



## Benthic ctenophores (Platyctenida: Coeloplanidae) in South Florida: predator–prey interactions

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**Abstract.** The primary goal of this study was to demonstrate, from field observations and laboratory experiments, some key trophic roles of benthic ctenophores as predators and prey in subtropical communities. We examined individuals of two benthic platyctenid species: *Coeloplana waltoni*, a minute epibiont on octocorals in exposed, open-water settings; and *Vallicula multiformis*, an associate of calm-water biofouling communities and floating *Sargassum* spp. Laboratory observations of individuals of both ctenophore species revealed frequent capture and ingestion of diverse zooplankton taxa, especially crustaceans. Laboratory predation trials demonstrated the capture of dolphinfish (*Coryphaena hippurus*) eggs and larvae by both ctenophore species. Dolphinfish eggs and larvae larger than individuals of *C. waltoni* were captured but not ingested during 2-h trial periods. These prey items were sometimes purloined and ingested by polyps of the ctenophore's octocoral host. Ingestion of dolphinfish eggs and larvae by individuals of *C. waltoni* was observed, however, after longer periods of exposure to prey. In predation trials, dolphinfish eggs and larvae were both captured and ingested by larger individuals of the ctenophore species *V. multiformis*. Field and laboratory observations revealed diverse invertebrate and fish taxa that prey on both ctenophore species. In the laboratory, the mean daily per capita consumption of individuals of *C. waltoni* by a pomacanthid fish ranged 0.5–2.8 individuals, and ranged 2.6–3.6 individuals for predation by an ovulid mollusc. Field population densities of these predators ranged 0.1–0.7 individuals per m<sup>2</sup> for the pomacanthid, and 0.2–1.1 individuals per m<sup>2</sup> for the mollusc. Laboratory feeding observations demonstrated frequent consumption of individuals of *V. multiformis* by a sea anemone, and by three species of brachyuran crabs. Field observations revealed eight fishes that probably feed incidentally on individuals of *V. multiformis*. These findings add to the limited knowledge base of predator–prey dynamics in both *C. waltoni* and *V. multiformis*.

*Additional key words:* ctenophore feeding, predators, zooplankton, fish larvae, biofouling community

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Numerous studies have been conducted on the predators and prey of pelagic ctenophores (Reeve & Walter 1978; Kremer et al. 1986; Costello &

Coverdale 1998; Sullivan & Gifford 2004; Titelman et al. 2012). Much of this work has resulted from the realization that ctenophores play a pivotal role in affecting pelagic food chains and trophic structure, fisheries stocks, and the success of invasive species (Costello et al. 2012). A more recent

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concern demanding attention is the possible ecological ascendancy of ctenophores due to human activities leading to environmental degradation and climate change (Purcell 2012). The predatory ctenophore *Mnemiopsis leidyi* exists in high abundances in native and invaded pelagic ecosystems along North American Atlantic coasts (Costello et al. 2012), northern Europe (Rüsgård et al. 2007; Javidpour et al. 2009), inland seas such as the Black Sea and Caspian Sea (Vinogradov et al. 2005), and the Mediterranean Sea (Fuentes et al. 2010). In the early 1980s, the accidental introduction of *M. leidyi* in the Black Sea was in large part responsible for unprecedented changes in the pelagic food chain, leading to sharp declines in the anchovy catch (Kideys 2002). Then, in 1997, the introduction of *Beroe ovata*, a well-known pelagic predatory ctenophore, resulted in the population control of *M. leidyi*, which contributed to the recovery of the Black Sea ecosystem. Other reported predators of ctenophores are various cnidarian scyphozoans (Condon & Steinberg 2008; Hosia & Titelman 2011), bony and cartilaginous fishes, and sea turtles (Oviatt & Kremer 1977; Link & Ford 2006; Bos et al. 2017), some capable of exerting control over ctenophore population growth.

In contrast to the notable attention devoted to pelagic ctenophores, little has been published on the predator–prey interactions of benthic ctenophores, except for general and limited remarks on zooplankton prey capture in the laboratory (Rankin 1956; Matsumoto 1999) and field (Alamaru et al. 2015), including laboratory maintenance of ctenophores by feeding them mainly crustacean larvae (Gnanamuthu & Nair Velappan 1948; Freeman 1967; Matsumoto & Gowlett-Holmes 1996). Such studies may have been hindered by the relatively small sizes and cryptic habits of benthic ctenophores. While small crustaceans (e.g., copepods, cladocerans, and zoea larvae) and other small zooplankton taxa (e.g., veligers, polychaete, and oligochaete worms) have been reported as prey, some benthic ctenophores are adept at ingesting larger prey items. Published and anecdotal information indicate that some benthic ctenophores can consume large food items, with prey body lengths up to one-half, and even exceeding, that of the ctenophore predators. Marcus (1957) noted the ingestion of a large crustacean appendage by *Vallicula multiformis*, and Gnanamuthu & Nair Velappan (1948) observed that individuals of *Ctenoplana bengalensis* consumed large prawn fragments, which they attributed to an expansive and everted stomodaeum. Larger food items may also be pushed into the inner pharynx of

*V. multiformis* by the tentacles, assisted by the contraction inwards of the oral lappets (Rankin 1956). Furthermore, benthic ctenophore ectosymbionts of sea stars were observed in several instances feeding on fishes, crabs, and a tube worm off Halmahera, Indonesia (<http://www.blennywatcher.com/2013/05/21/death-by-ctenophore/>; Ned & Anna DeLoach, unpubl. data).

In consideration of ctenophores as prey, we were unable to find any published study documenting predation on benthic ctenophores. However, online blogs and other forums have reported examples of predator–prey interactions in tropical Indo-Pacific sites of high biodiversity. These observations are of particular interest because they have been made *in situ* by naturalist divers who often provided behavioral details and photographic documentation. For example, in the Banda Sea (East Timor), an aglajid opisthobranch was reported eating an individual of *Coeloplana* sp. (B. Francisco unpubl. data; <http://www.seaslugforum.net/find/15543>; see p. 30 in Coleman 2008).

The primary aims of this study were centered around the predator–prey ecologies and behaviors of two coeloplanid ctenophores in subtropical southeast Florida to determine: (a) efficacy and rates of prey capture (zooplankton; eggs and larvae of fish) by ctenophores; and (b) predation rates of two known predators (a fish and a snail) on individuals of the nearly microscopic *Coeloplana waltoni* GLYNN, BAYER & RENEGAR 2014 associated with their octocoral hosts. Both of these aspects of the study were based on laboratory experiments. Furthermore, to determine the identity of possible predators of the small and fairly cryptic *V. multiformis* Rankin 1956, (c) field observations were conducted on macroscopic consumers in the ctenophore's habitat, and (d) laboratory feeding experiments were performed with suspected predators. Finally, (e) field sampling of known and suspected predators of the two ctenophore species was conducted to help assess their relationship with ctenophore prey abundances.

## Methods

### Species and study sites

The benthic ctenophore species in this study, *Coeloplana waltoni* and *Vallicula multiformis*, are members of the order Platyctenida and family Coeloplanidae. Members of this family lack comb rows as adults, and many species occur as commensals on algae and invertebrate hosts. Information on

the biology, distributions, study sites, and environments relating to these species can be found in Rankin (1956), Matsumoto & Gowlett-Holmes (1996), Matsumoto (1999), Glynn et al. (2014, 2017), and Alamaru et al. (2015).

In this study, the principal habitat of *C. waltoni* encompassed octocoral communities off Dania and Hollywood beaches at 3–8 m depth, while *V. multiformis* was a seasonally abundant member of biofouling communities at 10–50 cm depth at Crandon Park Marina (CPM), Biscayne Bay, southeast Florida (Fig. 1). Neither of the habitats is exposed at low tide. The shallow-water biofouling community is established on floating docks and thus is continuously submerged. Strong currents and turbulent conditions often occur at the octocoral sites; weak currents and calm waters prevail in the biofouling communities (Glynn et al. 2017). Mean monthly temperature/salinity (T/S) conditions are less variable annually at exposed octocoral sites subject predominantly to northerly Florida Current flow than at sheltered biofouling community sites that are influenced by freshwater input from runoff, canal effluents, and groundwater discharge (Glynn et al. 2017). Mean seasonal salinity values in the north region of Biscayne Bay, during a 4-year period (2005–2009), were 25.0‰ (wet season) and 30.4‰ (dry season), dropping below 10‰ during heavy precipitation events (Stabenau et al. 2015). Annual extreme T/S conditions were less variable at exposed (e.g., 20–32°C; 32–39‰) than protected sites (e.g., 16–34°C; 30–41‰). Laboratory seawater temperature was maintained at 24–27°C, and salinity at 32–35‰.

