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Nocturnally swarming Caribbean polychaetes of St. John, U.S. Virgin Islands, USA

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Abstract

Nocturnally swarming polychaetes were sampled over a ten-year period (2007–2017) in shallow waters of the Virgin Islands National Park, St. John, United States Virgin Islands. While sampling was qualitative and conducted over different years, months and lunar phases, some patterns were noted in the emergence of swarming polychaetes. Three families (Nereididae, Opheliidae, and Syllidae) had members that swarmed on most nights, while reproductive epitokes from two families appeared only during specific lunar phases: Goniadidae around the full moon and Phyllodocidae around the new moon. Additional polychaete families represented included Amphinomidae, Dorvilleidae, and Scalibregmatidae, whose members swarmed during the waning or waxing lunar phases. This overview offers new information about the timing of reproductive swarming in Caribbean polychaetes and suggests some connections between lunar phases and the swarming of different families.

Key words: Annelida, Polychaeta, lunar cycle, reproduction, swarming

Introduction

Many studies document correlations between lunar cycle phases and marine animal reproduction. Particularly notable are the mass spawning events during specific lunar phases for corals (Boch *et al*. 2011; Wolstenholme *et al*. 2018) and palolo worms (Caspers 1984; Pamungkas & Glasby 2015). The effect of lunar cycle periodicity on reproductive behavior has been well-documented for many other coral reef organisms, including cnidarians (Reitzel *et al*. 2013), mysid shrimp (McFarland & Kotchian 1982), the bioluminescent polychaete *Odontosyllis enopla* Verrill, 1900 (Fischer & Fischer 1995), and fishes (McFarland *et al*. 1985; Stallings *et al.* 2016). Correlations between reproductive periodicity and lunar phases have also been documented for some deep-sea invertebrates, including deep water octocorals, sea urchins, starfish, and sea anemones (Mercier *et al.* 2011) at depths where there is no lunar illumination.

Polychaetes have evolved a myriad of reproductive strategies that include forming reproductive swimming individuals, epitokes, which broadcast their gametes at night (Clark 1961; Schroeder & Hermans 1975; Wilson 1991). Many epitokous polychaetes form epitokes through epigamy, where the entire atoke is transformed into a reproductive swarmer (Rouse & Pleijel 2001). Other polychaetes (many syllids) form epitokous stolons through schizogamy, where only the posterior body is modified to produce an epitoke (Nygren 1999; Rouse & Pleijel 2001). Synchronized spawning is thought to maximize the likelihood of fertilization for broadcast swarmers (Rouse & Pleijel 2001), and for many epitokous polychaetes, the precise synchronization of swarming and spawning is linked to specific lunar phases (Aiyar & Panikkar 1937; Clark 1961; Wilson 1991; Bentley *et al*. 1999).

While the taxonomic literature for Caribbean polychaetes is continually being updated, it is not generally sufficient to accurately identify the epitokes, which have often undergone dramatic body changes for swimming and gamete production. Depending on the species, epitokes exhibit varying degrees of metamorphosis, or changes in body morphology, which range from modified natatory (swimming) chaetae (e.g. amphinomids, goniadids and phyllodocids) (Böggemann 2005; Schroeder & Hermans 1975) to the transformation of an entire

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body region (nereidids and syllids) (Fischer 1999; Nygren 1999; Read 2007; Pamungkas & Glasby 2015). Greatly enlarged eyes and elongated dorsal cirri are among the many morphological changes in epigamous epitokes, especially noticeable in the nereidids and syllids (Schroeder & Hermans 1975; Nygren 1999). The schizogamous epitokes (stolons) produced by Syllidae exhibit great diversity, as they may be headless, sexually dimorphic, or serve as egg-brooding females (Frank 1999; Nygren 1999). Since some epitokes bear little resemblance to atokous forms, they are frequently misidentified, referred to as new species (Pamungkas & Glasby 2015), or simply set aside and labeled unknown. Research that focuses on polychaete epitokes can yield valuable information on reproductive cycles and associated metamorphoses, and may help with the identification of cryptic species (Read 2007; Pamungkas & Glasby 2015). Increased sampling efforts, conducted over different seasons and lunar phases, can provide new material useful in the development of more comprehensive taxonomic literature.

