

Capricious commensalisms: Consumption of coral spawn by the ruby brittle star (*Ophioderma rubicundum*)

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Abstract

Many reef invertebrates reproduce through simultaneous broadcast spawning, with an apparent advantage of overwhelming potential predators and maximizing propagule survival. Although reef fish have been observed to consume coral gamete bundles during spawning events, there are no published records of such predation by benthic invertebrates. Here, we document several instances of the ruby brittle star, *Ophioderma rubicundum*, capturing and consuming egg-sperm bundles of the mountainous star coral, *Orbicella faveolata*, and the symmetrical brain coral, *Pseudodiploria strigosa*, during spawning events in the Cayman Islands in 2012 and the Florida Keys in 2022. These observations are widely separated in space and time (>600 km, 10 years), suggesting that this behavior may be ubiquitous on western Atlantic reefs. Since *O. rubicundum* spawns on the same or subsequent nights as these coral species, we hypothesize that this opportunistic feeding behavior takes advantage of the coral's lipid-rich bundles to recover energy reserves expended by the brittle star during gametogenesis. The consumption of coral gametes by adult brittle stars suggests a novel trophic link between reef invertebrates, and also provides evidence that ophiuroid-coral symbioses may oscillate between commensalism and parasitism depending on the ontogeny and reproductive status of both animals. Our observations provide insights into the nuanced, dynamic associations between coral reef invertebrates and may have implications for coral fecundity and resilience.

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**Capricious commensalisms: Consumption of coral spawn by the
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KEYWORDS

Coral reef, predation, trophic interactions, *Ophioderma rubicundum*, coral spawning, symbiosis

1 ABSTRACT

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3 Many reef invertebrates reproduce through simultaneous broadcast spawning, with an
4 apparent advantage of overwhelming potential predators and maximizing propagule survival.
5 Although reef fish have been observed to consume coral gamete bundles during spawning
6 events, there are no published records of such predation by benthic invertebrates. Here, we
7 document several instances of the ruby brittle star, *Ophioderma rubicundum*, capturing and
8 consuming egg-sperm bundles of the mountainous star coral, *Orbicella faveolata*, and the
9 symmetrical brain coral, *Pseudodiploria strigosa*, during spawning events in the Cayman Islands
10 in 2012 and the Florida Keys in 2022. These observations are widely separated in space and time
11 (>600 km, 10 years), suggesting that this behavior may be ubiquitous on western Atlantic reefs.
12 Since *O. rubicundum* spawns on the same or subsequent nights as these coral species, we
13 hypothesize that this opportunistic feeding behavior takes advantage of the coral's lipid-rich
14 bundles to recover energy reserves expended by the brittle star during gametogenesis. The
15 consumption of coral gametes by adult brittle stars suggests a novel trophic link between reef
16 invertebrates, and also provides evidence that ophiuroid-coral symbioses may oscillate between
17 commensalism and parasitism depending on the ontogeny and reproductive status of both
18 animals. Our observations provide insights into the nuanced, dynamic associations between coral
19 reef invertebrates and may have implications for coral fecundity and resilience.
20

21 INTRODUCTION

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23
24 Most reef-building scleractinian coral species reproduce through broadcast spawning,
25 whereby gametes are released into the water column for external fertilization (Baird et al. 2009).
26 In many cases, multiple coral species and invertebrate taxa spawn in near synchrony, within
27 minutes or hours of one another (Harrison et al. 1984; Babcock et al. 1986). Mass spawning may
28 have evolved to maximize fertilization success by generating high concentrations of gametes
29 (Oliver and Babcock 1992; Levitan et al. 2011; Moláček et al. 2012), but also as a strategy to
30 minimize predation losses by saturating predator feeding capacity and reducing the impact on
31 any single spawning individual or species (Harrison et al. 1984; Alino & Coll 1989; Hughes et
32 al. 2000).