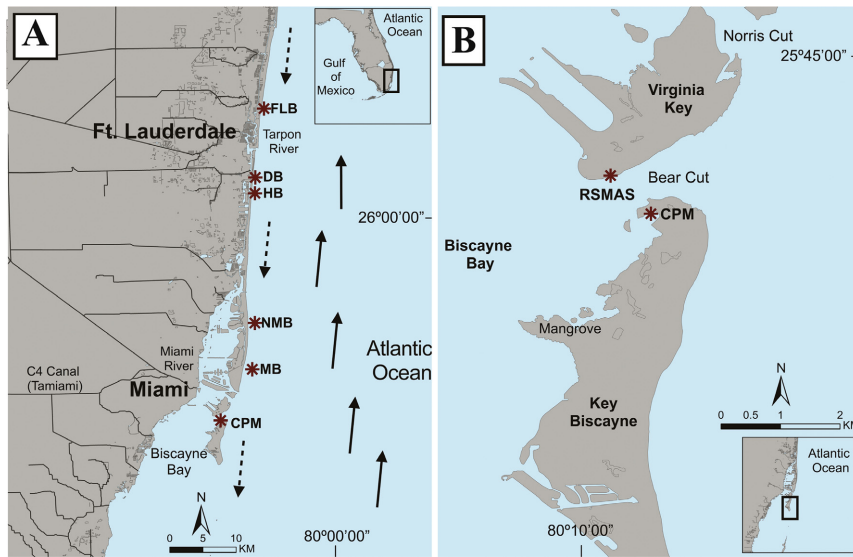
### Ctenophores as predators, laboratory studies

Ctenophores were collected and maintained on their natural substrates in the laboratory for 2–3 d before the feeding trials. Survival of ctenophores and their host substrates (octocorals, algae) was high before and after trials. Both ctenophore species were fed live nauplii of *Artemia* sp. and rotifers (*Brachionus* sp.) at least weekly. See Glynn et al. (2017) for details on the maintenance of laboratory animals. Observations of prey capture, chiefly zooplankton, by individuals of *C. waltoni* and *V. multiformis* were recorded in the laboratory during routine maintenance of ctenophores and their natural substrates. Also, prey capture by individuals of *C. waltoni* was observed day and night in the field. Individuals of *V. multiformis* were not observed feeding in the field due to the frequent presence of large bull sharks (*Carcharhinus lucas*) near the

biofouling community, which prevented observations from being made *in situ*.

The predatory behaviors and prey capture efficiency of each ctenophore species was observed in 1-L beakers of sand-filtered (10- $\mu$ m pore size) seawater. In each predation trial, a 50-mL subsample of potential prey of predetermined density was added to 950 mL of seawater to total 1 L for the experimental trials. Natural densities (22–58 individuals per L) of individuals of *C. waltoni* present on a colony of the octocoral host *Eunicea succinea* PALLAS 1766 were employed in predator trials. Each octocoral host was suspended naturally in an upright position in beakers with a looped nylon line. Treatments also included live octocoral stems alone, and dead (briefly frozen) octocoral stems, which served as controls. The live and dead octocoral controls were employed to determine prey losses due to octocoral feeding in the absence of ctenophores, and losses from adhesion and fragmentation, respectively. Stems were 10–12 cm in length and contained 100–500 polyps each, with mean mouth diameters of 1.7–2.8 mm. The predators (numerous individuals of *C. waltoni* on one octocoral stem in 1 L of seawater) in the three treatments were offered zooplankton, fish eggs, or recently hatched fish larvae for feeding periods of 2 h. Eggs and larvae of the dolphinfish *Coryphaena hippurus* LINNAEUS 1758 were selected for study because this species spawns in drifting rafts of *Sargassum* spp., which naturally travel across and sometimes accumulate in octocoral communities where individuals of *C. waltoni* are found. Additionally, *Sargassum* spp. form a natural substrate for individuals of *V. multiformis* and occur commonly as large wind-blown rafts in our study site at CPM.

In trials with *V. multiformis*, individuals were introduced on sprigs of the alga *Halimeda tuna*, 6–8 cm in length, and with a displacement volume of 3–4 mL. Prey were introduced to the experimental beakers as described for *C. waltoni*. Individuals of both ctenophore species remained firmly affixed to their respective natural substrates during the 2-h trials. Circulation in the beakers was generated with a magnetic stirrer set at a low and constant rate, resulting in a current flow of 3–4 cm s<sup>-1</sup>. Congo Red dye introduced at the surface, to observe visually the path of water flow, dispersed fully throughout the beaker in 30–45 s. Emson & Whitfield (1991) and Eeckhaut et al. (1997) demonstrated that tentacle extension is passive, generated by drag forces induced by water flow. We note, however, that individuals of both ctenophore species commonly extended tentacles three to four times their



**Fig. 1.** Location of study sites, southeastern coast of Florida. **A.** Fort Lauderdale Beach south to Crandon Park Marina, Key Biscayne. Mean current flow over the SE Florida shelf is predominantly northward most of the year (solid arrows); in the autumn season, the mean nearshore surface current briefly changes course (broken arrows) and is directed southward (Soloviev et al. 2017). **B.** Virginia Key and Key Biscayne. FLB, Ft. Lauderdale Beach; DB, Dania Beach; HB, Hollywood Beach; NMB, North Miami Beach; MB, Miami Beach; RSMAS, Rosenstiel School of Marine and Atmospheric Science; CPM, Crandon Park Marina.

body lengths in Petri dishes with no water movement. Since feeding commonly occurred in both species in our holding tanks under light, each beaker was illuminated with a ProLux LED fiber optic daylight illuminator (TechniQuip, Pleasanton, CA, USA) in the range of 100–150 lumens at a distance of 10 cm from the top of each beaker. Ctenophore fishing behaviors and predator–prey interactions were observed continuously during the course of all trials. Individuals of both ctenophore species also were offered dolphinfish eggs and larvae for several hours after the experimental trials, and then examined microscopically for signs of ingestion.

Zooplankton samples for the feeding trials were collected from the dock at the University of Miami Rosenstiel School of Marine and Atmospheric Science (RSMAS) with a 64- $\mu\text{m}$  mesh net during daylight hours. Taxa were identified from descriptions in Johnson & Allen (2005) and Martin et al. (2014), and counted and measured (maximum body dimensions) in known volumes of seawater with a dissecting microscope at 8–35 $\times$  magnification. Zooplankters were allowed to settle for  $\sim$ 0.5 h to permit separation of detritus, which settled to the bottom, from live plankton that remained actively swimming in the water above. Live zooplankters were employed in the predation trials  $\sim$ 2 h after collection. The trials with individuals of *V. multiformis* usually consisted of two beakers, one experimental and one control.

Trials with individuals of *C. waltoni* that were offered zooplankton prey consisted of one experimental beaker and two control beakers (the second control beaker contained a freshly killed octocoral, *E. succinea*, alone; see Table S1).

Eggs and larvae of dolphinfish from locally captured brood stock were obtained from the University of Miami Experimental Hatchery, RSMAS, Virginia Key, Biscayne Bay, Miami. The dolphinfish, *C. hippurus*, is a tropical and subtropical species that occurs abundantly in Florida waters, as well as worldwide (Gibbs & Collette 1959; Oxenford 1999). All eggs and larvae were procured the same day of the predation trials and killed immediately after use in order to avoid accidental introductions. The maximum dimensions of live individual ctenophores, expanded octocoral polyps, zooplankters, dolphinfish eggs, and dolphinfish larvae employed in predation trials were measured under a dissecting microscope. The trial numbers for experimental and control treatments are noted below (Tables 1 and 2) and in Tables S1 and S2.

### Ctenophores as prey, laboratory experiments

We used two potential predators of *C. waltoni* that are commonly observed in the Dania Beach octocoral communities: *Centropyge argi* WOODS & KANAZAWA 1951, the Caribbean Pygmy Angelfish;

**Table 1.** Estimates of per capita prey loss during 2-h experimental feeding trials including one or two focus predator species and one of three prey types.