In this study, nocturnally swarming polychaetes were collected intermittently over the course of ten years (2007–2017) in the Virgin Islands National Park, in St. John, U.S. Virgin Islands (USVI). Observations from this study indicate that some polychaetes swarmed during specific lunar phases, while members of other families swarmed throughout the lunar cycle. These results may allow for a better understanding of polychaete reproductive cycles in coral reef systems in the northeastern Caribbean Sea.

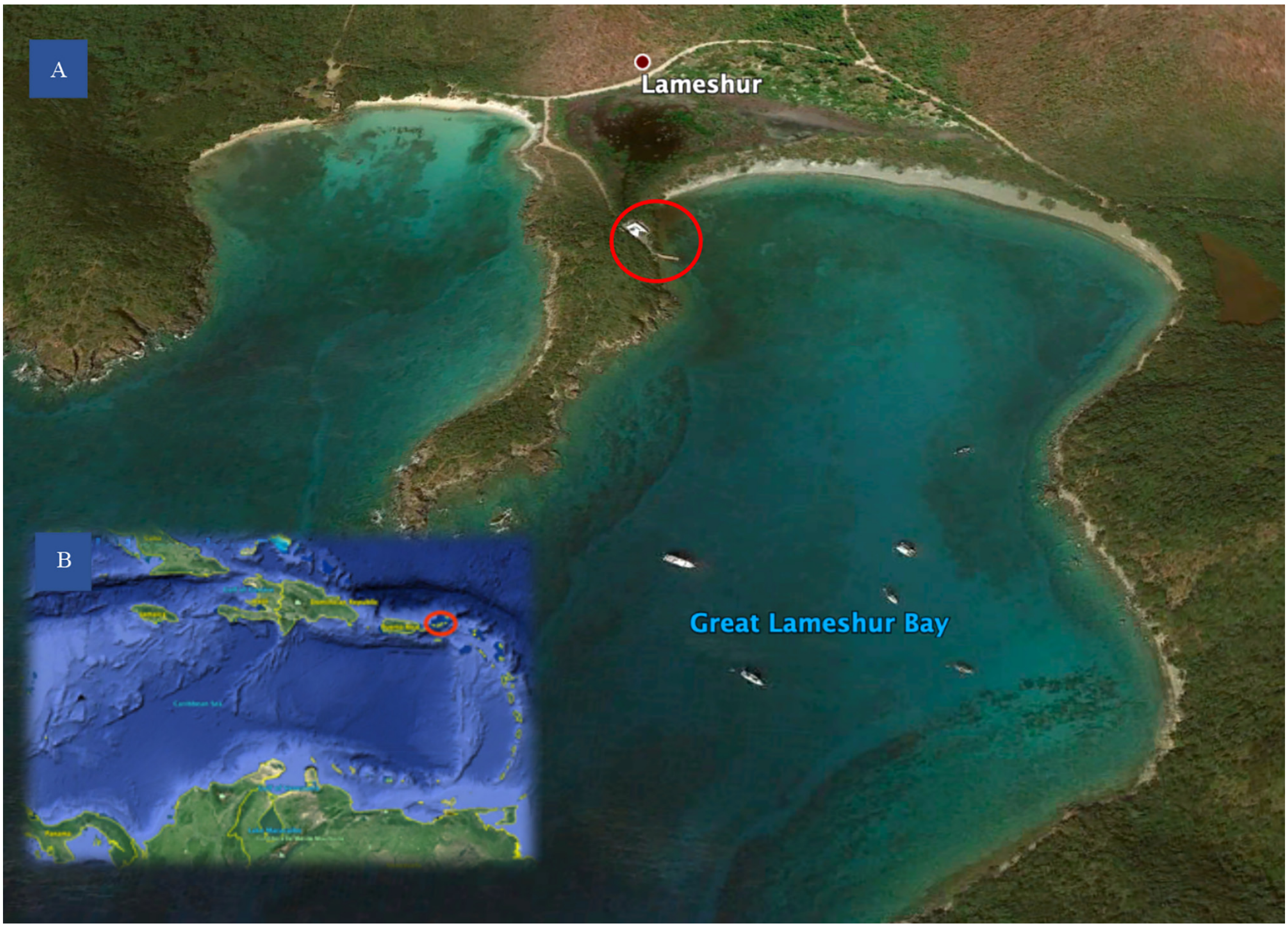

FIGURE 1. A. Aerial view of Great Lameshur Bay with USVI National Park Service dock.
B. Region of the U.S. Virgin Islands (red oval) in northeastern edge of the Caribbean Sea (18° 19.1’ N, 64° 43.5’ W). Images obtained from *Google Earth Pro*.

