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LUMINESCENT SYLLID (*ODONTOSYLLIS* SP.) COURTSHIP DISPLAY DENSITIES VARY ACROSS MARINE HABITATS AROUND SOUTH WATER CAYE, BELIZE

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ABSTRACT: Bright–green luminescent clouds frequently occur at the surface of shallow waters of the Caribbean Sea. These clouds are produced by syllid polychaetes during courtship. Although temporal variation in the occurrence of these courtship displays has been documented throughout the diurnal and lunar cycle, other factors such as habitat type have not been well studied. In this study, we investigated how syllid courtship–display densities varied across 3 substrate types (grassbed, rubble, and coral) over a 3 day period. In line with previous studies, we found that syllid courtship displays occurred over seagrass and rubble substrates; however, we also found that display densities were significantly higher over shallow coral substrates than over either seagrass or rubble habitats. These findings reflect published observations and newly collected observational data from other locations throughout the Caribbean. Future work across species, time and regions is required in order to better understand the factors underlying syllid display densities.

KEY WORDS: bioluminescent, mate–signaling, swarming

INTRODUCTION

The emission of visible light from living organisms following a chemical reaction (generally termed “bioluminescence”) is commonly reported from shallow waters throughout the Caribbean. The expression of luminescence in marine organisms can serve a number of important functions. For example, species of ctenophores, cnidarians, dinoflagellates and copepods luminesce as a defensive strategy (reviewed in Haddock et al. 2010). Other organisms, such as flashlight fish, brittle stars, polychaetes and ostracods use luminescence not only for defense, but also for courtship and/or for attracting and/or finding prey (reviewed in Haddock et al. 2010). In some locations, many luminescent species coexist which can lead to both stunning and complicated light shows, particularly at certain times of the lunar cycle. Although reports of luminescence have garnered scientific attention, we still know very little about many marine luminescent species and the conditions (temperature, depth, habitat type, etc.) that dictate luminescent behaviors.

Syllid polychaetes within the genus *Odontosyllis* (Claparède 1864) can be found in many locations throughout the Caribbean, and some species emit substantial visible light at the sea surface during courtship (Galloway and Welch 1911, Huntsman 1948, Russel 1989, Markert et al. 1961, Gaston and Hall 2000). In fact, it has been reported that the swirling green luminescence of syllid females can be easily seen up to 50 m away (Gaston and Hall 2000). Work on the mating systems of luminescent *Odontosyllis* spp. has shown that both male and female worms luminesce as they swarm which facilitates mate–finding and the eventual union of gametes in the water column (Fischer and Fischer 1995, Deheyn and Latz 2009). Male *Odontosyllis* luminesce internally producing short duration (< 2 second) flashes as they move in a relatively straight line towards females. On the other hand, females

produce a diffuse external luminescent display as they swim in tight circular patterns (Galloway and Welch 1911, Markert et al. 1961, Tsuji and Hill 1983, Gaston and Hall 2000). Tsuji and Hill (1983) reported that male flashes start *O. phosphorea* (Moore 1909) swarming behaviors in the shallow Pacific waters near San Diego, whereas female displays in other species, such as *O. enopla* (Verrill 1900) and *O. luminosa* (San Martin 1990), initiate swarming in areas surrounding Bermuda and Belize (Galloway and Welch 1911, Markert et al. 1961, Gaston and Hall 2000). It has been suggested that the female light producing chemicals are emitted with mucus (Galloway and Welch 1911) and can be associated with the release of gametes (Deheyn and Latz 2009). The result is a luminous cloud that persists for minutes and can be seen above and below the water. Depending on the time and location, syllid luminescent courtship displays can be abundant. For example, Gaston and Hall (2000) observed as many as 50 females displaying/minute within a 20 m x 30 m viewing area in Belize, and Tsuji and Hill (1983) reported more than 200 displays/minute around a floating viewing dock in San Diego.

