Non-native brittle star interactions with native octocoral epizoites: an endemic benthic ctenophore in peril?

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Abstract
Widespread and large populations of the non-native eastern Pacific ophiuroid brittle star Ophiothela mirabilis now occur in southeastern Florida, extending the range of this recently introduced species from southern Brazil northward to the eastern Caribbean Sea and Florida. The Florida brittle stars, representing two lineages, are epibionts on shallow (3–18 m depth), tropical/subtropical plexaurid (e.g., Eunicea spp., Muricea spp.) and gorgoniid (Antillogorgia spp.) octocorals. The scope of this study includes recent distributional records of O. mirabilis in south Florida, field abundances in relation to the cohabiting endemic ctenophore Coeloplana waltoni, behavioral observations of the ophiuroid, ctenophore and the predatory amphipod Caprella penantis, as well as a laboratory experiment testing the effects of the non-native ophiuroid on the native ctenophore. Individuals of O. mirabilis have been collected near St. Lucie Inlet, extending its northern-most range by about 110 km since 2019. Two years of field sampling have demonstrated significant declines of the native, benthic ctenophore with increasing abundances of the non-native ophiuroid. Evidence suggests that the ophiuroid is negatively affecting the abundances of the ctenophore through interference competition, greatly aided by its abrasive armature of calcareous spines, plates and hooks. This detrimental effect justifies considering O. mirabilis as an invasive species in south Florida. Sporadic and intense predation by a caprellid amphipod also probably contributes to the ctenophore’s decline, but to a lesser extent than that caused by the ophiuroid. Adding to the risk of extinction of C. waltoni is its narrow requirement of living octocorals as hosts and restricted distribution in southeast Florida and the Bahamas.

Introduction

The introduction of non-native marine species on native biota has been shown to decrease diversity, cause local species extirpations, extinctions, and at the ecosystem level induce changes in community structure and function (Katsanevai et al. 2014; Anton et al. 2019). Such impacts are concerning in terms of the recent acceleration in marine bioinvasions (Seebens et al. 2017; Pyšek et al. 2020). This is especially alarming considering the introduction of non-native species in coral reefs, an ecosystem already in serious decline due to diverse anthropogenic disturbances (Madin and Madin 2015; Hubbard et al. 2016; Hughes et al. 2018).

The present study concerns the non-native brittle star, Ophiothela mirabilis, which was first reported in the western Atlantic from the south coast of Brazil in 2000 (Hendler et al. 2012). This brittle star possesses several traits that allow for rapid colonization of new habitats in Atlantic tropical and subtropical waters. In just 20 years, O. mirabilis has undergone a notable range expansion of 6000 km in the
western Atlantic Ocean. Individuals of *O. mirabilis* are vagile, highly active epizoites usually associated with diverse benthic taxa, especially octocorals and sponges (Mantelatto et al. 2016; Fortunato and Lôbo-Hajdu 2021; Tavares et al. 2021). In south Florida, *O. mirabilis* has a higher occurrence on octocorals than other benthos (Glynn et al. 2020). 

Studies addressing the invasive status of *O. mirabilis* are few, suggesting damage to octocoral host tissues (Ferry et al. 2020) and a competitive impact on co-occurring benthic ctenophores (Glynn et al. 2020, 2021). Based on the negative impacts to benthic ctenophores in the present study, we believe it is appropriate to regard the non-native ophiuroid as an invasive species.

Non-native species can become invasive shortly after arrival, rapidly disrupting benthic community structure and consuming ecologically important native demersal fishes. Introduced in the 1940s (Creed et al. 2017), sun corals (*Tubastrea* spp.) have caused the competitive exclusion of numerous native species in Brazil (De Paula and Creed 2004), the Caribbean Sea, Florida, the Gulf of Mexico (Fenner 2001; Fenner and Banks 2004; Sammarco et al. 2015) and the eastern Atlantic (López et al. 2019; Capel, 2020). *Tubastrea* spp. aggressively exclude benthic species by rapid overgrowth, sweater polyps and tentacles, and extracoelenteric digestion employing mesenterial filaments (Lages et al. 2011; Silva et al. 2014; Sammarco et al. 2015; Miranda et al. 2016; Luz et al. 2017; Guilhem et al. 2020). The Indo-Pacific Lionfish, *Pterois miles*, spread rapidly throughout the Greater Caribbean and the Gulf of Mexico in early 2000 (Johnston and Purkis 2015). Subsequently, the mesopredator has consumed a broad variety of native fishes and invertebrates, including juveniles of commercially important groupers and snappers (Hixon 2016).

