

1 **Recent declines in invasive macroalgae on coral reefs in Kāneʻohe Bay, Hawaiʻi: evidence**
2 **for phase shift reversals.**

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12

13 **Abstract**

14 The non-native red algae *Eucheuma denticulatum* (Burman) Collins and Hervey and
15 *Gracilaria salicornia* C. Ag. were spatially dominant components of the reef flat communities
16 of Kāneʻohe Bay, Oʻahu, Hawaiʻi for approximately 20 years. In 2014 and 2015, *E.*
17 *denticulatum* and *G. salicornia* abundance declined abruptly on Kāneʻohe Bay reefs,
18 independent of efforts to control *E. denticulatum* through manual removal and stocking
19 reefs with hatchery-raised herbivorous sea urchins. The proximate cause of these declines
20 appears to be grazing by herbivorous fishes, but the declines also coincided with two
21 successive summers of high water temperatures. Field experiments with *E. denticulatum* in
22 the fall of 2014 showed that rates of tissue removal by herbivorous fishes exceeded growth
23 rates on the reef flats and reef slopes of 13 patch reefs.

24 One of two long-term time-series of the abundance of herbivorous fishes at Kāneʻohe Bay
25 patch and fringing reefs sites shows an increase in the numbers of herbivorous fishes from
26 2007 through 2013 on reefs where *E. denticulatum* and *G. salicornia* declined in cover. The

27 second record from a different site in Kāneʻohe Bay does not show a significant increase in
28 herbivorous fish biomass over the same time period.

29 High water temperatures may have acted synergistically with grazing to bring about the
30 decline of *E. denticulatum*. During the summers of 2014 and 2015, surface water
31 temperatures in Kāneʻohe Bay exceeded 30°C; sufficiently high to cause coral bleaching.
32 Laboratory studies of *E. denticulatum* thalli held at a range of water temperatures showed
33 that growth rates decreased at temperatures above 28-29 °C. This decrease may have
34 increased the apparent loss of tissue due to herbivory. Comparable responses to variation in
35 water temperature were not observed in *G. salicornia*.

36 The recent decline in *E. denticulatum* and *G. salicornia* abundance occurred approximately
37 40 years after their introduction to Kāneʻohe Bay and 20 years after they became
38 widespread and competitive with corals. The declines of these spatially dominant algae
39 constitute a phase reversal, and the first reversal that has been attributed in large part to
40 naturally occurring grazing by herbivorous fish.

41

42 **1 Introduction**

43 On most coral reefs, macroalgal cover is minimal in zones of active coral growth; when
44 macroalgae are abundant in these zones, it is generally because a phase shift has occurred.
45 The term phase shift refers to a large-scale, abrupt and persistent transition in ecological
46 structure, dynamics and/or function (Hughes 1994, de Young et al. 2008, Möllmann et al.
47 2015). Shifts from coral to macroalgal dominance are among the most frequently reported
48 phase shifts in marine ecosystems (e.g., Smith et al. 1981, Done 1992, Hughes 1994, Connell
49 1997, McClanahan et al. 2001, Ledlie et al. 2007, Maliao et al. 2008, Cheal 2010). A wide
50 range of natural and anthropogenic drivers of coral-macroalgal phase shifts have been
51 identified or proposed, including disease outbreaks in coral and herbivore populations,
52 hurricanes, tsunamis, coral bleaching, depletion of herbivores through overfishing,
53 eutrophication and human-mediated biological invasions. These drivers often act
54 simultaneously or sequentially, which can increase susceptibility to or persistence of phase
55 shifts (de Young et al. 2008).

56 Some researchers have speculated that phase shifts from coral to -macroalgae are
57 irreversible (Scheffer et al. 2001, Rogers and Miller 2006, Ledlie et al. 2007, Hughes et al.
58 2011, Mumby et al. 2013), due to low resilience and strong hysteresis (i.e., resistance to
59 ecological recovery after environmental conditions have returned to a pre-degradation
60 state). However, data from long-term monitoring at sites of historical phase shifts may alter
61 the irreversibility view. Several cases of reversals in coral-macroalgal phase shifts have been
62 reported. Most of these reversals occurred on Caribbean reefs, where recovery of grazing
63 urchin populations to pre-phase-shift levels coincided with large-scale reductions in
64 macroalgal cover and a return to coral dominance (e.g., Edmunds and Carpenter 2001,
65 Miller et al. 2003, Idjadi et al. 2006). An additional phase-shift reversal has been reported
66 from Hawai'i (Stimson and Conklin 2008).

67 An early example of a coral-macroalgal phase shift was the proliferation of the green
68 macroalga *Dictyosphaeria cavernosa* (Forsskål) Børgesen in Kāne'ōhe Bay, O'ahu, Hawai'i.
69 *D. cavernosa* began replacing reef building corals on the patch and fringing reefs of
70 Kāne'ōhe Bay in the late 1960s, presumably in response to nutrient enrichment from
71 sewage discharges and direct coral mortality caused by freshwater inflows (Banner 1968,
72 Banner and Bailey 1970, Smith et al. 1981). Despite the diversion of sewage discharges from
73 Kāne'ōhe Bay in 1977-1978, *D. cavernosa* persisted as a spatially dominant component of
74 reef slopes throughout the bay for the next 30 years (Stimson & Conklin 2008). In 2006, *D.*
75 *cavernosa* in Kāne'ōhe Bay underwent a rapid decline in abundance; maximum *D. cavernosa*
76 cover on previously infested reefs decreased to < 1% over a 5-mo period. The decline in *D.*
77 *cavernosa* appeared to be triggered by light limitation during an extended period of high
78 turbidity and high cloud cover, which coincided with the season of slowest growth in the
79 annual *D. cavernosa* growth cycle (Stimson & Conklin 2008). The lack of regrowth of *D.*
80 *cavernosa* following the rapid decline may have been prevented because nutrient
81 concentrations in the bay were lower than when the alga became abundant in the 1960s; *D.*
82 *cavernosa* growth in Kāne'ōhe Bay is strongly nitrogen-limited and dissolved nitrogen
83 concentrations in the bay water column have decreased substantially in the last 40 years
84 (Larned and Stimson 1996, Stimson 2015). The decline in *D. cavernosa* was followed by a
85 rapid increase in live coral cover on reef slopes (Stimson 2017); these two events comprised
86 a major phase-shift reversal.

87 In the early 1970's, several species of economically important red macroalgae were
88 intentionally introduced to southern Kāneʻohe Bay for aquaculture trials. By the early 2000's
89 established populations of some of these species were present in all sectors of the bay,
90 where they overgrew and killed reef-flat corals (Rodgers and Cox 1999, Smith et al. 2004,
91 Conklin and Smith 2005), causing a second coral-macroalgal phase shift that persisted until
92 the initiation of the present study in 2014. The red macroalgae that contributed to that
93 phase shift were dominated by two species, *Eucheuma denticulatum* and *Gracilaria*
94 *salicornia*.

95 In this paper, we have assembled records of the extent and abundance of *E. denticulatum*
96 and *G. salicornia* from multiple unpublished sources. Collectively, these records provide
97 evidence of a second phase shift reversal in Kāneʻohe Bay, approximately 10 years after the
98 reversal associated with the decline of *D. cavernosa*. Detection of such phase-shift reversals
99 requires long term monitoring of coral reef communities that have long-term resilience to
100 the effects of macroalgal proliferations (Hughes et al. 2010, Graham et al. 2013). Here, long-
101 term resilience refers to the potential for recovery from a prolonged degraded state, as
102 distinct from initial resistance to degradation (Nyström et al. 2008). If long-term resilience
103 applies to many coral reefs, then the emerging view that coral-macroalgal phase shifts are
104 irreversible should be reevaluated. In addition to documenting the second phase-shift
105 reversal in Kāneʻohe Bay, we present the results of experiments designed to test the effect
106 of grazing and high sea-water temperatures as potential drivers of the second phase-shift
107 reversal.

