in abundance (75%) occurred within a 30-day survey period. The consistent environmental conditions during the survey period, dominance of *G. salicornia* despite the presence of abundant herbivorous fish populations, and multiple observations of physical grazing by the green turtle, *Chelonia mydas*, on *G. salicornia* support our conclusion that *C. mydas* was the primary driver of the rapid decline of a persistent invasive macroalgae within a Hawaiian marine reserve. These findings highlight the need for high herbivore functional diversity with species-specific differences in dietary preference and feeding strategy, which should more efficiently suppress the growth and spread of any given macroalga and indirectly benefit coral reefs.

### Introduction

Since the 1950s, 19 algal species were intentionally (e.g., aquaculture food) and/or accidentally (e.g., ballast water) introduced into Hawai‘i (Glenn and Doty 1990). A few of these species were successful in expanding their distribution and abundance in the well-studied estuarine ecosystem of Kāne‘ohe Bay, O‘ahu (Bahr et al. 2015a). These non-native species flourished due to nutrient enrichment from continuous sewage effluent discharge for nearly two decades, causing a phase shift from a coral-dominated to an algal-dominated ecosystem. Sewage diversion in the late 1970s led to natural recovery and a reverse phase shift favoring coral reefs; however, a few non-native invasive algal species persisted. Of these, *Gracilaria salicornia* has been the most successful, spreading extensively throughout Kāne‘ohe Bay and growing in large entangled clumps that overgrow and compete with corals consequently stripping reefs of their complexity (Rodgers & Cox 1999, Smith et al. 2004). When the rate of consumption by herbivores falls below algal growth rates, algal phase shifts will persist (Hughes et al. 2007, Mumby 2009).

The island of Moku o Lo‘e in Kāne‘ohe Bay is home to the Hawai‘i Institute of Marine Biology (HIMB) and is surrounded by a 0.30 km<sup>2</sup> no-take marine reserve (Hawai‘i Marine Laboratory Refuge) established in 1967. *Gracilaria salicornia* was first introduced to Kāne‘ohe Bay on Moku o Lo‘e in 1978 (Russell 1992) and has since increased in distribution and abundance to become the most dominant alga (57.6% of total average macroalgae cover by species, Stamoulis et al. 2017)

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Figure 1. Green turtle, *Chelonia mydas*, feeding on *Gracilaria salicornia* in the back lagoon of Moku o Lo'e, Kāne'ohe Bay, O'ahu, Hawai'i in March 2017. Photo by KD Bahr.

within the marine reserve. In March 2017, the Hawaiian green turtle, *Chelonia mydas*, was observed feeding on *G. salicornia* in the back lagoon of Moku o Lo'e (Figure 1, Online Resource 1), where *C. mydas* have been rarely observed in over 45 years (G. Balazs unpublished data; J. Stimson, pers. comm., 2017). Since this initial sighting, *C. mydas* have consistently visited the back lagoon and areas surrounding Moku o Lo'e, feeding on *G. salicornia*. In response to unusual observations of *C. mydas* with a concomitant rapid decline in *G. salicornia*, we hypothesized that *G. salicornia* abundance would continue to decline in the lagoonal areas around Moku o Lo'e and we expeditiously established survey sites within the marine reserve.

### Materials and Methods

The Hawai'i Marine Laboratory Refuge encompasses a fringing reef that has been heavily altered by dredging, which has produced channels/inlets, spits, and a number of moats. The shallow (0.25-1.5 m) reef flat consists of algal-dominated sand and coral rubble, enclosed within a coral-dominated fringing reef crest that descends steeply to a mud and silt bay floor (depth approximately 13 m). Survey sites ( $n = 32$ ) were haphazardly established around Moku o Lo'e, within the Hawai'i Marine Laboratory Refuge, across a range of habitats including reef flats, lagoons and channels (Figure 2). The two sites in the enclosed north lagoon of Moku o Lo'e originally were designated as control sites due to their inaccessibility to *C. mydas*; however, *C. mydas* managed to access this lagoonal area during the unusually high tide levels (up to 34 cm above predicted levels) that occurred in late April 2017 (NOAA National Ocean Service, Moku o Lo'e station 1612480, [www.tidesandcurrents.noaa.gov](http://www.tidesandcurrents.noaa.gov)). Surveys visually estimating benthic composition were conducted on 9 April 2017 in clear, calm conditions from the surface to depths  $<2$  m, with each 5-min observation period generally covering a swath of 25 m in length and 4 m in width (sensu Bahr et al. 2015b, Jokiel et al. 2015). This method has been quantitatively evaluated and produces results