33 On the Great Barrier Reef, planktivorous fish in the families Caesionidae (fusiliers),
34 Chaetodontidae (butterflyfishes), and Pomacentridae (damselfishes) have been found to feed on
35 substantial quantities of coral propagules during mass spawning events (Westneat & Resing
36 1988; Alino & Coll 1989; Pratchett et al. 2001; Baird et al. 2001; McCormick 2003). In the
37 western Atlantic, butterflyfishes have been reported to prey intensely on *Diploria*
38 *labyrinthiformis* gamete bundles as they are released (Muller & Vermeij 2011; Chamberland et
39 al. 2017). Although these trophic links between fish and corals are well established (Pratchett et
40 al. 2001), there are remarkably few publications describing consumption of coral spawn by
41 invertebrates or other marine organisms (Schmahl et al. 2008).

42 Ophiuroids, commonly known as brittle stars, are among the most biodiverse and prolific
43 invertebrates on Caribbean coral reefs (Kissling & Taylor 1977; Stöhr et al. 2022). Despite their
44 abundance, these cryptic animals are rarely seen, hidden within the reef structure by day and
45 primarily emerging at night to feed (Fell 1966; Birkeland 1988; Hendler et al. 1995; Pomory
46 2003). The ruby brittle star, *Ophioderma rubicundum*, is widely distributed on shallow reefs

47 throughout the western Atlantic but rarely found to be the most abundant ophiuroid (Clark 1933).
48 They have been described as “opportunistic omnivores” that feed on small organisms, including
49 dinoflagellates, diatoms, foraminiferans, hydroids, polychaetes, crustaceans and mollusks (Reese
50 1966; Binyon 1972). In some cases, *O. rubicundum* have been reported to exhibit predatory
51 behavior, seizing prey from the benthos or water column by coiling an arm around it before
52 transporting it to the mouth (Reese 1966; Reimer & Reimer 1975; Birkeland 1988; Hendler et al.
53 1995). Here, we report several observations of *O. rubicundum* capturing and feeding on coral
54 egg-sperm bundles in two locations in the western Atlantic.

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57 **FIELD OBSERVATIONS**

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Cayman Islands, September 2012

60 On 6th September 2012, five nights after the full moon (AFM), divers observed a coral
61 spawning event at Ironshore Gardens in Half Moon Bay, East End, Grand Cayman (19° 17'
62 29.1" N, 81° 08' 37.1" W). Throughout the dive, several adult *Ophioderma rubicundum* were
63 photographed climbing atop spawning coral colonies. At 22:13, one *O. rubicundum* was
64 observed to crawl onto the surface of an *Orbicella faveolata* colony as it readied its gamete
65 bundles for release (Fig. 1a). From 22:26 - 22:32, four *O. rubicundum* were photographed
66 consuming gamete bundles of a *Pseudodiploria strigosa* colony as it spawned (Fig. 1b, c). In
67 both coral species, the brittle stars captured multiple gamete bundles at once with one or two
68 arms, using the arm-coil behavior described by Reimer and Reimer (1975).

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Florida Keys, USA, August 2022

71 On 17th August 2022, six nights AFM, divers from the National Oceanic and
72 Atmospheric Administration’s Southeast Fisheries Science Center (NOAA SEFSC), and the
73 University of Miami’s Rosenstiel School of Marine, Atmospheric, and Earth Science observed
74 *O. faveolata* spawning at Horseshoe Reef in Key Largo, FL (24° 39' 40.26" N, 80° 59' 39.06"
75 W). At 00:14 on 18th August, an adult *O. rubicundum* was filmed extending two arms from its
76 shelter within a spawning *O. faveolata* colony, waving them over the coral as the coral began to
77 release gamete bundles (Fig. 2). Additional video footage then shows the same brittle star,
78 having emerged completely and perched on the colony’s surface, capturing numerous egg-sperm
79 bundles (Video 1). Two of the brittle star’s arms were coiled around approximately a dozen
80 gamete bundles each, and were observed to move the bundles toward the mouth.