Demonstrating the invasive status of *O. mirabilis* has been more problematic.

Marine organisms exhibiting complex body structures often host numerous symbiotic metazoan associates, thus promoting local and regional biodiversity. These associations are realized across a broad range of seascape depths, from the shallow littoral zone (Bayer 1961; Goh et al. 1999; Sánchez 2016) to mesophotic (Maggione et al. 2020) and deep continental margin environments (Buhl–Mortensen et al. 2010). Early on, Bayer (1961) recognized the great variety of organisms associated with tropical western Atlantic octocorals—zooxanthellae (dinoflagellates), parasitic copepods, cirripeds, pycnogonids, and gastropods, epizoic cnidarians, ctenophores, polychaete worms, porcellanid and spider crabs, hippolytid shrimp, and ophiuroid echinoderms. Our knowledge of the diversity of octocoral communities, including octocoral microbes (viruses, bacteria), fungi, protozoans, invertebrates and fishes has been greatly augmented recently (e.g., Van Oppen et al. 2005; Sánchez 2016; McCauley et al. 2020) in shallow western Atlantic, Indo-Pacific, and eastern Pacific regions, but is still greatly understudied.

The focus of this study is on the non-native ophiuroid *Ophiothela mirabilis* and its interactions with the native benthic ctenophore *Coeloplana waltoni*, both octocoral epizoites. We provide recent data on the occurrence and abundance of the non-native ophiuroid on octocorals across approximately 78 km of coastline, from Hallandale Beach to West Palm Beach, Florida. A seven-day laboratory experiment simulating ophiuroid-ctenophore interactions was performed to further investigate this competitive association and the cause of natural variations in epizoite ctenophore relative abundances. Motivation for the experiment was based on an observed negative relationship between field ctenophore abundances and the presence of ophiuroids. Thus, the null hypothesis states that *O. mirabilis* should not influence the abundance of co-occurring *C. waltoni*. Attention is also directed to the recent and unexpected occurrence of the amphipod, *Caprella penantis*, a sporadic co-inhabitant of octocorals. The abundances and behaviors of the ophiuroid and caprellid suggest competitive and predatory interactions, respectively, leading to negative impacts affecting the abundance of the benthic ctenophore. This study offers an opportunity to address questions relating to extinction research in the earliest stages of invasion (Sax and Gaines 2008). A time-lag to extinction may exist for the benthic ctenophore under competition by the introduced ophiuroid and intense predation by the caprellid. To understand this, the ophiuroid invasion needs to be tracked to follow how the ophiuroid changes the abundance of the ctenophore. Interference competition by the ophiuroid may transform the ctenophore’s microhabitat sufficiently to endanger their presence.

**Materials and methods**

**Species**

Six plexaurid and three gorgoniid octocoral host species were sampled in this study with an emphasis on *Eunicea asperula* (Milne Edwards and Haime 1857), *Eunicea clavigera* (Bayer 1961), *Eunicea flexuosa* (Lamouroux 1821), *Eunicea tourneforti* (Milne Edwards and Haime 1857) and *Muricea elongata* Lamouroux, 1821. Table 2 in Glynn et al. (2020) lists all octocoral species examined in this and previous studies with corresponding museum catalog numbers. Sánchez and Wirshing (2005) provide species-specific characteristics. The non-native ophiuroid *Ophiothela mirabilis* Verrill (1867) consists of beige and orange color morphs in Florida, in two closely related lineages (Alitto et al. 2020; Glynn et al. 2020). *Coeloplana waltoni* (Glynn et al. 2014) is a native South Florida benthic ctenophore (Glynn et al. 2014). *Caprella cf. penantis* (Leach 1814) an octocoral
epizoite, belongs to a complex of cryptic, amphipod species and is probably not cosmopolitan in distribution (Cabezas et al. 2013; Paz-Rios et al. 2014).

