Removal of corallivorous snails as a proactive conservation tool

Corallivorous snail feeding is a common source of tissue loss for the threatened coral *Acropora palmata*, accounting for roughly one-quarter of tissue loss in monitored study plots over seven years. However, corallivory by *Coralliophila abbreviata* is one of the few major sources of partial mortality (contrasting with threats such as bleaching, disease, or storm disturbances) that may be locally managed. We conducted a field experiment to explore the effectiveness and feasibility of snail removal. Long-term monitoring plots on six reefs in the upper Florida Keys were assigned to one of three removal treatments: 1) removal from *A. palmata* only, 2) removal from all host coral species, or 3) no-removal controls. During the initial removal in June 2011, 639 snails were removed from twelve 150 m^2 plots. Snails were removed two additional times during a seven month "removal phase", then counted at five surveys over the next 19 months to track recolonization. At the conclusion, snails were collected, measured, and sexed. Before-After-Control-Impact analysis revealed that both snail abundance and feeding scar prevalence were reduced in removal treatments compared to the control, but there was no difference between removal treatments. Recolonization by snails to baseline abundance is estimated to be 4.3 years and did not differ between removal treatments. Recolonization rate was significantly correlated with baseline snail abundance. Maximum snail size decreased from 47.0 mm to 34.6 mm in the removal treatments. The effort required to remove snails from *A. palmata* was 30 diver minutes per 150 m^2 plot, compared with 51 minutes to remove snails from all host corals. Since there was no additional benefit observed with removing snails from all host species, removals can be more efficiently focused on only *A. palmata* colonies, and in areas where *C. abbreviata* abundance is high, to effectively conserve *A. palmata* in targeted areas.

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7 Introduction

8   Predator control is most commonly considered as a management strategy for invasive

9   predators (Baxter et al. 2008; Barbour et al. 2011; Morris Jr et al. 2011) or outbreaks of endemic

10   predators (Yamaguchi 1986; Sanz-Aguilar et al. 2009). Previous attempts to cull corallivores,

11   specifically *Acanthaster planci*, have largely been aimed at localized outbreaks with the goal of

12   preserving coral tissue over a large area (Yamaguchi 1986). These efforts have been deemed

13   ineffective due to the large numbers and migrating aggregations of these predators (Yamaguchi

14   1986; Johnson et al. 1990). However, removal of a relatively sedentary predator from targeted

15   populations of a threatened coral species has not been evaluated.

16   Ecological theory on predator-prey dynamics can provide insight on situations when predator

17   removal may be effective in protecting prey. Sinclair et al. (1998) present a framework whereby

18   controlling natural predators may improve the outcome for management of declining or

19   reintroduced populations of threatened species. In this framework, the appropriate scale of

20   intervention depends on the functional and numerical response of predators to changing prey

21   abundance. In cases where the effects of predation are depensatory and prey abundance is so low

22   that they are vulnerable to stochastic events, predator control could provide benefit to prey

23   populations (Sinclair et al. 1998). Rotjan and Lewis (2008), in a review of corallivory, suggest

24   that the rapid pace of coral decline over the past two decades, largely from factors other than

25   predation, may have indeed reached such a depensatory threshold such that predation is exerting

26   undue influence, potentially compromising coral reef resilience.

27   On reefs in the western Atlantic, the dominant framework builder, *Acropora palmata,* is

28   preyed upon by the corallivorous snail *Coralliophila abbreviata.* Although disease, storms, and

29   bleaching have largely driven the range-wide decline of *A. palmata* populations, snail predation is

30 recognized as one of the top three threats to the persistence and recovery of these populations

31 (Bruckner 2002; Williams and Miller 2012). In the upper Florida Keys, there has been a 50%

32 decline in *A. palmata* tissue abundance since 2004. Although the main culprit has been disease,

33 feeding by *C. abbreviata* accounted for an estimated one-quarter of the observed tissue loss

34 (Williams and Miller 2012). It is unknown whether or not the *C. abbreviata* population is

35 increasing; however, typical predators of shelled gastropods are grunts, wrasses, trunkfish,

36 triggerfish, and pufferfish (Randall 1967). Therefore it is possible that reduced predation on

37 snails due to overfishing may have increased snail abundance (Burkepile and Hay 2007), though

38 specific data to support this hypothesis are lacking. Regardless, as *A. palmata* populations

39 decline, snails have been observed to become more concentrated on the remaining *A. palmata*

40 (Bruckner et al. 1997; Bruckner 2000; Baums et al. 2003a; Williams and Miller 2012) rather than

41 declining themselves, suggesting increasing per capita impact on prey.

42   *C. abbreviata* preys on multiple coral host species including acroporids, *Orbicella* spp.,

43 *Diploria* spp. *Colpophylia natans*, *Agaricia* spp., and occasionally on other mounding coral

44 species (Miller 1981). Snails found on *A. palmata* are larger, older, have higher fecundity

45 (Johnston and Miller 2007), and consume more coral tissue than on other coral host species

46 (Bruckner 2000). The snails are typically found in groups (Bruckner et al. 1997; Bruckner 2000;

47 Baums et al. 2003a), feeding on coral tissue and leaving a feeding scar of exposed skeleton. They

48 are relatively sedentary, often remaining on a prey colony until no living tissue remains, at which

49 point they migrate to a neighboring colony (Bruckner 2000; Williams and Miller 2012).

50 Individual snails can consume up to 16 cm^2 of tissue per day (Brawley and Adey 1982; Baums et

51 al. 2003b), though they do not feed continuously throughout the year at that rate (Bruckner et al.

52 1997). In addition to directly removing *A. palmata* tissue during feeding, *C. abbreviata* may

53 indirectly affect corals by way of vectoring disease (Williams and Miller 2005) or attracting other

54   predators such as butterflyfish (Brawley and Adey 1982) and *Hermodice carunculata* (DW, pers

55   obs). Thus, *C. abbreviata* has substantial direct and potential indirect effects on *A. palmata*.

56   Because this predator has low mobility and a relatively long lifespan (up to 15 years; Johnston

57   and Miller 2007), it may be feasible to locally reduce their abundance to conserve *A. palmata*.

58   *Acropora palmata* was listed as threatened under the US Endangered Species Act (NMFS

59   2006) and has been proposed for uplisting to endangered (NMFS 2012) based on devastating

60   declines throughout its range. The ESA listing carries with it a mandate to pursue management

61   actions to foster recovery of the species (ESA, section 4f). Although predation is not the primary

62   factor causing decline of this species, recent trajectories suggest it may be a fundamental factor

63   inhibiting recovery and, at present, predation may be the most locally tractable threat. Even in

64   regions where *A. palmata* is relatively rare, such as the Florida Keys, its distribution is clumped

65   making targeted removal efforts logistically feasible. Therefore, both ecological and

66   legal/management conditions point to removal of *C. abbreviata* as a potential conservation action

67   that could be feasible at the local level. Earlier work (Miller 2001) showed removing *C.*

68   *abbreviata* snails on a colony scale can conserve *A. palmata* tissue, but nothing is known about

69   effectiveness in terms of recolonization rates or at a larger 'reef scale'. The current study utilized

70   long-term fixed monitoring plots of *A. palmata* colonies to conduct experimental *C. abbreviata*

71   (here after 'snail') removals to 1) determine the rate at which snails recolonize *A. palmata*

72   colonies, 2) evaluate detectable impacts on the host *A. palmata* population, 3) compare the size

73   distribution of recolonizing versus original snail populations, and 4) evaluate the costs of removal

74   for resource managers.

