Enhanced susceptibility to predation in corals of compromised condition

Allan J Bright, Caitlin M Cameron, Margaret W Miller

The marine gastropod, *Coralliophila abbreviata*, is an obligate corallivore that causes substantial mortality in Caribbean *Acropora* spp. Considering the imperiled status of *Acropora cervicornis* and *A. palmata*, a better understanding of ecological interactions resulting in tissue loss may enable more effective conservation strategies. We examined differences in susceptibility of *A. cervicornis* to *C. abbreviata* predation based on coral tissue condition. Coral tissue condition was a strong determinant of snail prey choice, with snails preferring *A. cervicornis* fragments that were diseased or mechanically damaged over healthy fragments. In addition, snails always chose fragments undergoing active predation by another snail, while showing no preference for a non-feeding snail when compared with an undisturbed prey fragment. These results indicate that the condition of *A. cervicornis* prey influenced foraging behavior of *C. abbreviata*, creating a potential feedback that may exacerbate damage from predation in coral populations compromised by other types of disturbance.

1   Enhanced susceptibility to predation in corals of compromised condition

2   **Abstract**

3   The marine gastropod, *Coralliophila abbreviata*, is an obligate corallivore that causes substantial

4   mortality in Caribbean *Acropora* spp. Considering the imperiled status of *Acropora cervicornis*

5   and *A. palmata*, a better understanding of ecological interactions resulting in tissue loss may

6   enable more effective conservation strategies. We examined differences in susceptibility of *A.*

7   *cervicornis* to *C. abbreviata* predation based on coral tissue condition. Coral tissue condition was

8   a strong determinant of snail prey choice, with snails preferring *A. cervicornis* fragments that

9   were diseased or mechanically damaged over healthy fragments. In addition, snails always chose

10 fragments undergoing active predation by another snail, while showing no preference for a non-

11 feeding snail when compared with an undisturbed prey fragment. These results indicate that the

12 condition of *A. cervicornis* prey influenced foraging behavior of *C. abbreviata*, creating a

13 potential feedback that may exacerbate damage from predation in coral populations

14 compromised by other types of disturbance.

15

16 Allan J. Bright[1,2], Caitlin M. Cameron[1,2], Margaret W. Miller[2]

17 [1]Cooperative Institute for Marine and Atmospheric Studies, University of Miami, 4600

18 Rickenbacker Cswy, Miami, FL 33149, USA

19 [2]National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Dr.,

20 Miami FL 33149, USA

21 Corresponding author: Allan J. Bright; University of Miami, 4600 Rickenbacker Cswy, Miami,

22 FL 33149, USA; Email: allan.bright@noaa.gov; Telephone: 305-365-4561

Introduction

24 Corallivory is widely understood to have significant, if sometimes underestimated, effects on

25 scleractinian coral populations (Rotjan & Lewis, 2008). Depending on the type and intensity of

26 predation, corallivory may result in positive or negative ecological responses (Cole, Pratchett &

27 Jones, 2008). While, at the community level, moderate predation pressure has sometimes been

28 positively correlated with an increase in species diversity (Menge & Sutherland, 1976), for an

29 individual coral, predation often equates to partial mortality that may compromise physiological

30 processes such as growth (Meesters, Noordeloos & Bak, 1994) and reproductive success (Van

31 Veghel & Bak, 1994). Predation can also be associated with negative indirect effects; if tissue

32 regeneration is incomplete or too slow following predation, spatial competitors such as algae and

33 sponges can colonize the dead areas, potentially introducing a myriad of negative interactions

34 (Bak & Steward-Van Es, 1980). Additionally, some corallivores are known to vector disease

35 (Sussman et al., 2003; Williams & Miller, 2005), and tissue lesions (likely including those from

36 partial predation) have been cited as a pre-requisite to disease transmission in *Acropora*

37 *cervicornis* (Gignoux-Wolfson, Marks & Vollmer, 2012).

