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LUNAR PERIODICITY AND BIOLUMINESCENCE OF SWARMING *ODONTOSYLLIS LUMINOSA* (POLYCHAETA: SYLLIDAE) IN BELIZE

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ABSTRACT Few benthic polychaetes have the notoriety of the bioluminescent "glowworm", *Odontosyllis luminosa* San Martin, 1990, that inhabits soft-sediment habitats of the Caribbean. A few nights after a full moon, apparently during most months of the year, a most unusual phenomenon occurs. Female glowworms leave the sediments, swim toward the water surface, and release a bioluminescent egg mass, causing a bright green glow near the water's surface. The female's luminescence attracts the males, which also glow briefly. The tiny worm has a bright glow, and viewing it is a favorite pasttime in the Caribbean. Over 50 years ago investigators linked the bioluminescence of *Odontosyllis* with the mysterious lights described by Christopher Columbus in November 1492. Reproduction of *O. luminosa* peaks during summer, when the water's surface is brilliantly lit with females for 10–15 min on the first few evenings following a full moon. Spent females apparently survive to spawn again. They return to the sediments to build new tubes after spawning.

Introduction

The tropical grassbeds of Belize are inhabited by a unique benthic polychaete, *Odontosyllis luminosa* San Martin, 1990 (Annelida: Syllidae), that periodically leaves the sediments to reproduce at the water's surface. This is the bioluminescent "glowworm", that inhabits soft-sediment habitats of the Caribbean. The species was described only recently (San Martin 1990), but its behavior is familiar to persons throughout tropical waters of the Western Hemisphere. During evenings following a full moon, apparently during most months of the year, these worms release a glowing mass near the water's surface. This glow is surprisingly bright, and is easily visible from 30–50 m away.

Over 50 years ago investigators linked the bioluminescence of *Odontosyllis* with the mysterious lights described by Christopher Columbus in November 1492 as his ship approached an anchorage site in Rum Cay, Bahamas (Crawshay 1935). Despite this long history, details of the reproductive biology of *O. luminosa* remained undescribed. Previous authors documented the ecology of *Odontosyllis enopla* in Bermuda (Goodrich 1933, Huntsman 1948, Markert et al. 1961, Wilkens and Wolken 1981, Fischer and Fischer 1995), and assumed that it was the species that Columbus saw in the Caribbean. The description of this new Caribbean species by San Martin makes it more likely that what Columbus saw that night from the *Santa Maria* was *O. luminosa*, not *O. enopla*.

The purpose of this study was to investigate the reproductive ecology of *O. luminosa*, and describe its behavior. We also compared our observations with previous studies of *Odontosyllis* congeners and proposed directions for future studies.

Materials And Methods

The study was conducted near South Water Caye, Belize (16°48.5'N; 88°05'W), a 6.0-ha (15-acre) island located about 32 km (20 mi) SW of Dangriga and 1.6 km (1 mi) north of the Smithsonian's Caribbean Coral Reef Ecosystems research facility on Carrie Bow Caye. South Water Caye sits astride the Belize Barrier Reef and is bordered on the west by extensive turtlegrass beds (*Thalassia testudinum*) of the barrier reef lagoon and on the east by the coral forereef. South Water Caye supports a modest human population throughout the year, and the marine ecosystems surrounding the island remain nearly pristine.

Data for this study were collected primarily during the spring, summer, and fall of 1999, with additional observations made during May 1997, and March and May of 1998. A study area about 20 m by 30 m was established over the lagoon to water depths of 2–3 m adjacent to the International Zoological Expeditions (IZE) pier for evening observations. Habitats of this area were 70% turtlegrass and 30% bare sand (coarse sand; primarily derived from coralline algae, *Halimeda opuntia*). This allowed us to count the number of swarming worms in an established region, and determine the timing of spawning activity during the days following a full moon. We also recorded weather (wind speed, direction, cloud cover) and tidal conditions during swarming events.

Females and males were collected for laboratory observations during spawning episodes of May 1998, and February, March, and May 1999. Specimens were maintained in aquaria on South Water Caye. A stereomicroscope was set up to provide magnified viewing of tube-building behavior.

Observations that we made during spring of 1997 and 1998 established that most spawning occurred during the first days following the full moon, so we focused our observation efforts at those times. We began collecting data in late May 1999 on the night preceding the full moon, and continued nightly until the activity waned (Figures 1 and 2). Observations began at dusk, and lasted until no females were seen swarming that evening. We made instantaneous observations by counting the number of females observed in the area at a set time (5-min intervals beginning at sunset). It took about 1–2 min to tally the number of females swarming in the study area at a given time. Data were pooled in Figure 2 to illustrate the timing of swarming. Error bars are not provided, because all observations occurred at the same time of day and same location (non-random sampling).