Methods

Long-term *Acropora palmata* demographic monitoring plots (7 m radius) at six sites in the upper Florida Keys National Marine Sanctuary (FKNMS) were used to implement a Before-After-Control-Impact (BACI) type design (Green 1979; Smith 2006) to evaluate the effects of snail removal. This design is useful in natural settings because initial variation among individual plots can be partitioned from treatment effects by comparing each plot's trajectory over time (before vs. after a manipulation) among plots subjected to different treatments. Each site included three plots numbered one to three when initially established for monitoring at least 1 year prior to the start of the experiment. Three snail removal treatments were assigned according to plot number: 1) removal of snails from *A. palmata* colonies only ("Ap Only"), 2) removal of snails from all host corals in the plot ("All Hosts"; mainly *A. palmata, Diploria* spp., *Orbicella* spp., and *Colpophylia natans*), and 3) "Control" in which snails were counted on the host corals in the plots, but were not removed.

Removal

This experiment proceeded in two phases (described in detail below); the first phase is referred to as the 'removal phase' and consisted of three removals beginning with an 'initial removal' of snails that provided the 'baseline' snail abundance and ending with a 'final removal'. The second phase is the 'recolonization phase' consisting of five surveys beginning after 'final removal' and ending at the 'final survey' when the snails were collected for analysis.

Removal of snails from host corals was performed by two SCUBA divers that were experienced in finding this somewhat cryptic gastropod species. Individual host colonies were searched, and when snails were found in the removal plots, the diver recorded the host species and number of snails on the colony. Snails were removed and placed in zip-top bags, pooled according to host species. Snail shell length was measured to the nearest 0.1 mm using Vernier

99   calipers. Due to the high abundance and small size of *Agaricia* spp. colonies, it was not feasible

100   to systematically locate all the colonies. However, when *Agaricia* colonies were encountered in

101   the All Hosts and Control plots, they were searched, and snails found in the All Host plots were

102   removed. Initial removal was conducted during 14-16 June 2011. Three weeks later we returned

103   to the treatment (Ap Only and All Hosts) plots to remove and measure any snails that were

104   overlooked in the initial removal. The snails from these two 'removals' were added together as

105   the 'baseline' snail abundance for each plot and will be referred to as the "initial" removal.

106   Snails were removed from all *A. palmata* colonies in the treatment plots again in September

107   2011 and January 2012 ('removal phase'). Thereafter, snails found on *A. palmata* were counted

108   but not removed in May 2012, September 2012, January 2013, May 2013 and August 2013

109   ('recolonization phase'). At the final survey in August 2013, all host colonies were measured

110   (length, width, height, and % live) and surveyed for snails in all plots. Snails were collected from

111   all hosts in the All Hosts treatment plots and *A. palmata* only in the Ap Only treatment plots. All

112   snails collected at the final survey were measured to compare the recolonized population with the

113   initial population. Shells were crushed to determine the presence (designating males) or absence

114   (designating females) of a penis. The time spent searching the host colonies and removing

115   encountered snails was recorded during the final survey and the averages among plots were used

116   to evaluate the 'effort' of each removal treatment.

117   During the removal and recolonization phases, routine monitoring of *A. palmata* in the study

118   plots continued as described in Williams et al. (2008). Once per year (fall), all *A. palmata*

119   colonies in each plot were counted and the length, width, and height were measured and % live

120   tissue was visually estimated. Tissue abundance was estimated as a live area index (LAI),

121   calculated by taking the colony's average dimension (average of length, width, and height)

122   squared and multiplying it by the visual estimate of % live tissue cover. The LAI is summed for

123   all colonies to get total tissue abundance for the 150 m^2 study plot. Three times per year a

124   randomly selected subset of tagged *A. palmata* colonies was further assessed for size, % live

125   tissue, and presence of disease, snails, and snail feeding scars. This work was done under permit

126   numbers FKNMS-2010-033, FKNMS-2010-130 and FKNMS-2012-030 from the Florida Keys

127   National Marine Sanctuary.

128   **Analyses**

129   *Effectiveness of Removal*

130   We examined the total number of snails found on *A. palmata* colonies in the plot (ApSnails),

131   the tissue abundance (LAI) of all *A. palmata* in the study plot (ApLAI), and the prevalence of

132   disease and feeding scars among a subset of tagged *A. palmata* colonies. We used a BACI

133   (Before-After-Control-Impact) design to compare the statistical interaction between time and

134   treatment for the removal treatments and control. The total number of ApSnails and the ApLAI

135   was compared among treatments using the initial (June 2011) and final (August 2013) surveys.

136   Because the prevalence of both disease and feeding scars vary temporally (Williams and Miller

137   2012), we compared the peak in prevalence from the year before the removal and the subsequent

138   peak observed after the removal. For disease prevalence we compared fall 2010 (before) and fall

139   2011 (after) and for feeding scars we compared spring 2011 (survey prior to removal) and spring

140   2012 (first survey after final removal). Each variable (ApSnails, ApLAI, and prevalence of

141   disease and feeding scars) was rank transformed to meet the assumption of normality and

142   homoscedasticity, and a repeated measures ANOVA was run on the ranks to look for significant

143   ($p \leq 0.05$) within-subject interactions between time (the Before/After factor) and treatments (the

144   Control/Impact factor) indicating that the trend in the measured parameter varied significantly

145   between treatments.

146   *Recolonization*

147   We examined the rate at which snails recolonized *A. palmata* in removal plots over the

148 recolonization phase. The number of snails present following the final removal in January 2012

149 was assumed to be zero and the number found at each subsequent survey during this

150 recolonization phase was plotted over time for each study plot and linear regression was used to

151 determine the equation for the line. With y set to the baseline snail abundance for that plot, we

152 solved for the projected date (x) that the number of snails in that plot would return to its baseline

153 abundance observed at the initial removal. The difference between the projected date and the date

154 of the January 2012 removal was calculated as the treatment 'effect duration' for that plot. A

155 Wilcoxon Matched-Pairs test was used to compare the baseline snail abundance, recolonization

156 rate, and effect duration between Ap Only and All Hosts removal treatments paired within site.

157 *Snail size*

158 In order to compare the population of recolonized versus initial snails, shell length of the

159 collected snails was measured and the data were log transformed to achieve normality. A two-way

160 ANOVA was used to compare shell lengths between the two removal treatments and time (initial

161 removal vs final survey). The size-frequency distributions of males and females at the final

162 survey could not be compared between treatments due to small sample size ($n \leq 39$; Table 1), but

163 the proportion of the population that was male was calculated as the number of male snails

164 divided be the total number of snails.