108

109 **1.1 Introduction, expansion and ecology of *Eucheuma denticulatum* and *Gracilaria*** 110 ***salicornia* in Kāneʻohe Bay**

111 Macroalgae in the genera *Eucheuma* and *Kappaphycus* are the principal sources of the food
112 additive kappa-carrageenan, and are raised in marine aquaculture systems in tropical and
113 subtropical regions within and outside of their native ranges (Pickering et al. 2007, Bindu
114 and Levine 2011). Established populations of non-native *Eucheuma* and *Kappaphycus* have
115 been observed on coral reefs adjacent to aquaculture facilities in India and South and
116 Central America; the presumed sources of these populations are spores or thallus fragments

117 that drift out of the facilities (Barrios 2005, Chandrasekaran et al. 2008, Sellers et al. 2015).
118 The same process of intentional introduction, propagule dispersal and establishment on
119 adjacent reefs may apply to the establishment of *Eucheuma* and *Kappaphycus* species in
120 Kāneʻohe Bay. From 1970 to 1976, thalli from the putative species *Eucheuma denticulatum*,
121 *Kappaphycus striatum* (formerly *Eucheuma striatum*) and *Kappaphycus alvarezii* were
122 introduced from the Philippines and Pohnpei to southern Kāneʻohe Bay for aquaculture
123 trials (Russell 1983, Russell and Balazs 2009). The main site of the trials was on the fringing
124 reef flat of Moku o Loe in the southern bay (Fig. 1), where unattached thalli of both species
125 were grown in mesh pens. Visual surveys carried out between 1976 and 2002 documented
126 the subsequent expansions of the *Eucheuma* and *Kappaphycus* ranges in Kāneʻohe Bay.
127 Results of the first survey in 1976 indicated that *Kappaphycus striatum* (as '*Eucheuma*
128 *striatum*') thalli had drifted down the Moku o Loe reef slope to the bay bottom, but not to
129 shallow habitats on other patch and fringing reefs (Russell 1983). In the early 1980s, thalli
130 identified as *Eucheuma spinosum* (possibly equivalent to *E. denticulatum*) were observed on
131 a reef flat adjacent to Moku o Loe (Morrissey 1985). In 1996, taxa identified as *Kappaphycus*
132 *striatum* and *Kappaphycus alvarezii* were observed on most patch and fringing reef flats in
133 the south and central portions of Kāneʻohe Bay, up to 6 km from Moku o Loe (Rodgers and
134 Cox 1999). In repeated surveys in 1999 and 2002, *Eucheuma* and *Kappaphycus* (as
135 "*Kappaphycus* spp.") were observed on reef flats throughout Kāneʻohe Bay, including the
136 northern-most fringing reef that extends out of the bay to the outer coast (Conklin and
137 Smith 2005).

138 As indicated by the shifting terminology used in the surveys cited above, the taxonomic
139 identities of *Eucheuma* and *Kappaphycus* species in Hawaiʻi have changed several times in
140 the last 40 years. Field identifications have varied between studies due to the taxonomic
141 changes and to the morphological plasticity of these taxa. Genetic analyses have since
142 confirmed the presence of two taxa in Kāneʻohe Bay, *Eucheuma* clade E (i.e., *E.*
143 *denticulatum*) and *Kappaphycus* clade B (Conklin et al. 2009). The *Eucheuma* taxon used for
144 experiments in the current study corresponds to *E. denticulatum*. The current study also
145 includes assessments of survey data collected by multiple researchers prior to and after
146 publication of the genetic analyses (Conklin et al. 2009). For consistency, we refer to the

147 taxa in all pre-2014 studies as *Eucheuma/Kappaphycus*. The taxon in post-2014 surveys and
148 field and laboratory experiments is referred to as *E. denticulatum*.

149 Fertile *E. denticulatum* thalli have been reported from Kāneʻohe Bay (Conklin et al. 2009),
150 but propagation and dispersal appear to be dominated by vegetative fragments. These
151 fragments settle and grow to form interwoven mats of branched thalli. Until the current
152 study, *E. denticulatum* occurred on reef flats over a wide exposure range in Kāneʻohe Bay,
153 from the high-energy barrier reef and northern fringing reef to low-energy reefs in the lee of
154 the barrier reef. Persistence on high-energy reef flats was facilitated by branch growth into
155 reef interstices and attachment to coral and limestone substrata (Conklin and Smith 2005).
156 On low-energy reefs, detached thalli also accumulated in gaps between coral heads, in sand
157 pockets between corals and on reef slopes (Conklin and Smith 2005, Stimson 2013). The
158 propensity of *E. denticulatum* to overgrow and kill live corals on Kāneʻohe Bay reef flats led
159 to the initiation of a control program in 2005. The control program initially focused on
160 manual removal of *E. denticulatum* from selected reefs; manual removal was combined with
161 biological control based on hatchery-raised sea urchins in 2010 (Pala 2008, Westbrook et al.
162 2015).

163 *Gracilaria salicornia* was first introduced to Kāneʻohe Bay for aquaculture trials in 1978; the
164 point of introduction was a fringing reef of Moku o Loe (Rodgers and Cox 1999). In contrast
165 to *E. denticulatum*, field identifications of *G. salicornia* are reliable and the taxonomy has
166 been stable throughout its history in Kāneʻohe Bay (Abbott 1985, Sherwood et al. 2010).
167 Visual surveys of *G. salicornia* on Kāneʻohe Bay reefs did not commence until 1996. At that
168 time, *G. salicornia* was present on most of the fringing and patch reef flats in the southern
169 bay, and on several reef flats in the central bay (Rodgers and Cox 1999). By 1999, the *G.*
170 *salicornia* range had expanded in the central bay and in 2002, *G. salicornia* was observed on
171 the northern fringing reef (Conklin and Smith 2005). By 2009, the *G. salicornia* range
172 extended across Kāneʻohe Bay (Hawaiʻi State Division of Aquatic Resources (HDAR),
173 unpublished survey data).

174 *G. salicornia* is restricted to moderate to low energy environments in Kāneʻohe Bay,
175 including intertidal zones. Reproduction of the species in Hawaiʻi appears to be limited to
176 vegetative fragmentation (Nishimoto 2000, Smith et al. 2002). Fragments settle and attach

177 to limestone substrates with small holdfasts, then grow to form mats of densely interwoven
178 thalli; mats can exceed 1 m diameter and can overgrow and kill corals (Martinez et al. 2012,
179 Stimson 2013). Large thalli are often detached from anchoring substrate, transported across
180 reef flats by wind-driven currents, and deposited on leeward reefs slopes (Stimson 2013).

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

190

191 **2 Methods**

192 2.1 Study site

193 The field studies reported here were conducted on multiple reefs in Kāneʻohe Bay, a
194 partially enclosed, 46 km² embayment on the northeast coast of the Island of Oʻahu (Fig. 1).
195 The bay is subdivided into northern, central and southern sectors based on circulation
196 patterns (Smith et al. 1981). A peninsula and a 5-km-long barrier reef protect the south and
197 central sectors from oceanic swells driven by the prevailing NE trade winds. Within the bay,
198 there are approximately 60 individual patch reefs (30 to > 200 m diameter), and a fringing
199 reef borders the landward shore. The identification numbers for patch reefs used here
200 follow Roy (1970). Patch reefs in the southern and central sectors generally have shallow
201 sand-dominated inner reef flats and shallow coral- and limestone-dominated outer reef
202 flats. Reef flats in the northern bay have lower sand cover and higher coral and limestone
203 cover. Reef slope substrates are a mixture of live coral, collapsed coral heads, fine sediment,
204 and rubble. Live coral cover decreases with depth to the bay bottom at ~ 15 m depth

205 (Hunter and Evans 1995). Most of the bay bottom consists of fine carbonate and terrestrial
206 sediments. Tidal amplitude in Kāneʻohe Bay is approximately 1 m.

207

208 **2.2 Surveys of algal cover**

209 Unpublished data from four multi-year surveys with different starting dates (designated
210 Surveys A, B, C and D) were used to assess changes in *Kappaphycus/Eucheuma* and *G.*
211 *salicornia* cover in Kāneʻohe Bay. All four surveys were initially designed to investigate the
212 distribution and cover of corals and the invasive green alga, *Dictyosphaeria cavernosa*. Each
213 survey included observations on the cover of *Kappaphycus/Eucheuma* and *G. salicornia*, but
214 those data have not previously been assembled and analyzed.