Field sampling

Octocoral collections were made at the Dania Beach study site (80°06.344′, 26°03.506′) over a 19 month period, July 2018–February 2020. The octocorals sampled were chiefly species of *Eunicea* and *Muricea elongata*. Octocoral side branches approximately 15–20 cm in length, from colonies with *Ophiothela mirabilis* present, were cut free, bagged separately and then transported to the laboratory in an insulated cooler chest supplied with aerated seawater. The number of colonies sampled in each collection ranged from 16 to 30, and the ophiuroids collected were predominantly the beige color morphs. See Glynn et al. (2020) for additional details of routine field sampling. According to a social media report of unverified sightings of individuals of *O. mirabilis* at Blue Heron Bridge in West Palm Beach city, Florida (26.7844°N, 80.0484°W), a single survey was performed at this site on 20 October 2020. This is a brackish water lagoon environment in the intracoastal waterway. Circulation at this location is strong with a twice-daily tidal influx of ocean water. All specimens at the Blue Heron Bridge site were collected under a Special Activity License (SAL-20–2267-SR) issued to Phillip R. Gillette by the Florida Fish and Wildlife Conservation Commission, Division of Marine Fisheries Management, Tallahassee, Florida.

Sampling to determine the spatial pattern of occurrence of *O. mirabilis* involved observations at several sites off Palm Beach and Broward counties. Ten to 40 plexaurid and 10–40 gorgoniid colonies were examined at 22 sites from April to December 2020. Colonies were sampled along a fixed 30 m² transect at 13 sites and randomly selected in a 200 m² area around a fixed center point at the remaining nine sites. Occurrence and abundances at survey sites were estimated according to the following qualitative scale: rare 0 to 1–2 ind on <5% of colonies, moderately common, 5–10 ind on 5–20% of colonies, abundant, 20+ ind on several branches of over 20% of colonies. At 16 of the sites located north and south of Port Everglades, prevalence was calculated quantitatively (% of colonies with *O. mirabilis* present) and prevalence interpolated using an inverse distance weighted (IDW) method in QGIS (Bartier and Keller 1996). Geographic positions were obtained by means of GPS.

Behavioral observations

The feeding behavior of individuals of *Ophiothela mirabilis* were viewed in the field during the day and night. Competitive and predatory observations were made on octocoral branches with their normal complement of epizoites within two to three hours after collection under subdued lighting in the laboratory using a microscope (8–35X). Interactions between individuals of *O. mirabilis* and their octocoral hosts were observed in the laboratory during feeding and non-feeding periods.

Experimental procedure

The plexaurid octocoral host species used in the laboratory experiment were *Eunicea succinea* (Pallas 1766) and *Eunicea tourneforti* (Milne Edwards and Haime 1857). These octocoral species were the only two consistently found hosting both the non-native ophiuroid *Ophiothela mirabilis* (Verrill 1867) and the endemic benthic ctenophore *Coeloplana waltoni* (Glynn et al. 2014). The common beige color morph of *O. mirabilis* was studied in this experiment (Glynn et al. 2020). The experimental animals were collected off Lauderdale by the Sea, Florida (26.1920°N, 80.0964°W) on 27 October 2020 at four to five meters depth. The basal end of each lateral branch was trimmed until the branch measured 10 cm in length. A total of 10 separate 4 L containers, each with a vertically oriented octocoral branch with (experimental) or without (control) individuals of the non-native brittle star were randomly placed in a linear array with respect to the light source. All octocoral branches contained ctenophore epizoites with initial densities: experimental (with brittle stars), mean *C. waltoni* density (no. ind. 10 cm⁻¹ branch) 7.2, range 6–9, controls (without brittle stars), mean *C. waltoni* density 7.6, range 6–10. Initial experimental *O. mirabilis* density, mean 5.0, range 3–6, control 0. The water was gently aerated and stirred continuously with magnetic stirring bars, creating a flow rate of approximately 8 cm s⁻¹. One liter of water with naturally present plankton was changed out daily in each container. Both brittle stars and ctenophores were observed feeding on plankton during daylight hours. Ctenophores were occasionally observed feeding at night. The experiment was conducted for seven days; data on epizoite densities and location on octocoral hosts were collected daily. Caprellids were absent from the experiment.

Statistical analyses

Two generalized linear mixed models (GLMMs) were fit to densities of the three epizoite species (*Ophiothela mirabilis, Coeloplana waltoni, Caprella penantis*) inhabiting the 10 cm octocoral branches (406 total branches collected over 16 surveys) using the R package glmmTMB (Brooks, 2017). The first model, to analyze trends in counts of each species over the survey period, employed a zero-inflated first-order negative binomial (NB1) response structure (φ = 6.79) with a random intercept for each survey (a branch random effect was dropped due to zero estimated variance). Fixed effects...
included species, time (continuous), and their interaction. The second model, to examine the relationship between the abundance of C. waltoni and co-occurring epizoites O. mirabilis and C. penantis, was fit using a standard NB1 response structure (ϕ = 9.53) with a random intercept for each survey and time as a continuous fixed effect. Additional species fixed effects, including potential interactions and polynomial degrees, were selected by AIC from models fit by maximum likelihood, with the final models fit by restricted maximum likelihood. Visual examination of simulated scaled residuals indicated assumptions were met sufficiently for both models. Inference on parameters was performed by employing F tests with denominator degrees of freedom estimated using the inner-outer method (Pinheiro and Bates 2000).