Prey	Trial number	Focus predator species	Percent loss* Experiment – control	Total no. prey offered (50 mL <sup>-1</sup> )	Loss per individual predator
Mesozooplankton	1	<i>Coeloplana waltoni</i>	23.8	82	0.89
	1	<i>Eunicea succinea</i>	36.5	82	0.25
	2	<i>Coeloplana waltoni</i>	28.0	109	0.92
	2	<i>Eunicea succinea</i>	30.4	67	0.08
<i>Coryphaena hippurus</i> Eggs	1	<i>Coeloplana waltoni</i>	19.2	52	0.17
	2	<i>Coeloplana waltoni</i>	18.2	44	0.22
Larvae	1	<i>Coeloplana waltoni</i>	50.0	50	1.92
	2	<i>Coeloplana waltoni</i>	7.1	71	0.26

\* Percent loss was determined by subtracting the control (focus predator absent) prey density losses from the experimental prey density losses.

**Table 2.** Estimates of per capita prey loss during 2-h experimental feeding trials including *Vallicula multiformis* and one of three prey types.

Prey	Trial number	Percent loss*	Total no. prey offered (50 mL <sup>-1</sup> )	Loss per individual predator
Mesozooplankton	1	17.1	116	1.24
	2	21.0	94	0.99
<i>Coryphaena hippurus</i> Eggs	1	12.0	50	0.60
	2	2.0	50	0.09
Larvae	1	26.0	50	0.81
	2	4.0	50	0.12

\* Percent loss was determined by subtracting the control (predator absent) prey density losses from the experimental prey density losses.

and *Cyphoma gibbosum* LINNAEUS 1758, the flamingo tongue gastropod. These predators were introduced to laboratory aquaria containing *C. waltoni* on an octocoral colony. These predators were selected because they were often observed nipping or grazing on octocorals in the field. The four octocoral host species, members of the family Plexauridae, were *Eunicea clavigera* Bayer 1961, *Eunicea (Eunicea) succinea*, *Eunicea (Euniceopsis) tourneforti* MILNE EDWARDS & HAIME 1857, and *Muricea elongata* LAMOUROUX 1821. Two branch tips, 10 cm in length, from individuals of each species, were positioned upright in coral carbonate platforms (see fig. 3 in Glynn et al. 2017). The three angelfish (*C. argi*) were donated by Ocean View Aquariums, and the five individuals of *C. gibbosum* were collected from octocorals at Ft. Lauderdale and Hollywood beaches, Florida. Predator sizes were: *C. argi*, 5–7 cm total length; *C. gibbosum*, 3–5 cm shell length. The octocoral species were maintained in a 50-gallon (~200 L) holding aquarium and fed daily (nauplii of

*Artemia*, microalgae [*Nannochloropsis oculata* and *Isochrysis galbana*, from Reed Mariculture, California]) between trials. The aquarium was supplied with live rock (a marine limestone rock with a diverse array of live microorganisms, algae, and invertebrates), a protein skimmer, and an external canister filter (with a physical filter medium). Lighting on a 12-h cycle was supplied with metal halide (250 W) 14 K color temperature lamps to mimic seawater illumination. Seawater was prepared using dechlorinated tap water with Instant Ocean salt mix. Freshly collected octocoral branches, with their ctenophore ectosymbionts, were employed in each trial.

Twelve trials, 72 h in duration, were performed with either a fish or a mollusc predator. One predator was introduced into a 10-gallon (~40 L) aquarium with eight octocoral branches (two branches per species), each with its natural complement of ctenophores. The initial numbers of ctenophores ranged 7–17 per branch. In each trial, a control tank

containing an equal number of octocoral branches with ctenophores was used to determine background ctenophore losses and mortality in the absence of predation. The *C. argi* trials were performed in February and March 2014, and *C. gibbosum* from March through May 2014. A total of three fish and five gastropods were employed in the predation trials. These test individuals were employed repeatedly and allowed 2–3 weeks of respite between trials, during which time they were fed lightly.

### Potential predators of ctenophores, field surveys

To determine the abundances of the predators *C. gibbosum* and *C. argi* in the field (the two known predators of *C. waltoni*), octocoral communities dominated by *Eunicea* spp., *Muricea* spp., and *Antilloorgia* sp. were selected for sampling. These sampling sites were located at six locations from Ft. Lauderdale Beach, Florida to North Miami Beach, Florida (Fig. 1) at 6–8 m depth, with each census plot subdivided into 3 × 3 m areas with corner-emplaced steel rods and connecting lines. All octocoral colonies inside the plots were searched visually by SCUBA divers for *C. gibbosum*, and the numbers of *C. argi* were noted from the outer plot boundaries during 2- to 3-min observation periods. The fish were found not to be unduly disturbed during the censuses, quickly returning to their territories within 1–2 min following the initiation of sampling protocol.

Abundances of potential predators of *V. multiformis* were monitored at three observation sites from October 2016 through April 2017, weekly or twice monthly, for 20-min periods each at CPM (Key Biscayne), South Dock #2, piers 3 and 4. These sites supported an abundance of algae including *Acanthophora spicifera* (VAHL) BØRGESEN 1910 and *H. tuna* (J. ELLIS & SOLANDER) J.V. LAMOUREUX 1816, which are frequented by individuals of *V. multiformis* (see Glynn et al. 2017). Observers visually surveyed, photographed, and identified potential invertebrate and fish predators by lying motionless on the floating dock from 10:00 to 12:30 hours, and made observations to a depth of 0.5 m along a 1-m length of the biofouling community. Contact with the substrate and the type of feeding were noted. “Directed biting” was defined as the selection of a particular prey item, and “grazing” as the biting and ingestion of numerous, and often diverse, prey items.

Potential predators of *V. multiformis* were isolated and identified (to the lowest possible taxonomic level) from algal masses collected at CPM, Key Biscayne. In order to compare predator and prey

abundances in different collections, the displacement volume of the algal substrate, after draining excess water, was measured to the nearest mL in a graduated cylinder. These possible predators were selected on the basis of their abundance and co-occurrence with *V. multiformis* and, in most cases, their known predatory behaviors with other species. The date, hour, sea surface temperature, salinity, moon phase, and tidal cycle were recorded at the time of collection. We measured the size of each candidate predator and then isolated each individual in the laboratory in a holding dish, with seawater changes performed every 48–72 h. For each timed trial, a single potential predator was introduced to a clear polyethylene dish (13.5 cm diameter, 2.5 cm high) with seawater (~350 mL) and allowed to acclimate under indirect lighting for 1 h. Then, two ctenophores were introduced 3–5 cm from a test predator, in line of sight of visual predators (crabs, isopods) or near non-visual predators (actinians, polychaete worms, brittle stars). For trials with actinians, two ctenophores were introduced within reach of tentacles. Interactions (escape, capture, ingestion) between the predator and ctenophore were observed for 1 h. Elapsed times between prey introduction and the first and second predation events were recorded. A few predation trials did not follow this protocol, and are so noted in Table 4 below.

### Data analyses

Since enumeration data represented the chief source of measurements in this study, appropriate statistical testing required largely non-parametric methods, which are noted where applied. Standard parametric statistics were also used in predator–prey body size comparisons and in the analysis of experimental consumption rates of *C. waltoni* by a fish and mollusc predator. For the latter analysis, a repeated-measures generalized linear mixed model with a Poisson response structure was fit, using Kenward–Roger degrees of freedom and standard error adjustments. Pairwise differences were tested using Tukey–Kramer adjustments. Statistical testing was executed using SAS procedure PROC-MIXED.