We collected benthic samples from turtlegrass beds at the NW end of South Water Caye (water 1.0 m deep) to determine population density of *O. luminosa*. Specimens of benthos were washed free of sediments on a 0.5mm sieve. Sediments were generally coarse coralline-algae sand (as above). Benthic organisms were sorted under stereomicroscopy. Additional benthic samples were collected from coral rubble in the turtlegrass beds. Fish that preyed on swarming benthos were collected with a pole-mounted sweep net (1 mm mesh), and their gut contents were sorted and identified under stereomicroscopy.

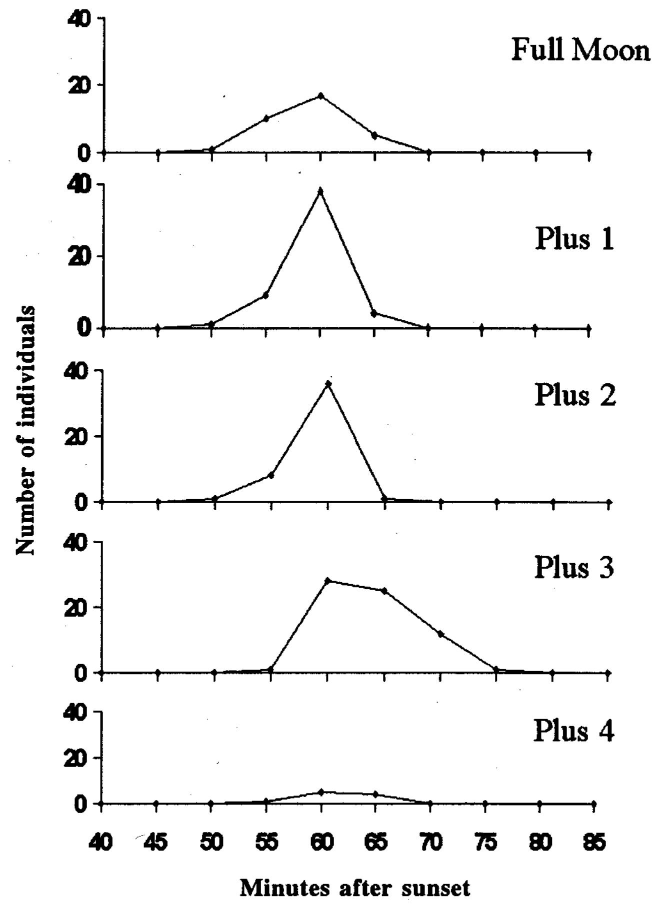

Figure 1. Numbers of female *Odontosyllis luminosa* observed luminescing in the study region (20- by 30-m area) near South Water Caye, Belize during the full moon and 4 nights that followed (30 May–3 June 1999). Data are instantaneous counts taken at 5-min intervals.

RESULTS

The greatest densities of spawning *Odontosyllis luminosa* during our 1999 study were observed on the first 3 evenings after the full moon (Figure 1). Timing of this reproductive activity was remarkably consistent from day to day, despite changes in weather conditions, tidal cycle, or current direction. For instance, cloud cover was less than 20% during the first 2 evenings of observation (Full Moon and Plus 1; Figure 1), but it was overcast with 80% cloud cover on the 3rd evening (Plus 2). As a result, it was dark much earlier on the 3rd night, yet the timing of reproductive activity remained similar. Winds were relatively calm during the first 2 evenings, and a falling tide carried the bioluminescing worms to the south. On the 3rd evening a 15-k wind blew from the NE and increased the surface currents carrying the worms southward. These differences in environmental conditions seemed to have no effect on timing of spawning activity, as evidenced by Figure 1. This consistency occurred despite the daily variance in tidal cycle (about 50 min per day).

The greatest reproductive activity of *O. luminosa* during our May–June 1999 study occurred at about 60 min after sunset (Figure 1). This timing of spawning activity is evident in Figure 2, which summarizes observations over the 5-day period. Females began bioluminescing at the surface at about 45–50 min after sunset, and peaked in activity at about 60 min; few were still spawning by 70–75 min. We noted that the peak of activity on days 1–2 after a full moon was actually at 58 min after sunset, when up to 55 females were observed in the study area, but that pattern is not reflected in the illustration since we recorded on 5-min intervals.