comparable to more laborious techniques; however, some variance between resurveys is to be expected (see Jokiel et al. 2015). Each area was classified as percent benthic composition (estimated in 5% increments) of *G. salicornia*, live coral, rubble and sand using an underwater look box. Turf algae was observed at a single site on the reef flat during the resurvey with an estimated percent cover of 15%. Since we were only interested in *G. salicornia* due to its abundance and multiple observations of grazing by *C. mydas*, we removed this single observation of turf algae from statistical analyses. Resurveys were conducted 30 days later on 9 May 2017 at identical sites with the same observer (Figure 2), locating sites using a Garmin GPSMAP 78s. Since *C. mydas* accessed our two control sites, *G. salicornia* abundance was pooled across all sites and compared between survey dates. A t-test assuming unequal variance was used to determine if there was a significant decline in *G. salicornia* abundance between surveys at sites that contained algae. A t-test was also used to determine changes in the benthic composition of coral, rubble, and sand across sites between surveys. The assumptions of independent observations, normal distribution and homoscedasticity of the residuals were met by the data. Environmental data, including photosynthetically active radiation (PAR), ultraviolet radiation (UV), seawater temperature, precipitation, and wind strength and direction, were monitored continuously throughout the surveying period at an automated weather station located at HIMB on Moku o Lo'e (<http://www.pacioos.hawaii.edu/weather/obs-mokuoloe/>). Average daily environmental parameters during the survey period (9 April – 9 May) were compared to the same time period for the two previous years using a one-way analysis of variance (ANOVA).

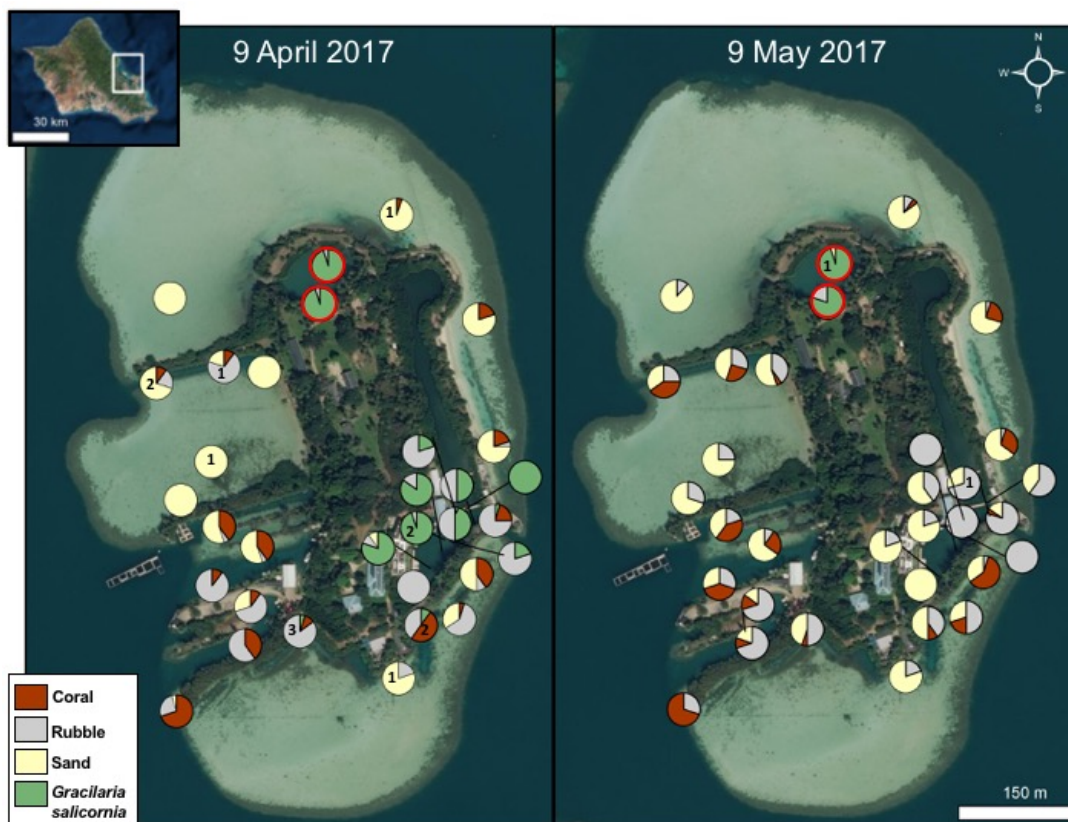


Figure 2. Surveyed sites around Moku o Lo'e, Kāne'ohe Bay, O'ahu, Hawai'i in April (left) and May (right) depicting proportion of substratum classified as coral (brown), rubble (grey), sand (yellow), or *Gracilaria salicornia* (green). Numbers within pie charts indicate number of turtles observed at each site during the survey. Red outlined pie charts denote areas with limited accessibility (only during high tides) to *Chelonia mydas*.

## Results

Significant declines in *G. salicornia* abundance were observed across sites that contained algae in April 2017 (t-test;  $df = 26$ ,  $t = -2.81$ ,  $p = 0.0096$ ) (Table 1, Figure 2). Within 30 days, the mean ( $\pm$  s.e.) percent change in algal cover (relative to initial percent cover) was  $75.0 \pm 13.6\%$  (Table 1). The largest decrease in percent cover (99%) occurred inside the back lagoon of Moku o Lo'e (Figures 2 and 3). Of the two enclosed sites, one had no change in percent cover of *G. salicornia* (95%) during the May survey and the other decreased by 15% (Figure 2). Benthic cover of coral ( $p = 0.8420$ ), sand ( $p = 0.2350$ ), and rubble ( $p = 0.5469$ ) did not significantly change between the surveys across sites (Table 1).