38

39 While predation among healthy coral populations can promote a stable equilibrium, within

40 degraded coral populations, the per capita relative impact of corallivory is likely to increase as

41 coral cover decreases, potentially affecting the fitness and recovery of affected coral populations

42 (Jayewardene, Donahue & Birkeland, 2009). This was observed on surveyed reefs in Jamaica

43 where populations of *A. cervicornis* were reduced by the acute disturbance of Hurricane Allen.

44 As a result, predation by the corallivorous gastropod, *Coralliophila abbreviata*, was concentrated

45   on remaining individuals resulting in further population declines of *A. cervicornis* rather than

46   recovery (Knowlton, Lang & Keller, 1990).

47

48   Abiotic and biotic disturbances such as hurricanes, disease and bleaching not only reduce coral

49   populations, but may affect the 'condition' of the remaining colonies yielding broken branches,

50   lesions, compromised immune response (Bak & Criens, 1981), growth (Bak, 1983) and

51   reproduction (Rinkevich & Loya, 1979). Furthermore, studies have shown that stressed corals

52   are more susceptible to ambient predation (Morton, Blackmore & Kwok, 2002; Wolf & Nugues,

53   2013) suggesting that predation pressure on a focal coral may increase as a result of disturbance-

54   related physiological stress in addition to a potential numerical effect (i.e. higher ratio of

55   predators to surviving prey). Field studies on the impact of predation following disturbances such

56   as Knowlton, Lang & Keller (1990) cannot distinguish the relative influence of diminished coral

57   abundance versus coral condition.

58

59   The *Acropora-Coralliophila* relationship provides a good model for evaluating the relative

60   influence of coral condition (i.e. healthy, diseased, damaged, etc.) on predator behavior.

61   Considering the region-wide declines of *Acropora* spp., many populations may exist below a

62   threshold abundance where they are now at heightened vulnerability to predation pressure.

63   *Coralliophila abbreviata* is an obligate corallivore with an asymmetrical preference for

64   *Acropora* spp. prey (Johnston & Miller, 2014) and may thus pose a substantive risk to the

65   recovery of decimated *Acropora* populations. In the Florida Keys, predation by *C. abbreviata*

66   was the most prevalent factor causing tissue loss among remnant populations of *A. palmata*,

67   accounting for approximately 29% of all tissue mortality (Williams & Miller, 2012), and is

68   recognized as one of the top three proximal threats to the recovery of wild (Bruckner, 2002) and

69   restored *Acropora* populations (Johnson et al., 2011) throughout the Caribbean. Currently,

70   management actions are underway throughout the Caribbean to enhance *Acropora* population

71   recovery via conservation and restocking strategies. Understanding the interactions of factors

72   contributing to the loss of Caribbean acroporids may allow for more effective conservation

73   strategies for these species. We took advantage of the experimental system offered by *in situ*

74   nursery propagation of *A. cervicornis* to conduct field choice assays testing the hypothesis that

75   susceptibility to colonization by the corallivore, *C. abbreviata*, would be enhanced for corals

76   with disease or mechanical damage relative to an apparently healthy coral.

77

78   **Materials and Methods**

79   This study was conducted at a coral field nursery operated by the Coral Restoration Foundation

80   (CRF) located off Tavernier, Florida (24° 59'N, 80° 26'W) from June to September 2013 (under

81   permit # FKNMS-2013-065). The nursery is located on sand bottom surrounded by seagrass at a

82   depth of 10 m and provided *Acropora cervicornis* fragments for use in choice experiments.

83   *Coralliophila abbreviata* were collected from Pickles Reef (24° 59'N, 80° 24'W), transported

84   2.2 km to the nursery and kept in holding cages until use in choice experiments. Snails were held

85   separately based on the host species from which they were collected: *A. cervicornis* ($n = 38$) or

86   *A. palmata* ($n = 55$). Snails were starved for at least one week prior to use in choice trials.