Past assessment of *Odontosyllis* spp. courtship behaviors in Belize and Bermuda indicated that display densities varied in relation to diurnal and lunar cycles (Huntsman 1948, Markert et al. 1961, Gaston and Hall 2000). On nights when no moon was visible at sunset, courtship displays of *O. enopla* and *O. luminosa* began 40–50 min post–sunset and peaked in density 8–10 min later. Displays also peaked in abundance 2–3 nights after the full moon (Markert et al. 1961, Gaston and Hall 2000). Like luminescent displaying ostracods (Gerrish et al. 2009), syllids may initiate courtship at moonset; however, this possibility has not yet been assessed. Temporal cycles in the luminescent courtship displays of *Odontosyllis* spp. appear to be tightly associated with the phase of the

moon and ambient light levels, and some species show seasonal variation in their activity (Markert et al. 1961, Tsuji and Hill 1983, Gaston and Hall 2000).

Spatial–habitat variability across marine environments modulates species occurrence through the availability of feeding, refuge and mating opportunities. Because syllid courtship is dependent on visible light signals, habitat features such as water depth, ambient light and the reflectivity of substrates may dictate the presence and abundance of luminescent displays. In Bermuda and Belize, *Odontosyllis* spp. displays have been primarily associated with near–shore rocky rubble (Markert et al. 1961, Fischer and Fischer 1995) and grassbed environments (Gaston and Hall 2000), respectively. Available surveys of luminescent syllid courtship have primarily taken place in habitats visible from shore, so little is known about their courtship activities in shallow offshore habitats.

To help fill in this informational gap, we conducted a quantitative survey of *Odontosyllis* sp. courtship–display densities from boats anchored at similar depths across different offshore adjacent habitats (coral, rubble and seagrass) at a single location (South Water Caye, Belize). To supplement our study observations, we also present a qualitative summary of newly collected data on *Odontosyllis* sp. displays over various substrates and depths throughout Caribbean locations.

MATERIALS AND METHODS

Field observations

Seagrass, rock rubble and coral patch reef habitats were selected just south of South Water Caye, Belize (16°48'43.2"N, 88°04'58.3"W) (Figure 1) where *Odontosyllis* sp. courtship displays had previously been observed and studied (Gaston and Hall 2000). Observations were made during 3 consecutive

nights (6–8 January) in 2016. These nights were prior to the new moon so there was no moon present in the sky immediately following sunset. Across the 3 collection nights there was minimal variation in wind (5–8 kph), timing of sunset (17:32–17:34) and tidal conditions (21–24 cm high tide peak between 19:17 and 20:47; Mobile Geographics LLC). Since the luminescent chemicals of syllids mix into the water column, they serve as a natural means to gauge flow and drift within surface water habitats. Little to no drifting of displays was observed. Each night 3 observers anchored kayaks at 3 points, one in each of 3 habitat types: coral, rubble and grassbed. The grassbed habitat was dominated by *Thalassia testudinum* at moderate density (100–300 blades/m²). Sites were selected and anchors were moved during the daytime to new locations within each habitat before the sampling period each night. Just prior to the sampling period, kayaks were attached to the anchors so that each observer was completely surrounded by the appropriate habitat. The 3 observers rotated between the 3 habitats over the course of the 3 sampling nights to minimize observer bias in any one habitat. Observations began each night about 60 minutes after astronomical sunset near the end of nautical twilight at 18:30. Observers in each habitat recorded the number of luminescent clouds observed every 5 minutes for a 60 minute period that ended at 19:30. Any displays occurring within ~5 m (visible) radius of the kayak were counted, and, given the time and distances between luminescent clouds, each event was assumed to be independent

To verify identification, *Odontosyllis* sp. were collected by sweeping a 250 µm net through the luminescent clouds. Using a dissecting microscope, individuals were clearly categorized as *Odontosyllis* and all specimens collected appeared to belong to a single species. The species is most likely *O. luminosa* (as suggested in Gaston and Hall 2000) or *O. enopla* (as suggested in Crayshaw 1935 or Verdes et al. 2016), but given the current uncertainty about species designations (and what actually comprises a species) within the *Odontosyllis* genus (Verdes et al. 2016) we conservatively refer to the polychaete in this study as *Odontosyllis* sp.

