



Benthic ctenophores (Platyctenida: Coeloplanidae) in south Florida: environmental conditions, habitats, abundances, and behaviors

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Abstract. Two benthic ctenophores, *Coeloplana waltoni* and *Vallicula multiformis*, are contrasted in terms of their coastal environments, habitats, abundances, seasonal occurrences, and behavior in south Florida. *Coeloplana waltoni* occurs as an epibiont on octocorals in open water settings, and *V. multiformis* is present in bio-fouling communities, associated with macroalgae, bryozoans, and inanimate substrates in protected, back-water habitats. In our study, individuals of *C. waltoni* were found under moderate to strong current flow and relatively constant temperature and salinity (*T/S*) conditions, whereas individuals of *V. multiformis* occurred at sites of low current flow and more variable *T/S* conditions. In *C. waltoni*, individuals generally adhered tightly to host colony surfaces, whereas in *V. multiformis*, individuals often disassociated from substrates and floated free. Mean population densities of *C. waltoni* ranged ~500–850 individuals 100 mL⁻¹ (measured as the displacement volume of the octocoral habitat), and densities of *V. multiformis* ranged 5–360 individuals 100 mL⁻¹ (measured as the displacement volume of the biofouling habitat). Abundance of *C. waltoni* was significantly highest in the 2014 warm season (June–October) when numerous minute (≤ 0.5 mm body length) juveniles were present. *Vallicula multiformis* was abundant in the 2015 and 2016 warm seasons (July–October), and also relatively abundant in the 2016 cool season (March–April). Ctenophore abundance and surface seawater temperature indicate a significant positive response to warm-season conditions in *C. waltoni*, whereas numbers of *V. multiformis* did not show any effect of seawater temperature. Recently settled individuals of *V. multiformis* (≤ 1.0 mm) occurred throughout the year. Individuals of *V. multiformis* recruited to fiber-coated sponges during warm and cool periods, with mean body sizes increasing in one cohort from 1.41 to 6.46 mm over a 39-d period, suggesting a growth rate of ~4% d⁻¹. Feeding in both species involves tentacle capture of water-borne zooplankton and particulate organic matter. Individuals of *C. waltoni* were also observed inserting tentacles into octocoral polyps, possibly pilfering food. Chlorophyll *a* was detected in extracts of both ctenophore species. The high abundances and feeding behavior of benthic ctenophores could have a strong influence on octocoral and biofouling communities.

Additional key words: Ctenophora, seasonal occurrences, behavior, cryptic fauna, subtropical

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Ctenophore research has focused largely on pelagic taxa, especially species prominent in plankton food webs (Harbison et al. 1984; Link & Ford 2006; Purcell 2012), and on invasive species that can contribute to the collapse of fisheries and entire marine ecosystems (Kideys 2002; Finenko et al. 2006). In addition, recent phylogenomic studies have raised the level of interest in ctenophores due to evidence suggesting their basal position in animal evolution (Ryan et al. 2013; Dunn et al. 2014; Moroz et al. 2014). Several studies have entertained the hypothesis that ctenophores are the sister group of all metazoans, including sponges, placozoans, and cnidarians (e.g., Jékely et al. 2015; Whelan et al. 2015). Studies of benthic ctenophores in the order Platyctenida were initiated in the late 19th century (e.g., Kowalevsky 1880; Korotneff 1886, 1888) with emphasis, to the present, on the description of new species and their geographic distributions (e.g., Song & Hwang 2010; Glynn et al. 2014; Alamaru et al. 2015). The generally small size and often cryptic nature of the platyctenes have not been conducive to in-depth studies of their biology and ecology.

Most species in the order Platyctenida are flattened along their oral-aboral axis, and part of the stomodeum is typically everted as a creeping foot. In the family Coeloplanidae, to which this study's two subject species belong, the comb rows are lost in development, but elongate, laterally branched tentacles are prominent. Coeloplanids are usually small (<6 cm along the tentacular axis) and occur at shallow depths in warm waters globally. Some are active swimmers or drifters, but others are benthic creepers that glide over substrates much like free-living flatworms.

This study offers new information on the ecology of the two known coeloplanid ctenophores, *Coeloplana waltoni* GLYNN, BAYER, & RENEGAR 2014 and *Vallicula multififormis* RANKIN 1956; present in south Florida. Considered here are the environmental conditions (sea temperature, salinity, current flow) where these species occur, their habitats, population densities, and seasonal variations in abundance. Also noted are ctenophore attachment and movements on their substrates, and fishing behavior (prey capture). The great majority of studies on the Coeloplanidae have focused on descriptions of new species, their associations with specific hosts or substrates, and their distributional records and morphology (see Matsumoto & Gowlett-Holmes 1996; Matsumoto 1999; Alamaru et al. 2015 for entries to this literature). In this study, we report ecological observations as a basis for investigations into the roles and importance of benthic ctenophores at population and community levels.

Methods

Species, study areas

Coeloplana waltoni is a minute (0.2–4 mm in length), benthic ctenophore associated with octocorals (subclass Alcyonarea), and known since the 1960s from shallow depths off south Florida (Bayer 1961; Glynn et al. 2014). This species was rediscovered in south Florida in 2011 and described in 2014. It has been reported from the southeast coast of Florida and recently observed on octocorals in the Bahamas (2016; Moorhead, pers. obs.; Fig. 1A, B). *Vallicula multififormis*, slightly larger (0.5–10 mm in length) than *C. waltoni*, was first observed associated with floating collectors and rafts (presumably of wood construction), and on algae and hydroids at the University of Miami marine school, Virginia Key, Miami, Florida in 1945 (Smith 1945), and later described from specimens associated with macroalgae and various invertebrates adhering to mangrove roots in Kingston Harbor, Jamaica, in the early 1950s (Rankin 1951, 1956). *Vallicula multififormis* is a wide-ranging species associated with diverse biota in and beyond the wider Caribbean region (Fig. 1C,D). It has been reported from the Bahamas and Bermuda (Pearse et al. 2002); Brazil (Marcus 1957); Canary Islands (Moro et al. 2011); Gulf of Aqaba, Red Sea (Alamaru et al. 2015); Gulf of Kutch, India (Prasade et al. 2015); Kane'ohe Bay, Hawaii (Galt 1998; Carlton & Eldredge 2009); and San Diego Bay, California (Mills & Haddock 2007). The latter record was reported during the 1997 El Niño event when subtropical waters occurred along the temperate southern California coast. In addition to the broad geographic distribution of *V. multififormis*, it also has been reported in great abundance at some localities, such as 3000 individuals m⁻² in Hawaii (Galt 1998). *Coeloplana waltoni* and *V. multififormis* are members of the Coeloplanidae, a species-rich family with 32 described species in the order Platyctenida, phylum Ctenophora (Matsumoto & Gowlett-Holmes 1996; Mills 1998; Matsumoto 1999). Specimens of both species are deposited in the collections of the Marine Invertebrate Museum, Rosenstiel Marine School (University of Miami Marine Laboratory, UMML): *C. waltoni*, UMML 9.1, 9.2, 9.5; *V. multififormis*, UMML 9.3, 9.4, 9.6 (Fig. 1A–D).