87

88   Treatment chambers were made by modifying plastic compartment boxes (40 x 23 x 8 cm). Each

89   chamber contained two choice arenas with a removable lid, which was secured with cable ties

90   during trial periods (Fig. 1A). A single choice arena consisted of a Y-maze with the subject snail

91 staged at one end facing two treatment lanes and a treatment coral loosely secured at the end of

92 each lane. Rectangular cutouts covered with window-screen mesh were at each end of the

93 treatment chamber to facilitate flow. Chambers were oriented relative to predominant currents to

94 allow water flow from the treatment coral toward the snail staging area. To minimize water

95 exchange between treatment lanes and arenas, Velcro felt was glued to the top of the walls of

96 each treatment lane allowing the lid to lay flush with no gaps. Each of ten experimental

97 chambers was secured to a cinder block and set on sand bottom approximately 1 m apart (Fig.

98 1B).

99

100 Three types of prey choice experiments were conducted (Fig. 1C-E): healthy coral versus

101 diseased coral (H v D, $n = 52$), healthy coral versus coral with mechanical damage (H v M, $n =$

102 58) and healthy coral versus coral with active snail predation (H v P; $n = 3$). Prior to the start of

103 the experiment, healthy fragments were snipped from apparently healthy nursery colonies and

104 the cut surfaces were allowed to heal for at least two weeks in the field in order to yield

105 completely undisturbed, healthy tissue. Disease progression is intermittent in *A. cervicornis*

106 requiring actively diseased samples to be identified immediately at the start of a trial. Thus,

107 diseased branch tips were collected from cultured coral with active tissue loss and snipped

108 immediately prior to trials within an area of already-dead skeleton (i.e. no tissue disturbance),

109 approximately 2 cm from the tissue margin. Fragments with mechanical damage were prepared

110 by snipping branch tips from healthy coral, and, immediately prior to the start of a trial, a 3–5 cm

111 long abrasion was created with a clean, dead *A. cervicornis* branch. This treatment was included

112 to mimic the type of damage inflicted from abrasion during storms or hurricanes. At the end of

113   any trial, if a snail was actively feeding on a healthy coral, the coral and feeding snail were

114   immediately transferred to serve as a choice in a subsequent H v P trial (Fig. 1E).

115

116   *Coralliophila abbreviata* are known to be gregarious (Bruckner, Bruckner & Williams, 1997); so

117   there is an aspect of prey choice that may be purely social. Thus, we also tested snail preference

118   between a healthy coral fragment versus a solitary snail with no coral (H v S, $n = 45$). In these

119   trials, a treatment snail was tethered via a small length of twine glued to its shell at the treatment

120   end of one of the Y-maze lanes with a healthy coral at the end of the other lane (Fig. S1).

121

122   The position of the healthy coral and treatment coral/snail was alternated between the two lanes

123   in subsequent trials. Following each trial, the chamber was flushed of all sand and debris, and the

124   walls and floors were rigorously wiped down with a brush or a diver's gloved-hand to reduce

125   carryover of mucus or other potential cues. Trials were pooled among those conducted during

126   daytime (8:00 am to approximately 4:00 pm; ~8 h duration) and nighttime (sunset to a few hours

127   after sunrise; ~16 h duration).

128

129   During each trial, subject snails were left alone to choose a treatment lane. If the subject snail did

130   not travel more than 5 cm down a treatment lane or remained in the staging area, the trial was

131   determined as 'no choice' and excluded from analyses (n represents only the trials where a

132   choice was made; Table 1; see Table S1 for daytime and nighttime trials separated). The

133   proportion of trials in which a choice was made (i.e. response rate) ranged from 41 to 72% across

134   the three treatments (D, M and S), which is well within the range of response rates reported in

135   other published Y-maze choice studies using gastropod subjects (range: 27 to 100%; Nakashima,

136   1995; Avila, 1998; Rilov, Gasith & Benayahu, 2002).