215 Survey A was initiated in 1970 (Maragos 1972) (prior to the introductions of
216 *Kappaphycus/Eucheuma* and *G. salicornia*) and was repeated in 1983, 1990 and 1999
217 (Hunter and Evans 1995, S. K. Rodgers unpublished data). This survey consisted of paired 25-
218 m transects running from the reef crest downslope; macroalgal cover estimates from the
219 upper 5 m of each transect were used here. The surveys were conducted at 14 sites in
220 southern, central and northern Kāneʻohe Bay. Detailed methods for Survey A are in Maragos
221 (1972) and Hunter and Evans (1995). Survey B commenced in 1992 and was repeated in
222 2014. This survey consisted of cover estimates in large quadrats (4 m wide and extending 3
223 m down the reef slope from the crest) distributed at 10-20 m intervals along the perimeter
224 of the reef slope on 34 patch reefs in southern, central and northern Kāneʻohe Bay.
225 Estimates of cover of coral and macroalgal species were made visually by a snorkeler
226 floating above the reef slope looking perpendicular to the slope. Detailed methods for
227 Survey B are in Stimson et al. (2001). Survey C commenced in 1996 and was repeated in
228 1997, 2006, 2008, 2009, 2013, 2014, and 2016. This survey consisted of triplicate transects
229 spaced 5-m apart, at two sites on each of five patch reefs (Patch reefs 4, 8, 29, 30 and 44)
230 and the fringing reef of Moku o Loe. The transects extended 40 m onto the reef flat from
231 the crest, and 5 m down the reef slope. Detailed methods for Survey C are in Stimson et al.
232 (2001). Survey D commenced in 2006 on three patch reefs in central Kāneʻohe Bay (Reefs
233 19, 20 and 21) and was repeated approximately 3 times per year until 2017. This survey
234 consisted of 1 or 2 transects per reef; each transect extended approximately 30 m across

235 the center of the reef flat and 5 m down slope at each end of the 30-m section. Detailed
236 methods for Survey D are in Stimson and Conklin (2008).

237 A fifth survey of macroalgal cover (Survey E) on Kāneʻohe Bay reefs was carried out in 2014
238 in conjunction with the field study of *E. denticulatum* growth and grazing intensity reported
239 below. In Survey E, 25-m transects were used to estimate the cover of macroalgae, coral
240 and other substrata on the reef flats and upper 3 m of the reef slopes at 12 reefs (Reefs 6, 9,
241 12, 15, 16, 17, 19, 22, 23, 28, 33, 40). As these reefs were selected to represent a range of *E.*
242 *denticulatum* cover, they were not a randomly selected subset of the reefs in Kāneʻohe Bay.
243 At each of the Survey E reefs, 3-9 transects were surveyed on the reef flat and 3-6 transects
244 were surveyed on the reef slope approximately 2 m below the crest; the number of
245 transects varied with reef area. The occurrence of corals and macroalgae were scored at 20
246 cm intervals along each line to obtain a % cover value.

247 No surveys of macroalga and corals on Kāneʻohe Bay reefs were carried out in 2015, but by
248 January 2016, it was apparent that the cover of *E. denticulatum* had declined markedly. In
249 order to quickly assess the extent and magnitude of this decline, Survey F was carried out. *E.*
250 *denticulatum* cover was visually estimated on 11 reefs in January 2016 (Reefs 9, 11, 12, 13,
251 15, 17, 22, 23, 24, 28, 38). A single straight transect was swum across each reef flat in a NE
252 to SW direction and passing through the approximate center of the reef (30-180-m long
253 transects, width 1 to 2 m depending on water depth). The number and approximate
254 diameter of *E. denticulatum* thalli were recorded within these transects. Thallus counts and
255 sizes in combination with the transect dimensions were converted to percent cover
256 estimates.

257 Some of the reefs used in Surveys C, D, and E were also used in invasive algae control
258 programs by HDAR and The Nature Conservancy. These programs were intended to prevent
259 further range expansion of non-native macroalgae by manual removal and by stocking reef
260 flats with the herbivorous sea urchin *Tripneustes gratilla*. The control programs began in
261 2010. The year that macroalgal removal commenced on each reef (hereafter 'manipulated
262 reef') and the potential effects on algal coverage are presented in the Results section.

263

264 **2.3 *Eucheuma denticulatum* growth and grazing intensity on reef flats and slopes**

265 *E. denticulatum* thallus growth rates and grazing intensity were measured in a field
266 experiment conducted on 13 reefs on 13 dates in the summer, autumn and winter of 2014.
267 Twelve runs of the experiment were carried out on 12 patch reefs from August to October
268 of 2014, and 7 additional runs were carried out on the NE fringing reef of Moku o Loe from
269 June to December of 2014. *E. denticulatum* thalli for the experiment were collected from
270 reef flats and held overnight in outdoor tanks with flowing, unfiltered seawater. Thalli were
271 then divided into experimental units (approximately 30 g wet weight), shaken to remove
272 excess water, and weighed on an analytical balance to 0.1 g. Two thalli were attached to
273 vinyl-coated wire mesh platforms (15 x 30 cm) using fine plastic-coated wire, and one of the
274 thalli was enclosed in a plastic-mesh cage (12 x 12 x 12 cm, 6-mm mesh, mesh diameter ~0.5
275 mm) to exclude herbivorous fishes. The platforms with paired caged and uncaged *E.*
276 *denticulatum* thalli were transported by boat to the reef where they were to be used; thalli
277 were shaded and sprayed with seawater during transport. At each reef, approximately 20
278 platforms were positioned on the reef slope and 30 platforms were positioned on the reef
279 flat in predetermined configurations. The reef slope platforms were evenly spaced around
280 the reef perimeter at 2-m depth, and the reef flat platforms were arranged in a regular grid
281 across the entire flat. Platforms were retrieved after two days and the thalli were
282 reweighed. Specific growth or loss was calculated as weight change per initial weight per
283 day ($\text{g g}^{-1} \text{d}^{-1}$). Grazing intensity was calculated as the difference between specific growth or
284 loss rates of the caged and uncaged thalli on each platform.

285

286 **2.4 Effects of water temperature on *Eucheuma denticulatum* and *Gracilari salicornia*** 287 **growth**

288 Water temperatures of ~30°C were measured in shallow waters in Kāneʻohe Bay in the late
289 summers of 2014 and 2015 (www.pacioos.hawaii.edu) in association with coral bleaching
290 events both years (Bahr et al. 2015a, 2017). Outdoor laboratory experiments were
291 conducted in October and November 2016 to examine the effect of such high temperatures
292 on the growth of *E. denticulatum* and *G. salicornia*. Small *E. denticulatum* thalli (2-4 gm wet
293 weight) were held in six 6.4 l glass tanks supplied with unfiltered seawater at a rate of 300

294 ml per min⁻¹. Aeration was used to increase water motion in the tanks. The water in two
295 tanks was heated with aquarium heaters, the water in one tank was cooled with an
296 aquarium chiller and the water in the remaining three tanks was maintained at the
297 temperature of the laboratory seawater system. Temperatures were recorded in the tanks
298 using Hobo temperature loggers; the treatments produced a range of mean temperatures
299 from 24 to 31° C. The tanks were covered with one layer of window screen to reduce
300 irradiance by ~ 40% (measured with a Biospherical Instruments QSI-140 meter and 4- π
301 sensor). Three *E. denticulatum* thalli were placed in each tank at a depth of 7 cm. The thalli
302 were reweighed after 48 hr and specific growth rates of the three thalli in each tank were
303 averaged for subsequent analysis. Eight experimental runs were carried out in October
304 2016; all six treatments were included in each run but results from six of the 48 replicates
305 were excluded from analysis because of aeration or water supply problems. The mean
306 temperature in each tank over the 48 hour growth period was used in a regression analysis
307 to quantify the relationship between *E. denticulatum* growth rate and water temperature.

308 Effects of water temperature on *Gracilaria salicornia* growth were measured using the same
309 methods used for *E. denticulatum*, with the following modifications. Starting weights of *G.*
310 *salicornia* thalli were 2 to 3 g. Three 2-day experimental runs were carried out from
311 November 1, 2016 to November 7, 2016. Six tanks were used, two heated, one cooled and
312 three with ambient water temperature, treatment temperatures ranged from 24.5 to 30°C.

313

314 **2.5 Herbivorous fish abundance and biomass**

315 The abundance of herbivorous fishes has been visually estimated at Kāneʻohe Bay reefs in
316 two multi-year surveys that were extended for the current study. The first survey consisted
317 of counts of herbivorous surgeonfishes (Acanthuridae) around the perimeters of four small
318 patch reefs (~30 m in diameter) in the central bay (Reefs 19, 20, 21, 23). Repeat surveys
319 were carried out 106 times from early 2007 to late 2013. Each fish was assigned to one of
320 three size classes, and no attempt has been made to convert these counts to biomass. Total
321 length of acanthurid individuals on these reefs is generally less than 14 cm. Detailed
322 methods for the first fish survey are in Stimson et al. (2005). The second survey consisted of
323 counts and estimated lengths of herbivorous surgeonfishes and parrotfishes along 50 m

324 long belt transects located on a 750-m long section of the windward reef of Moku o Loe (Fig.
325 1). The transect belt extended from the crest 3 m onto the reef flat and 5 m down the reef
326 slope. The total length of the individual fish was estimated to the nearest cm. Length
327 estimates were converted to biomass estimates using the conversion factors in Stimson et
328 al. (2001). The individual biomass values were multiplied by the number of individuals in a
329 size class in a species, then these products were summed across the size classes and species
330 in a survey. The analysis presented here used the natural log of the biomass value of each
331 survey. Detailed methods for the second fish survey are in Stimson et al. (2001). A total of
332 41 Moku o Loe surveys were carried out from early 2007 to late 2013.