Materials and Methods

Polychaete sampling was conducted over a ten-year period (2007–2017) in Great Lameshur Bay, St. John, USVI (18° 19.1’ N, 64° 43.5’ W), within the Virgin Islands National Park (Figure 1). The NOAA tidal station in Great Lameshur Bay indicates that over the course of a year, the surface water temperature ranges from a low of 26º C in January/February to a high of 31º C in September/October (NOAA Tides and Currents), while the tidal range oscillates from about 0.2 meters on a neap tide, to about 0.4 meters on a spring tide (NOAA Tides and Currents). The greatest tidal range ever recorded for Great Lameshur Bay was 0.42 m during a spring tide (Tide-Forecast). Over 30 plankton collections were made in different years, months and lunar phases. Most of the sampling was done for 1–2 hours, at least one hour after sunset (7:30–9:30 p.m.) and before moonrise, at the National Park Service (NPS) dock (Figure 1), where the water depth was less than three meters. Within a 10-meter radius of the collection site, the seafloor substrate was composed primarily of dead coral rubble and coarse sand, along with *Aplysina* and *Ircinia* sponges, isolated patches of seagrass (*Thallasia testudinea*), and mats of green algae and cyanobacteria. Larger benthic invertebrates commonly seen at night around the dock included octopuses, coral-banded shrimp, arrow crabs and the echinoderms *Diadema antillarum*, *Holothuria mexicana*, and *Euapta lappa*. South of the dock, the shoreline consisted of volcanic rock, while north of the dock, it was rimmed by red mangroves (*Rhizophora mangle*). Live hard coral colonies near the dock were non-contiguous and less than 0.25 m in diameter.

TABLE 1. Compilation of planktonic polychaetes observed during different years, months and lunar phases from 2007 to 2017. Sunset and moonrise times for each collection night are included, along with lunar illumination percentages. Eight families of polychaetes were represented among the swarmers.

LUNAR PHASE	DATES	SUN SET (PM)	MOON RISE (PM)	LUNAR ILLUMI-NATION (%)	*Amphinomidae*	*Dorvilleidae*	*Goniadidae*	*Nereididae*	*Opheliidae*	*Phyllodocidae*	*Scalibregmatidae*	*Syllidae*
FULL MOON	Jun 19 2008	6:57	8:00	99.7			swarm		swarm			swarm
	Jul 26 2010	6:56	7:22	100			swarm					
	May 25 2013	6:49	7:34	100				few ind.				swarm
	May 21 2016	6:47	6:44	99.7								swarm
1 DAY PAST FULL	Jun 20 2008	6:57	8:45	97.9			swarm					
	May 26 2013	6:49	8:36	98.3								swarm
	May 22 2016	6:48	7:35	99.7								swarm
WANING GIBBOUS	Jun 21 2008	6:58	9:26	94.1	lg. swarm		swarm	lg. swarm	lg. swarm			lg. swarm
	Jul 5 2012	6:59	8:39	97.0			swarm	swarm				
	May 27 2013	6:50	9:34	93.5								swarm
	May 23 2016	6:48	8:25	98.1								swarm
3 - 4 DAYS PAST FULL WANING GIBBOUS	Jun 22 2008	6:58	10:05	88.5					lg. swarm			lg. swarm
	Jan 13 2009	6:02	8:54	93.5		swarm			swarm			
	Jan 14 2009	6:02	9:50	86.4				swarm	lg. swarm			swarm
	May 24 2016	6:49	9:15	94.5					swarm			swarm
	June 23 2008	6:58	10:44	81.1				swarm				
	May 25 2016	6:49	10:05	88.9					swarm			swarm
1 - 2 DAYS BEFORE THIRD QUARTER	May 26 2008	6:49	no rise	67.6	lg. swarm	swarm		swarm				swarm
	Jun 24 2008	6:58	11:17	72.2					swarm			swarm
	Jan 16 2009	6:04	11:38	67.7		swarm		swarm	swarm			swarm
THIRD QUARTER	Jan 17 2009	6:04	no rise	57.3				swarm	swarm			swarm
	Jan 18 2009	6:05	no rise	47.0								
WANING CRESCENT	Jun 2 2008	6:52	no rise	2.4	swarm				swarm	swarm		
	Jan 19 2009	6:05	no rise	37.0				swarm	swarm			swarm
NEW MOON	Jul 14 2007	6:59	no rise	0.1		swarm		swarm				
	May 24 2009	6:48	no rise	0.2				swarm				
	May 20 2012	6:47	no rise	0.1		swarm		swarm	swarm	swarm		
	Jul 19 2012	6:57	no rise	0.4		females						
	May 25 2017	6:49	no rise	0.2				swarm	swarm			swarm
FIRST QUARTER WAXING GIBBOUS	Jul 8 2011	6:59	12:45	57.9				swarm			1 female	
	May 25 2015	6:45	12:15	52.2				swarm	swarm			swarm