137

138   For each treatment except H v S, trials among the two host-source subject snails are pooled for

139   analysis as no difference was found between snails sourced from *A. palmata* and *A. cervicornis*.

140   Additionally, trials are pooled among daytime and nighttime for each treatment as no difference

141   was found in preferences expressed during daytime versus nighttime. Differences in frequencies

142   of choices made between healthy and treatment corals/snail were assessed using a Pearson's chi-

143   squared test. The variation in activity levels (i.e. proportion of trials in which a choice was made)

144   between daytime versus nighttime trials was analyzed using 2×2 contingency tables (Statistica

145   Statistical Software v6.0).

146

147   **Results and Discussion**

148   Coral condition significantly affected prey preference of *Coralliophila abbreviata* snails sourced

149   from *Acropora* spp. host colonies. In 70.8% of the trials, snails preferred corals with either

150   disease ($df = 1$, $p < 0.001$, Fig. 2A) or mechanical damage ($df = 1$, $p = 0.01$, Fig. 2A) over

151   apparently healthy corals. Other studies have shown similar results for the Pacific corallivorous

152   snail, *Drupella rugosa*, where snails were attracted to corals stressed by either mechanical

153   damage, low salinity or low water temperature suggesting that corals stressed by additional

154   factors beyond the scope of the present study may manifest a similar enhanced susceptibility to

155   corallivores (Morton, Blackmore & Kwok, 2002; Tsang & Ang, 2015).

156

157   It is well known that chemoreception is important in foraging behavior of marine benthic

158   organisms (Kohn, 1961; Hay, 2009). Although the specific mode of attractant to prey has not

159   been studied for *C. abbreviata*, it seems likely that variable chemical cues may underlie their

160   preferences. Abraded coral tissue releases mucus and interstitial content that contains primary

161   metabolites such as proteins and amino acids which may attract consumers (Hay, 2009). The

162   release of mucus and/or secretions by damaged cells were the suggested cause of attractants for

163   increases of the corallivorous snail, *D. rugosa,* to stressed corals in Hong Kong (Morton,

164   Blackmore & Kwok, 2002). Similarly, Kita et al. (2005) showed an increase in 'feeding-

165   attractant activity' by the corallivorous snail, *Drupella cornus*, when offered montiporic acids

166   isolated from the prey coral, *Montipora* sp., which are suggested to be expelled with coral

167   mucus. As this study only examined behavioral responses based on short distance cues, further

168   studies should determine a range of distances that snails are able to detect such cues to better

169   infer snail foraging patterns on a reef scale.

170

171   A similar mechanism that attracts snails to mechanically damaged corals may apply to diseased

172   coral tissue as it may result in tissue deterioration and the production of excess mucus. However,

173   although mechanically damaged corals used in this study appeared to produce more mucus and

174   expel more interstitial content than diseased corals, snails had a slightly stronger attraction to

175   diseased coral (75% of choices made) than mechanically damaged coral (65.5% of choices

176   made) suggesting there may be something more complex attracting the snails than simple

177   quantity of these exudates. Additionally, as this study did not induce disease for H v D treatment

178   corals, it is possible that an undescribed physiological difference in corals making them more

179   susceptible to disease may also make them more attractive to snails rather than the diseased

180   condition *per se*.

181

182   Though there was only opportunity to conduct limited trials of the H v P treatment ($n = 3$), 100%

183   elicited a choice and 100% chose the fragment under active predation (P) suggesting a strong

184   bias toward prey fragments with active conspecific snail feeding. To ensure that the subject snail

185   was not attracted to the mere presence of a conspecific, H v S trials were conducted and showed

186   no significant preference for the conspecific snail relative to a healthy coral (Fig. 2B). However,

187   the following of conspecific mucus trails has been reported for the marine mud snail, *Ilyanassa*

188   *obsolete* (Trott & Dimock, 1978) and has been suggested to account for aggregation behavior in

189   the corallivorous snail, *Cyphoma gibbosum* (Gerhart, 1986). Yet, considering that traces of

190   previous mucus trails were removed (see methods), this preference may be the result of damaged

191   coral tissue releasing interstitial attractants (described above) or feeding mucus produced by the

192   feeding snail.