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83 **DISCUSSION**

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86 This report presents the first visual documentation and description of benthic
87 invertebrates consuming gamete bundles from multiple coral species and from multiple locations
88 in the western Atlantic, and includes the first video footage of this behavior.

89 Despite numerous studies detailing predation by reef fish on coral spawn on the Great
90 Barrier Reef (Westneat & Resing 1988; Alino & Coll 1989; Pratchett et al. 2001; Baird et al.
91 2001; McCormick 2003), there are few accounts of such predation in the western Atlantic
92 (Muller & Vermeij 2011; Chamberland et al. 2017), and only one publication mentioning
predation of coral spawn by benthic invertebrates (Schmahl et al. 2008). A one-sentence report

93 exists of *Ophioderma rubicundum* predation during a coral spawning event in the Flower Garden
94 Banks (Schmahl et al. 2008): “Besides the occasional observations of brittle stars (*O.*
95 *rubicundum*) collecting gamete bundles with their arms as they retreat underneath a coral head,
96 no other predation [on coral spawn] has been observed,” with a photograph depicting *O.*
97 *rubicundum* atop a spawning *Orbicella franksi* colony (credited to E. L. Hickerson).

98 The feeding responses we documented in *O. rubicundum* matched those previously
99 described for this species. Presented with preferred prey items such as crab and fish meat, and
100 sea urchin viscerae, *O. rubicundum* quickly leave their hiding places, move toward the food
101 source, coil an arm around it, and transport it to the mouth for ingestion (Reimer & Reimer
102 1975). The arm-coiling behavior in our images and footage thus represents a strong feeding
103 response, suggesting that the brittle stars perceive coral gamete bundles as desirable prey items.

104 Observations of this behavior from locations as far apart as the Flower Garden Banks in
105 the Gulf of Mexico (Schmahl et al. 2008), Key Largo in the Florida Straits, and the Cayman
106 Islands in the Caribbean Sea, and (distances of >600 km), and over decadal timescales (pre-2008
107 to 2022) suggest that consumption of coral gametes by *O. rubicundum* may be pervasive on
108 Caribbean reefs. In addition, the observed consumption of gamete bundles from multiple species,
109 including *Pseudodiploria strigosa*, *Orbicella faveolata*, and *O. franksi* [Schmahl et al., 2008],
110 indicates that *O. rubicundum* may opportunistically feed on the spawn of any broadcast
111 spawning corals upon or near which they reside.

112 This behavior may be related to the reproductive status of each animal, since corals and
113 brittle stars often spawn on the same or subsequent nights. *Orbicella faveolata* and *P. strigosa*
114 typically spawn several hours after sunset, five to nine nights after the full moon (AFM) in
115 August and/or September (Szmant 1986; Wyers et al. 1991; Sánchez et al. 1999; Vize et al.
116 2005), while *O. rubicundum* spawns after sunset six to nine nights AFM from August through
117 November (Hendler 1979; Hagman et al. 1998; de Graaf et al. 1999; Hagman & Vize 2003;
118 Schmahl et al. 2008). These corals and ophiuroids both release eggs and sperm into the water
119 column for external fertilization (Fell 1966; Hendler et al., 1995), resulting in planktonic,
120 lecithotrophic larvae rich in polar lipids, wax esters, and triacylglycerols for buoyancy and
121 development (Giese 1966; Nevenzel 1970; Hendler 1979; Stimson 1987; Arai et al. 1992;
122 Villinski et al., 2002; Harii et al. 2007; Harii et al. 2010; Figueiredo et al. 2012; Padilla-Gamiño
123 et al. 2013).