Specimens were observed swarming over grassbeds in various water depths, from less than 0.1 m deep near

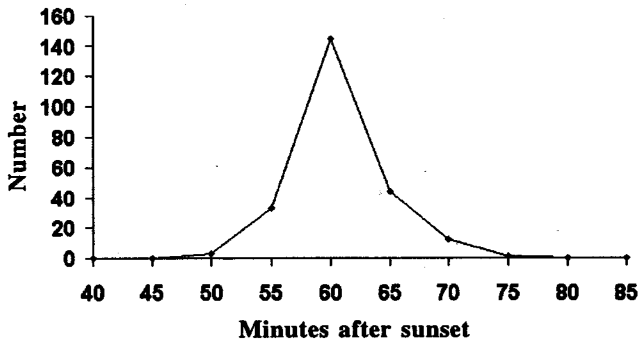

Figure 2. Total number of female *Odontosyllis luminosa* observed luminescing in the study region (20- by 30-m area) near South Water Caye, Belize, over a 5-day period. These are instantaneous counts taken at 5-min intervals beginning 40 min after sunset.

the shore to 6 m deep in the channel between South Water Caye and Carrie Bow Caye. Most activity occurred in the lagoon (where the most turtlegrass is located), but a few specimens were seen bioluminescing over the forereef on the east side of the island as well.

The reproductive behavior of *O. luminosa* was easily observed from piers and boats. Female *O. luminosa* left the bottom and drifted slowly on surface currents (within 1–2 cm of the water surface) where they periodically began luminescing. Several female specimens that we collected when they first began luminescing were full of oocytes, indicating that luminescence can occur without shedding of gametes. Specimens observed under stereomicroscopy confirmed this. Apparently both the oocytes and the bioluminescent material are released from the gonopores along the abdomen.

Males could be seen flashing a pattern of luminescence on turtlegrass blades below the females, apparently in response to glowing of the females. Males left the bottom, flashing bioluminescence as they swam rapidly toward the surface to join the females. This pattern was evident in deep water of the channel, where males swam for 5–6 m in a few seconds flashing as they went. Male *O. luminosa* (mean length, 12 mm) were generally smaller than females (mean length, 20 mm).

Once the males joined the females at the water's surface, females began quivering rapidly and periodically spinning in circles, while releasing a luminescent mass and (presumably) gametes. Males swam rapidly around the females bioluminescing and releasing their gametes. Sometimes several males encircled a single female. Each luminescent episode lasted for 45–65 sec, but some female worms repeated the episodes numerous times as they drifted near the surface. Generally, once males were attracted, the spawning of a female lasted just 2–3 min. Some females apparently were not successful in attracting males and did not undergo the oocyte-releasing behavior. Rather, they continued to periodically emit their bioluminescent mass while drifting at the surface.

A few female *O. luminosa* were observed luminescing at the water's surface following full moons during nearly every month of observation, but the greatest reproductive activity occurred during summer months (June–August). Activity increased during full moons of early spring (February and March), and counts of luminescing females numbered 2–3 per 5-min record in the observation area. Similarly low counts occurred during fall months of 1998 and 1999. Reproductive activity increased to a maximum of about 40 females bioluminescing per record during June (Figure 1; 1 female per 15 m^2). Apparently there were more *O. luminosa* spawning during July than June 1999, but an overgrowth of green algae (*Ulva rigida*) near the pier limited our observation. Although most activity occurred on evenings immediately after the full moon, a few females were seen during the first hour after sunset almost every night during May and June of 1999.

Specimens maintained in aquaria after spawning settled to the sediments to establish mucous tubes. These specimens were intact after spawning and their gametes were completely spent, characteristic of polytelic polychaetes that survive spawning events (Clark 1979). A few specimens autotomized during handling, but none of the whole specimens that we put into aquaria ruptured their body walls, even though some continued to release gametes after collection. Oocytes were observed on the bottom of the aquaria by morning, indicating that they were negatively buoyant.

The swarming *O. luminosa* were joined in the water column by other swarming benthic taxa, including amphipods, isopods, tanaids, and other species of polychaetes (nereidids, opheliids, and spionids). Several species of fish preyed on benthos as they swarmed in the water column. The most notable predatory fish was *Atherinomorus stipes*, a silverside (Atherinidae) that is common in turtlegrass beds (B. Chernoff, pers. Comm., Field Museum of Natural History, Chicago). The fishes indiscriminately fed on many of the swarming taxa as we watched and appeared to ingest *O. luminosa*. Several of the silversides began having spasms and suffered paralysis, apparently after feeding on *O. luminosa*. We collected some of these paralyzed silversides to confirm our observations, but all of them had empty guts. Apparently the fish regurgitated their ingested prey during spasms.

Odontosyllis luminosa were collected in benthic sediment samples from sandy sediments of turtlegrass beds during March 1999. Only 3 specimens were collected (density = about 1–3 m^{-2}). All 3 specimens inhabited sediments around the roots of turtlegrass short shoots, and none of those collected was sexually mature.