The principal study sites were located off Dania Beach, Broward County, 26°3'6.84"N; 80°6'26.53" W, and at the Crandon Park Marina (CPM), Key Biscayne, Miami-Dade County, 25°43'32.07"N;

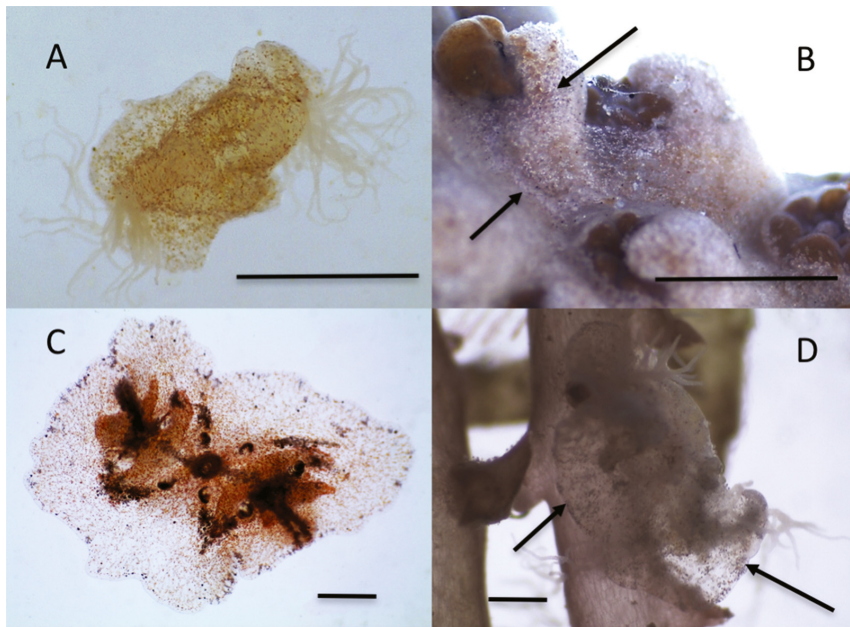


Fig. 1. *Coeloplana waltoni*, collected at Dania Beach, Florida, study site, November 18, 2016. **A.** Freed from octocoral (*Eunicea* sp.) host, both tentacles partially exposed. **B.** *In situ*, lying astride polyp of host *Eunicea tourneforti*. *Vallicula multiformis*, collected from Crandon Park Marina study site, Miami, Florida, November 16, 2016. **C.** Separated voluntarily from its macroalga host. **D.** Adhering to host *Acanthophora spicifera*, tentacle in upper position partially exposed. All scale bars=1 mm. Arrows denote ctenophores on hosts. Images were manipulated using Adobe® Photoshop® to enhance anatomical details and distinction between ctenophores and their hosts.

80°09'19.04"W (Fig. 2). The Dania Beach collection site is located in the John U. Lloyd Beach State Park, recently renamed Von D. Mizell and Eula Johnson State Park. Collections were also made nearby at Hollywood Beach (26°2'26.97"N; 80°6'29.04"W). The population of octocorals at Dania Beach occurs in a 2.72 km² area at 4–8 m depth. In addition to the CPM site, some collections also were made in Biscayne Bay at Hobie Beach Park, Virginia Key, 25°44'41.75"N; 80°10'19.62"W. The sampling domain in CPM at dock #2 south, piers 3 and 4, covered a collective area of 408 m² at 20–50 cm depth. Other collection and monitoring sites in Biscayne Bay and along the Florida reef tract are also noted in Fig. 2.

Environmental conditions

Sea surface temperature and salinity were measured approximately twice monthly (October 2013–December 2014) at the exposed Dania Beach site, and weekly (July 2015–October 2016) at the sheltered CPM site. Temperature at the two chief study sites was measured with a liquid analogue thermometer and salinity with an Aquafauna refractometer. Temperature and salinity conditions were monitored more frequently (15-min intervals) over the same period

(January–December 2004) at protected (mangrove site no. 10, 1 m depth; 25°23'51.7"N; 80°14'09.5"W) and exposed (Alina's Reef, 3 m depth; 25°23'10.32" N; 80°09'46.44"W) sites to better define protected and exposed site differences (DataForEVER, Everglades National Park). These data were obtained with sub-surface Yellow Springs Instruments (YSI), model 6600 V2 salinity/temperature meters (YSI Incorporated, Yellow Springs, OH, USA). Although discordant in space (35–70 km) and time (2004), the mangrove (no. 10) and Alina's Reef monitoring sites off the Ragged Keys (Fig. 2) were the only ones available with seasonal data recorded concurrently at the two ctenophore habitats. The chief interest in the interhabitat comparison was to gain an appreciation of the temperature and salinity differences in a protected nearshore site versus an offshore coral reef site.

Current rates were determined during daylight hours before 12:00 hours by timing the distance traveled by a float with a stopwatch and meter scale. Measurements were made at the Dania Beach and CPM collection sites at 1- to 9-d intervals over a nearly 4-month period. At the collection depths associated with *C. waltoni* (usually 4–6 m) and *V. multiformis* (usually 20–40 cm), surface and subsurface general current flow (direction and rate) were observed to be similar.

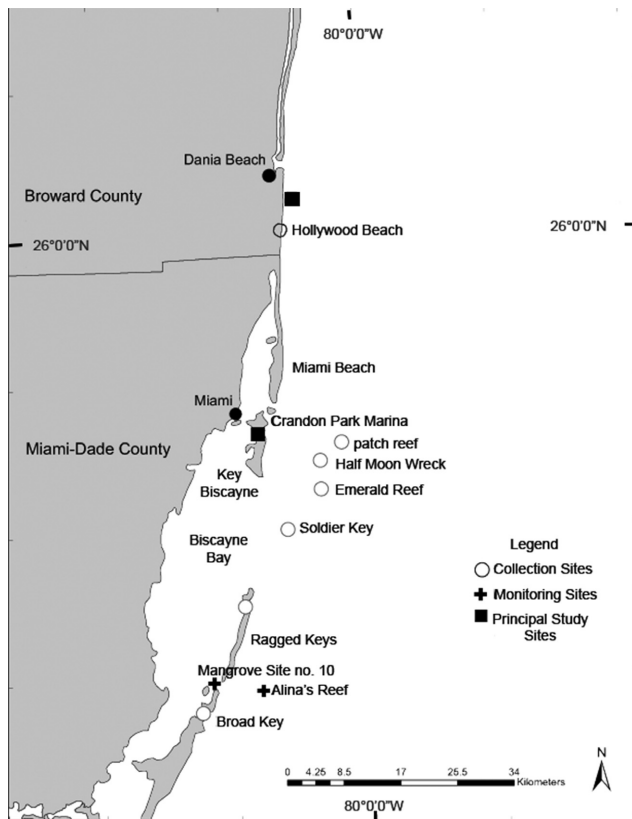


Fig. 2. Locator map of sampling sites off southeast Florida.