165 **Results**

166 **Removal**

167 Searching each 150 m^2 study plot required on average 30 person minutes ($\pm$ 16 minutes SD)

168 for *A. palmata* and an additional 21 person minutes ($\pm$ 10 minutes SD) when the other host

169 species were searched. A total of 279 snails were removed from *A. palmata* in the twelve 150 m^2

170   removal treatment plots (Table 1). In the follow-up removal three weeks later, an additional 40

171   were found for a total of 319 snails that were removed from *A. palmata* in the removal plots at

172   the initial survey in June 2011. A total of 157 snails were removed from other hosts in the 'all

173   hosts' treatment plots.

174   The mean number of snails found on *A. palmata* (ApSnails) in the removal plots remained

175   less than five per plot during the removal phase, then gradually increased after removals stopped

176   in January 2012 (Fig. 1). The interaction between time and treatment was significant for both the

177   total number of ApSnails per plot (Fig. 2a; p = 0.042) and the prevalence of feeding scars (Fig.

178   2d; p = 0.004); for both, the removal treatments decline significantly while the controls remained

179   unchanged. The tissue abundance (LAI) showed no change among all treatments (Fig. 2b). The

180   prevalence of disease was significantly higher in fall 2011 compared to fall 2010 (Fig. 2c; p =

181   0.016) with no significant treatment effects or interaction.

182   **Recolonization**

183   Despite high variability among individual removal plots, linear regressions of the number of

184   snails found at each survey (Fig. 3) yielded *r* values ≥ 0.7 within each plot. Both the baseline

185   abundance of ApSnails and the rate of snail recolonization (regression slopes of 0.002 to 0.050

186   snails d^{-1}) varied by an order of magnitude among reefs (Fig. 3). When treatment plots were

187   paired by site, neither the baseline abundance of ApSnails nor the recolonization rate differed

188   between treatments. If the Sand Island pair is excluded as an outlier (based on the extreme

189   number of snails found in the Sand Island All Hosts plot, Table 1), then the baseline number of

190   snails still does not differ between treatments, but the difference in recolonization rate between

191   treatments becomes marginally significant (Wilcoxon, Z = 2.02, n = 5, p = 0.043). The baseline

192   snail abundance and recolonization rate were highly correlated across all removal plots (Fig. 4).

193   Overall, calculated 'effect durations' ranged from 1.3 to 6.9 years (Fig. 3) with an overall average

194   of 4.3 ± 1.7 (± SD) years. Effect durations did not differ significantly between Ap Only removal

195   (4.5 ± 1.6 years; mean ± SD) and the All Hosts removal (5.5 ± 1.6 years; mean ± SD) treatments

196   (Wilcoxon, Z = 0.31, n = 6, p = 0.8).

Size frequency/Sex ratios

198   A two-way ANOVA on log-transformed shell lengths (size) was used to compare the

199   recolonized versus initial ApSnail populations between the two removal treatments (Fig. 5).

200   Mean shell length was significantly larger between the initial (24.4 mm ± 7.8 mm, pooled mean ±

201   SD; $F_{1, 465}$ = 8.61, p = 0.003; Fig. 5a-b) and final (22.1 mm ± 5.7 mm, pooled mean ± SD; Fig. 5c-

202   d) surveys but not between the two removal treatments ($F_{1, 465}$ = 1.09, p = 0.3) and there was no

203   significant interaction ($F_{1, 465}$ = 0.16, p = 0.7). A separate two-way ANOVA was also used to

204   compare the initial and final log transformed shell lengths between ApSnails (pooled treatments)

205   and the snails collected from other host corals in the All Hosts treatments (Fig. 6). Snails

206   collected from other host corals were significantly smaller (18.8 mm ± 3.6 mm, mean ± SD; $F_{1, 710}$

207   = 103.58, p < 0.001) than those collected from *A. palmata* (24.4 mm ± 7.8 mm, pooled mean ±

208   SD), and the snails collected at the initial survey were significantly larger (22.5 mm ± 7.2 mm,

209   pooled mean ± SD; $F_{1, 710}$ = 16.83, p < 0.001) than those collected at the final survey (20.3 mm ±

210   5.9 mm, pooled mean ± SD), but there was no significant interaction ($F_{1, 710}$ = 0.23, p = 0.6)

211   between host and time factors.

212   At the final survey, the proportion of males among ApSnails in the Ap Only treatment was

213   0.66 (54 males and 28 females) and 0.74 (52 males and 18 females) in the All Hosts treatment.

214   Unfortunately, we do not have gender ratios for the initial population, but as larger snails are

215   known to be female in this protandrous species (Johnston and Miller 2007), the larger snail sizes

216   of the initial population would be expected to reflect a lesser proportion of males relative to the

217   final population.

Discussion

Removal was effective in significantly decreasing both corallivore abundance and the prevalence of feeding scars observed 19 months following the snail removal. Consequent declines in the prevalence of disease and a parallel enhancement of total tissue abundance (LAI) might be expected, but both of these factors are strongly influenced by a multitude of additional known and unknown factors, thereby decreasing the ability to detect these parallel changes in the present study. However, based on the significantly lower prevalence of feeding scars we can deduce that less tissue was consumed by snails (Miller 2001).

The recolonization rate calculations, though complicated by high site-specific variability, indicate full recolonization to the baseline abundance of snails over a 4-year period. At the final survey, the average size of recolonizing snails was smaller than at the initial removal. Though the decrease in mean snail size was modest, the larger sized ApSnails (≥ 35 mm) were not observed to recolonize at all (Fig. 5). At the initial removal, the maximum snail size was 47.0 mm and at the final survey the maximum was 34.6 mm. The cumulative tissue consumption of smaller snails is expected to be less than for larger snails (Hayes 1989; Bruckner 2000; Baums et al. 2003b); thus, although this portion of the size distribution represented approximately 10% of the population, these larger snails likely were inflicting greater than 10% of the tissue loss.

In addition to the direct impact of feeding, fecundity is disproportionately higher in these large snails (Johnston and Miller 2007). At the initial removal there were 42 snails found with shell length > 34.6 mm. Based on the relationship between shell length and veliger production (Johnston and Miller 2007), we can estimate that these 42 snails, assuming they were all females, would have produced >715,000 veligers in one reproductive cycle (clutch). For comparison, if we look at the largest 10% of the final size distribution (females ranging from 29.8 to 34.6 mm), these 17 females are expected to yield approximately 155,000 veligers in one reproductive cycle.

242 In fact, all 46 female ApSnails found at the final survey combined would be predicted to yield

243 280,000 veligers in one clutch. Thus, the combination of fewer snails and the shift to smaller

244 sizes could potentially decrease snail reproductive output by more than 50%.

245   In the 4.3 years projected for full recolonization, it is possible that the snail size distribution

246 will also shift back to baseline size. Based on the size-age relationship reported by Johnston &

247 Miller (2007), the largest individual observed at the start of the experiment (i.e., 47 mm) might be

248 approximately 15 years old while the maximum size observed at the final survey would be

249 expected to be approximately 9 years old. However, it is also possible that the smaller sizes are

250 more vulnerable to predation due to thinner shells (e.g., Wainwright 1987) and will be kept from

251 attaining the larger less vulnerable sizes.