Data manipulation and statistical analyses

To explore how syllid display densities vary over different habitat substrates, we first summed the number of displays recorded over each habitat during the entire observational period (18:30–19:30); this was done independently for each of the 3 nights. We calculated

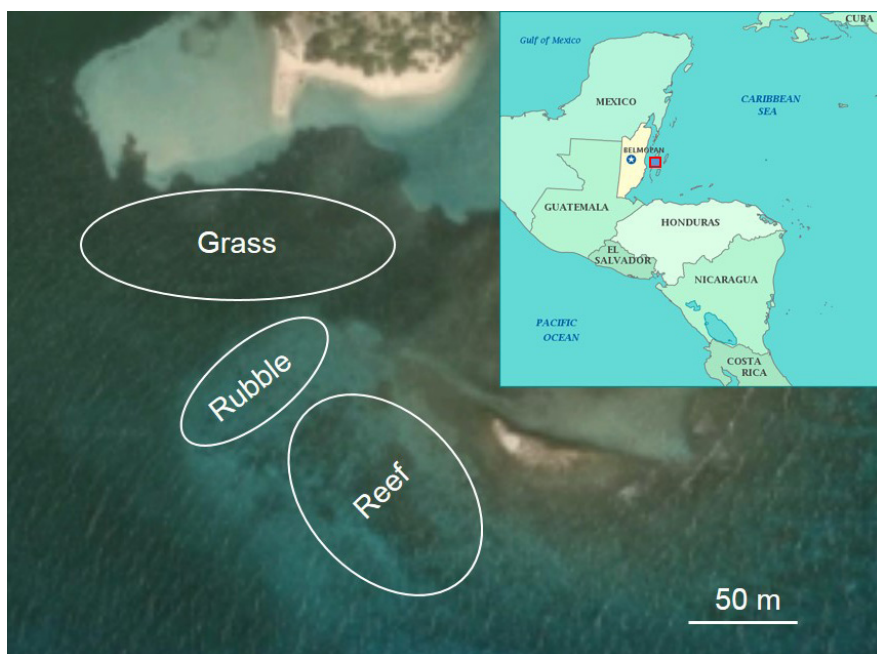


FIGURE 1. Geographic and habitat sampling locations in Belize, Central America (map inset modified from Online Atlas and habitat image modified from Google Earth).

proportions for each night independently by dividing the total number of displays within a habitat by the total number of displays observed across all habitats in one night. Habitat proportions were then compared using Analysis of Variance (ANOVA) and Scheffe's post-hoc analysis after arcsine square-root transformation. To examine syllid display density changes during our night-time observational period (18:30–19:30), we calculated display proportions for each 5 min observational time interval. Proportions were calculated by dividing the number of displays observed in a particular habitat during a 5 min observation period by the total number of displays observed in the whole night. These nightly proportions (per habitat type) were used to calculate interval means during the 1 h observational period. Since courtship displays did not occur in all habitats during each time interval (Table S1), assumptions of traditional statistical procedures for testing significance across time periods within nights were not met. We therefore employed descriptive statistics (e.g., percent) to outline general temporal trends.

Summary of syllid observations across regions

Odontosyllis courtship behaviors were documented at multiple sites throughout the Caribbean during our sampling of other luminescent taxa. This novel information includes the geographic location, date, seafloor substrate type, an approximate density of displays, and observational notes.

RESULTS

Female *Odontosyllis* sp. were observed initiating luminescent swarming as they swam in tight circles emitting a cloud of bright green luminescence that often lasted for at least 1 min at the surface of the water. Flashing male response was observed occasionally but data collection focused only on the longer-lasting and more visible female displays.