Ctenophore sampling

Population abundances of *C. waltoni* were sampled approximately twice monthly for 14 months (2013–2014) from the principal study site at Dania Beach (Fig. 2). Octocoral hosts occur there in a 2.72 km² area at 4–10 m depth. Terminal 10- to 12-cm-long branches of octocorals in the family Plexauridae were cut from colonies with scissors. The selection of branches was performed at random and without knowledge of ctenophore presence, as individuals of *C. waltoni* are visible only on rare occasions when feeding tentacles are extended. The branches and associated ctenophores were temporarily sealed in polyethylene bags and then transported to aquaria (20–200 L capacity) with circulating water and overhead lights supplying photosynthetically active radiation on a 12-h light:12-h dark cycle. About 0.5 cm of the outer rind (coenenchyme) was trimmed from the cut section of each octocoral branch, and then the axial skeleton was inserted into a tight-fitting predrilled hole in a carbonate block (Fig. 3). Individuals of *C. waltoni* were then located by examination under a dissecting microscope. To avoid injury when removed from octocoral hosts,

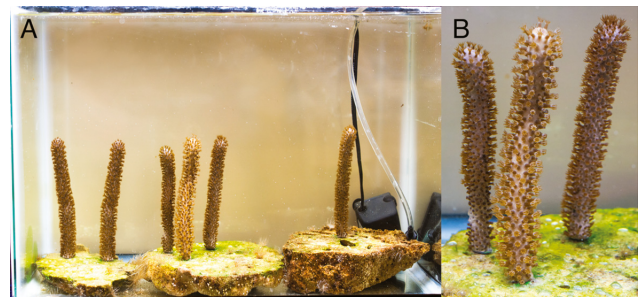


Fig. 3. Plexaurid octocoral hosts. **A.** In aquarium in normal upright growth position, with numerous *Coeloplana waltoni* ectosymbionts (not visible). Branch tips, 9–10 cm in length, inserted and stabilized in predrilled holes in coral carbonate platforms. **B.** Enlarged view of expanded polyps.

small areas of epidermal tissue were cut with sharp forceps and then lifted off together with the ctenophores. Maximum lengths of ctenophores were measured with an ocular micrometer along the tentacular planes within 1 h after removal and isolation.

Abundance of *V. multiformis* was sampled weekly for 16 months (2015–2016) from CPM, Key Biscayne. Care was taken to avoid making collections in previously sampled patches. Masses of macroalgae, bryozoans, and polychaete worm tubes, 200–500 mL displacement volume (DV), were pulled or scraped from the sides of boat slips 20–40 cm deep and immediately immersed in buckets filled with seawater. Only a few hours of direct sunlight were received daily at the CPM site due to a 30-cm-wide overhang. Samples of *Acanthophora spicifera* (VAHL) BØRGESSEN 1910 were specifically collected when present because this alga proved to be a frequent host substrate for *V. multiformis*. The biofouling masses, an amalgam of several taxa, were spread out in water-filled pans in the laboratory and illuminated with microscope lamps. Individuals of *V. multiformis* began emerging, floating upside down (oral side upper-most) at the surface film, from which they were removed to Petri dishes with eye droppers and spatulas. The collection of specimens was continued for 48–72 h, including the removal of individuals adhering to algae and other substrates. Due to frequent and marked shape changes, length measurements were delayed for 24 h, when most individuals were quiescent. The length measurements reported are maximum lengths along the tentacular plane and are best regarded as estimates (see Freeman 1967). In contrast to individuals of *C. waltoni*, the body shapes of individuals of *V. multiformis* were very labile and showed frequent expansion and contraction over several minutes.

To obtain comparable quantitative estimates of population densities for both ctenophore species on

their respective substrates, DV of each habitat substrate was measured in graduated cylinders and referenced to a standard volume (100 mL). We sampled biofouling masses for *V. multiformis*, and plexaurid octocoral branches (*Eunicea* spp., *Muricea elongata* LAMOUROUX 1821) for *C. waltoni*. Biofouling DVs were directly determined for each collection. Octocoral DVs were calculated by measuring the length of each sampled octocoral branch and calculating DV based on a standard volume of 2.4 mL (SD=1.27, $n=30$) per 10-cm branch tip as determined from previously sampled octocoral host taxa.

Inanimate scrubbing sponges were deployed at the CPM study site to test whether individuals of *V. multiformis* would settle on nonliving substrates, and also to gain insight to recruitment and dispersal potential. The sponges (trade name Fregon, manufactured and distributed by Somaki de México, SA), consisted of an exterior layer of polyethylene fibers, with dimensions 12.5×7.5×3.5 cm. They were suspended from the sides of the CPM boat slips, using monofilament line, 20–70 cm below the surface, and from 10 cm distant to superficial contact with the biofouling community. Fourteen sponges were deployed and ten collected, one at a time, over intervals of several days. Deployment was effected in the cool season (January–March), spring (April–May), and end of the warm season (October). Collected sponges were submerged in trays of seawater in the laboratory for 1–3 d, and the numbers of emerging ctenophores recorded, measured, and examined for reproductive activity. Collections were discontinued after 40–50 d, at which time much of the sponges' surfaces were covered with biofouling organisms, thus making it difficult to distinguish between settlement on inanimate versus live surfaces.

Laboratory observations

To sustain captive specimens of *C. waltoni* and their octocoral hosts, live rotifers (*Brachionus*) and *Artemia* nauplii were added to the holding aquaria approximately weekly. Prey capture and ingestion were observed by both taxa immediately after the addition of these food sources. Both ctenophores and octocorals remained in a healthy state for several months. To observe the behavior of ctenophores during food deprivation, one treatment involved maintaining both ctenophores and octocorals in sterile seawater (distilled water with Seachem Reef Salt mix adjusted to 35–36‰) without feeding.

No attempt was made to sustain specimens of *V. multiformis* in the laboratory beyond about 1 week

because of the species' ready availability nearby (CPM). The ctenophores were in a healthy state and feeding after 1 week, and were either returned to the wild or preserved in 70% ethanol or glutaraldehyde. Specimens collected from biofouling masses were transferred to petri dishes with filtered (2 µm) seawater. Specimens were also maintained in unfiltered seawater from the biofouling study site, which contained numerous protozoans and minute, diverse invertebrates (e.g., copepods, ostracods, nematodes, platyhelminths). The movements and feeding behavior of all metazoans observed under these conditions appeared healthy for up to a week's time.

The ctenophores were visualized under stereo-dissecting and compound microscopes, and various stains were employed: Neutral Red for viewing gut contents and tissue structures (Elliott & Tang 2009), Nile Blue for viewing cell nuclei, and food coloring to observe circulation within the gastrovascular system. Images and fluorescence in *C. waltoni* and *V. multiformis* were acquired using a Zeiss Axio Imager.Z2 with a Zeiss AxioCam MRC rev3 camera (Zeiss Axio, Jena, Germany), and Zeiss AxioVision software (Release 4.82).

Chlorophyll was detected and quantified in both ctenophore species (*C. waltoni*, one sample of 10 individuals; *V. multiformis*, one sample of four individuals). Each sample was extracted for 30 min with 10 mL of dimethyl sulfoxide (DMSO) at room temperature and then with an added 15 mL of 90% acetone at –20°C overnight, and measured fluorometrically before and after acidification for chlorophyll and phaeopigment concentrations (Burnison 1980; Parsons et al. 1984). Fluorescence measurements were made with a Turner Designs 10-AU fluorometer (Turner Designs, San Jose, CA, USA) equipped with an infrared-sensitive photomultiplier and calibrated using pure chlorophyll *a*.