252   Recolonizing individuals appear to be primarily migrants from surrounding reef areas rather

253 than larval recruits. Although there were small increases in the smallest size bins (Fig. 6a and c),

254 the smallest recolonizing individuals found (~ 8 mm) are expected to be ~ 3 years old (Johnston

255 and Miller 2007), significantly older than the 1.5 years duration of the recolonization phase in

256 this experiment (January 2012 - Aug 2013). However, if the other host corals were the only

257 source of snails that recolonized *A. palmata* colonies, then we would expect a difference in size

258 distribution and numbers of recolonizing snails between the two removal treatments (Fig. 5c-d),

259 which was not the case. Although the snails on other host corals in the Ap Only treatment were

260 not measured at the start of the experiment, they would likely have had the same size distribution

261 as those collected in the All Hosts treatment at the start (Fig. 6b). Presumably, if these other host

262 coral species were the primary source of recolonizing ApSnails, then the size distribution of

263 ApSnails at the final survey (Fig. 5c) would be similar to the distribution of the snails collected

264 from other host corals at the initial removal (Fig. 6b). Specifically, there were relatively few

265 snails larger than 24 mm on the other host corals, yet more than one-third of recolonizing snails

266   were larger than 24 mm (Fig. 6c). Instead, the size distribution of recolonizing snails in both

267   removal treatments looks the same (Fig. 5c-d). Although the mean snail size is overall smaller at

268   the final survey than at the start, the mean size of ApSnails is still significantly larger (22.1 mm)

269   in the final survey than snails collected from other hosts (18.8 mm) at the initial removal (Fig. 6).

270   In our experiment, no significant added benefit was derived from the additional effort

271   required to remove snails from all host corals (Fig. 1). Removing snails from *A. palmata* only

272   required 30 diver minutes versus 51 diver minutes for removal from all hosts. The density of

273   other host colonies in the plots was 5 ± 4.9 colonies (mean ± SD) and a total of 21 ± 15.6 (mean ±

274   SD) snails per plot were found on these other host colonies. If the site with the unusually high

275   number of snails was excluded, the recolonization rates were marginally faster in plots where the

276   snails were not removed from other hosts. It is possible that in areas where the other hosts species

277   are more abundant or are harboring greater numbers of snails, the additional effort to remove

278   them would be worthwhile.

279   We removed snails at three surveys roughly three months apart and each requiring roughly 30

280   minutes of diver time. Interestingly, during these three sequential removals, the average number

281   of snails found on the subsequent survey did not diminish (Fig. 1; mean of ~2 to 5 snails) so it

282   does not seem that the pool of colonizing snails was depletable at these temporal and spatial

283   scales. There is also indication that, at least in some plots, the rate of snail arrival may accelerate

284   over time, which is consistent with the aggregating behavior of snails (DW, pers obs).

285   In planning snail removal as an *A. palmata* conservation effort, the cost (diver time) and

286   benefit (reduced snail load) must be balanced. With the mean effect duration of four years, one

287   strategy could be to perform a removal at four year intervals. However, our results showing high

288   site variability and the strong correlation of recolonization rate with initial snail load (Fig. 4)

289   suggest that the frequency or need for subsequent removals may be indicated by the number of

290 snails that are found at the initial removal. In another view, the mean rate of snail recolonization

291 appears to increase after one year (Fig. 1), so annual removal might be a useful target, at least for

292 areas of high snail abundance (>0.2 m^{-2}). Removals in the warmer months are likely to be more

293 efficient when corallivorous snails are more actively feeding (Al-Horani et al. 2011).

294 Additionally, although their egg production cycle is not well established, it is more common to

295 find egg cases with mature veligers in mid-to-late summer (DW, pers obs), thus, removal prior to

296 that may reduce larval production.

297   Our sites were located on spur and groove formations on the shallow fore reef. However, our

298 study plots did not occupy the full extent of a reef 'spur', leaving contiguous reef areas populated

299 with snails. In practice, removal from all corals on a contiguous spur may further prolong the

300 effect duration of the removal. This may not be practical in areas where there are not natural

301 breaks in reef structure, but removal from contiguous stands of *A. palmata* may be possible.

302 Effect of *A. palmata* colony density on snail recolonization rate was not tested in this study;

303 however, other studies have found that *C. abbreviata* abundance is generally lower in higher

304 density 'thicket'-type stands (Bruckner et al. 1997; Miller et al. 2002; Baums et al. 2003a) of *A.*

305 *palmata* colonies, so removal effort could be more efficiently focused on *A. palmata* stands with

306 intermediate or low colony density rather than dense thickets. Although removing snails is not

307 technically difficult, *C. abbreviata* is fairly well camouflaged and divers need to be trained to

308 recognize them to ensure effective removal and to minimize collection of other non-corallivorous

309 species such as *Thais deltoidea* that are commonly found around *A. palmata*.

310   Given the ecologically and legally imperiled status of *A. palmata*, and the intractability of

311 managing or reducing many of its ongoing threats, proactive conservation measures that can be

312 implemented at a local level are needed. This experiment demonstrates the effectiveness of snail

313 removal at a local scale with a 30 minute diver investment effectively reducing corallivore loads

314 over an estimated four year time scale in seven meter radius plots containing *A. palmata*.

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Figure captions

Figure 1 Number of *Coralliophila abbreviata* found on *Acropora palmata* per plot (mean ± SE). The initial removal occurred in June 2011, remaining snails were removed through January 2012 (removal phase, gray dots) after which they were only counted and left in place during the survey phase (solid dots)

Figure 2 Before-After-Control-Impact analysis of a) the total number of *Coralliophila abbreviata* found on *Acropora palmata* in a study plot, b) the *A. palmata* tissue abundance as measured by the live area index (LAI, see text), c) the prevalence of white disease on a random subset of *A. palmata* colonies during the seasonal peak in disease before and after the initial removal, and d) the prevalence of *C. abbreviata* feeding scars on this random subset of *A. palmata* colonies at the survey prior to the initial removal and one year later. All points are mean ± standard error. Data were rank transformed for analysis and the p-values based on the transformed data are shown

Figure 3 Number of *Coralliophila abbreviata* snails found on *Acropora palmata* in each plot where they were removed from *Acropora palmata* only (Ap Only) and from all host coral species following the removal phase of the experiment. The dotted line indicates the baseline number of *C. abbreviata* that were removed from that treatment plot at the start of the experiment in June 2011. 'Effect duration' is the estimated time for the number of snails to reach the baseline (recolonization), according to the regression for each plot

410   Figure 4 Recolonization rate (number of snails per day) based on the slope of the linear

411   regressions (Fig. 3) versus the number of snails found in each study plot at the initial removal

412   Figure 5 Size and gender (Sept 2013 only) frequency distribution for the *Coralliophila*

413   *abbreviata* snails collected from *Acropora palmata* host colonies in the a) Ap Only (snails