Mean ( $\pm$  s.e.) daily seawater temperatures were significantly higher in 2017 ( $25.90 \pm 0.08^\circ\text{C}$ ) in comparison to 2016 ( $24.76 \pm 0.08^\circ\text{C}$ ) and 2015 ( $24.64 \pm 0.08^\circ\text{C}$ ) (One-way ANOVA  $F_{(2,89)} = 69.85$ ;  $p < 0.0001$ ) (Figures 3 and 4). Mean daily wind speeds were significantly lower in 2017 ( $13.38 \pm 0.90 \text{ km h}^{-1}$ ) compared to previous years ( $21.93 \pm 0.90 \text{ km h}^{-1}$  in 2015;  $19.25 \pm 0.90 \text{ km h}^{-1}$  in 2016) (One-way ANOVA  $F_{(2,89)} = 23.62$ ;  $p < 0.0001$ , Figures 3 and 4). Average daily rainfall was significantly higher in 2017 ( $0.25 \pm 0.05 \text{ mm h}^{-1}$ ) in comparison to 2015 ( $0.02 \pm 0.05 \text{ mm h}^{-1}$ ) (One-way ANOVA  $F_{(2,89)} = 4.55$ ;  $p = 0.0132$ ) (Figures 3 and 4). UV was lower in 2016 ( $0.057 \pm 0.003 \text{ W m}^{-2} \text{ h}^{-1}$ ) and 2017 ( $0.057 \pm 0.003 \text{ W m}^{-2} \text{ h}^{-1}$ ) compared to 2015 ( $0.072 \pm 0.003 \text{ W m}^{-2} \text{ h}^{-1}$ ) (One-way ANOVA  $F_{(2,89)} = 11.56$ ;  $p < 0.0001$ , Figures 3 and 4). Lastly, there were no significant differences in PAR flux across years (One-way ANOVA  $F_{(2,89)} = 1.28$ ;  $p = 0.2833$ ) (Figures 3 and 4).

Table 1. Benthic cover (%) averaged across sites ( $n=32$ ), and averaged across sites initially with ( $n=14$ ) and without ( $n=18$ ) *Gracilaria salicornia*.

Benthic Cover (%)	Average across sites $n=32$		Sites initially with algae $n=14$		Sites not initially with algae $n=18$	
	April 9 2017	May 9 2017	April 9 2017	May 9 2017	April 9 2017	May 9 2017
	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE
<i>Gracilaria salicornia</i>	22.0 $\pm$ 6.4	5.5 $\pm$ 3.8	51.0 $\pm$ 11.0	13.0 $\pm$ 8.5	0 $\pm$ 0	0 $\pm$ 0
Coral	13.0 $\pm$ 3.0	13.0 $\pm$ 3.0	6.0 $\pm$ 4.0	3.0 $\pm$ 2.0	18.0 $\pm$ 5.0	22.0 $\pm$ 5.0
Rubble	32.2 $\pm$ 5.9	37.0 $\pm$ 5.3	40.0 $\pm$ 8.7	53.5 $\pm$ 8.8	26.1 $\pm$ 8.0	24.2 $\pm$ 4.8
Sand	33.1 $\pm$ 7.0	43.6 $\pm$ 5.3	3.1 $\pm$ 2.5	31.1 $\pm$ 7.8	56.4 $\pm$ 9.0	53.3 $\pm$ 6.4

## Discussion

The persistent, alien invasive alga *Gracilaria salicornia* has dominated the protected waters surrounding Moku o Lo'e, Kāne'ohe Bay, Hawai'i since its introduction in 1978. During a short 30-day period (April – May 2017), the overall abundance of *G. salicornia* suddenly declined from 51% to 13% and some sites had a complete disappearance of this invasive alga. Environmental conditions remained in normal seasonal conditions for Kāne'ohe Bay; however, seawater conditions were warmer, calmer, and experienced more rainfall compared to the same time period in the two previous years (2015 and 2016) (Figures 3 and 4). Regardless, the environmental parameters experienced during the 30-day survey period remained within known tolerance thresholds for *G. salicornia*. Previous studies have revealed *G. salicornia* to be very resistant to extreme salinity (0-50 ppt) and temperature variations (8-37°C) (Smith et al. 2004, Phooprang et al. 2007) as well as survive hour-long periods of desiccation (Beach et al. 1997, Smith et al. 2004, Phooprang et al. 2007, Martinez et al. 2012).