DISCUSSION

Odontosyllis luminosa spawning occurs during the early evenings immediately following the full moon. Activity peaks 55–60 min after sunset, notably a time when the moon is still low or beneath the horizon; thus, the water is very dark except for bioluminescence. Twilight is also a time of reduced predation pressure in the plankton (Alldredge and King 1985). The peak reproductive activity that we observed did not vary with weather conditions, nor did it match particular tidal cycles, as suggested for *O. enopla* in Bermuda (Galloway and Welsh 1911).

Summer months are the height of reproduction for *O. luminosa* in Belize. Even though not apparent during our June 1999 study, the greatest reproductive activity may occur during a mid-summer full moon. Our primary observations occurred during early summer, and local residents of South Water Caye reported that activity usually peaks the third night after the full moon in midsummer. Our data indicated an extended period of activity on the third day (spawning lasted longer), but the number of females spawning at that time did not exceed the earlier 2 days.

Previous studies of *Odontosyllis* documented a similar pattern of reproduction on lunar cycles. The Bermuda "fireworm", *O. enopla*, reached its swarming peak 3 days after the full moon, and exhibited behaviors much like we observed (Markert et al. 1961). Females luminesced to attract males, which also luminesced. The swarming activity of *O. enopla* in Bermuda peaked at 56 min after sunset and nearly disappeared by 60 min. The entire display of *O. enopla* lasted only 15 min (Markert et al. 1961). *Odontosyllis luminosa* we observed began displaying about the same time as *O. enopla* (45–50 min), and the activity on any particular night ended within about 15 min. The cumulative data provided on Figure 2 shows that the majority of activity over a 5-day period was limited to 50–70 min after sunset.

Several authors provided reviews of the luminescence and lunar periodicity of *O. enopla* (Galloway and Welsh 1911, Goodrich 1933, Crawshay 1935, Huntsman 1948, Markert et al. 1961, Fischer and Fischer 1995) and its anatomy and physiology (Wilkens and Wolken 1981, Wolken and Florida 1984). Several other species of *Odontosyllis* are known to luminesce: *Odontosyllis hyalina* in Indonesia (Lummel 1932), *O. polycera* in New Zealand (Daly 1975), *O. undecimdonta* in Japan (Inoue et al. 1990, 1993, Tanino et al. 1996); and *O. phosphorea* in British Columbia (Potts 1913, Fraser 1915, Berkeley 1935). Eggs of *O. polycera* reportedly were negatively buoyant, as we observed for *O. luminosa*. Potts (1913) reported that males and females of *O. phosphorea* gathered at the water's surface, but males were not attracted by females as occurred with *O. luminosa* and *O. enopla*. Further, the swarming by *O. phosphorea* began before sunset and occurred during many months of the year (Berkeley 1935).

There are several dozen species of *Odontosyllis* described, but little is known about the reproductive biology or production of luminescence by most of them. Russell (1989) collected and described a new species, *O. twincayensis*, from Twin Cayes, Belize just a mile from our study site at South Water Caye. The short compound setae of *O. luminosa* distinguish them from *O. twincayensis*, and it is not known if the latter luminesces. *Odontosyllis fulgurans* and *O. detecta* are widely distributed and are known to occur in the Caribbean, but have different setae than *O. luminosa* (San Martin 1990). No other species of *Odontosyllis* are known from the region.

Crawshay (1935) compared *O. enopla* with an undescribed species that he observed in British Honduras (now Belize). The Belize species was possibly *O. luminosa*. He reported that the 2 species were "structurally similar, if not identical", but the Belize species began its reproduction "long after darkness had closed in". He observed the Belize species bioluminescing until 8:30 PM (about 2 hours after sunset). His other descriptions lacked detail, except to say that the episode of illumination by a female lasted just 5–10 min, and that the swarming might occur on successive nights, "but more usually will not recur until the same phase of a subsequent lunation". He reported that the swarming did not occur in all months (of 1921 and 1923), but was noted in January, April, May, July, October, and December. There is no way to determine for certain if Crayshaw was describing *O. luminosa*. What is certain is that its reproductive biology differed considerably from that of our observations.

There is much yet to learn about *O. luminosa*. We know little about the mechanism of its bioluminescence and almost nothing about its prespawning and postspawning behavior. It somehow maintains reproductive synchrony despite changing weather conditions, and we suspect that it avoids predation by chemical defense. This is a simple organism with a very complex reproductive ecology. It has been over 500 years since Columbus first saw this species bioluminescing in the waters of the Caribbean, yet we know little about details of its behavior. Most of its secrets remain to be explored.

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