## Results

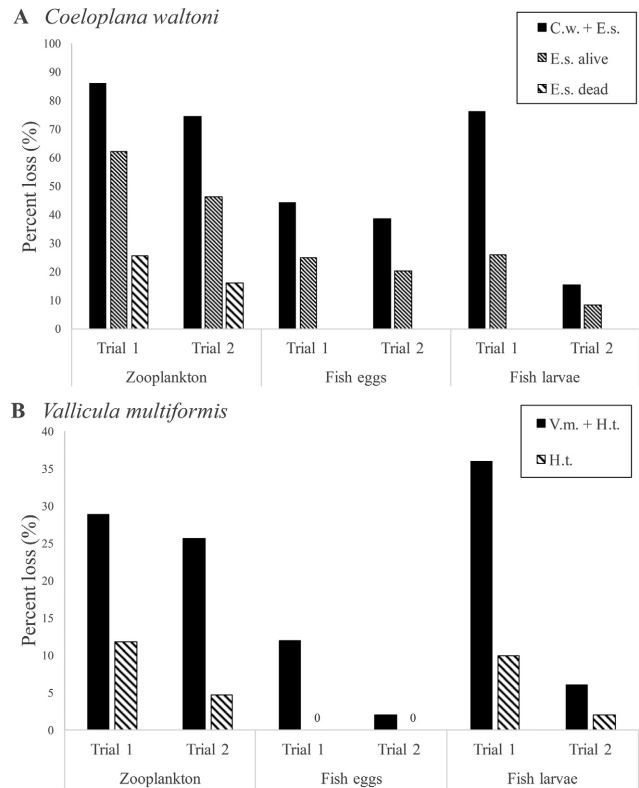
### Ctenophores as predators

Individuals of *Coeloplana waltoni* were frequently observed capturing and ingesting nauplii (*Artemia* sp.), rotifers (*Brachionus* sp.), and diverse taxa of zooplankton offered as food in the laboratory. In

laboratory feeding trials, individuals of *C. waltoni* quickly extended their tentacles and began capturing zooplankters, especially small copepods and veliger larvae (Fig. 2A, Table S1). Ingestion of captured prey was not observed during the 2-h trials; however, most captured zooplankters remained adhering to ctenophore tentacles over the entire trial period. Estimates of zooplankton prey loss (assumed to be due to capture by feeding individuals of *C. waltoni*) in trials 1 and 2 (Table S1, column 2) were 0.89 and 0.92 individuals  $2\text{ h}^{-1}$  (Table 1). Since individuals of both *C. waltoni* and *Eunicea succinea* were observed capturing prey, these rates were estimated from the differences of both predators feeding in trial 1 (experimental, 86.0% loss) and presence of octocorals alone feeding in trial 1 (control 1, 62.2% loss, Fig. 2A). The rate of zooplankton capture by octocoral polyps was estimated from the difference in prey loss in trials with live *E. succinea* and in trials with recently killed *E. succinea*. Estimates of daily loss rates due to octocoral polyps alone were 0.25 and 0.08 zooplankters  $2\text{ h}^{-1}$  (Table 1). Zooplankton losses also occurred in the dead octocoral control trials (Fig. 2A); this was a result of zooplankton adhesion to the dead octocoral stems, and mortality and fragmentation of zooplankters.

Dolphinfish eggs were readily captured by individuals of *C. waltoni*, but not ingested during the 2-h trials (Fig. 2A, Table S1). They were, however, observed ingested several hours after the predation trials. Eggs were captured and engulfed by polyps of the host octocoral *E. succinea*. On several occasions, eggs adhering to ctenophore tentacles in the process of retraction were purloined by octocoral polyps when the eggs were brought near the octocoral stem. Per capita estimates of egg capture rates (determined from the differences in egg loss between treatments with both ctenophores and octocoral vs. treatments with octocoral alone) were 0.17 and 0.22 eggs  $2\text{ h}^{-1}$  (Table 1). Egg loss rates were significantly lower than losses of zooplankton and dolphinfish larvae (Mann–Whitney *U*-test,  $U=0$ ,  $p=0.036$ ).

Recently hatched (<24 h) dolphinfish larvae were captured by individuals of *C. waltoni*, and sometimes covered by the oral surface of the ctenophore, but not ingested (Fig. 2A, Table S1). Fish larvae were also captured by the polyps of *E. succinea*, and occasionally purloined from the tentacles of individuals of *C. waltoni*. The large differences in capture rates in trials 1 and 2 are unexplained. Fish larvae loss rates were 1.92 and 0.26 per predator  $2\text{ h}^{-1}$  (Table 1). Microscopic examination showed that dolphinfish eggs and larvae were ingested by individuals of *C. waltoni* after several hours ( $\leq 5\text{ h}$ ) of



**Fig. 2.** Rates of predation (percent loss of prey) by *Coeloplana waltoni* and *Vallicula multiformis* in 2-h feeding trials with three different prey types offered: zooplankton, fish eggs, and fish larvae. **A.** Individuals of *Eunicea succinea* (E.s.), alive and dead, served as controls in zooplankton trials. **B.** The alga *Halimeda tuna* (H.t.), a live substrate, served as controls for all three prey types tested. See Tables S1 and S2 for predator and prey densities and sizes, and behavioral observations during the predation trials.

exposure to these food items. This suggests that feeding trials for this species should be extended to  $\sim 4\text{ h}$  in further work.

Incidental observations of individuals of *Vallicula multiformis* during collections revealed the capture and ingestion of relatively large crustacean limbs (periopods and antennae), 3–4 mm in length. Also of note, one individual of *V. multiformis* captured, in rapid succession, eight nauplii, 0.18–0.47 mm in length. These nauplii were ingested and visible in the gut in less than 2 min. Mesozooplankters offered to individuals of *V. multiformis* were readily captured, and occasionally ingested during the 2-h feeding trials (Fig. 2B, Table S2). The plankton samples were dominated by calanoid and cyclopoid copepods, about 20% smaller in mean size than their ctenophore predators. The losses of zooplankters in the two trials with individuals of *V.*

*multiformis* were 1.24 and 0.99 individuals per ctenophore predator (Table 2). However, all of these losses cannot be attributed to predation. While tentacle capture usually resulted in the mortality of potential prey, relatively few instances of ingestion were observed.

Dolphinfish egg capture and ingestion by individuals of *V. multiformis* were relatively high in trial 1 (0.60 eggs  $2\text{ h}^{-1}$ ) and low in trial 2 (0.09 eggs  $2\text{ h}^{-1}$ ) (Fig. 2B; Tables 2 and S2). The per capita capture rates of dolphinfish larvae by ctenophores, 0.12 and 0.81 larvae  $2\text{ h}^{-1}$  (Table 2), were comparable to those of individuals of *C. waltoni*. In experimental trial 1, some captured larvae were even ingested by individuals of *V. multiformis*. There were no evident differences in the loss rates of the three classes of prey tested (Mann–Whitney *U*-test,  $U=3$ ,  $p=0.400$ ).

The median loss rates of all three prey categories offered to individuals of *C. waltoni* and *V. multiformis* were 0.26 and 0.70 prey  $2\text{ h}^{-1}$ , respectively (Tables 1 and 2). These differences were marginally non-significant (Mann–Whitney *U*-test,  $U=8$ ,  $p=0.066$ ). The per capita mesozooplankton prey losses in two trials with the octocoral (*E. succinea*) alone, 0.08–0.25 zooplankters  $2\text{ h}^{-1}$ , were comparable to those of the ctenophores (Table 1).

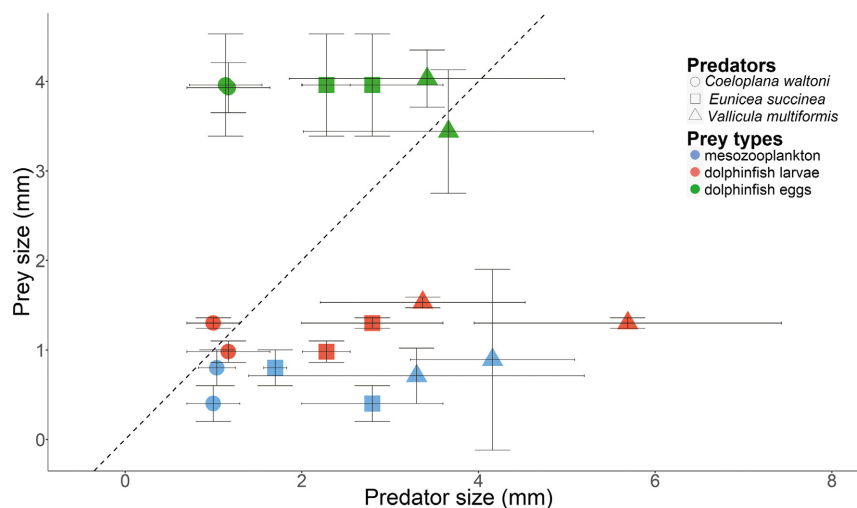
Variation in the relative sizes of predator and prey (Fig. 3) may have influenced observed variation in prey capture rates. Individuals of the two ctenophore species were generally larger or smaller than polyps of the octocoral. The large sizes of dolphinfish larvae in most trials (above the diagonal in Fig. 3) had a strong effect on the predator–prey size

ratios in those trials. There was also considerable variation in both predator and prey sizes within each trial, but duplicate trials were generally similar to each other.