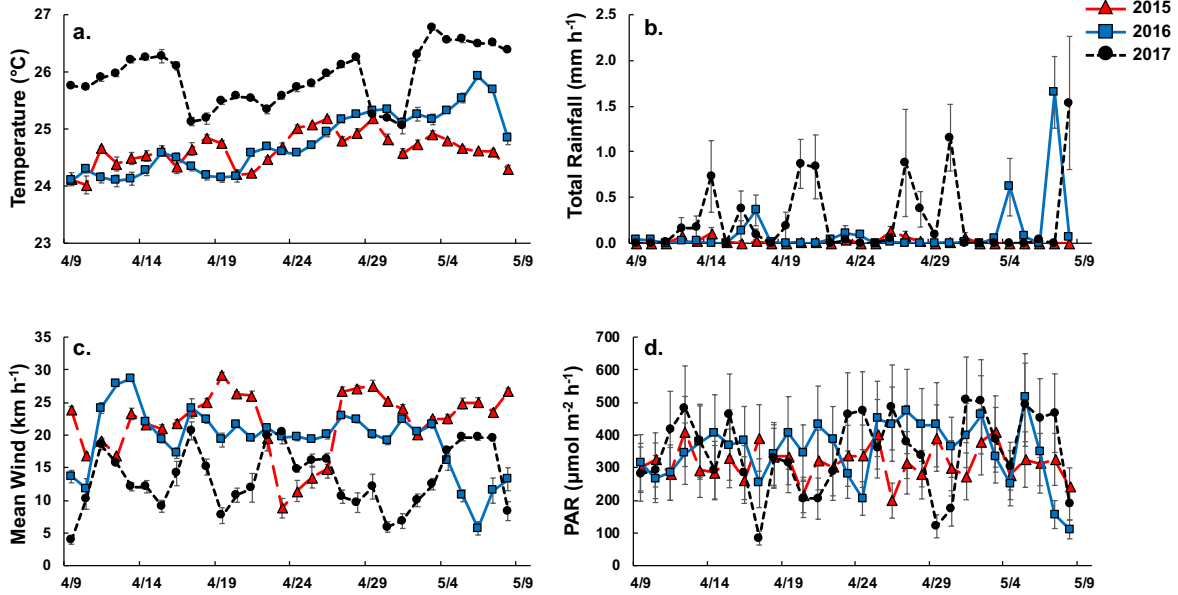


Figure 3. Mean hourly temperatures (°C) (a.), total rainfall (mm h<sup>-1</sup>) (b.), wind (km h<sup>-1</sup>) (c.), and PAR (μmol photons m<sup>-2</sup>) (d.) in 2015 (red triangle), 2016 (blue square), and 2017 (black circle). Data was obtained from Hawai‘i Institute of Marine Biology Weather Station (<http://www.pacioos.hawaii.edu/weather/obs-mokuoloe/>).

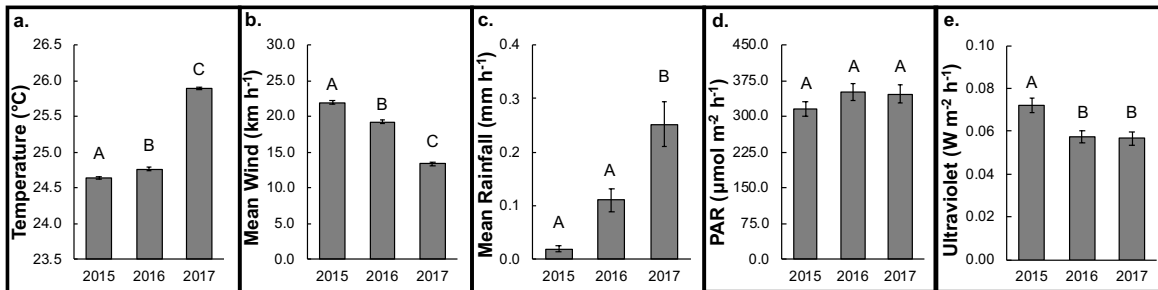


Figure 4. Environmental characteristics of mean daily temperature (°C) (a.), wind (km h<sup>-1</sup>) (b.), rainfall (mm h<sup>-1</sup>) (c.), PAR (μmol photons m<sup>-2</sup>) (d.), and ultraviolet radiation (d.) between 9 April – 9 May in 2015, 2016, and 2017. Levels not connected by the same letter are significantly different at p < 0.05. Data was obtained from Hawai‘i Institute of Marine Biology Weather Station (<http://www.pacioos.hawaii.edu/weather/obs-mokuoloe/>).

We hypothesize that the sudden decline in *G. salicornia* around Moku o Lo'e, Kāne'ōhe Bay, was likely linked to increased grazing pressure of the Hawaiian green turtle, *Chelonia mydas*. The population of *C. mydas* has increased dramatically since the state of Hawai'i banned commercial harvest in 1975 and protection was granted under the U.S. Endangered Species Act in 1978 (Balazs et al. 2015, Seminoff et al. 2015). Since 1973, annual monitoring and tagging of adult female turtles at the colonial nesting site of French Frigate Shoals in the Northwestern Hawaiian Islands, which accounts for >90% of all nesting within the Hawaiian Archipelago (Balazs 1976), has shown the Hawaiian population of *C. mydas* is increasing at a robust rate (Balazs et al. 2015, Seminoff et al. 2015). Although quantitative population estimates for Kāne'ōhe Bay are unavailable, satellite tracking of *C. mydas* from French Frigate Shoals revealed Kāne'ōhe Bay as an important foraging destination (Balazs et al. 2017), thereby suggesting an increase in the local population of *C. mydas* within the bay. It has been suggested that this population may be approaching its foraging habitat carrying capacity (i.e., foraging habitat is not sufficient and/or nutritionally sustainable for 'normal' somatic growth) (Balazs & Chaloupka 2004, Wabnitz et al. 2010), because these turtles have been documented feeding on non-native algae (Russell & Balazs 2009, 2015) and expanding their feeding grounds into new habitats (Clarke et al. 2012). A 36-year study (1976-2012) in Kāne'ōhe Bay revealed a shift in the diet of *C. mydas* from native algal species (e.g., *Amansia glomerata*, *Codium* spp., *Pterocladia capillacea*, *Ulva fasciata*) and a native seagrass (*Halophila hawaiiiana*) to abundant non-native species (*Acanthophora spicifera* 64%; *Hypnea musciformis*, 41.4%; *G. salicornia*, 37%) (Russell & Balazs 2000, 2009, 2015, Russell et al. 2003). *Gracilaria salicornia* was first detected in their diet in 1991, 13 years following this algal introduction, and has since comprised at least 10% of their diet (Russell & Balazs 2009, 2015). Additionally, *C. mydas* on the islands of Hawai'i and Moloka'i have been recently observed foraging on terrestrial, salt-tolerant turfgrass (*Paspalum vaginatum*) during high tides (McDermid et al. 2015) and on fallen tree leaves (*Heliotropium foertherianum*) in coastal waters off Hawai'i Island (McDermid et al. 2018).