Display densities ranged from 2–32 total displays observed in a given habitat during the 1 h observation period. ANOVA revealed a significant effect of habitat type on the proportion of syllid displays ($F_{2,6} = 8.08$, $p = 0.02$) (Figure 2). More specifically, syllids expressed significantly greater proportions of displays in reef habitats compared to either areas with rubble substrate (Scheffe, $p = 0.03$) or grassbed (Scheffe, $p = 0.04$) (Figure 2). Courtship displays did not differ between areas with rubble substrate and grassbed (Scheffe, $p = 0.99$). When examining syllid displays over time, luminescent courtships began about 5–10 min after the onset of nautical twilight in all habitats. In general, peak display densities tended to occur slightly earlier over the seagrass bed than over rubble or reef habitats (Figure 3). In addition, peak display densities appeared to occur within 20 min following

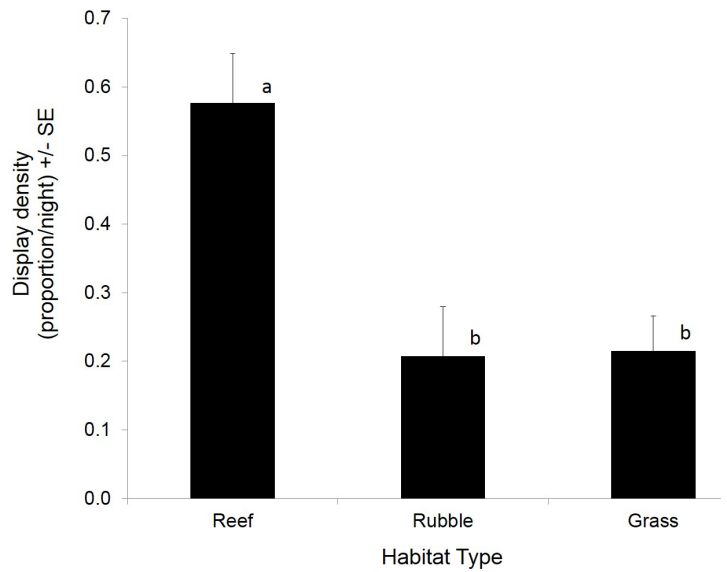


FIGURE 2. Proportion (mean \pm se) of total *Odontosyllis* sp. female courtship-display densities observed in each habitat type averaged across 3 nights in January 2016. Letters designate significant differences between groups (ANOVA with Scheffe's post-hoc analysis)

display initiation in all habitats. In general, the proportion of displaying syllids remained higher in coral habitats compared to either the rubble area or grassbed throughout the observational period, driving the habitat differences previously described.

Recent observations of *Odontosyllis* spp. displays have been made by our research group at multiple sites throughout the Caribbean (Belize, Honduras, Puerto Rico, Jamaica and Panama) (Table 1). At all locations, display densities peaked about 50–60 min post-sunset on the nights immediately following the full moon. The highest display densities (1–2 displays/m²) were observed in the shallow nearshore grassbed