333 **3 Results**

334 **3.1 Multi-year surveys of algal cover**

335 In survey A (commencing in 1970) *Kappaphycus/Eucheuma* occurred on the reef slopes of
336 only one of the 14 reefs and only in the 1983 and 1990 surveys. *G. salicornia* occurred on a
337 different reef and only in 1999. In survey B (commencing in 1992), *Kappaphycus/Eucheuma*
338 occurred on 19 of 34 reef slopes in the 1992 survey, with a mean cover of 0.5%, and on 12
339 of 30 reefs in 2014, with a mean cover of 1.46%. *G. salicornia* occurred on 6 of 34 reefs in
340 Survey B in 1992, with a mean cover of 0.2%, and was absent from all 30 reefs in 2014.
341 *Kappaphycus/Eucheuma* and *G. salicornia* are generally most abundant on reef flats in
342 Kāneʻohe Bay, therefore, Surveys A and B were less sensitive to the presence of both taxa
343 than Surveys C and D, which included reef flats.

344 In Survey C (commencing in 1996), mean *Kappaphycus/Eucheuma* cover increased from
345 1996 to 2008-2009 on reef flats, then declined by 2013 (Fig. 2A, un-manipulated reefs). In
346 2012, manual removal of *Kappaphycus/Eucheuma* commenced on Reef 29; the cover of
347 *Kappaphycus/Eucheuma* on this reef has been plotted separately in Fig. 2A. By 2014, no
348 *Kappaphycus/Eucheuma* cover was observed on the un-manipulated reefs and very little
349 was detected on Reef 29. The pattern of temporal variation in *G. salicornia* cover on the six
350 reefs used for Survey C was similar to that of *Kappaphycus/Eucheuma*; cover declined after
351 2008/09 on the un-manipulated reefs and virtually disappeared from all six reefs by 2014,
352 even though this species was not targeted for manual removal (Fig. 2B). The mean % cover

353 values are low on these reefs because the 40-m survey transects on some reefs crossed
354 large areas of sand substratum on the reef flat, with few attached macroalgal thalli.

355

356 In Survey D (commencing in 2006), *Eucheuma/Kappaphycus* reached its maximum cover on
357 Reef 19 by 2010 (Fig. 3A), then declined in the summer and fall of 2014, coincident with
358 both herbivorous urchin stocking in the HDAR control program and elevated water
359 temperatures. *Eucheuma/Kappaphycus* reached its maximum cover on Reef 20 in 2008,
360 then declined sharply but did not disappear until 2013; Reef 20 was stocked with urchins in
361 September 2013. *G. salicornia* cover peaked on Reefs 19 and 20 in 2007/2008, then
362 disappeared from Reef 19 by 2009, and persisted on Reef 20 until the time of the urchin
363 stocking in September 2013 (Fig. 3B). Neither species of algae established on Reef 21 during
364 the study.

365 **3.2 Surveys of algal cover in 2014**

366 A comparison of *E. denticulatum* cover on reef flats and reef slopes of the 10 unmanipulated
367 reefs in the summer and fall of 2014 (Survey E) showed that reef flats had significantly
368 higher cover by Wilcoxon's signed rank test ($P < 0.01$, Tab. 1). The cover of *E. denticulatum*
369 was about 5% on the reef flats of unmanipulated reefs and higher on the two manipulated
370 reefs; the manipulated reefs had been selected for macroalgal control by HDAR due to their
371 high initial *E. denticulatum* cover. *G. salicornia* only occurred on the reef flats of two of the
372 10 unmanipulated reefs in Survey E; *G. salicornia* cover on these reefs was 5% and 15%.
373 Since the reefs in Survey E were selected for the study of *E. denticulatum* growth and
374 grazing intensity, they do not comprise a random sample of reefs in Kāne'ōhe Bay in terms
375 of presence or cover of *E. denticulatum* and *G. salicornia*.

376

377 The cover estimates made in January 2016 indicated that *E. denticulatum* cover had sharply
378 declined since survey E in 2014. On four unmanipulated reefs with high *E. denticulatum*
379 cover in 2014 cover declined to 0 in 2016, and cover declined on an unmanipulated reef not
380 used in Survey E in 2014. Most of the remaining *E. denticulatum* thalli in 2016 had
381 morphological features characteristic of high grazing intensity, with short, tightly packed
382 branches and blunt apices.

383 **3.3 *Eucheuma denticulatum* growth and grazing intensity on reef flats and slopes**

384 Caged (ungrazed) *E. denticulatum* sustained net growth on reef flats and reef slopes during
385 the summer and fall of 2014. The mean specific growth rate of *E. denticulatum* thalli on reef
386 flats was $0.023 \text{ g g}^{-1} \text{ d}^{-1}$ on 12 patch reefs and $0.016 \text{ g g}^{-1} \text{ d}^{-1}$ on the fringing reef flat of Moku
387 o Loe. Mean specific growth rates *E. denticulatum* thalli on patch reef slopes ($0.012 \text{ g g}^{-1} \text{ d}^{-1}$)
388 and the Moku o Loe reef slope ($0.006 \text{ g g}^{-1} \text{ d}^{-1}$) were significantly lower than on the adjacent
389 reef flats (Table 2). All 4 of these mean specific growth rate values are significantly different
390 from 0. (The experiment coincided with a period of elevated water temperatures ($\sim 30^\circ \text{C}$)
391 and coral bleaching.

392

393 Grazing intensity, calculated as the difference between weight changes of caged and
394 uncaged *E. denticulatum* thalli on each experimental platform, was significantly higher on
395 patch reef slopes than on patch reef flats, but was not significantly different between these
396 habitats on the Moku o Loe fringing reef. Grazing intensity was a decreasing function of *E.*
397 *denticulatum* cover on reef flats (Fig. 4). Five runs of the experiment were carried out prior
398 to the end of August 2014, after which the average daily water temperature at Moku o Loe
399 rose above 28°C . In each of these early runs, mean grazing intensity exceeded mean
400 growth on both reef flats and reef slopes, suggesting that the high grazing intensity was not
401 necessarily the result of high temperature.

402

403 **3.4 Effects of water temperature on the growth of *Eucheuma denticulatum* and *Gracilaria*** 404 ***salicornia***

405 *E. denticulatum* growth in outdoor laboratory tanks increased with increasing temperature
406 from 25°C to 28°C , then declined at temperatures up to 30°C ; (Fig. 5A). A quadratic
407 polynomial curve fitted to the data was significant and explained 35% of the variation in *E.*
408 *denticulatum* specific growth rates ($F= 10.47$, $df = 2,43$, $P < 0.0001$). In contrast, the growth
409 rate of *G. salicornia* was neither a linear function of temperature ($F=2.81$, $df=2,16$, $P=0.113$)
410 or a curvilinear function.

411

412

413 3.5 Herbivorous fish abundance and biomass

414 Data from two surveys of herbivorous fishes were used to examine whether an increase in
415 herbivore density and biomass could have contributed to the reductions in *E. denticulatum*
416 and *G. salicornia* cover evident in Figures 2 and 3. A large recruitment of acanthurids was
417 responsible for a peak in herbivore abundance on Reefs 19, 20, 21 and 23 in summer 2014
418 (Fig. 6) however, this event did not result in a markedly higher acanthurid densities in
419 subsequent years. Over the period from 2007 to 2013, during which much of the decline in
420 *Eucheuma/Kappaphycus* and *G. salicornia* took place, there was a statistically significant
421 positive temporal trend in the density of acanthurids on three of the four reefs (Reefs 19,
422 20, 21, Table 3). The estimated biomass of scarids and acanthurids on the Moku o Loe reef
423 slope and outer reef flat did not increase significantly from 2007 to 2013 ($Y =$
424 $0.0001X+3.4856$, $R^2 = 0.0204$).