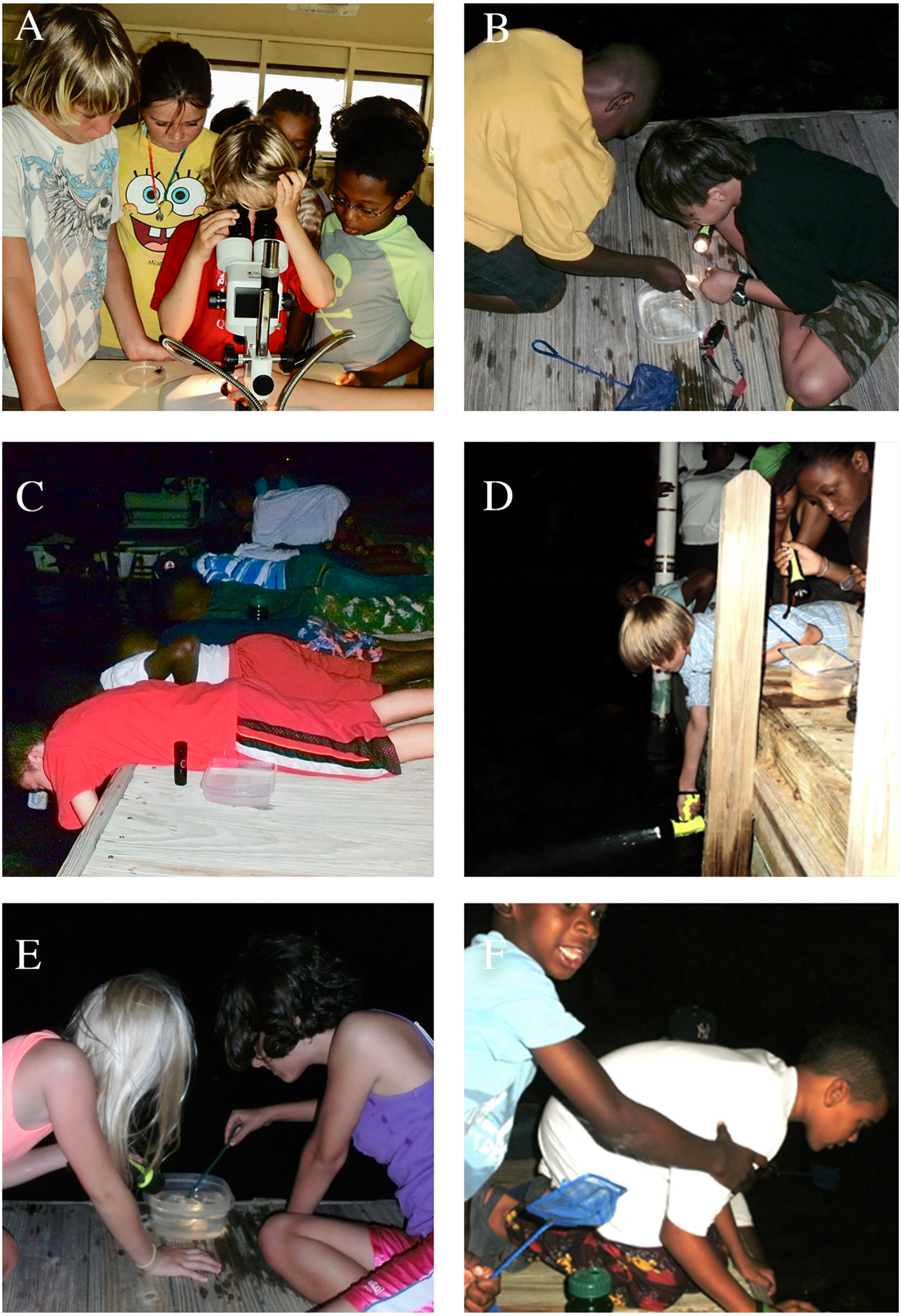

FIGURE 2. A. Young campers from the Virgin Islands Environmental Resource Station (VIERS) viewing recently caught polychaetes under a stereo microscope. **B–E.** VIERS campers collecting nocturnal plankton at the National Park Services dock in Great Lameshur Bay, St. John, USVI.