124 The seasonal production of eggs and sperm is energetically costly for iteroparous
125 invertebrates, requiring considerable investment of resources and space within the body cavity
126 (Greenfield et al. 1958; Giese 1966). Given the nearly concurrent timing of spawning in *O.*
127 *rubicundum* and various western Atlantic corals, we hypothesize that feeding on coral gamete
128 bundles can supplement the brittle stars’ depleted lipid stores and boost metabolic and/or
129 reproductive function (Greenfield et al. 1958). Lipids from coral bundles may help synthesize
130 new lipids in mature *O. rubicundum* (Giese 1966), which could be utilized to support gamete
131 development or replenish energy reserves. On the Great Barrier Reef, planktivorous fishes have
132 been found to amass considerable lipid stores as a result of coral gamete consumption (Pratchett
133 et al. 2001). Female *Pomacentrus amboiensis* that fed on large quantities of coral propagules
134 produced larvae with larger yolk sacs and oil globules than those that ate few or none
135 (McCormick 2003). Presumably, gravid *O. rubicundum* experience similar positive maternal
136 effects from feeding on lipid-rich coral spawn. Indirect coral gamete consumption may also
137 provide nutrition for reef organisms, evidenced by observations of targeted corallivory on gravid
138 polyps by parrotfish and spider crabs (Rotjan & Lewis 2009; Bright & Miller 2016). Overall,

139 coral spawning seems to present a convenient and valuable food source to enhance metabolic
140 and/or reproductive output in other reef organisms.

141 Associations between ophiuroids and anthozoans have been documented worldwide,
142 ranging from mutualisms to commensalisms (Grange 1991; Mosher and Watling 2009).
143 *Ophioderma rubicundum* live inside reef structures, relying on coral colonies as habitat and
144 shelter during daylight hours (Hendler et al. 1995; Pomory 2003), and perch atop colonies to
145 release their gametes when they spawn (Schmahl et al. 2008). Consequently, *O. rubicundum* are
146 typically considered commensals, since no costs or benefits are apparent for their coral hosts.
147 However, these observations warrant a reevaluation of ophiuroid-coral associations as potentially
148 shifting from commensalism to parasitism/predation during certain critical times of the year.

149 Similarly dynamic symbioses have been documented among other reef invertebrates, at
150 times impacted by the life stage of both animals. For instance, although cleaning behavior of the
151 obligate sponge-dwelling brittle star *Ophiothrix lineata* may benefit its host, *Callyspongia*
152 *vaginalis*, by increasing filtration efficiency, the ophiuroid has also been found to consume the
153 sponge's larvae, thus exhibiting characteristics of both mutualism and parasitism (Henkel and
154 Pawlik 2014). In addition, only larger echinoderms take shelter as commensals on or within coral
155 colonies, as larvae and juveniles are vulnerable to tentacle capture or entanglement with coral
156 mucus (Yamaguchi 1974; Lewis & Price 1975; Hendler & Littman 1986). Similar shifts as
157 organisms age may occur in epizoic bryozoans (e.g., *Hippoporidra*) and scleractinians living on
158 shells of hermit crabs. As these epizoites grow, they enlarge the internal habitable volume of the
159 shell, prolonging the use of the shell by the growing crab, effectively shifting the role of the
160 epizoite from commensal to mutualist (Taylor 2009).

161 These observations of predation of coral gametes by adult brittle stars highlight the
162 complexity of trophic dynamics during ontogeny and represent a previously unidentified
163 pathway of energy transfer among reef invertebrates. In light of these findings, we suggest that
164 further observations be made during coral spawning events, by divers and/or submersible camera
165 traps, to identify whether additional instances of predation on coral gametes have gone
166 undocumented, especially by other invertebrate species that reproduce around the same time as
167 corals.

168 Corals invest substantial amounts of energy into gametogenesis and spawning (Stimson
169 1987; Ward 1995). In fact, Leuzinger et al. (2003) found that *Acropora tenuis* allocated more
170 energy to reproductive tissues relative to somatic tissues than any other iteroparous marine
171 invertebrate. Most broadcast spawners, including *O. faveolata* and *P. strigosa*, have short annual
172 spawning periods and release gametes on just a few nights per year (Szmant 1986), limiting their
173 prospects for reproduction. Although reef fish can consume large quantities of coral gametes
174 during mass spawning events (Westneat & Resing 1988), predation occurs in the water column
175 and is likely to be distributed among the gametes of many colonies. In contrast, since brittle stars
176 are confined to a coral's surface, their feeding is presumably confined to the gamete bundles of
177 the very coral that it is using for shelter, therefore impacting fecundity more directly.