425

426

427 4 Discussion

428 The survey data reported here indicate that *E. denticulatum* and *G. salicornia* underwent a
429 substantial reduction in cover on Kāneʻohe Bay coral reefs in the 2009 to 2017 period and
430 that the areal cover of both species approached zero by 2016. These reductions in
431 macroalgal abundance are the second such alteration of Kāneʻohe Bay reef communities in
432 the last 10 years. The first of these was the abrupt decline in *D. cavernosa* cover in 2006,
433 which ended nearly four decades of *D. cavernosa* dominance on reef slopes through most of
434 Kāneʻohe Bay (Stimson and Conklin 2008). The abrupt decline of *D. cavernosa* was
435 attributed to persistent rain and overcast conditions over 42 days in February and March
436 2006. Support for this explanation came from outdoor laboratory experiments, conducted in
437 the spring of 2007 which showed that *D. cavernosa* growth was very slow at water
438 temperatures and irradiance levels comparable to those in February and March 2006
439 (Stimson and Conklin 2008). As of 2017, the abundance of *D. cavernosa* in Kāneʻohe Bay
440 remains very low. The meteorological conditions associated with the *D. cavernosa* decline in
441 2006 did not appear to have long-term adverse effects on *E. denticulatum* and *G. salicornia*
442 (Figs. 2, 3). In contrast, the declines in *E. denticulatum* and *G. salicornia* after 2013 appear to

443 be associated with high grazing pressure and possibly high summer water temperatures, as
444 discussed below.

445

446 The decline in *E. denticulatum* cover on Kāneʻohe Bay reefs after 2013, and that fact that
447 this decline occurred independently of manual and biological control efforts was not
448 recognized until January 2016, and was verified by Survey F. In retrospect, the decline in *E.*
449 *denticulatum* may have begun as early as 2008, based on the survey results from un-
450 manipulated reefs shown in Figure 2. The survey results for *G. salicornia* suggests that the
451 decline of this species could have begun at the same time on un-manipulated reefs (Figs.
452 2B). By 2016 both *E. denticulatum* and *G. salicornia* were virtually absent from all surveyed
453 reefs.

454

455 The reduction in *E. denticulatum* abundance on Kāneʻohe Bay reefs is likely to be wholly or
456 partly due to an increase in grazing pressure. Mean grazing intensity in the herbivory
457 experiments conducted on *E. denticulatum* in the summer and fall of 2014 equaled or
458 exceeded the growth rates of caged *E. denticulatum* thalli, which suggests that herbivores
459 reduced *E. denticulatum* abundance by consuming tissue in excess of production.

460 Additionally, data from one of two surveys of herbivorous fishes indicate that grazer
461 densities increased on several reefs over the 2007 to 2013 period and that a major
462 herbivore recruitment event occurred in 2014 (Table 3, Fig. 6); these increases in herbivore
463 densities may have caused the high grazing intensities we observed. No field measurements
464 of *G. salicornia* growth and grazing intensity were made in this study, but previous
465 experiments indicate that *G. salicornia* ranks higher in preference for Kāneʻohe Bay
466 herbivores than *E. denticulatum* (Stimson et al. 2001, Westbrook et al. 2015). Therefore, the
467 effect of high grazing pressure on the abundance of *G. salicornia* is likely to be similar to or
468 greater than the effect on *E. denticulatum* abundance.

469

470 Native acanthurids and scarids are the grazers most likely to be responsible for the high
471 grazing intensity we observed. Siganids do not occur in Hawaiʻi, pomacentrids and
472 macroalgae-grazing kyphosids are rarer than acanthurids or scarids, and large grazing
473 urchins are generally restricted to areas on and near the barrier reef (Hinegardner 1961).
474 Five common acanthurids in Kāneʻohe Bay have been directly observed feeding on *E.*

475 *denticulatum* and *G. salicornia*: *Zebrasoma velliferum*, *Acanthurus triostegus*, *Acanthurus*
476 *dusmerili*, *Zebrasoma flavescens* and *Naso unicornis* (Russell 1983, Bierwagen 2014,
477 authors' observations). In addition to herbivorous fishes, green sea turtles may have
478 contributed to the recent declines in *E. denticulatum* and *G. salicornia*. Green sea turtles
479 have been increasing in abundance in Hawai'i since protective management was initiated in
480 1978, and they are abundant in Kāne'ōhe Bay. *Kappaphycus/Eucheuma* and *G. salicornia*
481 both occur in the diets of green sea turtles in the bay (Russell and Balazs 2009). *G. salicornia*
482 is a particularly important component of green sea turtle diets; it is estimated to comprise >
483 30% of the macroalgae consumed by Kāne'ōhe Bay turtles (Russell and Balazs 2009, 2015).

484

485 Assuming that the rapid decline of *E. denticulatum* and *G. salicornia* was at least partly due
486 to an increase in grazing pressure, it appears to be the first example of a natural (i.e., non-
487 experimental), large scale reversal of macroalgal dominance of coral reefs attributable to
488 grazers other than sea urchins. Previous reports of reversals of coral-macroalgal phase shifts
489 in the Caribbean involved the recovery of urchin populations following their collapse in the
490 1980s, and subsequent increases in macroalgal grazing (Edmunds and Carpenter 2001,
491 Carpenter and Edmunds 2006, Myhre and Alcevedo-Gutiérrez 2007). Previous shifts from
492 macroalgal to coral dominance due to fish grazing are limited to field experiments (Bellwood
493 et al. 2006, Mumby et al. 2006, 2007, Hughes et al. 2007).

494

495 In addition to increased grazing pressure, elevated water temperatures may have
496 contributed to the decline in *E. denticulatum* in Kāne'ōhe Bay. The decline in *E.*
497 *denticulatum* cover evident in early 2016 followed two consecutive warm water events in
498 the late summers of 2014 and 2015. These events resulted in coral bleaching and mortality
499 in the bay in both years (Bahr et al. 2015a, 2017; Cunning et al. 2016). Water temperatures
500 at 2 m depth at Moku o Loe in southern Kāne'ōhe Bay reached 29.8 °C in 2014 and over 30
501 °C in 2015 (www.pacioos.hawaii.edu), and water temperatures at 2-3 m depth at 8 sites in
502 the bay were between 29 and 31.5°C from late August to early September of 2015 (Bahr et
503 al. 2017). In contrast to the research efforts focused on the responses of corals to the high
504 water temperatures of 2014 and 2015 in Kāne'ōhe Bay, the effects of high temperatures on
505 macroalgae have not been considered. A second hypothesis to account for the abrupt
506 decline of *E. denticulatum* is that the high temperature events in 2014 and 2015 reduced

507 thallus growth rates to the point that consumption by herbivores exceeded gross
508 productivity.

509

510 The results of the laboratory experiments on the effect of high temperature on the growth
511 of *E. denticulatum* indicate that the growth rate of this alga does decrease at high water
512 temperatures (Fig. 5). High temperature growth inhibition has been reported for several
513 species of tropical macroalgae (Pakker et al. 1995, Hwang et al. 2004, Tsai et al. 2005).
514 However, some species do not appear to be inhibited by naturally occurring high water
515 temperatures; we observed no inhibition of growth in *G. salicornia* over a temperature
516 range of 26 to 30°C (Fig. 6b). The failure to detect a decline in growth at high temperatures
517 in *G. salicornia* may be related to the differences between these two species in their
518 distribution among habitats in the bay. *E. denticulatum* utilizes reef slopes and those outer
519 reef flat habitats also occupied by corals. *G. salicornia* however, is almost entirely restricted
520 to inner reef flat areas, areas generally devoid of corals and potentially is subject to higher
521 temperatures associated with shallow waters and high-tide exposure.

522

523 While high water temperatures (> 28 °C) and high grazing pressure may have contributed
524 jointly to the decline of *E. denticulatum*, grazing alone was sufficient to cause the decline.
525 This conclusion is based on our observation that grazing loss rates exceeded tissue growth
526 rates in runs of the field experiment prior to August 2014, when temperatures were < 28° C.
527 Grazing appears to have been the primary cause for the decline in *G. salicornia* cover, given
528 that experimentally increasing water temperatures increase did not reduce *G. salicornia*
529 growth. Elevated water temperatures in 2014 and 2015 may have also caused grazing rates
530 to increase, by increasing metabolic rates in herbivorous fishes (and perhaps sea turtles),
531 thereby increasing food requirements (Clarke and Johnstone 1999, Smith 2008).

532

533 Studies of coral bleaching events that include responses by macroalgae, generally report an
534 increase in macroalgal abundance following the event (McClanahan 2000, Ostrander et al.
535 2000, McClanahan et al. 2001, DiazPulido and McCook 2002). The fact that this did not
536 occur in Kāneʻohe Bay after the 2014 and 2015 bleaching events may be associated with
537 rapid recovery of bleached corals and relatively low coral mortality (Bahr et al. 2017). It is
538 possible however, that the increase in *Eucheuma/Kappaphycus* and *G. salicornia* cover

539 evident in Figs. 2 and 3 was related to a bleaching event in 1996 that caused more severe
540 coral mortality (Bahr et al. 2017).