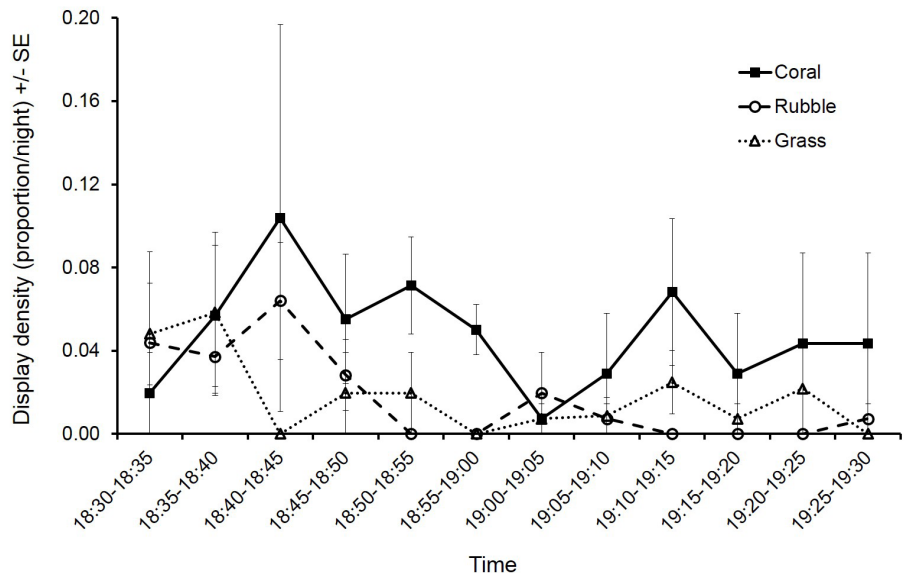


FIGURE 3. Proportion (mean \pm se) of *Odontosyllis* sp. female courtship display-densities observed in 3 different reef habitats recorded at 5 min intervals during the first hour of displays (immediately post nautical twilight) averaged across 3 nights in January 2016.

TABLE 1. *Odontosyllis* spp. courtship display observations made from 2015–2017 at multiple locations in the Caribbean.

Location	Lat/Lon	Dates	Substrate	Depth	Density	Notes
Belize, CA (South Water Caye, Carrie Bow Caye)	16°48'44.9"N, 88°04'59.0"W 16°48'11.9"N, 88°04'56.0"W	28 Dec 28 2015– 31 Jan 31 2016 and 12–18 Jan 2017	sea grass, rubble, coral patch reef, spur and groove	1 - 10m	High densities on nights following the full moon. Lower densities on nights throughout the lunar cycle.	
Roatan, Honduras, CA (Coco View)	16°21'30.7"N, 86°25'42.9"W 16°21'26.9"N, 86°25'56.5"W	21 May– 4 June 2016	sea grass, rubble, coral patch reef	0.25 - 3m	Extremely high densities in nearshore shallow grassbeds on nights following the full moon. Lower densities over the rubble, coral habitats and on other nights throughout the lunar cycle.	
Jamaica, WI (Discovery Bay)	18°28'17.8"N, 77°24'35.6"W	3–18 June 2015	coral patch reef	2 - 4m	Moderate to low densities on nights following full moon. Few to no displays observed throughout the lunar cycle.	Little to no observations of displays in nearshore seagrass and rubble habitats may be due to bright dock lighting.
Puerto Rico (Isla Magueyes)	17°57'11.9"N, 67°2'47.7"W 17°56'18.9"N, 67°2'45.6"W	19 July– 2 August 2016	sea grass, rubble, coral patch reef	1 - 4m	High densities on nights following the full moon. Displays especially abundant over patchy coral and rubble areas. Lower densities observed throughout the lunar cycle	Displays extended later into the night. Displays still present >90 minutes after sunset. Males exhibited a synchronous or entrained wave-like behavior with >30 males swarming toward a displaying female.
Panama, CA (Bocas Del Toro, Punta Manglar)	9°19'51.5"N, 82°15'17.4"W	11–24 May 2017	sea grass, rubble, coral patch reef	1 - 5m	Moderate to low densities on nights following full moon. Few to no displays observed throughout the lunar cycle.	

and rubble/grass boundary in Roatan. Relatively high densities were also observed across all habitat types in both Belize and Puerto Rico; however, we only observed male response entrainment or synchrony in Puerto Rico. Flashes from 20–30 male displays could be seen as they rapidly approached a female. The synchronized flash timing of the males created a rippling wave of light that moved across the ocean surface in the direction of a displaying female. *Odontosyllis* sp. display densities were relatively low in Panama even though the seagrass, rubble and coral habitats were not subjected to any artificial light and were teeming with other luminescent taxa (dinoflagellates and ostracods). In Jamaica, syllid display densities were also low which may have been due to the bright dock lights in the observed area and/or the intense offshore lighting from bauxite mines.