The Hawai'i Marine Laboratory Refuge surrounding Moku o Lo'e has been a no-take marine reserve for 50 years and contains a high diversity of abundant, herbivorous reef fishes (Stamoulis et al. 2017). If herbivorous fish grazing suppresses macroalgal proliferation, then macroalgae abundance should be inversely related to herbivore biomass (Stamoulis et al. 2017). Yet, prior to this study *G. salicornia* showed higher abundance in the marine reserve compared to similar adjacent patch reefs that lack protection from fishing, and had no association with herbivorous fish biomass, size distribution, or assemblage structure despite being the second most dominant algal species in herbivorous fish diet (Stamoulis et al. 2017). Further, herbivorous reef fish have small home ranges and reside predominantly within the marine reserve (Bierwagen et al. 2017, Stamoulis et al. 2017). This may be partly explained because the Hawai'i Marine Laboratory Refuge encompasses a fringing reef surrounded by relatively deep water, which forms a natural boundary that reef fishes seldom cross (Marshall et al. 2011). Therefore, the marine reserve consistently hosts a large, diverse population of herbivorous fishes. The previous dominance of *G. salicornia* within the Hawai'i Marine Laboratory Refuge despite the presence of abundant herbivorous fish populations supports our conclusion that the sudden increased grazing pressure by *C. mydas* was the primary driver of the rapid decline (30 days) of this persistent invasive macroalgae. This conclusion is further supported by the high percent cover of *G. salicornia* in enclosed lagoons around Moku o Lo'e that were permanently or temporally inaccessible to *C. mydas* but remained open to reef fishes and other herbivorous species during the surveying period. For example, two lagoons (954 m<sup>2</sup> and 200 m<sup>2</sup>) are enclosed with fences (see Figure 5) that permit entry to smaller animals (e.g., reef fishes), but are not accessible to *C. mydas*, and are monitored daily by HIMB researchers. These two lagoons maintained a mean percent cover of *G. salicornia* of 78.5% and 31.3%, respectively (D. Coffey, pers. comm., 2017).