541

542 The recent declines in *E. denticulatum* and *G. salicornia* cover on reef flats comprise the first
543 of two steps in a reversal of the coral-algal phase shift that followed the establishment of
544 these species in Kāneʻohe Bay. The second step in the phase shift reversal is the recovery of
545 coral cover. If corals recolonize the reef flat substrata made available by the loss of *E.*
546 *denticulatum* and *G. salicornia*, then a complete phase shift reversal will have occurred. The
547 potential for that recolonization exists. In a recent study of a 44-year (1970-2014) record of
548 Kāneʻohe Bay coral surveys, coral cover increased in most surveys over the last 20 years
549 (Stimson 2017). In the surveys where coral cover decreased over time or remained stable, it
550 was usually because the initial coral cover was high, i.e., the rates of change in coral cover
551 were inversely related to initial coral cover. Increased substrate availability due to the
552 decline of the *E. denticulatum*, and to a certain extent *G. salicornia*, and observations of
553 relatively rapid increases in coral cover reported by Stimson (2017), suggest that a complete
554 phase-shift reversal is underway, barring a setback to corals in future bleaching episodes.
555 Bahr et al. (2017) estimated that mortality of corals in the Kāneʻohe Bay due to bleaching
556 was 13% in 2014 and 22% in 2015, so while the cover of the macroalgae on reef flats has
557 been greatly reduced, the ability of the corals to regain spatial dominance may be limited by
558 periodic bleaching.

559

560 It is evidently not the case that coral-macroalgal phase shifts are irreversible, as some
561 researchers have suggested (Scheffer et al. 2001, Rogers and Miller 2006, Mumby et al.
562 2012, Mumby et al. 2013). However, detecting reversals of coral-macroalgal phase shifts
563 may require long-term monitoring programs. Furthermore, it may be necessary to monitor a
564 wide range of ancillary variables (e.g., grazer abundance) to identify causes of reversals. The
565 data sets assembled in this study document the expansion, reduction and near-
566 disappearance the dominant non-native red algae in Kāneʻohe Bay, and they suggest that an
567 increase in grazing intensity played a role in the phase-shift reversal. Graham et al. (2013)
568 have argued that major changes in environmental conditions (e.g., decreasing fishing
569 pressure, thereby increasing herbivory) are prerequisites for phase-shift reversals and that
570 ecological 'pulse' disturbances may also be required to initiate reversal. The ecological

571 disturbance in this case may have been the high water temperature events of 2014 and
 572 2015. The high water temperature events may have been functionally equivalent to the rain
 573 and overcast event that initiated the *D. cavernosa* phase shift reversal in Kāneʻohe Bay in
 574 2006 (Stimson and Conklin 2008), a phase shift which in many parts of the Bay lasted for at
 575 least 36 years.

576

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806 Fig. 1 Map of Kāneʻohe Bay, its fringing, patch and barrier reefs. Patch reefs are numbered
807 according to the system of Roy (1970).

808 Fig. 2. A) Change in *Kappaphycus/Eucheuma* cover on the reef flats and upper slopes of six
809 reefs in Survey C. Manual removal of *Kappaphycus/Eucheuma* on Reef 29 began in 2012,
810 urchin addition began in 2013. Points corresponding to “Unmanipulated reefs”, those not
811 subject to manual removal or urchin addition, are means \pm 1 standard error for all six reefs
812 until 2012, and thereafter the points represent the values from the five unmanipulated
813 reefs. B) Changes in *Gracilaria salicornia* cover on the reef flats and upper slopes of six
814 reefs in Survey C. Manual removal did not target *G. salicornia*.

815

816 Fig. 3. Changes in: A) *Kappaphycus/Eucheuma* cover and B) *Gracilaria salicornia* cover on
817 the reef flats and upper slopes of two reefs in Survey D. Large numbers of urchins
818 (*Tripneustes gratilla*) were outplanted on Reef 19 in 2014 and to Reef 20 in 2013 to
819 consume macroalga as part of a biological control program.

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

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825 Fig. 5. Specific growth rates of *E. denticulatum* thalli over a range of seawater
826 temperatures. Each data point represents the growth of three thalli.
827 Curves represents the fitted quadratic equation: $Y = -1.379 + 0.1004X - 0.0001782X^2$

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829 Fig. 6. Density of acanthurids over time on four patch reefs in central Kāneʻohe Bay.
830 Acanthurid density is expressed as number of fish per 100 m of reef perimeter

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835 Table 1.

836 Percentage cover of *Eucheuma denticulatum* in 2014 in survey E. The survey included
 837 separate estimates of algal cover on reef flats and reef slopes.

838

		Reef flat	Reef slope
Manipulated reefs	Mean % cover	13.7	2.8
	Range	0-27.4	0-5.5
	Sample size	2	2
Unmanipulated reefs	Mean % cover	5.7	0.5
	SD	7.6	1.1
	Sample size	10	10

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852 Table 2. Specific growth of *E. denticulatum* (caged thalli) and grazing intensity on *E.*
 853 *denticulatum* (difference between caged and uncaged weight change) on reef flats and reef
 854 slopes in Kāneʻohe Bay. “Patch reefs” refers to 12 patch reefs used for experimental runs.
 855 “Fringing reef” refers to the eight experimental runs the windward fringing reef of Moku o
 856 Loe. Values are means \pm 1 SD in $\text{g g}^{-1} \text{d}^{-1}$, with sample sizes in parentheses. “t”-tests are for
 857 comparisons between reef flats and reef slopes.

858

859 Growth rate in cages

860 Patch Reefs

861	Reef flat	Reef slope	t	P
862	0.023 \pm 0.010	0.012 \pm 0.005	5.61	<0.001
863	(12)	(12)		

864 Fringing reef

865	0.016 \pm 0.008	0.006 \pm 0.005	5.39	<0.01
866	(7)	(8)		

867 Grazing Intensity

868 Patch Reefs

869	0.023 \pm 0.017	0.047 \pm 0.035	2.29	<0.05
870	(12)	(12)		

871 Fringing reef

872	0.089 \pm 0.096	0.1541 \pm 0.121	1.53	ns
873	(7)	(8)		

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876 Table 3

877 Regression statistics for the test of the slopes of the regressions of numbers of acanthurids
 878 per 100 m of reef perimeter vs time (days)

879

880	Reef	slope	S _b	Number	F	P
881				of surveys		
882	19	0.0359	0.0054	40	44.58	<0.001
883	20	0.0434	0.0053	22	66.37	<0.001
884	21	0.0266	0.0062	33	18.56	<0.001
885	23	0.0135	0.0123	11	1.19	ns

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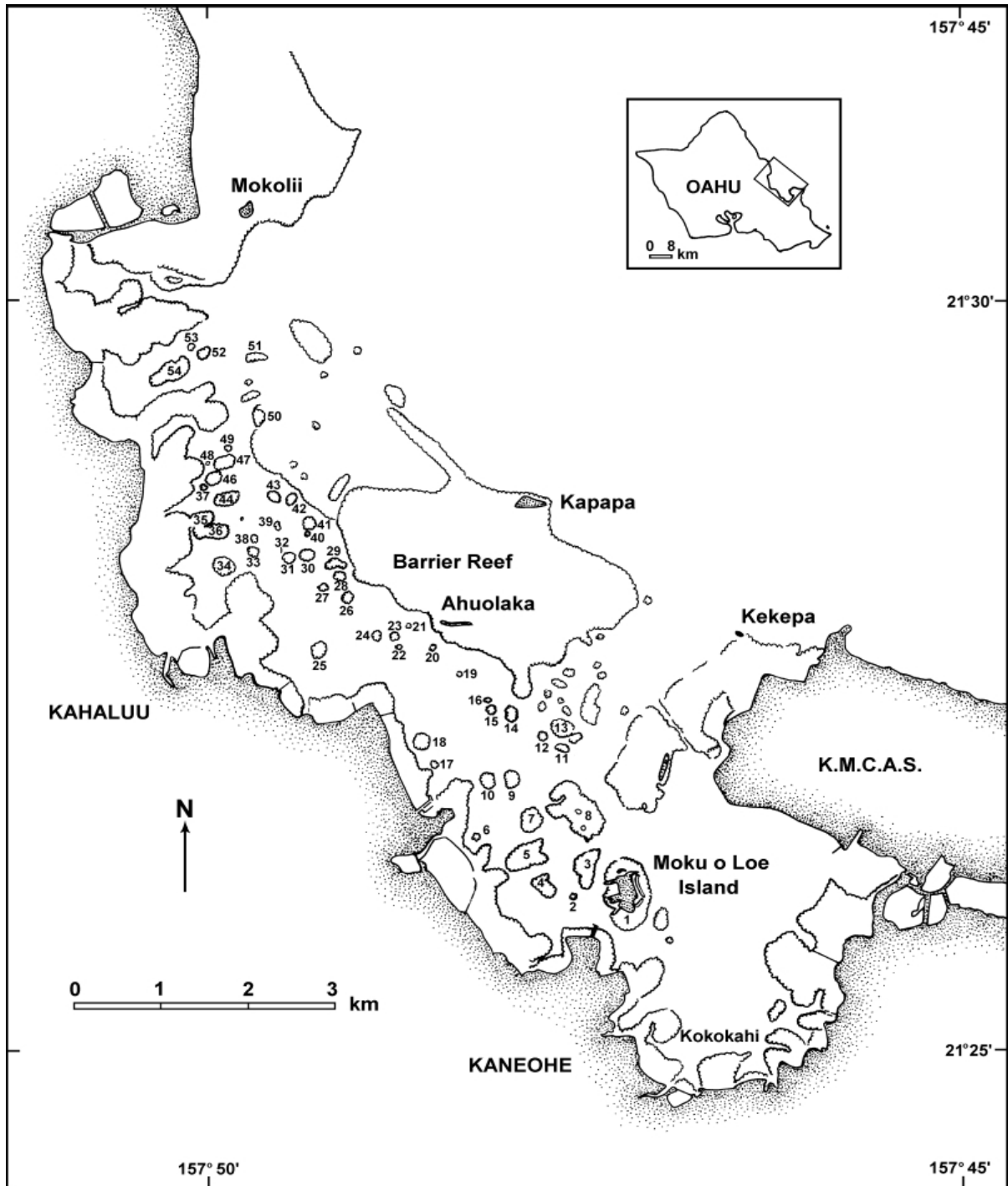
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898 Fig. 1 Map