193

194   Intraspecific behavioral differences in *C. abbreviata* sourced from *A. palmata* and *A. cervicornis*

195   colonies were evident in H v S trials (Fig. 2B) and in activity level based on time of day (Table

196   S1). Snails sourced from *A. cervicornis* showed a strong preference for healthy coral over a

197   solitary snail with no coral, while snails sourced from *A. palmata* showed no preference for

198   either treatment. Additionally, snails sourced from *A. palmata* were significantly more active at

199   night than during the day (evidenced by proportion of trials in which a choice was made),

200   whereas, snails sourced from *A. cervicornis* showed no difference in activity level between

201   daytime and nighttime trials. Intraspecific behavioral differences have been shown for a number

202 of marine species (e.g., Stachowicz & Hay, 2000; Crosby & Reese, 2005; Jordaens, Dillen &

203 Backeljau, 2009). In *C. abbreviata*, behavioral and population structural differences (e.g.

204 size/age structure, sex ratio, etc.) have been previously documented between acroporid and non-

205 acroporid host corals (Hayes, 1990; Baums, Miller & Szmant, 2003a; Johnston & Miller, 2007),

206 despite genetic results showing it to be a single species throughout the Caribbean (Johnston,

207 Miller & Baums, 2012). To our knowledge, no previous studies have documented intraspecific

208 behavioral differences of *C. abbreviata* between two *Acropora* spp. host corals as evident in our

209 results. One explanation may be that *A. cervicornis*-sourced snails were presented with their

210 native host prey species, whereas *A. palmata*-sourced snails were presented with a non-host prey

211 species. Some sort of host conditioning may result in differing attractiveness of native versus a

212 congeneric prey alternative. However, such differences were unexpected since the tissue of *A.*

213 *cervicornis* and *A. palmata* are qualitatively similar (thin tissues on perforate skeleton) and have

214 similar nutritional quality as indicated by C:N ratios (Ac = 6.1 ± 0.9, Szmant, Ferrer &

215 FitzGerald, 1990; Ap = 6.3 ± 0.3, Baums, Miller & Szmant, 2003b).

216

217 Coral disease and physical damage occur regularly on coral reefs, and, as changing climate is

218 predicted to bring increases in intensity and/or frequency of strong storms (McWilliams et al.,

219 2005; Knutson et al., 2010), as well as disease (Harvell et al., 2002), it is crucial to understand

220 how corals may be directly and indirectly affected by these disturbances. This study highlights

221 the enhanced vulnerability of remnant coral populations following acute disturbance events such

222 as storms or disease outbreaks due to corallivore behavioral preferences. The indirect effect of

223 attracting snail predators to these impacted corals implies ongoing tissue loss from predation

224 inhibiting potential recovery. Furthermore, there is likely a complex feedback between disease

225 risk and snail predation as *C. abbreviata* has been shown to vector disease among *A. cervicornis*

226 colonies (Williams & Miller, 2005). Although corallivory by invertebrates is relatively well-

227 documented, corallivore behavior and its potential influence on recovery of threatened or

228 endangered coral populations has received little attention. Understanding such behavioral

229 complexities can aid in epidemiological and predictive modelling of disease dynamics and

230 transmission in *Acropora* spp. populations as well as improved species recovery strategies such

231 as targeting snail removal efforts (Williams et al., 2014) following specific types of disturbance.