### Ctenophores as prey

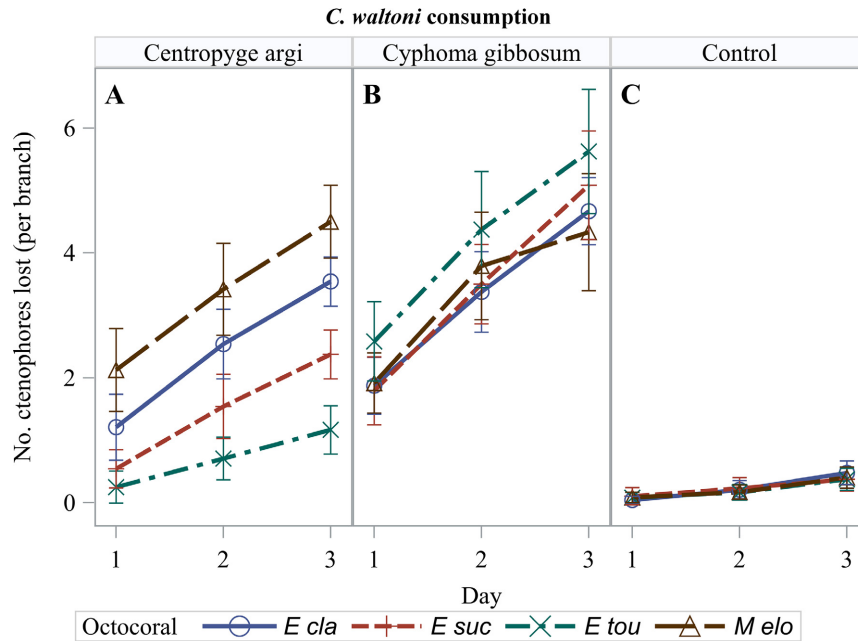
Predation on *C. waltoni* by a fish and a gastropod was high. Overall, predation rates were significantly different between the two predators ( $p=0.0085$ ; Table S3). Daily predation by individuals of the pomacanthid fish *Centropyge argi* was highly variable (Fig. 4A). Mean losses over 3 d ranged 1.2–5.0 individuals, which represented 4.6% and 40.0% of the initial numbers of ctenophores present. The greatest rates of loss occurred on octocoral colonies of *M. elongata*, but these rates were not significantly different from rates of loss on colonies of *Eunicea clavus*. Ctenophore losses due to grazing by individuals of the gastropod *Cyphoma gibbosum* were relatively consistent and did not differ significantly among octocoral host species (all  $p \geq 0.94$ ); the mean numbers of ctenophores lost ranged 4.6–5.2 over 3 d (Fig. 4B). These were equivalent to ctenophore losses of 32.6–44.4% over the experimental trials.

The mean rates of ctenophore losses in all control trials ( $n=24$ ) for *E. succinea*, *E. clavus*, *E. tourneforti*, and *M. elongata*, respectively, were 0.125, 0.153, 0.111, and 0.132 individuals per octocoral branch  $\text{d}^{-1}$ , or 2.96%, 3.70%, 2.69%, and 3.57% loss after 3 d (Fig. 4C). These differences were not significant ( $\chi^2_3=1.32$ ,  $p=0.724$ ), and are in line with



**Fig. 3.** Mean sizes of three predators (*Coeloplana waltoni*, *Eunicea succinea*, *Vallicula multiformis*) and mean sizes of three prey types (mesozooplankton, dolphinfish eggs, dolphinfish larvae) in laboratory predation trials (from Tables S1 and S2). Horizontal and vertical error bars (SD) show variation in predator and prey sizes in each of two trials.





**Fig. 4.** Rates of predation (number of prey lost) by a pomacanthid fish (A) and a gastropod mollusc (B) preying on *Coeloplana waltoni* from four species of octocoral hosts in 3-d feeding trials. C. Control loss rates. All error bars represent 95% confidence intervals. *E cla*, *Eunicea clavigera*; *E suc*, *Eunicea succinea*; *E tou*, *Eunicea tourneforti*; *M elo*, *Muricea elongata*.

the non-selective feeding field observations of Lasker et al. (1988). Also, these low rates of loss attest to the appropriate conditions in the control aquaria.

Mean daily per capita consumption rates of the ctenophore *C. waltoni* by individuals of *C. argi* ranged 0.46–2.78 individuals of *C. waltoni*; the consumption rates by individuals of *C. gibbosum* were slightly higher, from 2.64 to 3.58 ctenophores per d (Table 3). The coefficient of variation values indicates high and comparable variability in predation rates by fish and molluscs.

Field observations and laboratory predation trials were performed to gain insight into the natural predators of *V. multiformis*. Field observations conducted during daylight hours revealed a rich fish fauna associated with the biofouling community, with 19 species belonging to 17 families (Table S4). Nine species were observed biting or grazing on the benthos; however, the identity of many of the food items consumed could not be determined with an acceptable level of certainty. Five individuals of the decorator crab, *Omalacantha bicornuta* (LATREILLE 1825), performed directed biting 80% of the time. These crabs were observed clipping unidentified objects from algae. Six monitoring trials performed at night revealed two individuals of a decorator crab (? *O. bicornuta*) and a spiny lobster (*Panulirus argus* LATREILLE 1804). Both species were foraging in the benthos.

**Table 3.** Per capita daily consumption rates by fish (*Centropyge argi*) and molluscs (*Cyphoma gibbosum*) preying on *Coeloplana waltoni* during 72-h feeding trials.

Predator species	Octocoral hosts	Consumption*			CV (%)
		$\bar{x}$	SD	Range	
<i>Centropyge argi</i>	<i>Eunicea tourneforti</i>	0.46	0.21	0.3–0.7	45.6
	<i>Eunicea succinea</i>	1.22	0.33	0.7–1.7	27.0
	<i>Eunicea clavigera</i>	2.06	0.33	1.7–2.7	16.0
	<i>Muricea elongata</i>	2.78	0.62	2.0–4.3	22.3
	<i>Eunicea tourneforti</i>	3.58	1.11	2.0–5.3	31.0
<i>Cyphoma gibbosum</i>	<i>Eunicea succinea</i>	3.03	1.04	1.7–5.0	34.3
	<i>Eunicea clavigera</i>	2.72	0.52	2.0–3.3	19.1
	<i>Muricea elongata</i>	2.64	1.07	1.3–5.0	40.5

\* Number of ctenophores consumed per d.

Feeding trials in the laboratory provided information on possible ctenophore predators. Individuals of *Exaiptasia pallida* AGASSIZ IN VERRILL 1864, a sea anemone, and three species of brachyuran crabs

(*Macrocoeloma trispinosum* LATREILLE 1825, *Panopeus herbstii* H. MILNE EDWARDS 1834, and *Portunus (P.) sayi* GIBBES 1850) consistently and quickly attacked and ingested live individuals of *V. multiformis* (Table 4). Ctenophores were ensnared in the anemone's tentacles, which conveyed them to the mouth and then into the gullet (Fig. 5A). The crabs used their chelae to capture the ctenophores, and then moved them to their mouthparts (maxillae and mandibles), where they were manipulated, macerated, and ingested (Fig. 5B,C). Individuals of *M. trispinosum* were fed a steady diet of *V. multiformis*

for over 1 month to explore the possibility that the ctenophores might contain a repellent, toxic, or debilitating substance. The healthy state of the crabs suggested that *V. multiformis* provided an acceptable and sufficient food source.

Compared to the three species of brachyuran crabs, which ingested 68–100% of the ctenophores offered, individuals of the decorator crab *O. bicornuta* ingested only 16% of the ctenophores offered (Table 4). Individuals of this crab species usually detected individuals of *V. multiformis* when offered, but were not adept at capturing and handling the

**Table 4.** Potential natural predators of *Vallicula multiformis*, as observed from laboratory feeding trials, 2016–2017. All test animals are members of the biofouling community.