Laboratory experimental results of the effects of the ophiuroid O. mirabilis on the benthic cnidophore C. waltoni were tested according to the following procedure. A GLMM with a Poisson response was fit by maximum likelihood to C. waltoni counts across seven days of observation under experimental (O. mirabilis present, n = 5) and control (O. mirabilis absent n = 5) conditions. Correlation between repeated measurements was modeled with a heterogeneous first-order autoregressive [AR(1)] structure. Type III Wald tests with Kenward–Roger denominator degrees of freedom indicated that reductions in counts over time by treatment were best modeled as second-degree polynomials; there was no evidence that time or treatment effects differed between octocoral host species. Studentized residual plots indicated model assumptions were met sufficiently. To test the overall effect of O. mirabilis on C. waltoni abundance over time, a nested reduced model without treatment effects was fit as above and compared to the full model using a drop in deviance Chi-square test. Models were fit using SAS/STAT software, version 9.4, PROC GLIMMIX.

Results

Field observations

In field sampling surveys conducted from April to December 2020, Ophiouthea mirabilis was present on plexaurid and/or gorgoniid colonies at 18 of 22 sites, including the northernmost site surveyed near West Palm Beach (Fig. 1). Abundance varied spatially, with two hotspot locations identified, one on the inner reef (10 m depth) offshore of Port Everglades and another on the nearshore ridge complex (5 m depth) at Hollywood/Hallandale Beach. Individuals of O. mirabilis were found on 100% of colonies at three sites, were abundant at a further three, moderately common on plexaurid colonies at seven sites, moderately common on gorgoniid colonies at four sites and rare at four sites. Quantitative assessment around Port Everglades revealed that 24.37% (± 8.58% SE) of octocoral colonies hosted O. mirabilis, 29.60% (± 10.60% SE) of gorgoniids and 19.16% (± 8.03% SE) of plexaurids.

After about one hour of searching at the Blue Heron Bridge site, 10 individuals of O. mirabilis were observed on one of several colonies of the plumulariid hydrozoan [Denditheca dendritica (Nutting 1900)] examined (Fig. 2). The hydroid host colony, robust and arborescent in growth form (Calder 2013), was attached to the substrate under the bridge in the intracoastal waterway. Circulation at this location was strong, with a twice-daily tidal influx of ocean water.

Initial field evidence suggesting that interspecific interactions between brittle stars and cnidophores might influence epizoote abundances (including absences) was supported by sequential sampling at the Dania Beach study site. Across 16 quantitative surveys over a 19 month period, mean densities of individuals of C. waltoni ranged from 0 to 30.9 individuals per 10 cm octocoral branch length, mean densities of individuals of O. mirabilis ranged from 0 to 30.5 and mean densities of individuals of C. penantis ranged from 0 to 10 (Fig. 3). Based on the first statistical model (correlation-based $R^2 = 0.48$), there was strong evidence that trends in epizoite densities inhabiting octocoral hosts differed by species across the survey period ($p < 0.0001$). This was driven specifically by a decline in C. waltoni over time ($p = 0.0006$), which exhibited an average reduction in population size of 9.2% every 30 days (95% CI 4.1–14.0%). Overall trends in either direction were not significant for O. mirabilis ($p = 0.31$) or C. penantis ($p = 0.073$).

After accounting for the overall trend over time in total numbers of C. waltoni, the second statistical model (correlation-based $R^2 = 0.51$) revealed strong evidence of a linear association between the abundance of C. waltoni and counts of O. mirabilis ($p = 0.0007$). For each additional O. mirabilis individual present per 10 cm branch length, the abundance of C. waltoni displayed an expected 3.8% decline (95% CI 1.6–6.0%). In contrast, the abundance of C. waltoni showed evidence of a second-order relationship with counts of C. penantis ($p = 0.016$), exhibiting a positive association within the limited range of individuals observed. There was no evidence to suggest that these relationships varied over time, nor that an interaction between O. mirabilis and C. penantis was associated with the abundance of C. waltoni.