Data analyses

Ctenophore sample abundances were expressed as mean, standard deviation, median, and range statistics. Statistical testing was performed by parametric and nonparametric procedures depending on whether the data satisfied the assumptions of normality and homoscedasticity. Quantile regression was applied to assess the strength of relationship between ctenophore abundances to sea surface temperature at different quantiles of abundance (Cade & Noon 2003). The strength of relationship between ctenophore abundances and sea surface temperature was assessed by a generalized linear model using a quasi-Poisson exponential fit. The R programming

language (RStudio v.0.98.1091, © 2009–2014 RStudio, Inc., Boston, MA, USA) was used to perform quantile regression and generalized linear modeling statistical analyses. Abundance of *C. waltoni* was compared by employing the Kruskal–Wallis test and multiple comparisons (Daniel 1978). Differences in size-class abundance curves in warm and cool seasons were evaluated using the Kolmogorov–Smirnov two-sample test (Campbell 1989; Zaiontz 2014).

Results

Environmental conditions

Seasonal variations in subsurface temperature and salinity (T/S) were examined concurrently at two sites off Key Largo representative of habitats of *C. waltoni* and *V. multiformis*, an offshore coral reef with abundant octocorals (Alina's Reef) and a protected Biscayne Bay site (mangrove site no. 10) that is adjacent to a mangrove shoreline (Fig. 2) and sheltered by Pleistocene barrier islands. The reef site revealed narrower ranges of T/S than the protected site (Fig. 4). The maximum monthly subsurface seawater temperature range at the reef site was $\sim 4^\circ\text{C}$, compared with 9°C inside Biscayne Bay. Salinity extremes also were more pronounced at the protected bay site, with a high monthly range of 8‰ (October) compared with 4‰ (April) on the reef. The coarser biweekly and weekly T/S measurements at the two sampling sites also reflected the seasonal trends noted above (Table 1). In summary, nearshore sea surface and shallow subsurface temperature data over the period 2014–2016 indicated relatively warm conditions from May through October, and cool conditions from November through April.

Coastal circulation over octocoral communities in the upper Keys off southeastern Florida is dominantly in a northerly direction, a result of the northward flowing Florida Current (Lee & Williams 1999). This is most pronounced in the summer season, weakening in the fall with increasing eastern onshore winds. Mean current velocity at the Dania Beach collection site was 0.086 m s^{-1} measured over a 4-month period in the summer (Table 1). Mean water motion at the CPM site was 0.006 m s^{-1} over the same period, and this sluggish flow was due to tidal currents in and out of the enclosed basin.

Ctenophore abundances

Mean population densities of *C. waltoni* in 2013–2014 ranged 500–850 individuals $100\text{ mL}^{-1}\text{ DV}$ on 10-cm-long octocoral branch tips, with maximum

densities exceeding 1400 individuals (Fig. 5). The densities of *C. waltoni* were significantly highest in the warm season ($U=39.5$, $p<0.001$). The total numbers of *V. multiformis* observed in biofouling samples in 2015–2016 demonstrated high variability, ranging from 0–5 individuals to 100–359 individuals $100\text{ mL}^{-1}\text{ DV}$ (Fig. 6). No significant seasonal differences in abundance were evident ($U=530.5$, $p=0.245$).

Regression analyses of ctenophore abundances as a function of temperature also paralleled the above seasonal analyses. In *C. waltoni*, there was a highly significant exponential relationship of increasing abundance with temperature over a 6°C range ($p=2.19\text{e}^{-5}$, GLM quasi-Poisson exponential fit, Fig. 7). However, a Model II linear regression analysis indicated that abundance of *C. waltoni* was not significantly related to salinity ($F_{1,28}=0.141$, $p=0.710$). Abundance of *V. multiformis* was not positively related to temperature ($p=0.115$, Fig. 8) or to salinity ($F_{1,59}=0.0565$, $p=0.813$).

Abundances of *C. waltoni* differed among the host species sampled (Table 2). The median numbers of *C. waltoni* ranged from 13.5 to 17 individuals 10 cm^{-1} in three species of *Eunicea*, and these densities were statistically similar. The median density of *C. waltoni* on *M. elongata*, nine individuals per branch, was significantly lower than in *Eunicea* spp.

The colonization by individuals of *V. multiformis* to inanimate fiber-coated sponges was 2.6–7.7 individuals $100\text{ mL}^{-1}\text{ DV}$, and similar over periods of deployment from 5 to 49 d in the spring and late summer collections (Table 3). In mid-winter (January–March), 203 individuals, equivalent to 78.1 individuals $100\text{ mL}^{-1}\text{ DV}$, were associated with a single sponge. No ctenophores were found in two collections after 2 and 49 d. Mean body lengths in four collections in the spring season (April–May) demonstrated a consistent increase from 1.41 to 6.46 mm. Small (0.5–1.2 mm) individuals were present in all seasons, and gravid ctenophores were observed in May and October.

Ctenophore size structure

To gain insight into sexual reproductive activity (i.e., the seasonal occurrence of larval settlement and occurrence of juveniles), the body lengths of all individuals of both species were recorded for every collection. Asexual fission was never observed in either species over the course of this study. In *C. waltoni*, the size-class distributions were significantly different in the warm and cool seasons ($p<0.05$,