The majority of the sampling was done during the second half of the lunar cycle (full moon to new moon) (Table 1). Since planktonic organisms were not as abundant after moon rise, or during bright moonlit nights, most sampling efforts were biased toward darker nights when all planktonic fauna (e.g. cnidarians, crustaceans, chaetognaths and larval fish) were more evident. Some collections were purposely planned to coincide with the swarming of the bioluminescent syllid, *Odontosyllis enopla*, well-documented to swarm about 55 minutes after sunset, on the evenings that occur 1 to 2 days after a full moon (Huntsman 1948; Markert *et al.* 1961; Gaston & Hall 2000). The sampling was conducted by students from the University of Maine at Farmington, by young campers and counselors attending summer ecology camps at the Virgin Islands Environmental Resource Station (VIERS) (Figure 2), and by researchers conducting polychaete surveys in the Virgin Islands National Park.

Polychaetes swarming to underwater lights (hand-held underwater dive flashlights with differing intensities and wavelengths) were hand netted with small dip nets and observed live with stereomicroscopes. All epitokes were identified to the family or subfamily level, and some were identified to species, using taxonomic literature specific to the Caribbean. Body characteristics (pigmentation and size) were noted, as was the sex (if gametes were seen). For example, male and female goniadids and phyllodocids typically shed sperm or eggs while being captured. Female epitokes were also recognized when coelomic eggs could be seen with a stereomicroscope. Male epitokes of the nereidid species *Neanthes egregicirrata* (Treadwell, 1924) were recognized by their greatly elongated dorsal cirri. The polychaetes collected from 2007 through 2012 were fixed in buffered 10% formalin and preserved in 70% ethanol, while those collected from 2012 through 2017 were preserved in 95% ethanol. Most of the preserved samples were stored at the University of Maine at Farmington. Preserved polychaetes were examined using a Zeiss Stemi 2000 CS stereomicroscope, and macrophotographs of preserved specimens were taken with a SPOT Insight digital camera system.

Qualitative observations were made of polychaete emergence and the occurrence of "swarms" or "large swarms" (Table 1). Other non-polychaete planktonic fauna caught as "by catch" were noted as well. The times of sunset moonrise and predicted lunar phase illumination for Cruz Bay, St. John, USVI, were obtained from online sources (Time and Date 2019a, 2019b). Annual permits for collecting polychaetes within the U.S. Virgin Islands National Park were authorized by the National Park Service from 2007 through 2017 (Polychaete Survey St. John, U.S. Virgin Islands: Study #VIIS–09013).

Results

The largest swarms, in terms of overall biomass, seemed to occur on the second night following a full moon (Table 1). While occurring just after the full moon phase, these swarms also emerged before moonrise, so the water was still relatively dark. Over the 10-year study period, the polychaetes collected belonged to eight families: Amphinomindae, Dorvilleidae, Goniadidae, Nereididae, Ophelliidae, Phyllodocidae, Scalibregmatidae, and Syllidae (Table 1; Figures 3–5). Syllid epitokes were represented in the majority of the samples regardless of the lunar phase, and it was evident that many different species were present. Most of the syllids have not yet been identified, but epitokes belonging the subfamilies Autolytinae, Eusyllinae and Syllinae were recognized. Syllid swarms included male and female epitokes; occasionally, female epitokes were brooding (Figure 3A–D). Bioluminescent epitokes of *Odontosyllis enopla* swarmed about 50 minutes post-sunset, for 30 minutes, on the nights that occurred one and two days after a full moon. These *Odontosyllis* swarms were usually followed by large swarms of nereidids, syllids and opheliids. Nereidids and opheliids also occurred in most samples, regardless of the lunar phase (Table 1). Nereidid male and female epitokes were of several species, including *Neanthes egregicirrata*, the males of which could easily be recognized by a pair of greatly elongated dorsal cirri on the 6th chaetiger (Pettibone 1956; de León-González *et al*. 1999) (Figure 3 E–F). One opheliid species, *Polyophthalmus pictus* (Dujardin, 1839) swarmed on most nights (Figure 4a; Table 1), but no gametes were seen in the netted individuals.