Laboratory experiment

Based on analysis of the laboratory experiment there was strong evidence that the presence of Ophiouthea mirabilis negatively impacted the density of Coeloplana waltoni ($\chi^2 = 18.9, p = 0.0003$ Fig. 4). Mean (SE) C. waltoni density in the control group began at 7.6 (0.75) and declined to 5.0 (0.55) individuals per 10 cm branch length by day seven, while in the brittle star group mean density declined from
Fig. 1 Ophiothela mirabilis occurrence and abundance in southeast Florida. Main key: qualitative abundance categories of *O. mirabilis* on plexaurid (sea whips, genera *Eunicea* and/or *Muricea*, represented by circles) and gorgoniid (sea plume, genus *Antillogorgia*, represented by diamonds) colonies. Abundant denotes *O. mirabilis* present on over 20% of colonies, Moderate denotes *O. mirabilis* present on 5–19% of colonies, Rare denotes *O. mirabilis* present on <5% of colonies, Absent denotes *O. mirabilis* not found at the site. Ocean outfall locations, major cities and ports mapped for reference. Inset: Inverse Distance Weighted interpolation (IDW) of *O. mirabilis* prevalence around Port Everglades.

Fig. 2 *Ophiothela mirabilis*. (a), Adhering to hydrozoan colony *Dentitheca dendritica* under Blue Heron Bridge, Riviera Beach, Florida, 7 m depth, 28 July 2020. (b), six individuals from the same hydrozoan in various stages of fissiparity. Note salmon-pink patches on all individuals. At the center of the photograph, above the brittle star, is an unidentified caprellid amphipod.
7.2 (0.49) to 1.0 (0.63) individuals per 10 cm branch length. Ctenophores on octocoral branches remained roughly evenly spaced in the control group but clearly clumped at the ends of branches, separated from the ophiuroids, in the experimental treatment.

Behavioral observations

Interspecific behaviors were documented to gain insight into interactions possibly affecting epizoite abundances. Field observations of *Ophiothela mirabilis* revealed frequent suspension feeding during day and night with arms greatly extended and waving (as if searching) in passing currents. Identical activities were observed in the laboratory during feeding trials when offered *Artemia nauplii*.

Individuals of *Coeloplana waltoni* were nearly always inactive, firmly attached to coenosarc surfaces, and often near polyp bases with tentacles fully contracted (Fig. 5, Table 1). When individuals of *C. waltoni* were contacted by *O. mirabilis*, this often caused the ctenophore to move. In one instance, contact by *O. mirabilis* caused rapid contraction with the ctenophore assuming a crinkled body shape (see Fig. 3 in Glynn et al. 2014).

In two collections with individuals of the caprellid (*Caprella penantis*) present, 16.2% (5 of 31) and 100% (1 of 1) of the individuals of *C. waltoni* in the samples were attacked and eaten, no ctenophores were attacked in two collections (Table 1). The caprellid was not necessarily common, but when present effected intense predation on the ctenophore. The predatory caprellids in the 17 March sample moved quickly along the octocoral branch, ostensibly in a search mode, as soon as a ctenophore was encountered it was grasped, shredded, and consumed. In this same sample, two caprellids separately attacked an individual of *O. mirabilis*, but failed to penetrate the epidermis; each caprellid then moved further along the branch after a few seconds.
When present at moderate and high densities the ophiuroids were generally evenly spaced along the octocoral branch. However, in two high-density collections (January and November, Table 1) the ophiuroids were densely crowded with arms and discs overlapping. Ctenophores were not present in or near these aggregations.

**Fig. 5** *Ophiothela mirabilis* arms wrapped around the stem of *Muriacea* sp. near a resting individual of *Coeloplana waltoni* (indicated by an arrow). Collection locality: Dania Beach, Florida, 14 April 2021, 5–6 m depth

### Discussion

Our systematic surveys over a one-year period have demonstrated the presence of individuals of *Ophiothela mirabilis* at moderate to high abundances from Hallandale Beach to West Palm Beach, a distance along the coast of about 78 km. The clusters of high survey abundances immediately north and about 4 km south of the entrance to Port Everglades lend support to the hypothesized localized introduction of this non-native ophiuroid via high volume ship traffic (Glynn et al. 2020) as also proposed in several studies in Brazil (Bumbeer and Rocha 2016; Mantelatto et al. 2016; Araújo et al. 2018; Lawley et al. 2018).