414   removed from *A. palmata* only) and b) All Hosts (snails removed from all host coral species)

415   treatments at the initial removal (June 2011) and at the final survey (Sept 2013) for c) Ap Only

416   and d) All Hosts treatments

417   Figure 6 Size and gender (Sept 2013 only) frequency distribution for the *Coralliophila*

418   *abbreviata* snails collected from a) *Acropora palmata* host colonies and b) other host species at

419   the initial removal (June 2011) and at the final survey (Sept 2013) from c) *A. palmata* and d) and

420   other host coral species

Figure 1

Coralliophila abbreviata abundance in experimental plots

Number of *Coralliophila abbreviata* found on *Acropora palmata* per plot (mean ± SE). The initial removal occurred in June 2011, remaining snails were removed through January 2012 (removal phase, gray dots) after which they were only counted and left in place during the survey phase (solid dots).
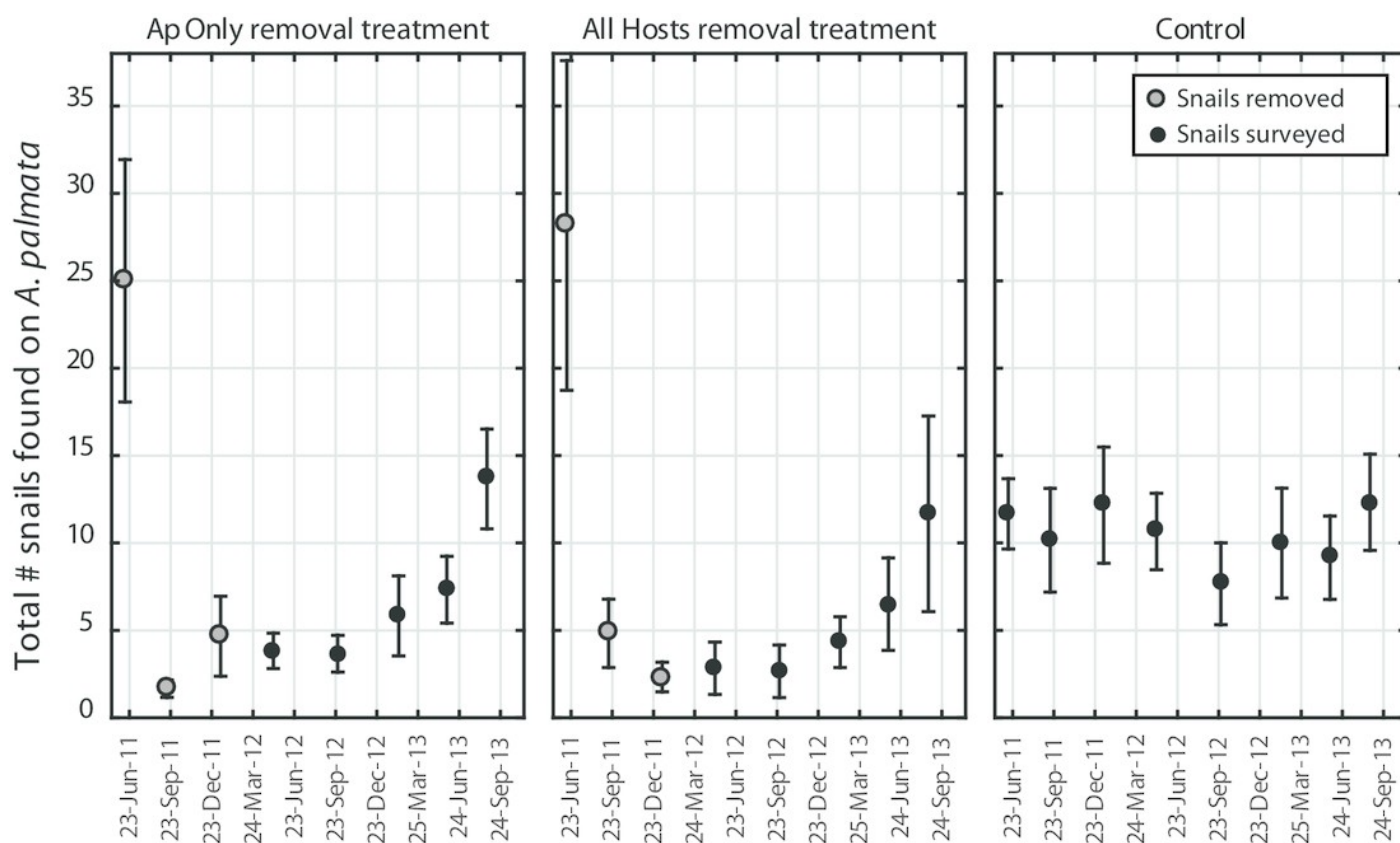
Figure 2