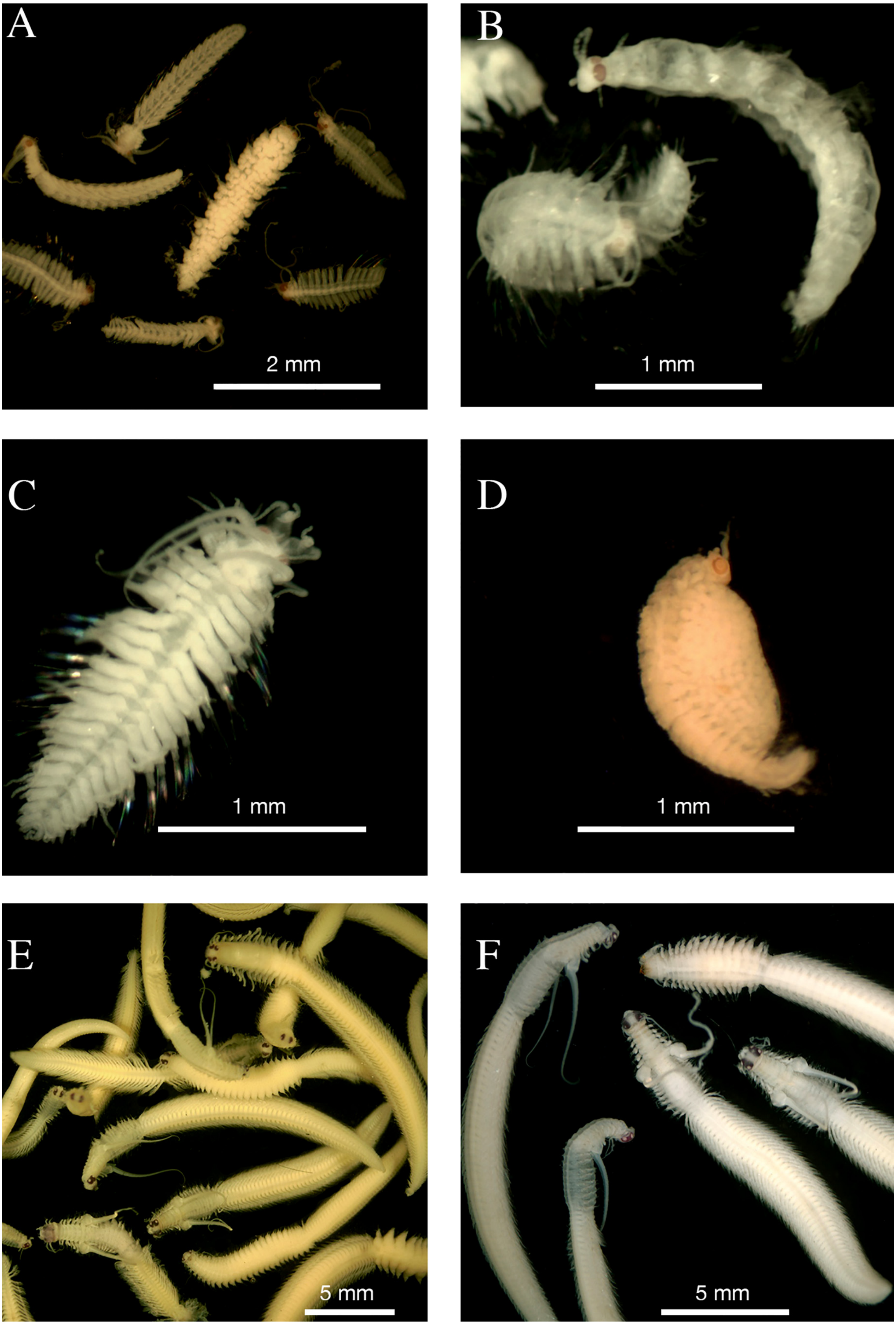

FIGURE 3. A. Syllid epitokes and one egg-filled stolon. **B.** Syllids. **C.** Syllid, male epitoke. **D.** Syllid, brooding female. **E.** *Neanthes egregicirrata* (males and females) (Nereididae). **F.** *Neanthes egregicirrata*, male epitokes (Nereididae).