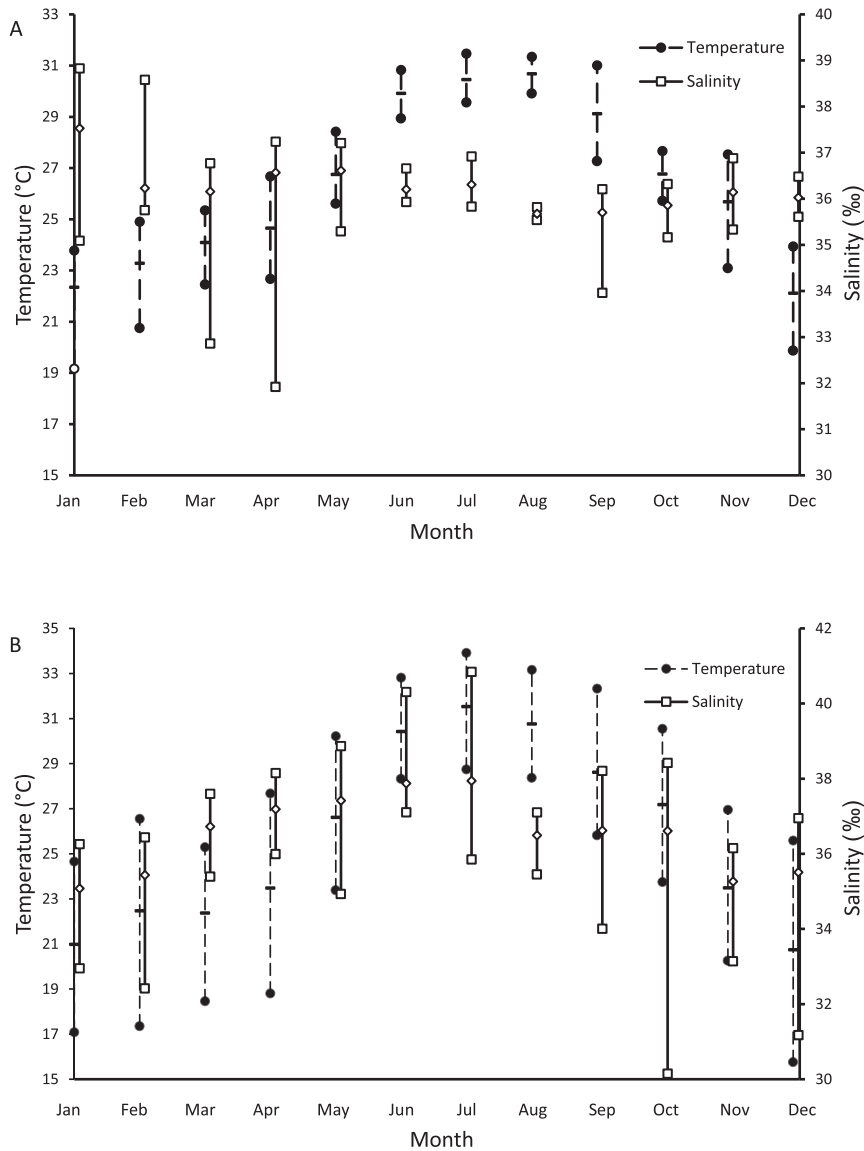


Fig. 4. Monthly bottom temperature and salinity in 2004 at (A) Alina's Reef, Florida Keys reef tract, and (B) protected mangrove site no. 10 in Biscayne Bay, Florida. For each month, the middle symbol (bar for temperature, open diamond for salinity) shows the mean value; upper and lower symbols (closed circles for temperature, open squares for salinity) show the maximum and minimum values, and broken lines show the range. Data were collected at 15-min intervals from bottom-type YSI instruments (DataForEVER, Everglades National Park, 2006).

Fig. 10). Two of the smallest size classes (0–0.2, 0.3–0.5 mm) demonstrated highest abundances in the warm season, making up a combined contribution of 15% of all samples (Fig. 9). These size classes contributed only 1% of all samples in the cool season.

The 15-month sampling of *V. multiformis* spanned two warm and one cool season periods, allowing for three pairwise seasonal size comparisons (Fig. 10). All seasonal size-class comparisons were nonsignificant ($p > 0.05$, Fig. 10). The warm season–cool season comparison was marginally nonsignificant, with

a cool season modal class of 1.0–1.49, notably smaller than the warm season modal class of 2.0–2.49.

Behavioral observations

The translucent bodies and multicolored pigment flecking in *C. waltoni* and *V. multiformis* rendered individuals of both species nearly invisible on the surfaces of their hosts. The multicolored pigment flecking (white, brown, purple) of individuals of *C. waltoni* blended with the octocoral's surface, which is peppered with similarly colored pigments and

Table 1. Summary of sea surface temperature, salinity, and current speed recorded over a 4-month period at collection sites for *Coeloplana waltoni* (Dania Beach, Florida) and *Vallicula multiformis* (Crandon Park Marina, Miami, Florida).

Location	Date	Property	Condition ^a		
			\bar{x}	SD	Range
Dania Beach 26°2'26.97"N 80°6'29.04"W	May 4–August 29, 2013	Temperature (°C)	29.5	1.02	28.3–30.6
		Salinity (‰)	35.12	0.54	34.0–36.0
		Current (m s ⁻¹)	0.086	0.03	0.001–0.15
Crandon Park Marina 25°43'32.07"N 80°09'19.04"W	May 6–August 30, 2013	Temperature (°C)	29.0	1.73	27.2–30.6
		Salinity (‰)	36.22	1.56	30.0–40.0
		Current (m s ⁻¹)	0.0076	0.0057	0–0.019

^a \bar{x} , mean; SD, standard deviation (30 observations for each data set).

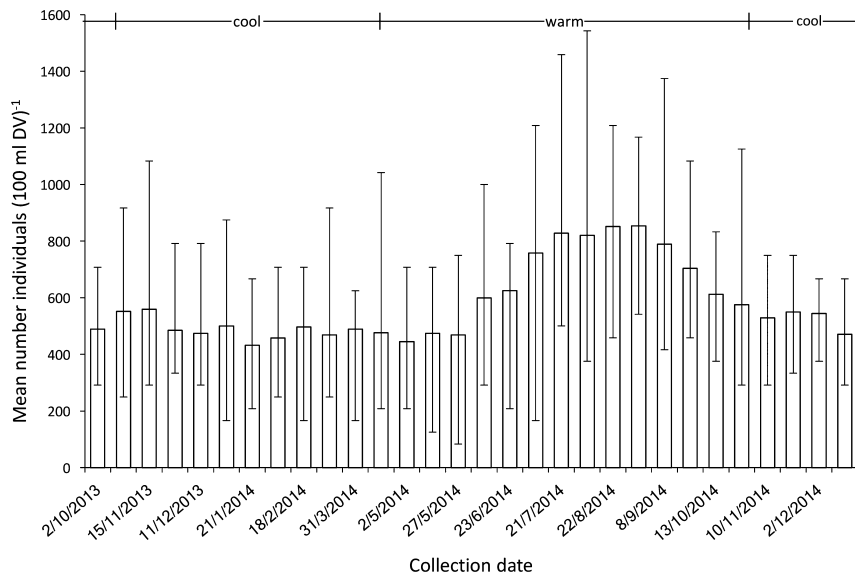


Fig. 5. *Coeloplana waltoni*, mean and extreme (maximum and minimum) densities on plexaurid octocoral branch tips sampled at Dania Beach, Florida, over a 14-month period, 2013–2014. Density values are number of ctenophore individuals per 100 mL octocoral displacement volumes (DV). Each value is based on samples of sixteen 10-cm-long branch tips of *Eunicea clavigera* ($n=4$), *E. succinea* ($n=5$), *E. tourneforti* ($n=3$), and *Muricea elongata* ($n=4$). Seasonal thermal periods observed at this collection site are indicated along the top margin of the graph (warm period, monthly mean $\geq 25^\circ\text{C}$; cool period, monthly mean $< 25^\circ\text{C}$).

white spotting where calcareous spicules show through the epidermis. Some individuals of *C. waltoni* exhibited a pale green hue even though collected from various octocoral hosts (*Eunicea* spp., *M. elongata*) that were predominantly brown in color. When present on species of green algae, such as *Halimeda opuntia* (LINNAEUS) J.V. LAMOUROUX 1816, *Halimeda tuna* (J. ELLIS & SOLANDER) J.V. LAMOUROUX 1816, and *Caulerpa sertularioides* (S. GMELIN) M. HOWE 1905, individuals of *V.*

multiformis displayed prominent green pigmentation. Individuals of *V. multiformis* associated with *A. spicifera* often displayed a dark-brown or purplish-brown body hue, typical of this algal species (see Fig. 1D).

Acetone extractions from individuals of both species exhibited fluorescence, likely indicating the presence of chlorophyll. Chlorophyll *a* was then identified and quantified fluorometrically from DMSO-acetone extracts. After we adjusted for the

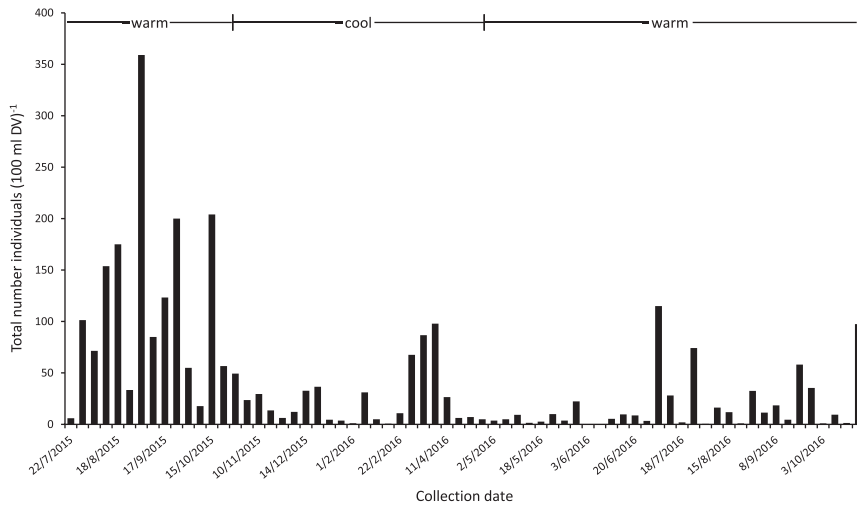


Fig. 6. *Vallicula multiformis*, total number of individuals extracted from biofouling communities sampled at Crandon Park Marina, Miami, Florida, over a 15+ month period, 2015–2016. Density values are total number of ctenophores adjusted to 100 mL displacement volume of biofouling mass sampled. Seasonal thermal periods observed at this collection site are indicated along the top margin of the graph (warm period, monthly mean $\geq 25^{\circ}\text{C}$; cool period, monthly mean $< 25^{\circ}\text{C}$).