In just 20 years, individuals of *O. mirabilis* have colonized coastlines spanning more than 6000 km of latitude (Tavares et al. 2021), from their first reported presence in southern Brazil (Hendler et al. 2012) northward along the South American coast to the Caribbean Sea (Hendler and Brugnears 2013; Ferry et al. 2020) and southeastern Florida (Glynn et al. 2019). Their northern-most occurrence on the Florida east coast, observed on 28 September 2019, was at Deerfield Beach, 26.3184°N, 80.0998°W (Glynn et al. 2020). In the present study, individuals of *O. mirabilis* were found on a hydrozoan colony at Blue Heron Bridge, Riviera Beach, 44 km north of Deerfield Beach in a brackish environment. The presence of the brittle stars at this site is not unexpected considering their occurrence in estuarine habitats in Brazil (Derviche et al. 2021). It is not known if this record represents migration over a one-year period or if the ophiuroids were already present there and un-reported.

### Table 1

| Collection         | n | Mean density of C.w./O.m./C.p. | Predation (C.w. → C.p.) | Observations                                                                 |
|--------------------|---|-------------------------------|-------------------------|------------------------------------------------------------------------------|
| 5 January 2019     | 16 | 4.5/27.0/0                   | 0→(0%)                 | O.m. arm briefly contacting C.w., no response. O.m. highly aggregated          |
| 17 March 2019      | 20 | 30.9/14.0/10.0               | 5→(16.2%)              | C.p. moving rapidly along branches locating and quickly shredding C.w. tissues with ingestion. Two C.p. unsuccessfully attacked O.m., but could not cut through epidermal armor. O.m. arm contacted C.w. aboral surface, C.w. contracted into spherical shape. C.w. on octocoral stem away from O.m. |
| 21 April 2019      | 39 | 7.6/7.3/0.2                  | 0→(0%)                 | C.w. moved when brushed by arms of O.m. C.p. with amorphous detritus in gnathopod, but not ingested |
| 27 October 2019    | 25 | 2.1/6.0/3.3                  | 0→(0%)                 | C.w. inactive. O.m. active with arm waving. C.w. moved when contacted by O.m. C.p. actively moving along branches |
| 8 November 2019    | 26 | 0.4/18.2/0                   | 0→(0%)                 | O.m. aggregating at high density                                             |
| 5 December 2019    | 30 | 1.0/19.5/0.3                 | 1→(100.0%)             | O.m. and C.p. in intermittent contact, no interaction. One C.p. quickly shredded and ingested one C.w. |

aNumber of 10-cm long octocoral branches observed. Observation time for all samples ≤ 2 h

bMean values are for epizoite densities on 10 cm octocoral branches. C.w. *Coeloplana waltoni*, O.m. *Ophiothela mirabilis*, C.p. *Caprella penantis*. Observed microscopically (10–30X) under subdued lighting

cTotal number of C.w. (prey) attacked and consumed by C.p. (predator). Percent values denote the proportion of all individuals of *C. waltoni* present on a single sampled branch that were consumed.
near absence of shallow water octocorals in the vicinity of Deerfield Beach (Palm Beach County), nearly 50 km north of Riviera Beach (Jones et al. 2020) would not seem likely to inhibit a more northern range extension of individuals of *O. mirabilis* since this ophiuroid is known to associate with numerous other taxa in Florida (Glynn et al. 2020), Brazil (Bumbeer and Rocha 2016; Mantelatto et al. 2016; Fortunato and Lóbo-Hajdu 2021), and the eastern Pacific (Granja–Fernández et al. 2014). However, the present distributions of non-native western Atlantic and native eastern Pacific *O. mirabilis* are generally restricted to these amphi-american tropical/subtropical biogeographic realms (Costello et al. 2017, Travares et al. 2020).

An ecological niche model analysis, employed by Derviche et al. (2021), based on current *O. mirabilis* distributions and abundances, predicted suitable western Atlantic habitats beyond present-day occurrences and widespread dispersion and range expansion in the future. They reported that the occurrence of *O. mirabilis* correlates chiefly with mean calcite concentration and mean sea surface temperature. If this prediction is realized the ophiuroid could colonize numerous suitable habitats in warm temperate southwestern and northwestern Atlantic environments. This would include range expansions to southeastern Brazil and to the Carolinian province along the east coast of the USA. Also included would be large areas of the Caribbean Sea and the northern Gulf of Mexico. Derviche and co-workers suggested that the calcite mineral would be required for ophiuroid skel etogenesi s, especially during ase xual fission, and that physiological functions are impaired at mean sea temperatures less than 21.75 °C. These workers also noted increasing population densities of *O. mirabilis* from inner shelf to estuarine habitats at the Paranaguá estuarine complex in southern Brazil.