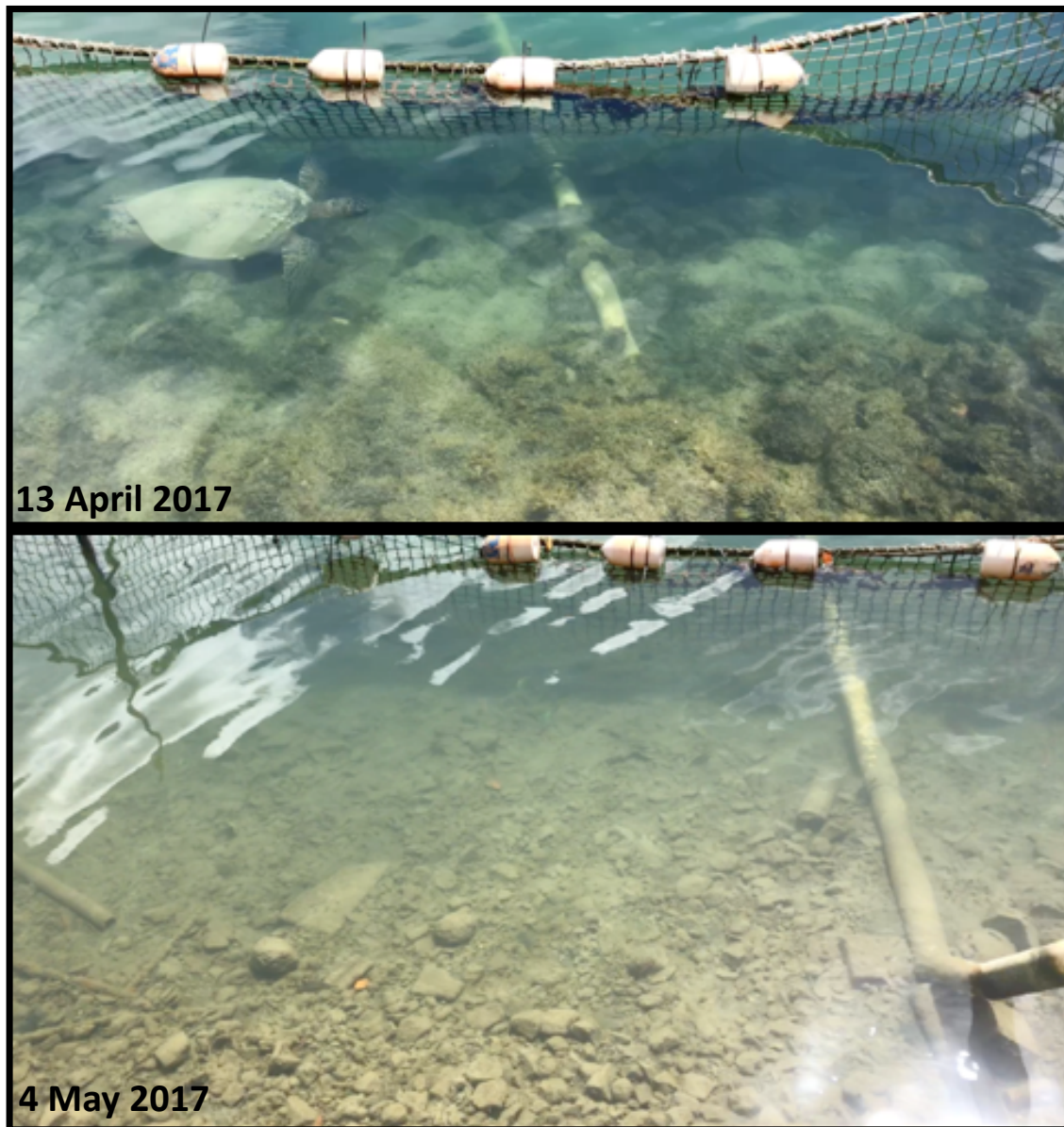


Figure 5. Back lagoon of Moku o Lo'e, Kāne'ohe Bay, O'ahu, Hawai'i adjacent to a fenced enclosure on 13 April 2017 (top) and same area 21 days later on 4 May 2017 (bottom). Photo by KD Bahr.

Prior to this study, *G. salicornia* was found in all habitats surrounding Moku o Lo'e and achieved its highest abundance on reef flats (Bierwagen et al. 2017, Hawai'i Division of Aquatic Resources 2009, Stamoulis et al. 2017); however, we observed no *G. salicornia* on reef flats during our surveys. Grazing rates by herbivorous fish differ among habitats in Kāne'ohe Bay with the highest grazing pressure occurring on the reef slope and crest near the edge of patch reefs and decreases with distance towards the center of the reef flat (Bierwagen et al. 2017, Conklin 2007). The reef slope and crest are structurally complex habitats that provide refuge from predation (Madin et al. 2011, Stimson et al. 2001) and the lower grazing pressure in open reef flat habitats suggests reef fishes avoid foraging far from shelter (Bierwagen et al. 2017, Stamoulis et al. 2017). In contrast,

*C. mydas* is a large, roving herbivore (Brill et al. 1995) that moves freely in and out of the marine reserve and exploits all foraging habitats (reef flats, lagoons and channels) within it. The sudden and rapid decline of *G. salicornia* on reef flats and lower grazing pressure by herbivorous fish suggest grazing by *C. mydas* prior to the survey period, particularly since several *C. mydas* were observed during the initial April survey in the reef flat at high tide when this habitat is most accessible.

Research and management efforts by the State of Hawai'i Division of Aquatic Resources and The Nature Conservancy have been ongoing since 1999 to control the distribution and limit the abundance of *G. salicornia* and other invasive species in Kāneʻohe Bay using manual and biocontrol (e.g., *Tripnustes gratilla*) measures (Stimson et al. 2007, Neilson et al. 2018). In contrast, *C. mydas* was potentially able to clear an average of 75% of *G. salicornia* within 30 days in the waters surrounding Moku o Loʻe. The intensive grazing pressure by *C. mydas* may reduce the abundance of *G. salicornia* to levels where other herbivorous species will be able to control further growth (Conklin 2007). However, unless grazing intensity remains high across all reef habitats, fragmentation (Smith et al. 2002) through foraging and egestion of potentially viable fragments (Bierwagen et al. 2017) may continue to facilitate the propagation of this invasive macroalga.

The environmental conditions around Moku o Loʻe within tolerance thresholds for *G. salicornia*, dominance of *G. salicornia* despite the presence of abundant herbivorous fish populations, and multiple observations of physical grazing by *C. mydas* on *G. salicornia* support our conclusion that *C. mydas* was the primary driver of the rapid decline of a persistent invasive macroalgae within the Hawai'i Marine Laboratory Refuge. Within a week following the May survey, *C. mydas* were no longer observed in the waters around Moku o Loʻe and have been observed utilizing new habitats in the south end of Kāneʻohe Bay (e.g., Nuʻupia Ponds) that have high densities of *G. salicornia*. The primary drivers of this sudden and substantial surge of foraging by *C. mydas* targeting *G. salicornia* remains unknown. Therefore, investigations are continuing in the Kāneʻohe Bay region to track the feeding behavior of *C. mydas* and possible expansions into previously unused or underused habitats.