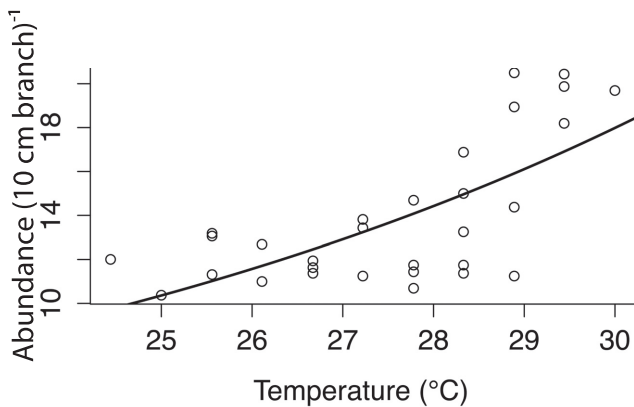


Fig. 7. Exponential relationship between abundance of *Coeloplana waltoni* and increasing temperature.

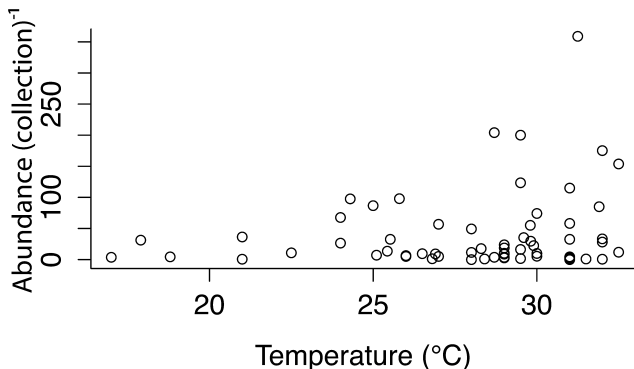


Fig. 8. Nonsignificant relationship between abundance of *Vallicula multiformis* and increasing temperature.

numbers of individuals analyzed in each sample, extracts from samples of *C. waltoni* and *V. multiformis* had 0.0194 and 0.0095 μg of chlorophyll *a* per individual, respectively.

Observations of laboratory-acclimated individuals of *C. waltoni* revealed that their resting sites and fishing behavior (i.e., tentacle extension and prey capture) were closely related to the morphology and disposition of the calices of the octocoral host. Individuals of *C. waltoni* resting on the colony surfaces of their hosts *Eunicea* spp. remained between or at the bases of crowded (closely spaced) calices. They were able to extend their fishing tentacles from these sites due to the low relief of the calices. In the host *M. elongata*, the calices are also closely crowded and sharply pointed, protruding farther off colony surfaces than in *Eunicea* spp. Individuals of *C. waltoni* associated with the host *M. elongata* in the laboratory and engaged in fishing were observed to move to the upper-most tips of the pointed and upwardly directed calices where they were fully exposed to surrounding waters. In observations of midday feeding at the Dania Beach collection site, we encountered several individuals of *C. waltoni* with tentacles extending up to 12–15 mm, many times the body length, from octocoral hosts. Turbulent sea conditions, however, did not allow a view of the ctenophores’ orientation on their octocoral hosts under natural conditions.

Individuals of *C. waltoni* adhered tightly to their octocoral hosts and assumed free-floating

Table 2. Mean and median abundance of *Coeloplana waltoni* observed in octocoral collections obtained approximately twice monthly at Dania Beach, Florida, study site, October 2, 2013–December 18, 2014. Statistical results are from number of individuals counted on 10-cm-long branch tips collected *in situ* from four octocoral species.

Octocoral species	Mean (SD)	Median	Range	Number examined
<i>Eunicea clavigera</i> BAYER 1961	14.74 (4.80)	13.5 ^a	6–28	120
<i>Eunicea (Eunicea) succinea</i> PALLAS 1766	14.40 (4.34)	14 ^a	7–33	150
<i>Eunicea (Euniceopsis) tourneforti</i> MILNE EDWARDS & HAIME 1857	17.86 (5.35)	17 ^a	10–37	90
<i>Muricea elongata</i> LAMOUROUX 1821	9.48 (3.41)	9	2–20	120

^aMedian abundances not statistically different (Kruskal–Wallis multiple comparisons procedure, $\alpha=0.15$).

Table 3. Settlement by individuals of *Vallicula multiformis* onto artificial fiber-coated sponges; table entries show colonization rates, size changes, reproductive condition, and sample densities per displacement volume (DV) of sampled habitat. -, data not collected.

Season	Days submerged	Collection date	Number present	Sizes (mm) ^a			Number gravid	No. individuals 100 mL ⁻¹ DV
				\bar{x} (SD)	Range	% d ⁻¹		
Spring	7	15/4/2016	15	1.41 (1.09)	0.5–4.3	-	0	6.2
April–May	14	22/4/2016	7	2.49 (1.68)	1.0–2.7	8.46	0	5.0
27.3°C (24.0–31.0) ^b	28	5/5/2016	6	4.18 (2.16)	1.2–6.5	3.77	0	5.0
<i>n</i> =20	39	18/5/2016	5	6.46 (3.04)	2.5–9.7	4.23	4	2.6
	49	27/5/2016	8	2.87 (2.03)	0.9–7.1	4.95	2	3.6
	56	3/6/2016	0	-	-	-	-	0
Winter								
January–March	69	30/3/2016	203	2.44 (1.60)	0.5–8.1		0	78.1
21.4°C (17.0–25.0)								
<i>n</i> =9								
Summer (late)–Fall	2	7/10/2016	0	-	-		-	0
September–October	5	10/10/2016	10	6.61 (3.04)	1.2–10.4		2	7.7
27.8°C (24.8–31.0)	8	13/10/2016	12	3.39 (1.59)	1.8–6.5		8	9.2
<i>n</i> =13								

^aGrowth rates (% d⁻¹) are mean daily compound growth rates calculated over the number of day intervals submerged (i.e., 7, 11, 14 d) and overall (39 d).

^bSeasonal mean (maximum–minimum) sea surface temperatures recorded at Crandon Park Marina biofouling communities in months noted (2016), 10:00–11:30 hours.