Marked variability occurred in epizoite densities in the 16 collections over the 19-month sampling period as reported in prior studies in southeast Florida (Glynn et al. 2020). For individuals of *O. mirabilis* and *Coeloplana waltoni* this is probably in part a reflection of the patchy occurrence and the sampling protocol for these species; the identical octocoral patches, colonies, and branches were not repeatedly sampled at the Dania Beach study site. The occurrence of individuals of *Caprella penantis* was sporadic, observed in only four collections. Aquarium observations revealed this amphipod to be highly mobile, moving quickly over a given octocoral branch, and often swimming and moving between branches. It is likely that this predatory amphipod naturally moves frequently among octocoral branches within and among colonies in search of prey.

Ophiuroids were not present on dead octocoral branches (Glynn et al. 2020). Their absence could offer a refuge for *C. waltoni*, however, the ctenophore was absent from dead branches as well. Dead branches are usually quickly colo nized by algae and hydroids, a likely inhospitable habitat for mobile epizoites. Live octocoral host tissues bearing nema toxysts, sclerites, and chemical defenses (Pawlik et al. 1987; Harvell and Fenical 1989; Yoffe et al. 2012) would provide an advantage in predator avoidance, thus offering a suitable microhabitat.

Since octocorals engage heavily in suspension feeding, capturing particulate organic matter (Lasker 1981) and microzooplankton (Glynn et al. 2018a), the interference of polyp expansion by individuals of *O. mirabilis* was sug gested to be a potentially significant threat against satisfying the trophic requirements of octocoral hosts (Araújo et al. 2018; Ferry et al. 2020), although a recent study suggests this may not be consequential (Glynn et al. 2021). From the current study—which has demonstrated an inverse relationship in the abundance of ophiuroids and ctenophores in field collections, and decreasing ctenophore abundance in the presence of ophiuroids in a laboratory experiment—it appears that the major effect of the non-native ophiuroid is on the displacement, by interference competition, of the cohabiting benthic ctenophore. This sort of negative impact on biodiversity is the predominant effect of marine invasive species in European seas (Katsanevakis et al. 2014). It is not yet known if *O. mirabilis* will negatively impact the abundances of octocoral hosts, but if this occurs then local biodiversity would be greatly diminished. Invasive azooxanthellate sun corals are displacing ecosystem engineers (e.g., reef-building corals and zoantharians) in Brazil, having a depressing effect on biodiversity, nearly two decades after their first sightings (Miranda et al. 2016; Luz and Kitahara 2017). It is too early to determine if the ophiuroid can drive *C. waltoni* to extinction and perhaps begin to impact octocorals and other associated epizoites.

Several studies have described the kleptocommensal and kleptoparasitic trophic relationships of hydroids and other invertebrate epizoites associated with sponges, octocorals, bryozoans, and polychaetes, and polychaete worms (e.g., Gotto 1969; Pupe et al. 2008). Bavestrello et al. (1996) observed caprellids seizing previously captured nauplii from hydroid polyps; a nudibranch grazing preferentially on hydroid polyps that previously ingested zooplankton, an example of the consumption of a prey item plus its ingested prey, was termed kleptopredation by Willis et al. (2017). The symbiotic status of the benthic ctenophore and its octocoral host is not clear since we have observed the ctenophore purloining food (unidentified organic detritus) captured by its host’s polyps, and octocoral polyps have been observed removing captured fish eggs from the tentacles of ctenophore epizoites (Glynn et al. 2018a). Further study is necessary to determine the significance of these trophic resources, the relative amounts garnered by the symbiotic partners, and how field conditions affect these interactions.

The alacrity with which individuals of *Caprella penantis* attacked, shredded and consumed relatively large fragments
of benthic ctenophores suggests that this crustacean species is an occasional, if not frequent, predator of individuals of *C. waltoni*. No defensive responses by *C. waltoni*, such as rapid tentacle extension (Glynn et al. 2018b), were observed beyond slow fleeing movements, which were ineffective. From feeding observations conducted in northern Florida, Gulf of Mexico, Caine (1974) noted that individuals of *C. penantis* depended primarily on filter feeding and substrate scraping. Contrary to the observations of Caine (1974) and Paz–Rios et al. (2014) on the relative ineffectiveness of caprellids as predators, we observed that all individuals engaged in feeding moved quickly over octocorals, occasionally swimming, potentially in search of ctenophore prey. This is the first documented record of a ctenophore species consumed by a caprellid (Saunders 1966; Sano et al. 2003; Guerra–García and Tierno de Figueroa 2009). Most caprellids are detritivores, 86% in the global survey conducted by Guerra–García and Tierno de Figueroa (2009), however, several species are facultative and obligate predators, consuming sponges, polychaete worms, copepods and amphipods.