178 Although any loss of gametes, by definition, decreases an animal's reproductive fitness,
179 the overall impact of ophiuroid predation likely depends on (1) the coral colony's size, (2) the
180 total number of bundles it releases during a spawning event, (3) how many brittle stars feed on
181 its surface, and (4) how many bundles each brittle star consumes. Coral fecundity increases
182 disproportionately with colony size (Hall & Hughes 1996), likely because smaller colonies invest
183 more energy in somatic growth rather than reproduction. Our observations include a single *O.*
184 *rubicundum* with two arms coiled around approximately one dozen gamete bundles each (Video

185 1), and four adult brittle stars feeding atop a single *P. strigosa* colony (Fig. 1c). In large colonies
 186 that release thousands of gametes at once, fecundity may be only minimally affected if a few
 187 dozen bundles are captured. However, the fecundity of a smaller colony, which releases fewer
 188 bundles, may diminish considerably if several dozen are eaten upon release, or if multiple brittle
 189 stars feed on its surface. Consequently, future studies should quantify the amount of coral gamete
 190 bundles that mature brittle stars consume, particularly as a proportion of a colony's total output.

191 If ophiuroid predation does impact coral fecundity, it might be assumed that corals have
 192 evolved mechanisms to discourage or prevent brittle stars from climbing on them or from
 193 consuming gamete bundles. In fact, toxic compounds have indeed been isolated from the eggs of
 194 various broadcast spawning marine invertebrates, including corals in the genus *Montipora*,
 195 perhaps for the purpose of deterring predation (Lucas et al. 1979; Fusetani et al. 1996; Marquis et
 196 al. 2005; Hagedorn et al. 2015), but this may equally well have evolved in response to fish
 197 predation. Selective forces may have also driven the production of large numbers of propagules
 198 as a general strategy to swamp predators of all kinds, whether vertebrate or invertebrate.

199 The two coral species whose gametes were consumed are particularly vulnerable; *O.*
 200 *faveolata* was listed as “threatened” under the US Endangered Species Act in 2014, and *P.*
 201 *strigosa* was recently reclassified as “critically endangered” by IUCN (Rodríguez-Martínez et al.
 202 2022), having experienced considerable declines in recent years due to stony coral tissue loss
 203 disease (Camacho-Vite et al. 2022). As coral populations decline and their spawning becomes
 204 less synchronized (Gardner et al. 2003; Levitan & McGovern 2005; Shlesinger & Loya 2019),
 205 any additional pressures on their fecundity may decrease fertilization success, reduce
 206 recruitment, and inhibit community recovery following disturbance (Oliver & Babcock 1992;
 207 Hughes & Tanner, 2000; Hughes et al., 2000). Consequently, trophic interactions with brittle
 208 stars may have important implications for coral reproductive fitness and resilience, warranting
 209 further investigation into the nuanced associations between reef invertebrates.