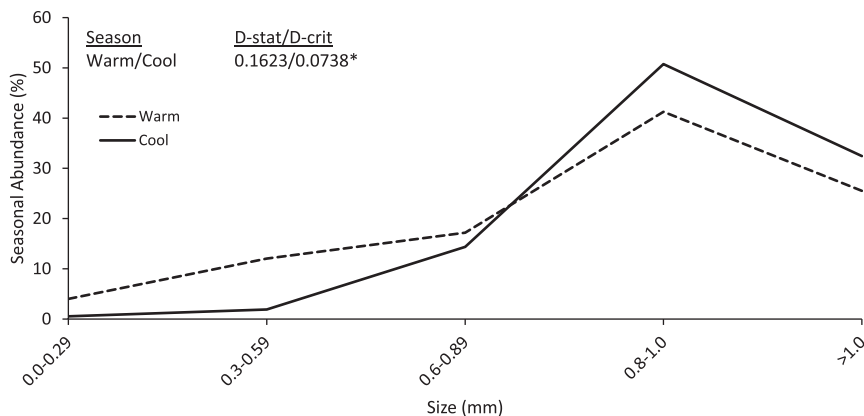


Fig. 9. *Coeloplana waltoni*, size-class abundances in warm and cool seasons. Kolmogorov–Smirnov D-statistic test results in inset.

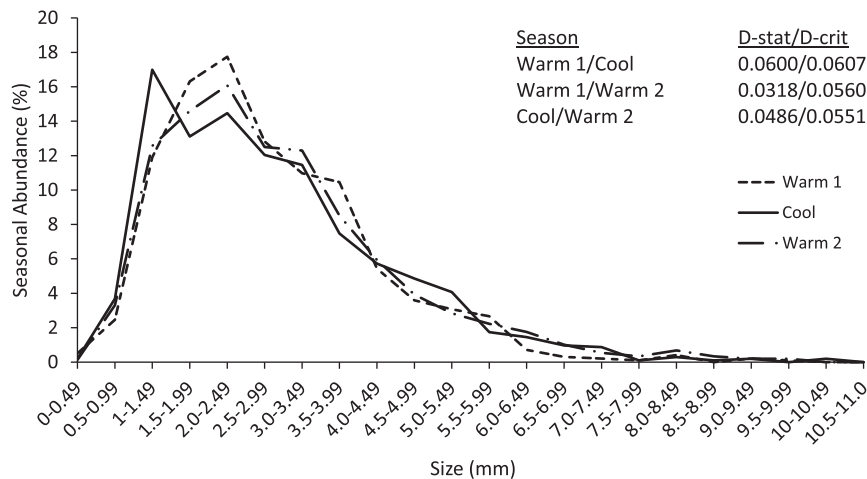


Fig. 10. *Vallicula multiformis*, size-class abundances in warm (two collections) and cool seasons. Kolmogorov–Smirnov D-statistic test results in inset.

movements only when forcefully (but carefully) removed from their resting site soon after collection. Some individuals, however, were found floating freely in the laboratory after 24 h. In *V. multiformis*, individuals were loosely associated with their living or inanimate substrates. Within an hour after collection, they became free and assumed a floating posture for up to several hours. In the free-floating state in both species, individuals adhered to the aqueous surface film with the oral side nearly always uppermost. Rankin (1956), however, noted that the free-floating posture in *V. multiformis* was aboral-side uppermost. Neither species demonstrated clumping or contact with other individuals while resting or fishing.

On numerous occasions, several different individuals of *C. waltoni* were observed to insert their tentacles into the polyps of their octocoral hosts, including *Eunicea* (*Eunicea*) *succinea* (PALLAS) 1766 forma *succinea*, *Eunicea* (*Euniceopsis*) *clavigera* F.M. BAYER 1961, *Eunicea* (*Euniceopsis*) *tourneforti* MILNE EDWARDS & HAIME 1857 forma *atra* VERRILL 1901, and *M. elongata*. Tentacle insertion occurred most often when the polyps were partially or fully retracted. Also, sizeable portions of the ctenophores, from 0.5 to 0.75 body lengths (led by their tentacles), were observed to enter octocoral host polyps. In such instances, the octocoral polyps were retracted and partially or entirely withdrawn into their respective calices. This behavior of entering the host's polyps seemed to be more common when we did not feed ctenophores. During such periods of food deprivation, individuals of *C. waltoni* aggregated around the oral disks of retracted polyps, sometimes completely covering them, and then inserted their tentacles and bodies.

From late May through late July 2014, several large individuals of *C. waltoni* were observed in pairs, tightly interlocked at the tentacle sheath openings. One of the paired individuals would insert a tentacle into the tentacle sheath of the other. Carmine red stain applied to the tentacles demonstrated that an unknown substance was transferred from one ctenophore to the other. The material transferred was isolated from the tentacle sheath and stained with Nile Blue, which revealed the presence of cell nuclei at 400 \times magnification. Beyond this, we were unable to determine the nature of this substance. On one occasion (20:00–21:00 hours, April 5, 2016), a similar pairwise interlocking of tentacles and tentacle insertion were observed in *V. multiformis*; however, there was no transfer of particulate matter.

Although observed clearly on only one occasion, rotifer capture and transfer in *V. multiformis* was swift, with the tentacle and entangled prey moved to the oral surface and mouth in 1–2 s. The ctenophore was free of the substrate during this observation. Afterward, the tentacle was moved to the aboral surface and quickly retracted into the tentacle sheath.

No sexual products (ova, spermatozoa, or brooded larvae) were visible through the body wall of individuals of *C. waltoni*; however, larger individuals changed color from various shades of brown and purple to yellow-orange in the warm season (May–September). During this time, a high proportion of small individuals entered the sampled populations, indicative of sexual or asexual (fission) reproduction. Conspicuous swellings were often observed in individuals of *V. multiformis*, particularly in the warm season. On several occasions,

brooded cydippid larvae were released from these swellings and continued swimming in the laboratory for several hours.

Discussion

Individuals of *C. waltoni* and *V. multiformis* experience very different physical environmental conditions, the former obligately associated with octocorals on exposed reef tracts and the latter occurring facultatively on diverse substrates in biofouling communities in the protected waters of Biscayne Bay. At our study sites in southeastern Florida, reef tract temperature and salinity conditions varied less than in Biscayne Bay. Also, nearly year round strong northerly current flow and frequent high turbulence conditions were observed at exposed sites. The notable adhesive behavior of individuals of *C. waltoni* on their octocoral hosts would offer a distinct advantage in preventing separation during periods of strong current flow and high turbulence.

Abundance of *C. waltoni* was significantly elevated in the warm season; this was related to high numbers of juveniles, indicative of reproduction. In *V. multiformis*, abundance was high in both the warm and cool seasons, with highest densities when temperatures were near or above 30°C. The modal size class of *V. multiformis* in the cool season (marginally nonsignificant) consisted of juveniles, suggesting year-round reproduction. *Vallicula multiformis* is most abundant in the Gulf of Aqaba, Red Sea in the winter season during water column mixing and massive algal blooms, with hundreds of individuals reported on *Sargassum* (Alamaru et al. 2015). The relatively low abundances of *V. multiformis* in many samples in southeastern Florida at and below 25°C could also be due to habitat availability. Several species of algae decline in abundance in the cool months in south Florida (Lirman & Biber 2000; Collado-Vides et al. 2005). *Acanthophora spicifera*, which is the preferred habitat of *V. multiformis*, was less abundant at the CPM site (although not quantified) in the cool season. Thus, this critically important microhabitat was probably under-represented during the cool season in the bulk sampling of the biofouling community.