The Hawai'i Marine Laboratory Refuge has been established for 50 years, yet the invasive *G. salicornia* has dominated extensive areas of the reef since its introduction despite the presence of high herbivore richness and diversity. The results of this study could magnify the importance of the species-specific impacts of the large, roving herbivore *C. mydas*. Identifying the functional role of specific herbivore species as well as the role of herbivore richness and diversity in driving the community dynamics of coral reef ecosystems has become increasingly important (Bellwood et al. 2003, Burkepile & Hay 2008, 2010). Smaller herbivorous fish within the marine reserve such as bluespine unicornfish, *Naso unicornis*, preferentially consume the apices of *G. salicornia* mats before utilizing the thicker portions (Bierwagen et al. 2017); whereas, *C. mydas* were observed consuming entire mats. These findings highlight the need for high herbivore functional diversity with species-specific differences in dietary preference and feeding strategy, which should more efficiently suppress the growth and spread of any given macroalga and indirectly benefit coral reefs (Lubchenco & Gaines 1981, Duffy 2002, Burkepile & Hay 2010). The disturbance in algal cover by *C. mydas* can also alter the successional trajectory of the coral reef community (Hixon & Brostoff 1996), especially in areas that underwent a complete shift in benthic habitat composition. Ongoing management efforts to limit the distribution and abundance of invasive algal species must consider the key role *C. mydas* may play in Hawaiian coral reef ecosystems.



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### References

- Bahr, K.D., Jokiel, P.L., R.J. Toonen. 2015a. The unnatural history of Kāne‘ohe Bay: coral reef resilience in the face of centuries of anthropogenic impacts. *PeerJ* 3:e950.
- Bahr, K.D., Jokiel, P.L., K.S. Rodgers. 2015b. The 2014 coral bleaching and freshwater flood events in Kāne‘ohe Bay, Hawai‘i. *PeerJ* 3:e1136.
- Balazs, G.H. 1976. Green turtle migrations in the Hawaiian Archipelago. *Biological Conservation* 9(2):125-140.
- Balazs, G.H. & M. Chaloupka. 2004. Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian Archipelago. *Marine Biology* 145:1043-1059.
- Balazs, G.H., Parker, D.M., M.R. Rice. 2017. Ocean pathways and residential foraging locations for satellite tracked green turtle breeding at French Frigate Shoals in the Hawaiian Islands. *Micronesica* 2017-04:1-19.
- Balazs, G.H., Van Houtan, K.S., Hargrove, S.A., Brunson, S.M., S.K. Murakawa. 2015. A review of the demographic features of Hawaiian green turtles (*Chelonia mydas*). *Chelonian Conservation and Biology* 14:119-129.
- Beach, K.S., Borgeas, H.B., Nishimura, N.J., C.M. Smith. 1997. In vivo absorbance spectra and the ecophysiology of reef macroalgae. *Coral Reefs* 16(1):21-28.
- Bellwood, D.R., A.S. Hoey, & J.H. Choat. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* 6:281285.
- Bierwagen, S.L., Price, D.K., Pack, A.A., C.G. Meyer. 2017. Bluespine unicornfish (*Naso unicornis*) are both natural control agents and mobile vectors for invasive algae in a Hawaiian Marine Reserve. *Marine Biology* 164(1):25.
- Brill, R.W., Balazs, G.H., Holland, K.N., Chang, R.K., Sullivan, S., J.C. George. 1995. Daily movements, habitat use, and submergence intervals of normal and tumor-bearing juvenile green turtles (*Chelonia mydas* L.) within a foraging area in the Hawaiian islands. *Journal of Experimental Marine Biology and Ecology* 185(2):203-218.
- Burkepile, D.E., & M.E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences* 105(42):16201-16206.
- Burkepile, D.E., & M.E. Hay. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS ONE* 5(1):e8963.
- Clarke, D.L., Balazs, G., S. Hargrove. 2012. Hawaiian green turtles up and down the Anahulu River. In: Jones TT, Wallace BP (eds) 31st Annual Symposium on Sea Turtle Biology and Conservation, San Diego, CA, USA, 2011. NOAA Technical Memorandum, p 322.
- Conklin, E.J. 2007. The influence of preferential foraging, alien algal species, and predation risk on the interaction between herbivorous fishes and reef macroalgae. Ph.D. thesis, University of Hawai‘i.
- Duffy, J.E. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos* 99(2):201-219.
- Glenn, E.P., Doty, M.S. 1990. Growth of the seaweeds *Kappaphycus alvarezii*, *K. striatum* and *Euचेuma denticulatum* as affected by environment in Hawai‘i. *Aquaculture* 84:245-255