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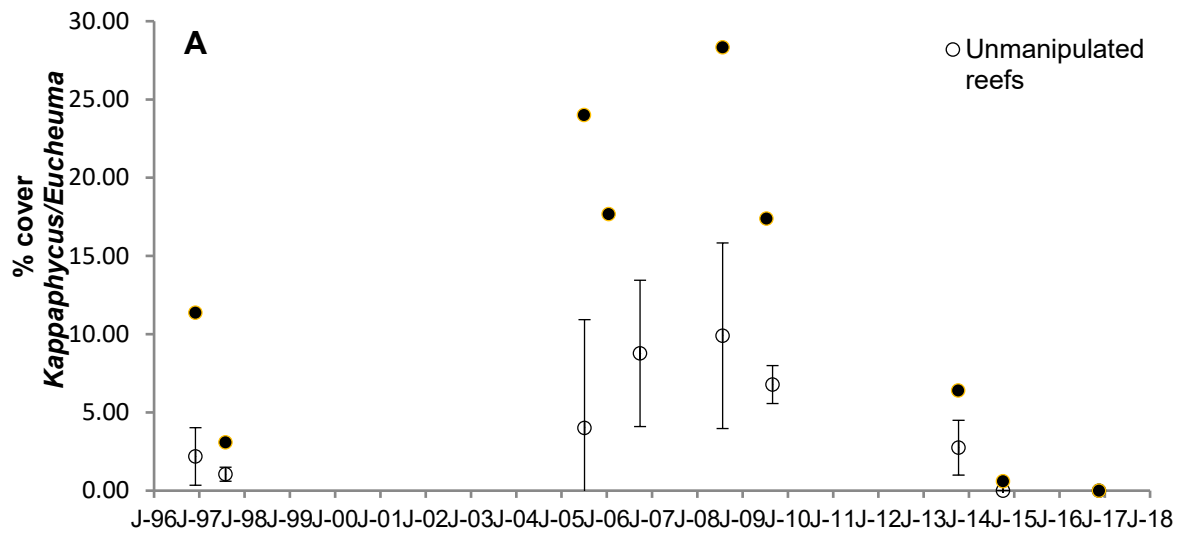
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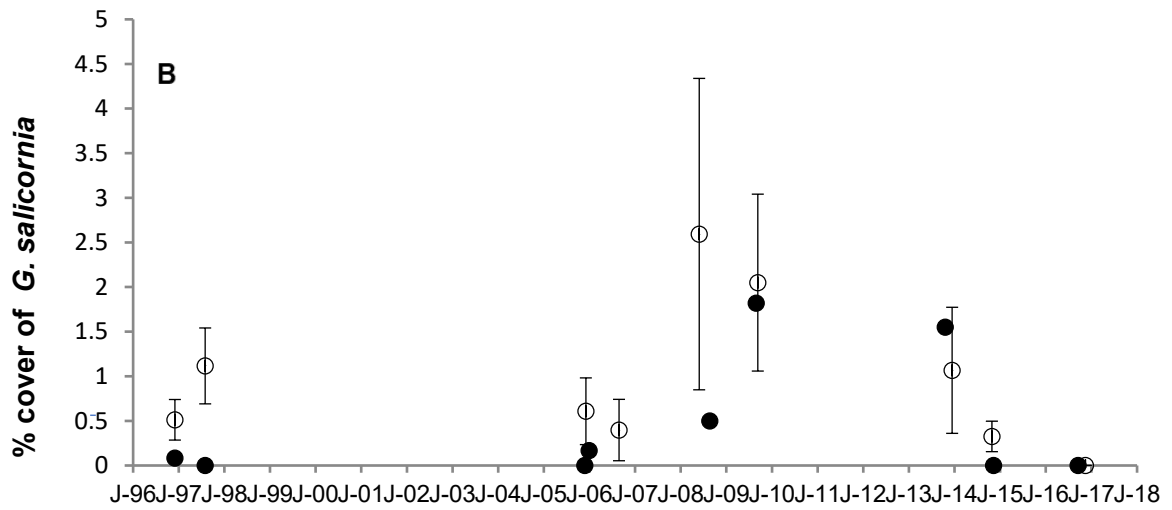
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905 Fig. 2 A



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907 Fig. 2B



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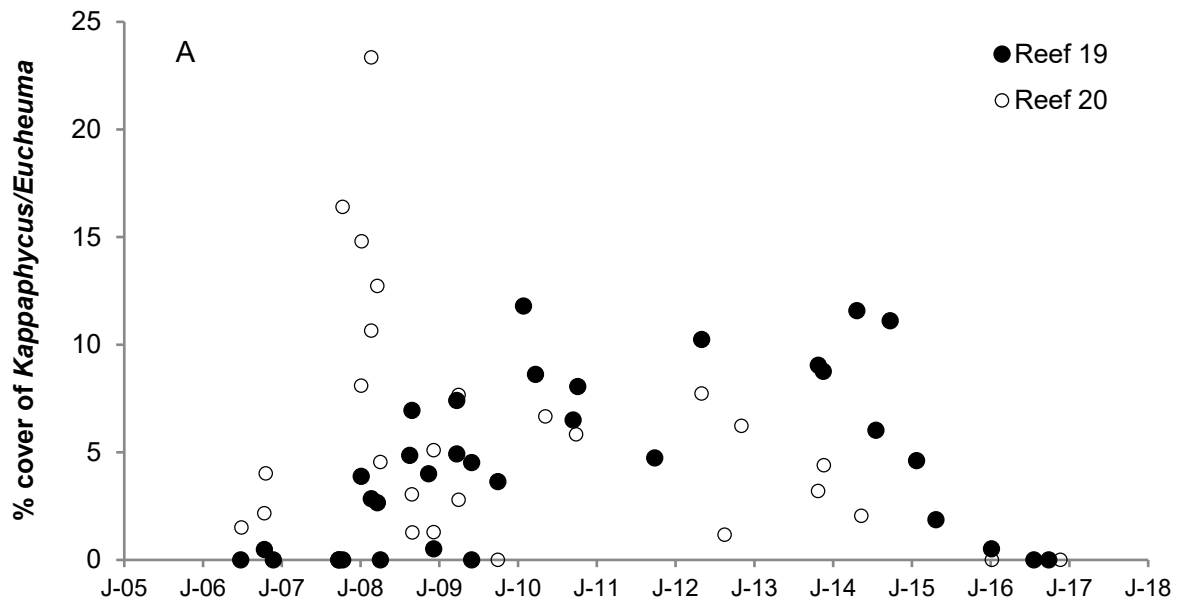
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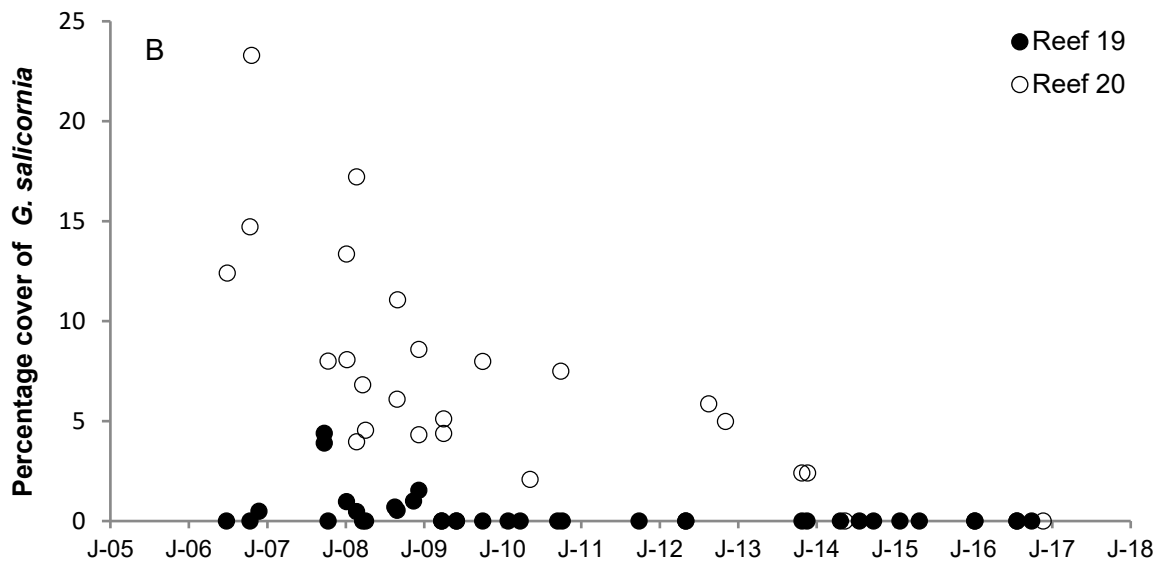
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918 Fig. 3A