Vallicula multiformis abundances in Jamaica (Rankin 1956) and Hawaii (Galt 1998) were reported to decline during periods of high rainfall and presumably low salinities. No significant reductions in ctenophore abundances were observed at the Biscayne Bay study site (CPM) in this study during the wet seasons of 2015 and 2016 when salinities

declined to ~30‰. The CPM site is located in the east bay region where freshwater inputs and salinity fluctuations are less marked than along the west bay shoreline. West Biscayne Bay salinities often range 15–20‰ for several weeks, which may approach the lower tolerance limit of *V. multiformis* (Lirman et al. 2003).

The settlement densities of *V. multiformis* on fiber-covered artificial sponges indicate that biotic substrates are not essential for the attraction and colonization of inanimate surfaces by this species. This finding is consistent with the reported occurrence of *V. multiformis* in plankton samples, under stones, and in sediments (Rankin 1956; Marcus 1957; Matsumoto 1999). Moreover, the minute (0.5 mm) to large sizes (>4 mm) of these settling ctenophores, including gravid individuals, indicate the likely recruitment of cydippid larvae as well as the dispersal of adults. No asexual fragmentation was observed during the entire course of this study. However, it was not possible to distinguish ctenophores that were residents of sponges from ctenophores that were in the process of dispersal to other substrates. A maximum settlement density of 78.1 individuals, observed after 69 d, was similar to mid-winter biofouling community densities of 60–90 individuals (Fig. 6). This high density could be explained by long-term accumulation of recruits and also their attraction to microfloral and faunal communities that had colonized the sponge surfaces after several weeks of immersion. As suggested by Alamaru et al. (2015), the global occurrence of *V. multiformis* in tropical and subtropical waters probably owes this widespread distribution to its ability to inhabit inanimate as well as a variety of biotic substrates.

The increasing mean sizes of individuals of *V. multiformis* observed on introduced artificial sponge substrates over a 39-d period in the spring season, from 1.41 to 6.46 mm (Table 3), may represent natural field growth of a cohort that colonized the sponges in mid-April 2016. A mean growth rate of 8.46% d⁻¹ was greatest by day 14, then decreased to about 4% d⁻¹ by day 39. Galt (1998) also reported rapid growth in *V. multiformis* over a 2.5-d trial, 27% per individual d⁻¹, which involved high ingestion rates of laboratory-fed *Artemia*. Ctenophore sample densities gradually decreased over this period, which could have been due to natural mortality. Four of five individuals were gravid by day 39, suggesting the attainment of sexual maturity in about 6 weeks.

Coeloplanids are generally closely associated with biotic substrates, the fidelity of host specificity often

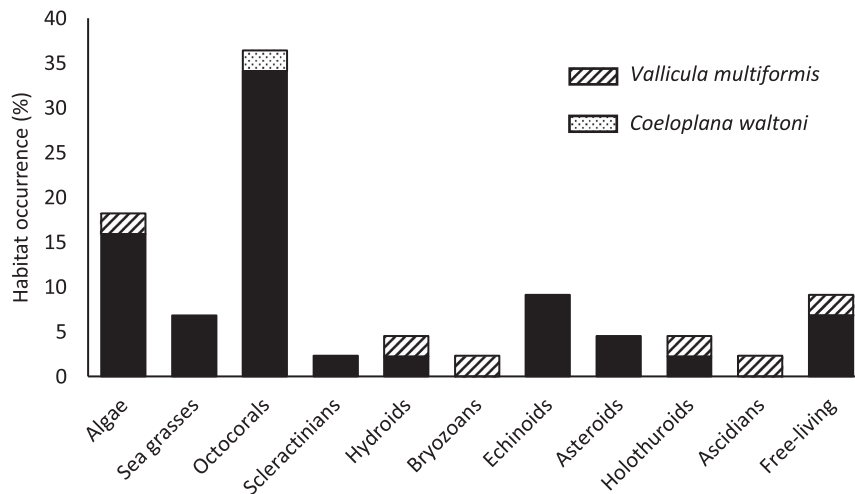


Fig. 11. Known habitats reported for 34 coeloplanid species. Sources: Walton Smith (1945), Rankin (1951, 1956), Marcus (1957), Freeman (1967), Emsen & Whitfield (1991), Matsumoto & Gowlett-Holmes (1996), Matsumoto (1999), Cavas & Yurdakoc (2005), Carlton & Eldredge (2009), Moro et al. (2011), Glynn et al. (2014), Prasade et al. (2015).

serving as an important guide to the identity of several species (Matsumoto & Gowlett-Holmes 1996; Matsumoto 1999; Alamaru et al. 2015). Like several other coeloplanid species, *C. waltoni* was observed to inhabit only octocorals (Fig. 11). Within the octocoral taxon, *C. waltoni* is known to associate with at least six genera and 11 species (Glynn et al. 2014). Individuals of other species of *Coeloplana* have been reported inhabiting sea grasses, scleractinian mushroom corals, and various echinoderms (echinoids, asteroids, and holothurians). In the present study, individuals of *V. multiformis* occurred most frequently on macroalgae (*A. spicifera*), but were also found on hydroids, bryozoans, ascidians (*Ascidia niger*), and on inanimate substrates (fiber-glass sponge pads).

The presence of chlorophyll *a* in *C. waltoni* and *V. multiformis* raises the possibility of a nutritional benefit to the ctenophore similar to the benefits demonstrated in zooxanthellate/coral holobionts (e.g., Stambler 2011). An unidentified unicellular alga (not *Symbiodinium*) was observed in the alimentary canals of both ctenophore species, but it is not known if this alga is the primary source of the detected chlorophyll *a*. Pianka (1974) noted that some pelagic ctenophores also harbor unicellular algae; however, the nature of this relationship remains unknown.

Coeloplanids involved in strong and enduring associations, commonly referred to as ectosymbionts or ectocommensals, are in intimate contact with their hosts. However, there is presently little understanding of host-symbiont interactions. Our observations suggest that individuals of *C. waltoni* probably benefit in three ways from their association

with octocorals: (1) predator avoidance, (2) provision of a fishing platform, and (3) a food source. Individuals of *C. waltoni* are nearly invisible against the host background by virtue of their translucent body and low profile when at rest, pressed tightly against the octocoral's surface. The ctenophore moves to the rims and spine tips of the calices of the host when feeding. Such perches allow concealment and unrestricted extension of tentacles while fishing. Red-stained zooplankton prey were captured and ingested by both ctenophores and their octocoral hosts. It is probable that the tentacle insertion by food-deprived individuals of *C. waltoni* is an effort to purloin zooplankters captured by host polyps. This means of food acquisition, similar to that of the feeding polyps of the hydroid *Proboscidea flavicirrata* that pilfer food (organic particulates) from polychaete tube worms (Cowles 2014), would argue for intermittent parasitism, at least during periods of food scarcity. Considering the weak host associations observed in *V. multiformis*, which include algae and sometimes inanimate substrates, individuals of this coeloplanid species would probably not benefit from acquiring food from hosts and would probably benefit most from predator avoidance and provision of a fishing platform.

Zooplankton prey capture by benthic ctenophores, coupled with the high year-round abundances of both species observed in this study, could markedly affect the mortality and settlement of recruiting benthos to octocoral and biofouling assemblages. This would have the logical effect of shaping the structure of these wide-ranging, subtropical communities.

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