DISCUSSION

Prior observations have reported high *Odontosyllis* sp. display densities over rubble and seagrass (Markert et al. 1961, Gaston and Hall 2000), but little information has been collected over other marine substrate types, including coral. By expanding the number of substrates investigated, we found the density of *Odontosyllis* spp. courtship displays to be significantly higher over coral reef than either rubble or seagrass

habitats in Belize. This result reflects our qualitative observations from Puerto Rico where courtship displays were also abundant over coral patches. Together, these observations suggest that coral habitats are important for syllid reproduction and emphasize the need to consider additional substrates when investigating distributions of marine luminescence in general. Extending quantitative assessments of syllid displays to include different substrate types may provide greater insight into the factors (i.e., food availability, refugia, etc.) dictating *Odontosyllis* spp. occurrence.

Although we assessed syllid display densities over different benthic environments, we did not specifically investigate syllid use of benthic habitats. The limited data available on benthic habitat use by luminescent syllids clearly indicates that both adults and juveniles burrow into web-like silken nets which they build upon substrates. Fischer and Fischer (1995) completed the most thorough published benthic habitat and life cycle description for a luminescent species (*O. enopla*) and found that, in the laboratory, all stages built silken tubes on hard substrates. In the field, they discovered juvenile tubes on the bottom/edges of small algal-covered rocks at the margin of seagrass beds. Alternatively, Deheyn and Latz (2009) found juvenile and adult stages of *O. phosphorea* from collections of the algae *Ulva* sp. and the bryozoan *Zoobotryon*

verticillatum. The degree to which syllid habitat use translates to the frequency of reproductive displays remains unclear. Only by combining benthic surveys with pelagic assessments of luminescent displays can we more fully understand the role marine habitats play in syllid life cycles.

Nearshore marine habitats are heavily manipulated by human activities. Because of this, it is critical to understand the responses of marine species to these activities and what this means for the biodiversity of a region. Luminescent organisms, like syllids, are readily disrupted in nearshore habitats by resort and dock lighting. Syllids in Belize and many places throughout the Caribbean begin their luminescent displays within 10–15 min of the end of nautical twilight (Galloway and Welch 1911, Markert et al. 1961, Gaston and Hall 2000) which corresponds to an ambient light level of about 0.008 lux. Based on the inverse–square law for light attenuation, syllids would have to be 126 m away from a non–diffused 100 W light bulb to reach a 0.008 lux threshold light level for initiating courtship. Thus, a single 100 W bulb hanging over the end of a dock could disrupt up to 49,000 m² of habitat which could have important life–history consequences not only for syllids, but for other luminescent species as well.

Human activities and manipulations can also have negative effects on the integrity of coral reefs, which provide critical habitat for numerous luminescent species. Increasing sedimentation and overfishing threaten the health of living corals in the Caribbean and can result in coral habitats tran-

sitioning into rubble. This may have two interrelated consequences for syllids. First, coral habitats may actually act as refugia for organisms experiencing nearshore habitat disruption, so coral loss could hamper the ability of syllids to move away from disturbed habitats. Second, results from our work suggest that transitions from coral to rubble could eliminate prime habitat for syllid courtship, reducing their mating opportunities and exacerbating the effects of nearshore human activities on these organisms.

Species delineations in the genus *Odontosyllis* are still being explored both morphologically and phylogenetically. Different microhabitat types could contain different populations or species of syllids. Microhabitat specialization allows congeneric coexistence in other luminescent courting species (Gerrish and Morin 2016). Two *Odontosyllis* species (*O. twin-cayensis* and *O. luminosa*) have been observed in the waters surrounding Belize (Russel 1989, Gaston and Hall 2000). However, preliminary phylogenetic analyses show that the genus *Odontosyllis* is not monophyletic (Verdes et al. 2016), meaning the taxonomy of luminescent syllids in the Caribbean likely will be revised. Our findings support the notion that syllids should be sampled across habitat types to capture the breadth of syllid species and determine the stability of syllid populations. By doing this we can gain a better understanding of the diversity of syllids within this region and further our knowledge of how different syllid species respond in the face of alterations to nearshore environments.

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