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920 Fig. 3B



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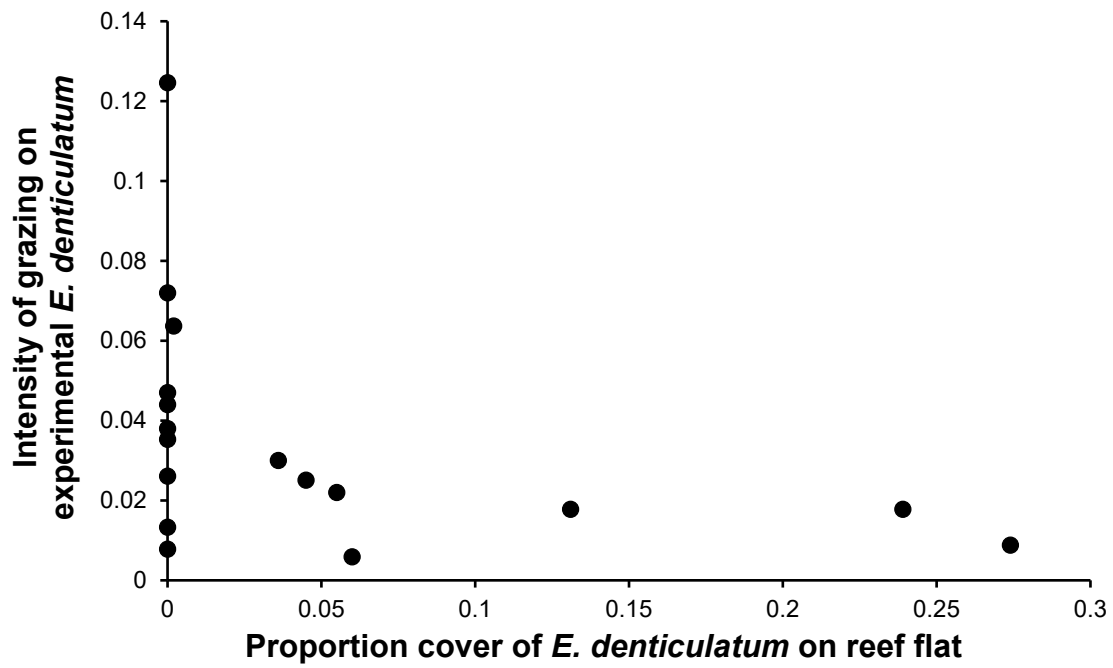
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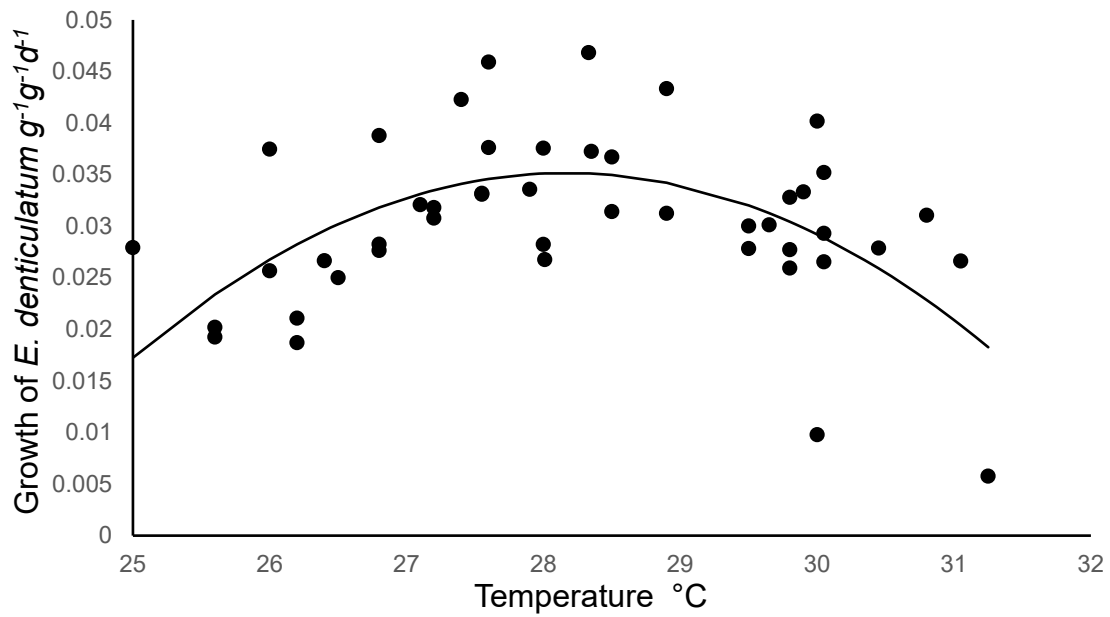
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928 Fig. 4



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930 Fig. 5



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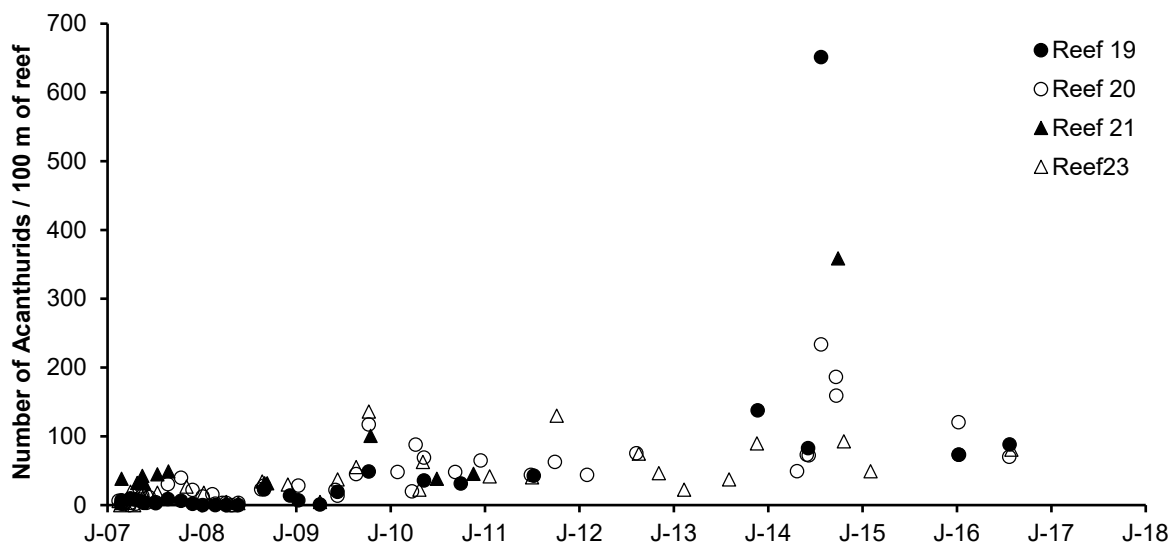
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937 Fig. 6



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