Before-After-Control-Impact analysis

Before-After-Control-Impact analysis of a) the total number of *Coralliophila abbreviata* found on *Acropora palmata* in a study plot, b) the *A. palmata* tissue abundance as measured by the live area index (LAI, see text), c) the prevalence of white disease on a random subset of *A. palmata* colonies during the seasonal peak in disease before and after the initial removal, and d) the prevalence of *C. abbreviata* feeding scars on this random subset of *A. palmata* colonies at the survey prior to the initial removal and one year later. All points are mean ± standard error. Data were rank transformed for analysis and the p-values based on the transformed data are shown.
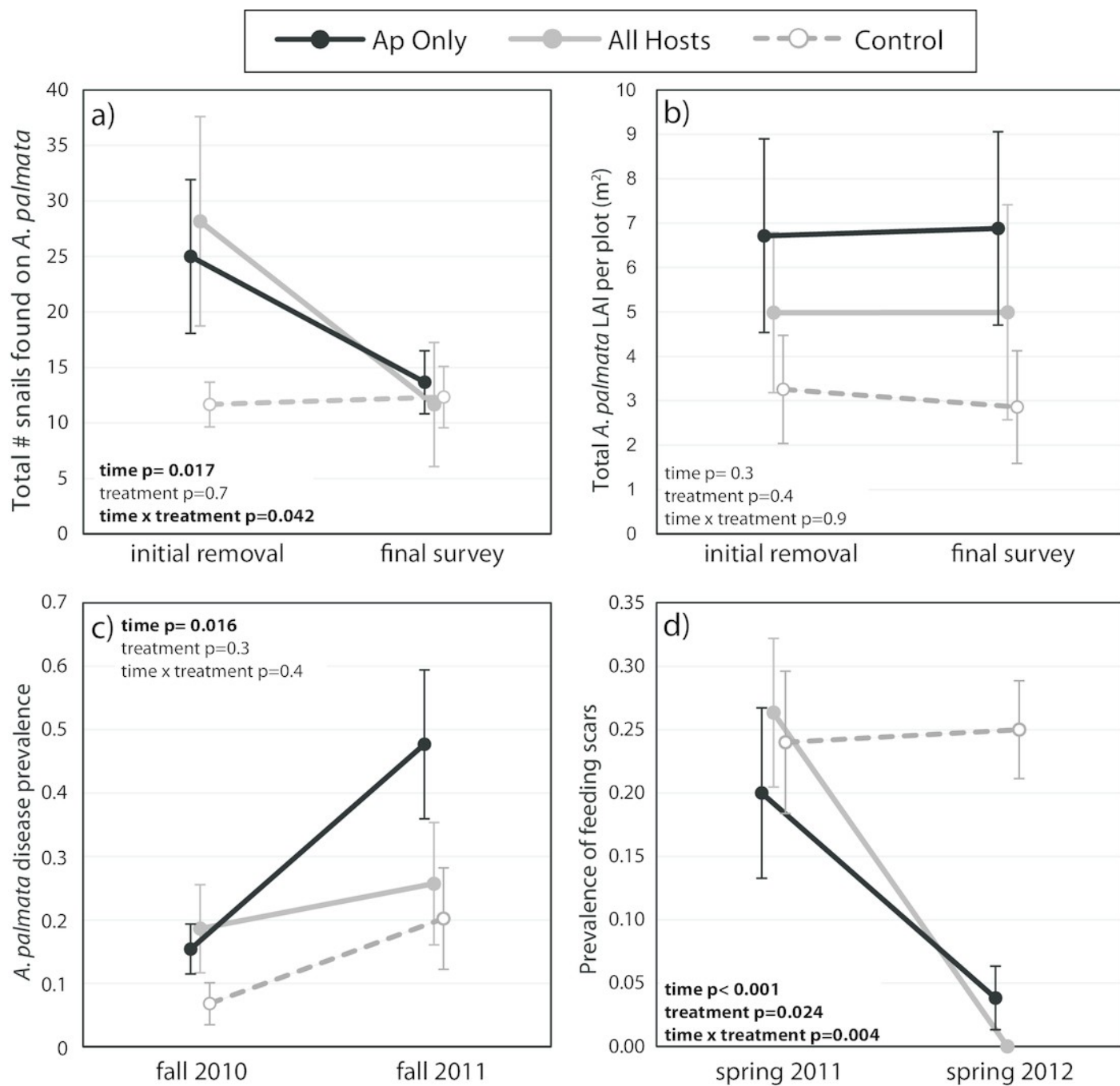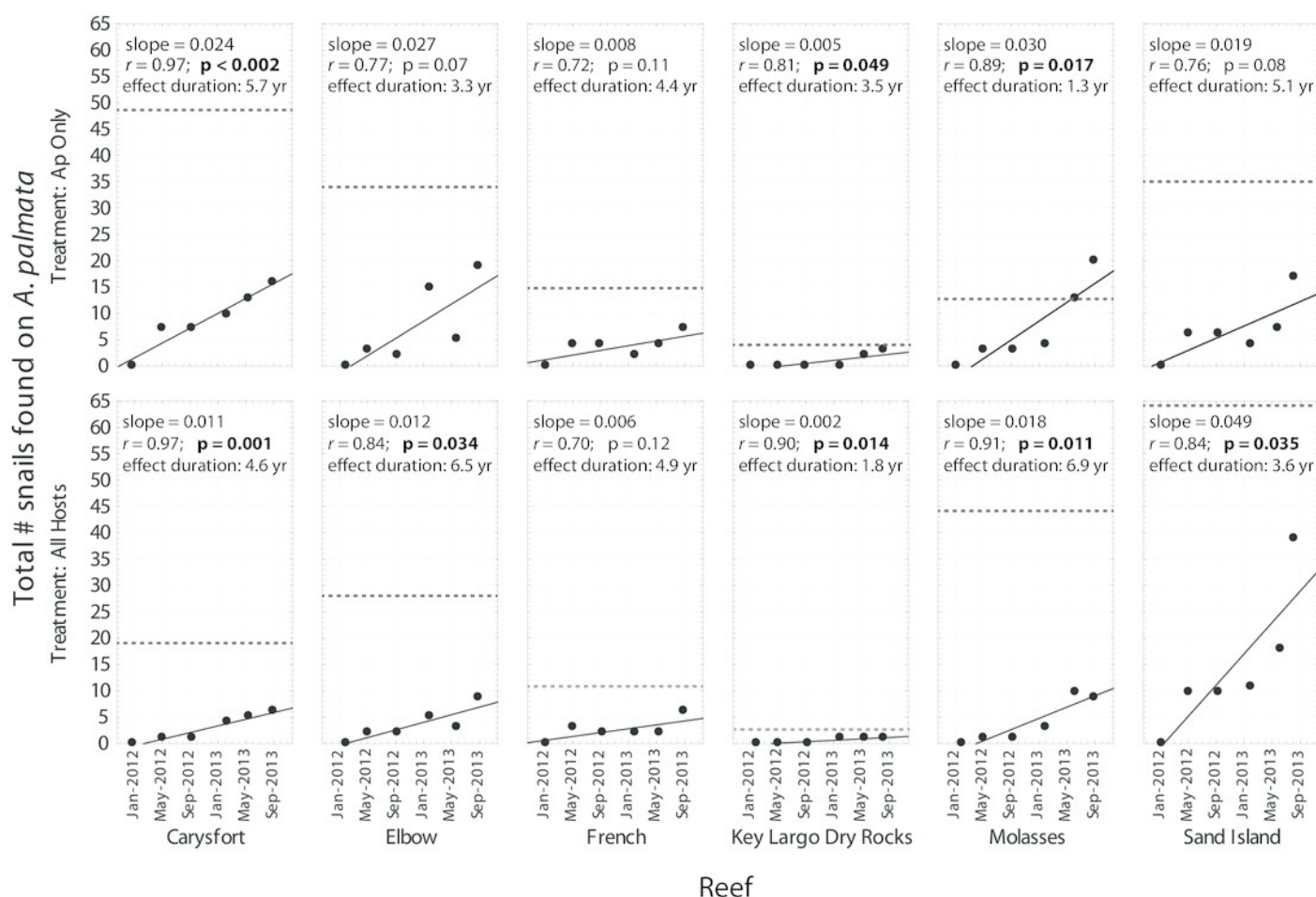
Figure 3