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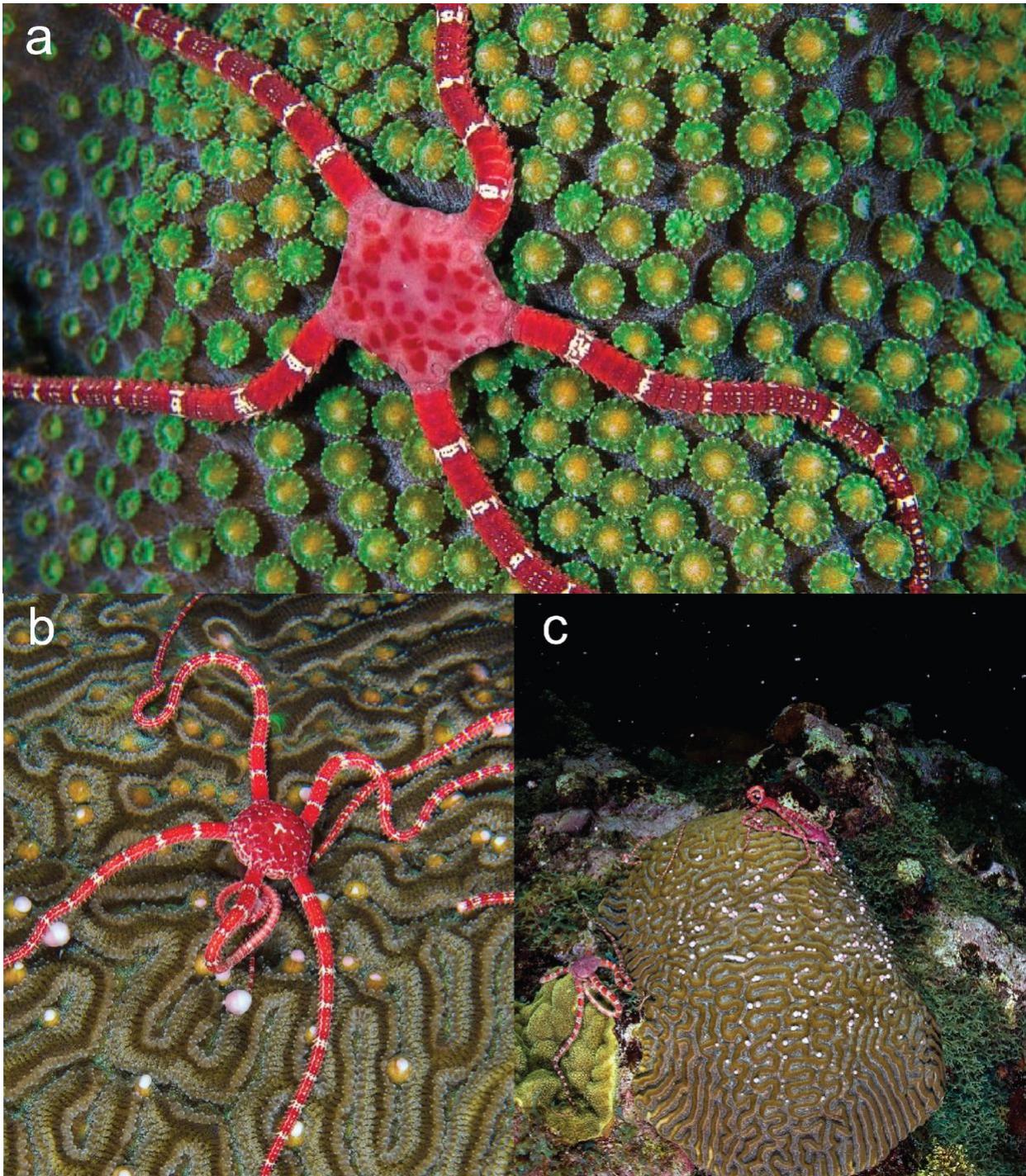
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Figure 1: Adult *Ophioderma rubicundum* climbing atop spawning scleractinian corals in Half Moon Bay, East End, Grand Cayman on 6th September 2012. (a) An adult *O. rubicundum* waits on the surface of an *Orbicella faveolata* colony as it stages gamete bundles in the mouths of each polyp, preparing to spawn. (b,c) Four adult *O. rubicundum* feed on *Pseudodiploria strigosa* gamete bundles as they are released, coiling an arm around the prey before passing it to the mouth.



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Figure 2: Screenshot from video footage depicting *Ophioderma rubicundum* (circled in white) emerging from its crevice within an *Orbicella faveolata* colony as the coral begins to spawn off Key Largo, FL in August 2022. Arm-waving behavior from *O. rubicundum* can be seen as parts of an *O. faveolata* colony have released gamete bundles, while the area near the brittle star's crevice are still "staging" gamete bundles for release.