

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

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1 ABSTRACT

2
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

22
23 Most reef-building scleractinian coral species reproduce through broadcast spawning,
24 whereby gametes are released into the water column for external fertilization (Baird et al. 2009).
25 In many cases, multiple coral species and invertebrate taxa spawn in near synchrony, within
26 minutes or hours of one another (Harrison et al. 1984; Babcock et al. 1986). Mass spawning may
27 have evolved to maximize fertilization success by generating high concentrations of gametes
28 (Oliver and Babcock 1992; Levitan et al. 2011; Moláček et al. 2012), but also as a strategy to
29 minimize predation losses by saturating predator feeding capacity and reducing the impact on
30 any single spawning individual or species (Harrison et al. 1984; Alino & Coll 1989; Hughes et
31 al. 2000).
32

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

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

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

FIELD OBSERVATIONS

Cayman Islands, September 2012

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

Florida Keys, USA, August 2022

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

DISCUSSION

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

Despite numerous studies detailing predation by reef fish on coral spawn on the Great Barrier Reef (Westneat & Resing 1988; Alino & Coll 1989; Pratchett et al. 2001; Baird et al. 2001; McCormick 2003), there are few accounts of such predation in the western Atlantic (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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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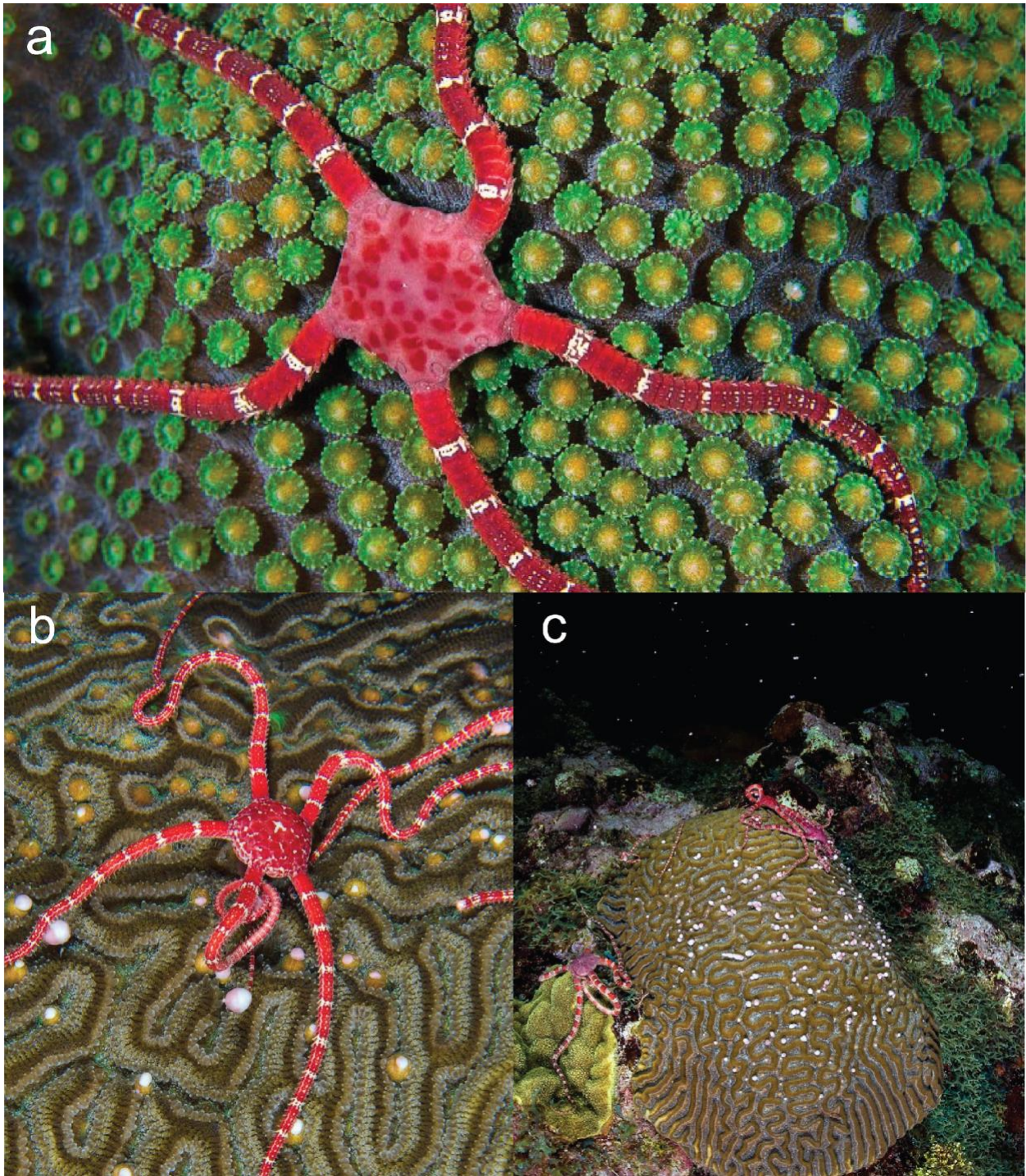


Figure 1: Adult *Ophioderma rubicundum* climbing atop spawning scleractinian corals in Half Moon Bay, East End, Grand Cayman on 6th September 2012. (a) An adult *O. rubicundum* waits on the surface of an *Orbicella faveolata* colony as it stages gamete bundles in the mouths of each polyp, preparing to 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.



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.