Coralliophila abbreviata recolonization

Number of *Coralliophila abbreviata* snails found on *Acropora palmata* in each plot where they were removed from *Acropora palmata* only (Ap Only) and from all host coral species following the removal phase of the experiment. The dotted line indicates the baseline number of *C. abbreviata* that were removed from that treatment plot at the start of the experiment in June 2011. 'Effect duration' is the estimated time for the number of snails to reach the baseline (recolonization), according to the regression for each plot.
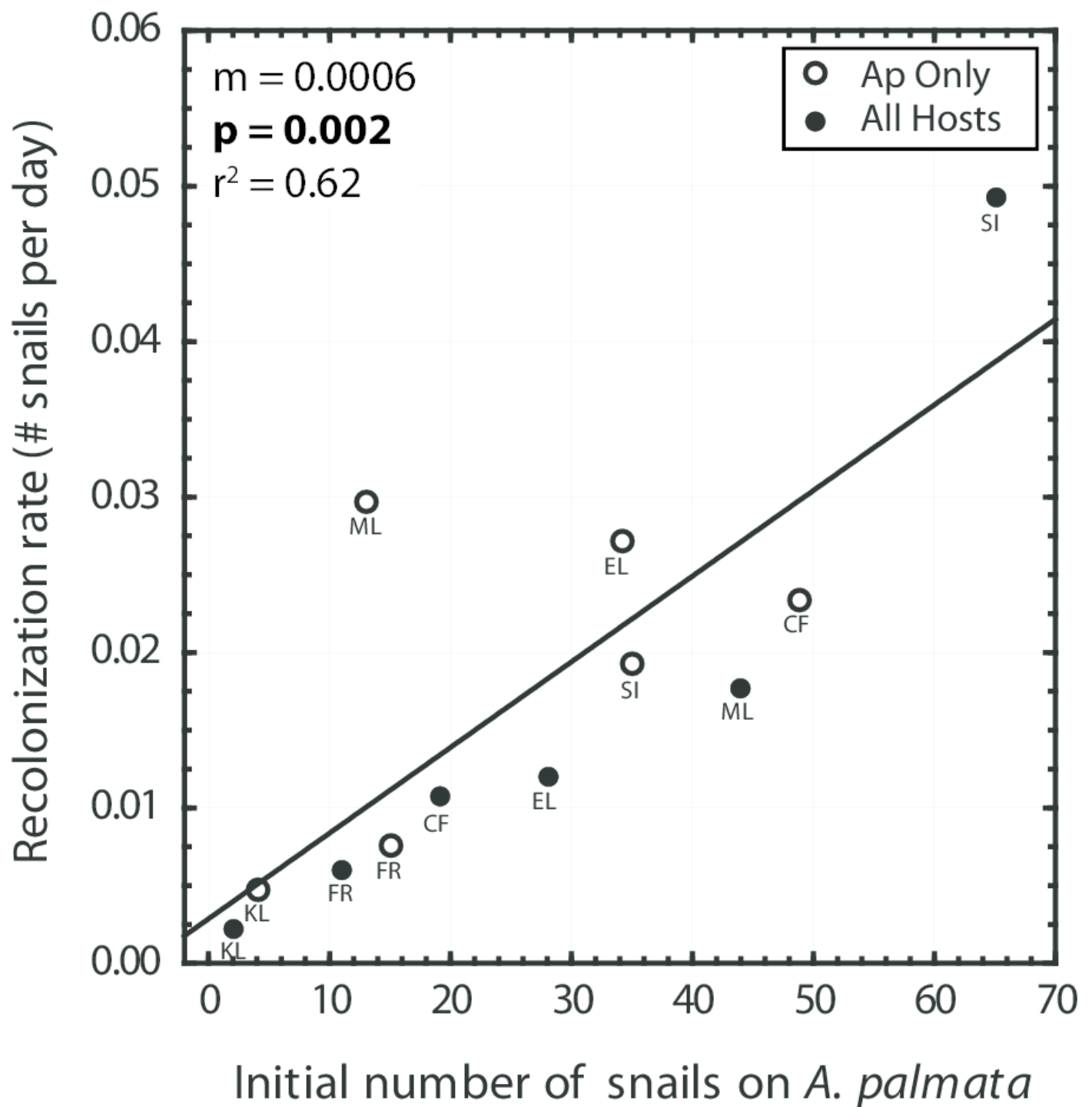
Figure 4

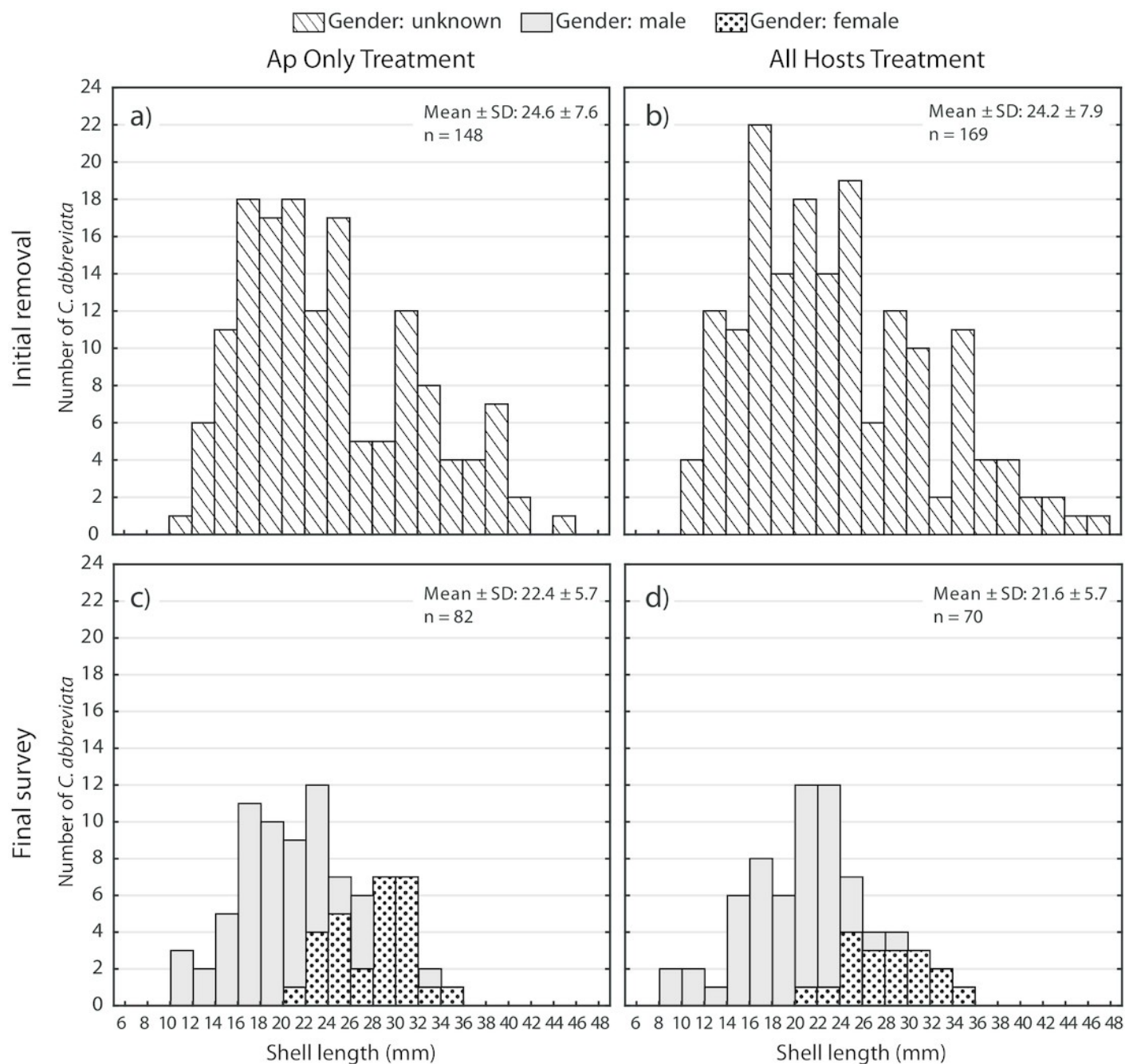*Coralliophila abbreviata* recolonization rate

Recolonization rate (number of snails per day) based on the slope of the linear regressions (Fig. 3) versus the number of snails found in each study plot at the initial removal.