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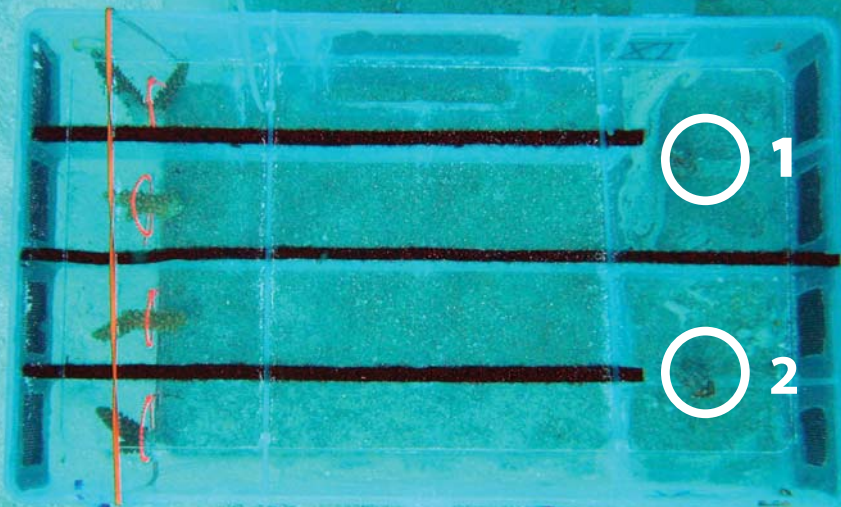
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Figure 1(on next page)

Photo examples of experimental Y-maze chamber design and treatment coral fragments.

(A) Experimental chamber design. Each chamber has two separate choice arenas, depicted as '1' and '2.' White circles depict the initial staging area for the subject snail. The treatment corals are attached at the far end of each treatment lane. (B) Cages were aligned in the same direction facing into the current. (C) Photo example of a treatment coral fragment with disease, (D) a fragment with mechanical damage and (E) a fragment with active snail predation.
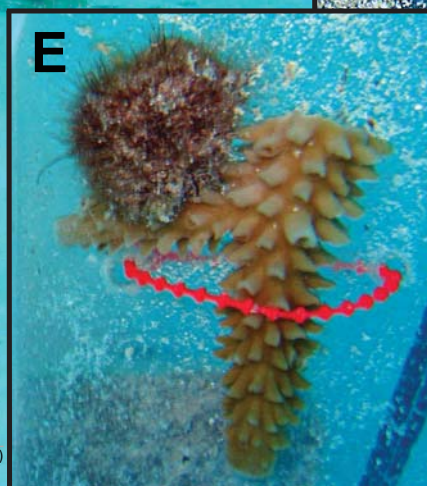
2

Results of Y-maze trials.