- Hawaii Division of Aquatic Resources. 2009. Aquatic Invasive Species Summary Report 2008-2009. Available at <http://dlnr.hawaii.gov/ais/files/2014/02/AIS-Annual-Report-2008-2009.pdf>
- Hixon, M.A., & W.N. Brostoff. 1996. Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecological Monographs* 66(1):67-90.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskij, N., Pratchett, M.S., Steneck, R.S., Willis, B.. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17(4):360-365.
- Jokiel, P.L., Rodgers, K.S., Brown, E.K., Kenyon, J.C., Aeby, G., Smith, W.R., F. Farrell. 2015. Comparison of methods used to estimate coral cover in the Hawaiian Islands *PeerJ* 3:e954.
- Lubchenco, J., & S.D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* 12(1): 405-437.
- Madin, E.M., Madin, J.S., D.J. Booth. 2011. Landscape of fear visible from space. *Scientific Reports*, 1, p.14.
- Marshall, A., Mills, J.S., Rhodes, K.L., J. McIlwain. 2011. Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve. *Coral Reefs* 30: 631-642.
- Martinez, J.A., Smith, C.M., R.H. Richmond. 2012. Invasive algal mats degrade coral reef physical habitat quality. *Estuarine, Coastal and Shelf Science*, 99: 42-49.
- McDermid, K.J., Lefebvre, J.A. and G.H. Balazs. 2015. Nonnative seashore *Paspalum*, *Paspalum vaginatum* (Poaceae), consumed by Hawaiian green sea turtles (*Chelonia mydas*): Evidence for nutritional benefits. *Pacific Science* 69: 48-57.
- McDermid, K.J., Jha, R., Rice, M.R., G.H. Balazs. 2018. Of turtles and trees: Nutritional analysis of tree heliotrope (*Heliotropium foertherianum*) leaves consumed by green turtles (*Chelonia mydas*) in Hawai'i. *Micronesica* 2018-02:1-11.
- Mumby, P.J. 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28:761-773.
- Neilson, B.J., C.B. Wall, F.T. Mancini, & C.A. Gewecke. 2018. Herbivore biocontrol and manual removal successfully reduce invasive macroalgae on coral reefs. *PeerJ* 6:e26796.
- Phooprong, S., Ogawa, H., K. Hayashizaki. 2007. Photosynthetic and respiratory responses of *Gracilaria salicornia* (C. Ag.) Dawson (Gracilariales, Rhodophyta) from Thailand and Japan. *Journal of applied phycology*, 19(6):795.
- Rodgers, K.S., E.F. Cox. 1999. The rate of spread of the introduced Rhodophytes, *Kappaphycus alvarezii*, *Kappaphycus striatum*, and *Gracilaria salicornia* and their present distributions in Kāneʻohe Bay, Oʻahu, Hawai'i. *Pacific Science* 53:232-241.
- Russell, D.J. 1992. The ecological invasion of Hawaiian reefs by two marine red algae, *Acanthophora spicifera* (Vahl) Boerg. and *Hypnea musciformis* (Wulfen) J. Ag., and their association with two native species, *Laurencia nidifica*. In J. Ag. and *Hypnea cervicornis* J. Ag. ICES Marine Science Symposium (Vol. 194, pp. 110-125).
- Russell, D.J., G.H. Balazs. 2000. Identification manual for dietary vegetation of the Hawaiian green turtle *Chelonia mydas*. NOAA technical memorandum NMFS; NOAA-TM-NMFS-SWFSC ; 294.
- Russell, D.J., G.H. Balazs. 2009. Dietary shifts by green turtles (*Chelonia mydas*) in the Kāneʻohe Bay region of the Hawaiian Islands: A 28-year study. *Pacific Science* 63:181-192.
- Russell DJ, Balazs GH (2015) Increased use of non-native algae species in the diet of the green turtle (*Chelonia mydas*) in a primary pasture ecosystem in Hawai'i. *Aquatic Ecosystem Health & Management* 18:342-346.
- Russell, D.J., Balazs, G.H., Phillips, R.C., A.K.H. Kam. 2003. Discovery of the sea grass *Halophila decipiens* (Hydrocharitaceae) in the diet of the Hawaiian green turtle, *Chelonia mydas*. *Pacific Science* 57:393-397.
- Seminoff, J.A., Allen, C.D., Balazs, G.H., Dutton, P.H., Eguchi, T., Haas, H., Hargrove, S.A., Jensen, M., Klemm, D.L., Lauritsen, A.M., S.L., MacPherson. 2015. Status review of the green turtle (*Chelonia mydas*) under the Endangered Species Act. NOAA Tech. Memor. NOAA-NMFS-SWFSC-539.

- Smith, J.E., Hunter, C.L., Conklin, E.J., Most, R., Sauvage, T., Squair, C. and Smith, C.M., 2004. Ecology of the invasive red alga *Gracilaria salicornia* (Rhodophyta) on O'ahu, Hawai'i. *Pacific Science* 58:325-343.
- Smith, J.E., Hunter, C.L., C.M. Smith. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. *Pacific Science* 56:299-315.
- Stamoulis, K.A., Friedlander, A.M., Meyer, C.G., Fernandez-Silva, I., R.J. Toonen. 2017. Coral reef grazer-benthos dynamics complicated by invasive algae in a small marine reserve. *Scientific Reports* 7:43819.
- Stimson, J., Cunha, T., J. Philippoff. 2007. Food preferences and related behavior of the browsing sea urchin *Tripneustes gratilla* (Linnaeus) and its potential for use as a biological control agent. *Marine Biology* 151:1761-1772.
- Stimson, J., Larned, S.T., E. Conklin. 2001. Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawai'i. *Coral Reefs* 19:343-357.
- Wabnitz, C.C., Balazs, G., Beavers, S., Bjorndal, K.A., Bolten, A.B., Christensen, V., Hargrove, S., D. Pauly. 2010. Ecosystem structure and processes at Kaloko Honokohau, focusing on the role of herbivores, including the green sea turtle *Chelonia mydas*, in reef resilience. *Marine Ecology Progress Series* 420:27-44.

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