Potential predator <sup>a</sup>	Size (mm)	Mean no. ctenophores ingested		No. trials (individuals) <sup>f</sup>	Remarks
		Per trial	%		
<i>Exaiptasia pallida</i> (AGASSIZ in VERRILL 1864)	6–7 <sup>b</sup>	1.4	70.0	12 (4)	Anemones sedentary, capture free-floating ctenophores
<i>Hesione picta</i> MÜLLER IN GRUBE 1858	30–38 <sup>c</sup>	0.3	27.3	11 (3)	A member of carnivorous family Hesionidae (Fauchald & Jumars 1979)
<i>Macrocoeloma trispinosum</i> (LATREILLE 1825)	10, 7 <sup>d</sup>	1.3	66.7	6 (2)	Aggressively attacked ctenophores, rapidly macerating and ingesting
<i>Omalacanthe bicornuta</i> (LATREILLE 1825)	9–20	0.4	16.0	19 (6)	Generally no reaction to ctenophore presence. Three large crabs ingested one ctenophore each. A 10-mm crab ingested two ctenophores
<i>Panopeus herbstii</i> (H. MILNE EDWARDS 1834)	14 <sup>d</sup>	1.0	100.0 <sup>e</sup>	4 (2)	Macerated and ingested ctenophores quickly
( <i>Portunus (P.) sayi</i> (GIBBES 1850) <sup>e</sup>	12 <sup>d,e</sup>	0.8	80.0	5 (3)	Present in floating <i>Sargassum</i> spp. Macerated and ingested ctenophores immediately
<i>Paracerceis sculpta</i> <sup>g</sup> (HOLMES 1904)	4–6	0	0	4 (3)	Often avoided contact with ctenophores
<i>Amphipholis squamata</i> <sup>h</sup> (DELLE CHIAJE 1828)	2–4	0.3	16.7	6 (2)	Ctenophores ignored; some ophiuroids executed avoidance responses
<i>Elacatinus macrodon</i> (BEEBE AND TEE-VAN 1928)	33	0	0	6 (2)	Ctenophore introduced at surface of 20-L aquarium
<i>Lutjanus griseus</i> (LINNAEUS 1758)	68	0.5	50.0	2 (1)	Ctenophore introduced at surface of 20-L aquarium. One ctenophore ingested whole; one bitten, then rejected, with fish showing mouth irritation
<i>Paraclinus nigripinnis</i> (STEINDACHNER 1867)	30	0	0	5 (1) <sup>e</sup>	Two ctenophores attacked, then rejected; fish showed mouth irritation

<sup>a</sup> Species names after WoRMS (2017).

<sup>b</sup> Maximum disk width.

<sup>c</sup> Live length.

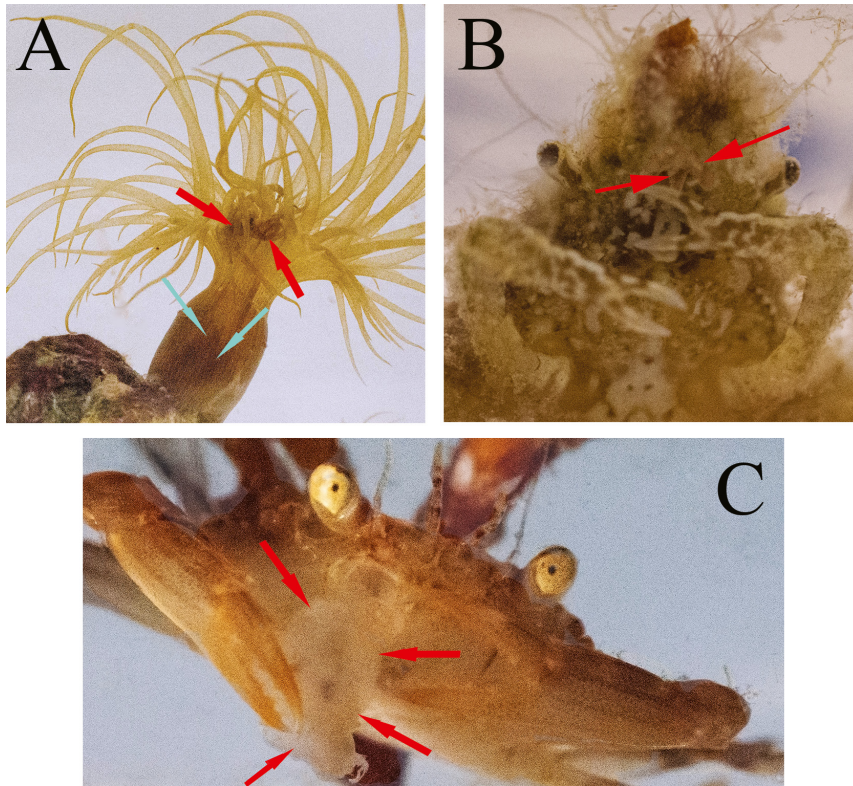
<sup>d</sup> Carapace width.

<sup>e</sup> One ctenophore offered.

<sup>f</sup> Number of predators tested.

<sup>g</sup> Probably an invasive species (Marchini et al. 2017).

<sup>h</sup> Probably a species complex (G. Hendler unpubl. data).



**Fig. 5.** **A.** *Exaiptasia pallida*, a 1.5-cm (column height) individual, ingesting a 3.8-mm individual of *Vallicula multiformis*, dark mass visible entering pharynx (arrows). Arrows point to earlier ingested ctenophore in gut. **B.** *Omalacantha bicornuta*, a 1-cm (carapace width) decorator crab, dismembering and ingesting a 4-mm individual of *V. multiformis*, a fragment visible entering mouth (arrows). **C.** *Portunus (P.) sayi*, a 1.2-cm (carapace width) *Sargassum* swimming crab, dismembering and ingesting a 7-mm individual of *V. multiformis* (arrows). All photographs from laboratory feeding trials.

ctenophore in the timed trials, perhaps due to the relatively small sizes of the ctenophores. Upon detection, the crab would actively flail its chelae, but fail to grasp the ctenophore. A small individual of *O. bicornuta*, with a carapace width of 10 mm, quickly detected, captured, and ingested two individuals of *V. multiformis* (Fig. 5B). Three individuals of the sargassum swimming crab, *Portunus (P.) sayi*, aggressively attacked and consumed ctenophores during timed trials (Fig. 5C). Other tested potential predators included a hesionid polychaete worm (*Hesione picta* MÜLLER IN GRUBE 1858); a sphaeromatid isopod (*Paracerceis sculpta* HOLMES 1904); an amphiuroid brittle star (*Amphipholis squamata* DELLE CHIAJE 1828); and three fishes, a juvenile lutjanid [*Lutjanus griseus* (LINNAEUS 1758)], adult gobiids (*Elacatinus macrodon* BEEBE & TEE-VAN 1928), and an adult labrisomid (*Paraclinus nigripinnis* STEINDACHNER 1867). Of the three invertebrates, the polychaete worm and brittle star ingested *V. multiformis*, but not quickly or consistently. Of the three fishes, only a single test individual, the juvenile snapper

(*L. griseus*), ingested a ctenophore. However, in one-half of the trials, the ctenophore was mouthed and then quickly rejected, with the snapper exhibiting apparent irritation.

#### Potential predators of ctenophores, field abundances

The sampled densities of the fish (*C. argi*) and mollusc (*C. gibbosum*) predators of *C. waltoni* were each  $<1 \text{ m}^{-2}$  in 11 of 12 censuses conducted in octocoral communities (Table 5). One community sampled off Miami Beach yielded a density of 1.1 individuals per  $\text{m}^2$  of *C. gibbosum*. In every survey, the predator abundances were highest in the best-developed (most dense) octocoral stands, namely at the Miami Beach sites compared to the three beach sites sampled farther north.

In 10 collections of the biofouling community, two potential predators of *V. multiformis* dominated the samples: the actinian *E. pallida*, individuals of which were observed preying on adult ctenophores in laboratory feeding trials; and the sabellid worm

**Table 5.** Population densities of fish and mollusc predators of *Coeloplana waltoni* in octocoral communities surveyed off southeast Florida.

Location	Date sampled	Predator abundances				Octocoral community structure*		
		<i>Centropygi argi</i>		<i>Cyphoma gibbosum</i>		Genera	Height (m)	Density (m <sup>-2</sup> )
		No.	Density (m <sup>-2</sup> )	No.	Density (m <sup>-2</sup> )			
Ft. Lauderdale Beach 26°02'54", 80°05'49"	March 17, 2017	3	0.3	4	0.4	<i>Eunicea</i> <i>Muricea</i> <i>Gorgonia</i>	0.5–1.0	1
Hollywood Beach 26°02'01", 80°06'33"	March 19, 2017	0	0	0	0			
Dania Beach 26°03'18", 80°06'31"	March 20, 2017	1	0.1	2	0.2			
Miami Beach 25°47'42", 80°06'46"	March 29, 2017	6	0.7	10	1.1	<i>Eunicea</i> <i>Antillogorgia</i>	1.0–2.0	9
North Miami Beach 25°51'28", 80°06'33"	April 1, 2017	4	0.4	3	0.3			
25°51'28", 80°06'32"	April 5, 2017	4	0.4	7	0.8			

\* Predominant octocoral genera at sampling sites; approximate heights and densities of octocoral colonies.