If the recent decline in abundance of *C. waltoni*, and local disappearance at some sites, is due primarily to *O. mirabilis*, then it is necessary to understand how this occurs. The ctenophores are exceedingly well camouflaged and typically quiescent when present on their octocoral hosts. Once a ctenophore has found a favorable perch for the extension of its ‘fishing’ tentacles, movement is infrequent. Our observations indicate that brittle star contact with individuals of *C. waltoni* is an irritation, often causing the ctenophores to move. We hypothesize that ctenophores on the move are more susceptible to dislodgment from their octocoral hosts. Dislodgment could occur during turbulent sea conditions, which are frequent off the southeast coast of Florida, or by fishes and other water column predators.

In our study, *Caprella penantis* voraciously consumed benthic ctenophores. However, caprellids are known to consume octocorals in other regions and researchers should be cognizant of this habit. A notable report of a caprellid infestation and predation on gorgonian sea fans in North Sulawesi, Indonesia, revealed massive consumption of coenenchyme (octocoral tissues including epidermis, mesoglea and gastrodermis) and skeletal fragments resulting in total colony mortality in three species (Scinto et al. 2008). Octocoral colonies of *Melithaea* sp. were most severely affected, irreparably damaged within a week. The caprellid responsible for the sea fan mortality was *Metaprotella sandalensis*, a common species on Indo-Pacific coral reefs. The morphology of the feeding appendages (molar process and mandibular palp) are characteristic of caprellid predators and scrapers (Caine 1977; Guerra–García and Tierno de Figueroa 2009). Mean caprellid infestation densities were 8.5 ind cm$^{-1}$ branch, equivalent to 85 individuals over a 10 cm long branch (Scinto et al. 2008), C. Cerrano, pers. comm.). These densities are an order of magnitude higher than those observed in south Florida (Table 1). Such a severe predation event triggering the death of entire octocoral colonies would also result in the loss of the associated symbiont community.

### Conclusion

The ophiuroid invasion of octocorals in southeast Florida is very recent, making it difficult to predict long-term effects. The apparent ongoing displacement of an endemic benthic ctenophore is the only negative effect thus far observed. No obvious signs of impairment to octocoral hosts are evident (Glynn et al. 2021). In light of the ophiuroids establishment in southeastern Brazil, over a period of about 20 years, its rapid and wide-ranging dispersal and possible repeated introductions, it is highly probable that it will continue to spread and become established throughout the western Atlantic warm water region where octocorals and other suitable substrata occur. Since the invasion of *Ophiothela mirabilis* in the western Atlantic region is so recent and still on-going, we strongly encourage continuing surveys to document its occurrence, abundance, and interactions with native species. Coastal and estuarine habitats with suitable environmental conditions in need of surveys and study are the Tropical Northwestern Atlantic province (wider Caribbean Sea) and the Warm Temperate Southwestern (southeastern Brazil) and Northwestern Atlantic (Northern Gulf of Mexico, Carolinian) provinces. Behavioral and experimental studies of non-native brittle star interactions vis-à-vis native epizoites are especially encouraged and may shed light on control measures should these be needed. Cryptogenic *Caprella penantis* should also receive attention considering its predatory impacts on *Coeloplana waltoni* and other octocoral epizoites.

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### Author contributions

PWG conceived study, processed samples, recorded behavioral observations, and prepared the manuscript. BMR assisted in field collections, processing samples, and manuscript preparation. BC performed the laboratory experiment. KD designed and completed all statistical analyses. JD, NM, and PRG performed field collections, observations, and processed samples. PRG collected...
specimens at Blue Heron Bridge, Riviera Beach, and performed all photographic documentation. Quantitative field collections were performed by NJ. All authors contributed intellectually to this study.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

**Declarations**

**Conflicts of interest** All authors declare that they have no conflicts of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Experiments and observations involving the invertebrates were approved by the IACUC committees at UM and NSU. The *Ophiothela* collection at Blue Heron Bridge was under FWC Special Activity License SAL-20–2267-SR.

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