Figure 5

Coralliophila abbreviata size and gender frequency distribution

Size and gender (Sept 2013 only) frequency distribution for the *Coralliophila abbreviata* snails collected from *Acropora palmata* host colonies in the a) Ap Only (snails removed from *A. palmata* only) and b) All Hosts (snails removed from all host coral species) treatments at the initial removal (June 2011) and at the final survey (Sept 2013) for c) Ap Only and d) All Hosts treatments.

Figure 6

Coralliophila abbreviata size and gender frequency distribution

Size and gender (Sept 2013 only) frequency distribution for the *Coralliophila abbreviata* snails collected from a) *Acropora palmata* host colonies and b) other host species at the initial removal (June 2011) and at the final survey (Sept 2013) from c) *A. palmata* and d) and other host coral species.
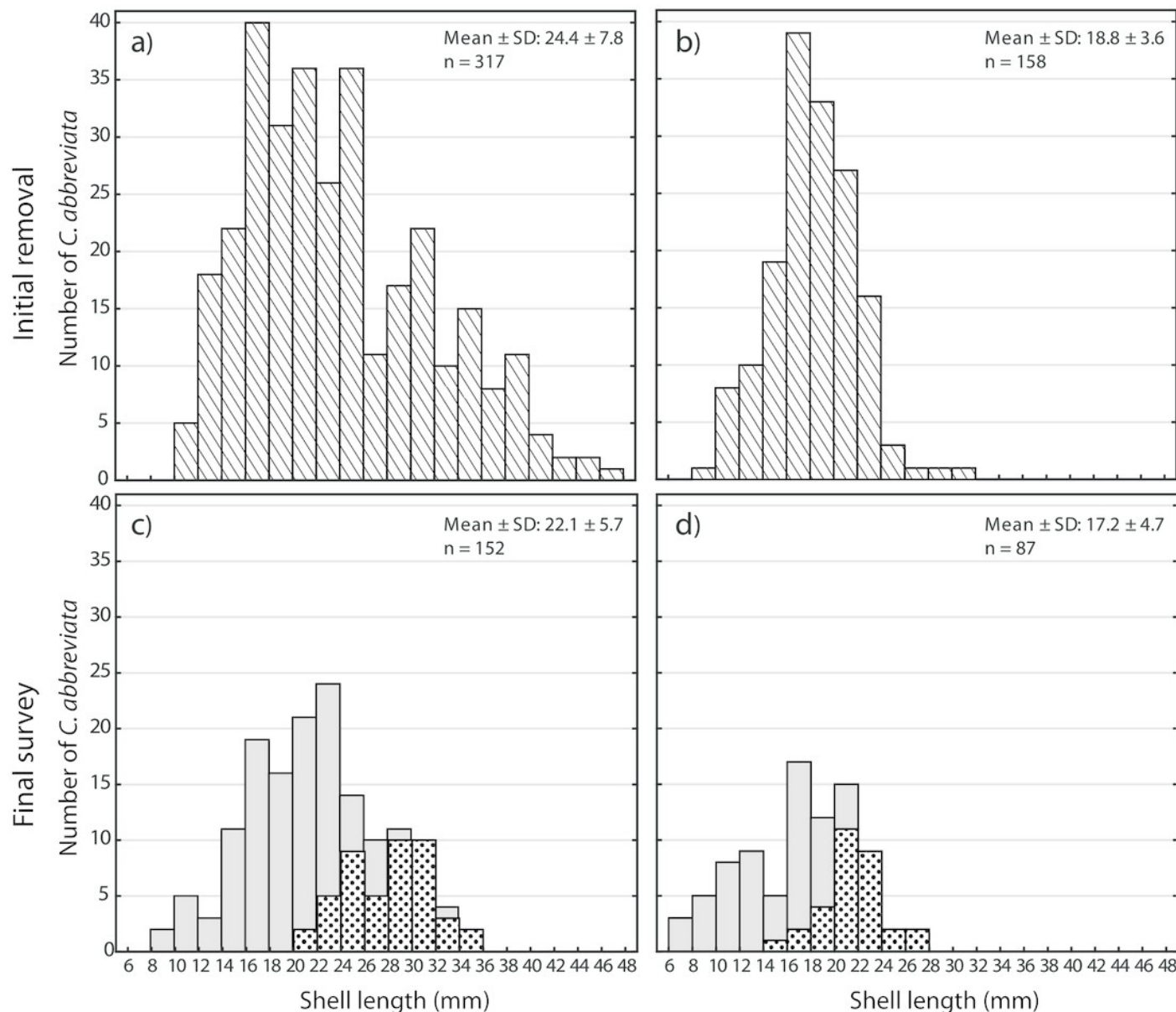
Table 1(on next page)

Summary of coral host colonies and *Coralliophila abbreviata* snails found in the study plots in the initial and final survey.

Observations at each study plot in three experimental treatments: removal of *Coralliophila abbreviata* snails from *Acropora palmata* only (Ap Only), from all coral host species (All Hosts) and controls in which snails were counted but not removed. Coral colonies and snails counted at the initial survey in June 2011 and the final survey in August 2013. *A. palmata* LAI (live area index) is calculated based on colony measurements described in the text.

Treatment	Reef	*A. palmata* colonies		*A. palmata* Snails		*A. palmata* LAI (m^2)		Other host colonies		Other host snails	
		Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final
Ap Only	Carysfort	32	21	49	16	8.4	8.4		0		4
	Elbow	55	76	34	19	15.2	14.8		1		0
	French	42	57	15	7	9.7	10.5		19		29
	Key Largo Dry Rocks	11	11	4	3	1.6	0.7		5		9
	Molasses	11	15	13	20	2.5	2.3		0		0
	Sand Island	18	21	35	17	2.8	4.7		1		1
All Hosts	Carysfort	8	13	19	6	6.7	2.3	3	3	61	34
	Elbow	28	31	28	9	5.0	4.8	2	1	11	3
	French	29	44	11	6	1.4	2.1	6	5	39	21
	Key Largo Dry Rocks	22	15	2	1	0.5	0.2	2	2	19	0
	Molasses	29	40	44	9	3.6	3.9	7	8	19	25
	Sand Island	41	51	65	39	12.7	16.6	1	1	9	4
Control	Carysfort	13	9	16	15	0.9	0.1	6	4	23	4
	Elbow	22	29	16	18	4.2	3.4	4	4	14	6
	French	24	20	8	5	1.9	1.2	15	15	29	31
	Key Largo Dry Rocks	10	9	11	10	3.0	2.5	6	6	10	10
	Molasses	22	31	15	21	8.7	8.7	7	6	7	8
	Sand Island	10	9	4	5	0.8	1.2	6	4	10	8