*Bispira* sp., a ciliary-mucoid suspension feeder, assumed to prey on cydippid larvae. Fauchald & Jumars (1979) noted that sabellids prey on small invertebrates, including larvae. Overall, these two species made up 34.7% (*E. pallida*) and 56.9% (*Bispira* sp.) of all individuals present (Table 6). Individuals of *E. pallida* were present in nine collections, and *Bispira* sp. in samples collected in May, July, and August. These two species were notably abundant in the May 1, 2017 sample, in which there was sparse presence of the alga *Acanthophora spicifera*. The displacement volume of the alga was only 50 mL, but yielded 67 and 112 individuals of the anemone and sabellid worm, respectively. To explore a possible relationship between the actinian and sabellid predators versus the abundances of *V. multiformis*, a Spearman rank correlation test was performed employing the adjusted sample population densities (Table 6). In both cases, the predator-prey correlations were weak and non-significant: *Exaiptasia/Vallicula*,  $r_s = -0.22$ ,  $p > 0.05$ ; *Bispira/Vallicula*,  $r_s = -0.41$ ,  $p > 0.05$ .

The tentacle ejection behavior performed by *V. multiformis* suggests the presence of an unknown, possibly small predator of this ctenophore. When agitated or probed, individuals of *V. multiformis* immediately (within seconds) fully extruded both tentacles, forming a dense tangle that could serve as a defensive response. Tentacle retraction was the

usual response of individuals of *C. waltoni* when disturbed.

## Discussion

### Ctenophores as predators

Like many pelagic tentaculate ctenophores that possess a capacious stomodaeum and feed on large prey (Haddock 2007), both ctenophore species in this study were observed to capture and ingest large prey relative to their respective body sizes. Several diverse taxa of zooplankton in the 0.4-mm size range were captured and occasionally ingested by individuals of *Coeloplana waltoni* of 1.0 mm mean body length. Also, this minute ctenophore captured dolphinfish larvae up to four times its length. These larvae remained entangled (and dead) for up to 2 h after capture in experimental trials, and were observed ingested by the ctenophores after longer exposure periods to prey. Individuals of *Vallicula multiformis* 5–8 mm in length readily captured and ingested dolphinfish eggs in the 1-mm size range. Also, dolphinfish larvae 3.5–4.0 mm in length were captured and ingested by individuals of *V. multiformis*. Among trials for each ctenophore species, both exhibited large and unexplained differences in the capture rates of fish larvae, amounting to nearly an order of magnitude difference (see Tables 1 and

**Table 6.** Abundances of *Vallicula multiformis* and several predatory species in biofouling communities sampled at Crandon Park Marina, Key Biscayne. Abundance is shown as the number of individuals in each sample, and as density (number relative to the displacement volume of the sampled alga substrate).

Species	Collection date	Predominant alga <sup>a</sup>	Displacement volume (mL)	No. per collection	Density <sup>b</sup> (L <sup>-1</sup> )	<i>Vallicula multiformis</i>		
						No.	Density	
<i>Exaiptasia pallida</i>	March 27, 2017	<i>Halimeda tuna</i>	375	9	24	8	21	
<i>Omalacantha bicornuta</i>				4	11			
<i>Paraclinus nigripinnis</i>				1	3			
<i>Exaiptasia pallida</i>	April 3, 2017	<i>Halimeda tuna</i>	917	51	56	2	2	
Unidentified actiniarian				1	1			
<i>Paracerceis sculpta</i>				4	4			
<i>Panopeus herbstii</i>	April 10, 2017	<i>Halimeda tuna</i>	500	1	1	1	2	
<i>Exaiptasia pallida</i>				28	56			
<i>Amphipholus squamata</i>				3	6			
<i>Exaiptasia pallida</i>	April 12, 2017	<i>Acanthophora spicifera</i>	234	15	64	0	0	
Unidentified actiniarian				2	9			
<i>Paracerceis sculpta</i>				5	21			
<i>Exaiptasia pallida</i>	April 17, 2017	<i>Acanthophora spicifera</i>	440	9	20	0	0	
<i>Paracerceis sculpta</i>		<i>Halimeda tuna</i>		2	4			
<i>Exaiptasia pallida</i>	May 1, 2017	<i>Acanthophora spicifera</i>	50	67	1340	1	20	
<i>Bispira</i> sp.				112	2240			
<i>Exaiptasia pallida</i>	May 8, 2017	<i>Acanthophora spicifera</i>	570	4	7	2	4	
<i>Bispira</i> sp.		<i>Valonia macrophrys</i>		60	105			
<i>Exaiptasia pallida</i>	July 24, 2017	<i>Valonia macrophrys</i>	690	18	26	0	0	
<i>Bispira</i> sp.		<i>Acanthophora spicifera</i>		100	145			
<i>Paracerceis sculpta</i>		22		32				
<i>Exaiptasia pallida</i>	July 31, 2017	<i>Acanthophora spicifera</i>	190	6	32	52	274	
<i>Bispira</i> sp.				42	221			
<i>Bispira</i> sp.	August 2, 2017	<i>Halimeda tuna</i>	410	25	61	33	80	
<i>Paracerceis sculpta</i>				<i>Acanthophora spicifera</i>	4			10
<i>Omalacantha bicornuta</i>				1	2			

<sup>a</sup> Identifications according to Littler & Littler (2000).

<sup>b</sup> Values rounded off to nearest number of individuals.

2, “loss per individual predator”). The capture rates were not related to predator–prey size differences, which were similar among trials, but could possibly have been due in part to the prior feeding history of the field-collected ctenophores.

We observed captures of several prey types by individuals of both ctenophore species under conditions of high variation in the sizes of both predators and prey. In light of those observations, it would be desirable to obtain the individual sizes of predators and the prey they actually capture and consume in order to more precisely define these size relationships. Our feeding observations support the wide range and large size of prey captured and often

consumed by benthic ctenophores (Gnanamuthu & Nair Velappan 1948; Rankin 1956; Marcus 1957; Matsumoto & Gowlett-Holmes 1996). In addition, present results extend the range of prey items captured by benthic ctenophores to include early developmental stages of commercially and recreationally important fish species.

Observations of benthic ctenophores feeding on fishes, crabs, and a tube worm were reported by N. and A. DeLoach (<http://www.seaslugforum.net/find/ctenopho>, and unpubl. data) at shallow depths off Makian, Indonesia. Those ctenophores, possibly a species of *Coeloplana*, were epizootic on sea stars. One of the captured fishes, likely *Limnichthys*

*nitidus*, a benthic species which inhabits sand patches, was about equal in length (2–3 cm) to the ctenophore, which slowly engulfed the fish. Similar feeding behavior was observed on several occasions at other localities in Indonesia.

In the predation trials using individuals of *C. waltoni*, the polyps of *Eunicea succinea*, which are short and stubby, exhibited much lower capture rates of zooplankton, fish eggs, or fish larvae than the ctenophores, <50% overall. Individuals of other western Atlantic gorgonian species examined by Lasker (1981) also did not readily capture zooplankton, and this was attributed to a reduced cnidom in these cnidarians. Both ctenophores and octocorals were observed capturing prey in our laboratory trials; however, the ctenophore's fishing tentacles were longer and had a greater reach than the octocoral's tentacles. Therefore, the ctenophores were more efficient at ensnaring passing prey. On several occasions, fish eggs captured and being reeled in by *C. waltoni* were filched by octocoral polyps and quickly ingested. Opposite behavior was observed by Glynn et al. (2017), who offered evidence of individuals of *C. waltoni* pilfering particulate organic matter from the guts of their octocoral host polyps.

Estimates of prey capture by individuals of *C. waltoni* were significantly highest for zooplankton and *Coryphaena hippurus* larvae (Fig. 2A, Table 1). The relatively low capture rates of fish eggs could be due to lack of stimulation compared to the swimming movements and escape responses of zooplankton and fish larvae, or due to some coating on the surface rendering the eggs less attractive. The tentacles and tentilla of the ctenophore *Coeloplana bannworthi* are covered with two types of sensory cells that can detect swimming planktonic organisms (Eeckhaut et al. 1997). Contact with prey by one of these sensory cells (hoplocytes) results in the elevation of collocytes, which are responsible for affixing the prey to the tentilla. This mechanism facilitating prey capture may also function in *C. waltoni*.