Percent of successful choice assay trials comparing snail preference of (A) healthy (H; white bars) *A. cervicornis* fragments vs. fragments with compromised condition (black bars; diseased [D] or mechanically damaged [M]) and (B) H vs. a conspecific snail (S; grey bars) presented separately for subject snails sourced from *A. cervicornis* and *A. palmata* hosts. Asterisks indicate significant results (Pearson Chi-squared tests, $p < 0.05$). (The total number of successful trials is given at the base of each bar)
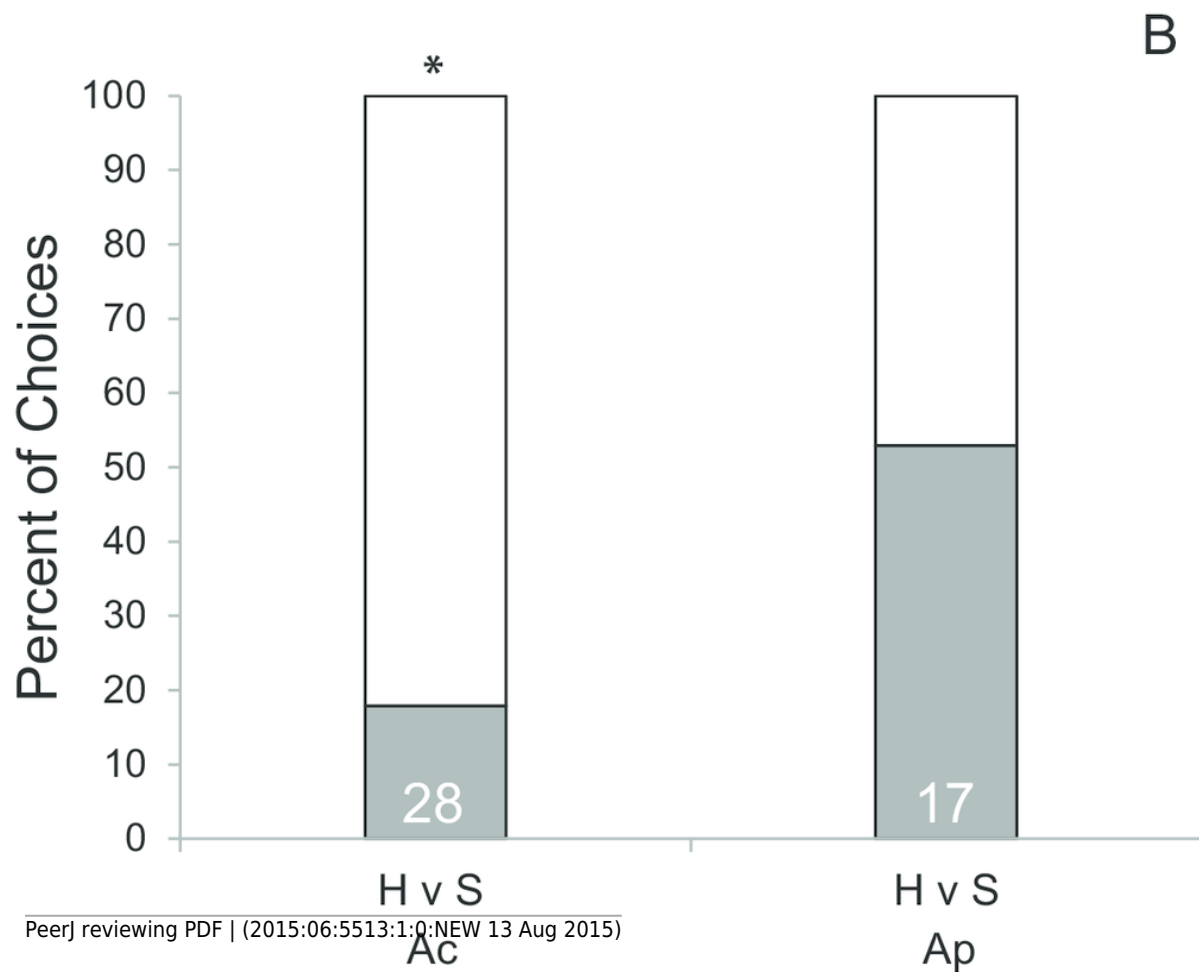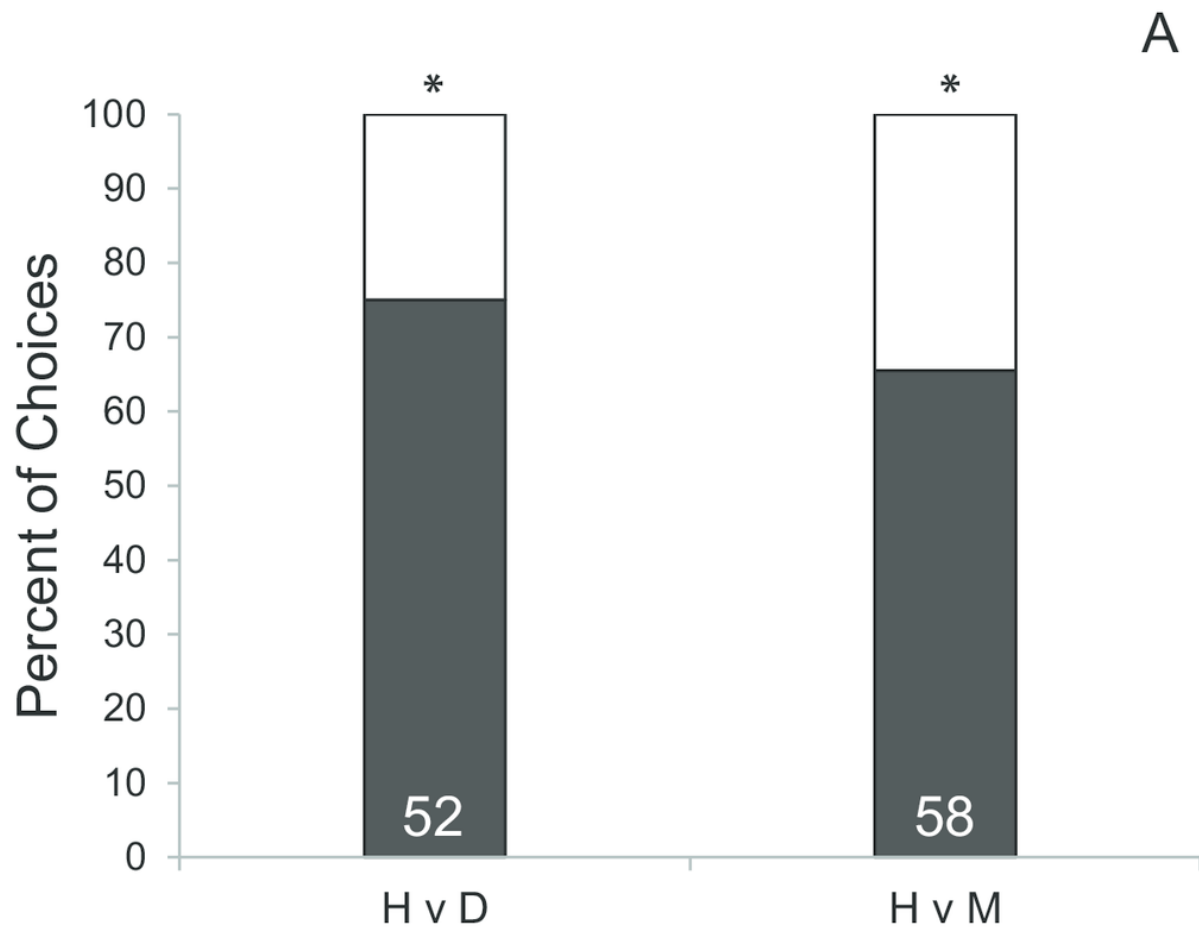
Table 1(on next page)

Summary of Y-maze trial treatments.

Paired choice experiments testing prey preferences by *Coralliophila abbreviata*. *N* gives the number of successful trials (for the treatment paired with H) with subject snails from each of two host corals, *Acropora cervicornis* (Ac) or *A. palmata* (Ap). The '# of no choice trials' represents additional trials conducted wherein the subject snail did not make a choice.

1

	Treatment	Origin	N			# of No Choice Trials
			Ac	Ap	Sum	
VERSUS	Healthy Coral (H)	5 cm branch tip snipped from nearby stock colony and allowed to heal for 2 weeks	-	-	-	-
	Diseased Coral (D)	4-9 cm branch tip with active disease snipped from nearby stock colony immediately prior to deployment in trial. Breaks were made on dead skeleton approximately 2 cm below active disease margin	29	23	52	32
	Mechanically Damaged Coral (M)	Healthy branch tip with 3-5 cm section actively abraded with a dead *A. cervicornis* branch immediately prior to deployment in a trial	32	26	58	23
	Solitary Snail (S)	Snail tethered at end of one treatment lane with no coral	28	17	45	65
	Coral with Active Snail Predation (P)	Snail feeding on a healthy fragment from an immediately prior trial	2	1	3	0

2