Is it possible that our relatively high rates of zooplankton capture by individuals of *V. multiformis*, 0.99 and 1.24 individuals  $2 \text{ h}^{-1}$ , are inflated? Galt (1998) reported a mean ingestion rate of 10 individuals of *Artemia*  $\text{h}^{-1}$  by *V. multiformis* in feeding trials in Hawaii, suggesting that the highest capture rates observed in our study may not be unrealistic. Indeed, they may be too low. The zooplankton capture rates by individuals of the much smaller *C. waltoni* were less than one-half those of individuals of *V. multiformis*, but more data are needed to evaluate this difference.

The reported occurrence of large numbers of *V. multiformis* associated with *Sargassum* spp. (Alamaru et al. 2015), and our finding of high abundances of this ctenophore in floating *Sargassum* that often accumulated at our CPM study site, were the chief motivation for including dolphinfish eggs and larvae in the predation trials. The community of organisms within the floating *Sargassum* in the Florida Current supports a species-rich fish fauna, including *Coryphaena hippurus* (Dooley 1972). Dolphinfish spawn in and near *Sargassum* from January through March, with possible spawning year round (Beardsley 1967). Thus, the early sexual products of dolphinfish would likely be available for consumption by individuals of *V. multiformis*.

Information available for pelagic spawning fish families associated with shallow-occurring octocoral communities indicates the occurrence of eggs and early juvenile larval stages of manageable size for capture and consumption by *C. waltoni*. For example, egg sizes and early larval stages are generally 0.6–1.7 mm in diameter and 1.5–3.5 mm in length in members of the Acanthuridae, Balistidae, Carangidae, Chaetodontidae, Haemulidae, Lutjanidae, Pomacanthidae, and Scaridae (Richards 2006). The extent to which species in these families spawn in or near octocoral communities would make this class of prey available to these ctenophores. In fact, all spawn on or near coral reefs and firm-bottom substrates where octocoral communities occur (fishbase, <http://www.fishbase.org/>).

### Ctenophores as prey

Due to the small size and cryptic nature of *C. waltoni* and *V. multiformis*, the ability to make detailed observations of predator attack behaviors under natural conditions was a challenge. The focused biting and overall grazing of octocorals by individuals of *Centropyge argi* and *Cyphoma gibbosum*, respectively, in the field prompted the aquarium predation experiments with *C. waltoni*, which supported the suspected predatory roles of the fish and mollusc species. The only other known report of a mollusc predator of benthic ctenophores is an aglajid opisthobranch that was observed attacking and ingesting an individual of *Coeloplana* sp. *toute de suite* in East Timor, Banda Sea (B. Francisco unpubl. data; Coleman 2008; Gosliner 2011). Gosliner (2011) noted the unique, weakly muscularized buccal bulb that may be better adapted to feed on the relatively soft bodies of ctenophores. Both the mollusc predator and ctenophore prey were

relatively large, each approximately 3–4 cm in length. This predation act occurred quickly, in 8–10 s.

The highly significant elevated mortality of *C. waltoni* due to predation by *C. argi* is related to the exposure of the ctenophores on the host species *Muricea elongata*. Glynn et al. (2017) found that, while feeding, individuals of *C. waltoni* tended to move to the uppermost tips of the sharply pointed calices of the octocoral *M. elongata*. By contrast, ctenophores on colonies of *Eunicea* spp. remained between or at the bases of calices, thus at more sheltered and less exposed sites to visual fish predators. No differences in ctenophore mortality were evident among the four octocoral host species subject to gastropod grazing. It is likely that *C. gibbosum* indiscriminately consumed ctenophores while grazing and denuding octocorals of their soft tissues.

Predation on individuals of *C. waltoni* would be expected to be elevated in areas with high population densities of *C. gibbosum*. Chiappone et al. (2003) found that *C. gibbosum* tended to be more abundant on coral reefs in the Florida Keys where large molluscan predators had been harvested. Field experiments involving the exclusion of fish and invertebrate predators of molluscs resulted in a 19-fold increase in *C. gibbosum* and an eightfold increase in octocoral damage (Burkepile & Hay 2007). In an extreme case, ctenophore population densities would be greatly impacted in areas experiencing outbreaks of *C. gibbosum*, which devastated octocoral communities at Mona Island, Puerto Rico in 2008 (Schärer & Nemeth 2010).

Trials to investigate predation on individuals of *V. multiformis* were devised after observations in the wild of biting and grazing by several fish and crustacean species that may be natural predators of *V. multiformis*. Considering the consistently high abundance of *Exaiptasia pallida* and its ready acceptance of individuals of *V. multiformis* as prey, this actinian may be the most important predator of adult ctenophores in biofouling communities in south Florida. Since polyps of *E. pallida* are often aggregated in dense colonies, reaching hundreds of individuals per 0.5 m<sup>2</sup>, sedentary individuals of *V. multiformis*, and especially free-floating ctenophores, would be at risk of capture. The bodies and tentacles of the anemone can be greatly extended, sweeping over several centimeters of biofouling substrates. Individuals of the hesionid polychaete *Hesione picta* ingested 27.3% of the individuals of *V. multiformis* offered as prey. Larger, non-interstitial hesionids are carnivores, feeding on a variety of small invertebrates (Fauchald & Jumars 1979); we suspect this species might be a

more important predator of ctenophores in the field than observed in laboratory trials. Predation trials demonstrated that brachyuran crabs (*Omalacantha bicornuta*, *Macrocoeloma trispinosum*, *Panopeus herbstii*, and *Portunus* [*Portunus*] *sayi*) readily accept individuals of *V. multiformis* as prey. *Portunus* (*P.*) *sayi* is an obligate associate of *Sargassum* spp., on which *V. multiformis* often occurs (Marcus 1957; Alamaru et al. 2015). Species of *Coeloplana* that are associated with *Sargassum* (Tanaka 1931; Matsumoto & Gowlett-Holmes 1996; Matsumoto 1999) may also be subject to predation by *Portunus* (*P.*) *sayi*. Some fishes, such as *Lutjanus griseus*, may target and ingest individuals of *V. multiformis*, and also commonly reject the ctenophore, and exhibit signs of irritation around the mouth. Some fish species regarded as herbivores or generalist carnivores have been observed feeding on large pelagic ctenophores in the Red Sea, without apparent irritation or ill effects (Bos et al. 2017).

### Concluding remarks

This study has revealed novel complexities of predator–prey interactions in south Florida benthic ctenophores. As predators, even minute ctenophores are capable of subduing diverse and relatively large prey, including fish eggs and larvae. To understand the degree to which these predators can influence or control associated prey populations, and possibly community structure, is a challenge awaiting further study. As prey, benthic ctenophores are directly and indirectly consumed by diverse predators and herbivore grazers. A sea anemone, a mollusc, brachyuran crabs, and fishes are among the commonly observed consumer taxa. The extent to which these predators can influence ctenophore population growth and persistence also remains to be investigated. In this study, we have observed several intriguing offensive and defensive predatory behaviors that invite continued investigation, adding to the limited knowledge base of the natural history of these species.

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### Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article:

**Table S1.** Feeding trials in *Coeloplana waltoni* and behavioral responses to zooplankton, and eggs and larvae of *Coryphaena hippurus* offered as prey. Treatment: ctenophore predator + host substrate + prey. Control: host substrate + prey. *C.w.*, *Coeloplana waltoni*; *E.s.*, *Eunicea succinea*; *C.h.*, *Coryphaena hippurus*; zplk, mesozooplankton; –, predators not present in trials.

**Table S2.** Feeding trials in *Vallicula multiformis* and behavioral responses to zooplankton, and eggs and larvae of *Coryphaena hippurus* offered as prey. Treatment: ctenophore predator + host substrate + prey. Control: host substrate + prey. *V.m.*, *Vallicula multiformis*; *H.t.*, *Halimeda tuna*; *C.h.*, *Coryphaena hippurus*; zplk, mesozooplankton; –, predators not present in trials.

**Table S3.** ANOVA table of test statistics for predation rates on ctenophores (*Coeloplana waltoni*), living on four species of octocorals, by a fish (*Centropyge argi*) and a mollusc (*Cyphoma gibbosum*).

**Table S4.** Visual observations of potential vagile predators of *Vallicula multiformis* at a field site, Crandon Park Marina, Key Biscayne, October 17, 2016–May 3, 2017.