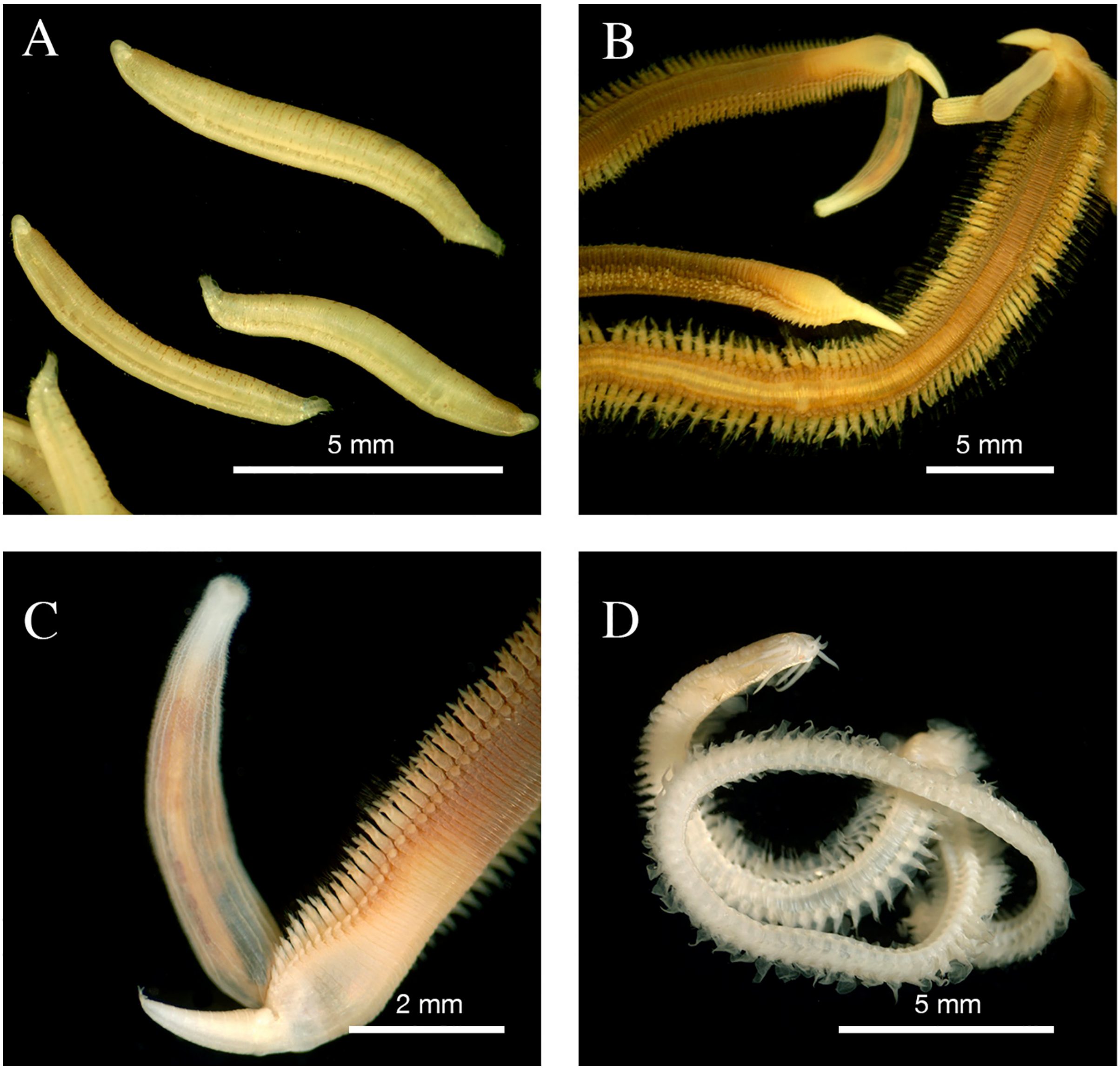

FIGURE 4. A. *Polyophthalmus pictus* (Opheliidae). **B.** Goniadids. **C.** Goniadid, anterior end with fully everted proboscis. **D.** Phyllodocid.

The goniadid and phyllodocid epitokes (15+ cm body length) swam serpent-like to the lights, and always self-fragmented to shed eggs and sperm after being collected. The goniadids (Figure 4B–C) appeared only around the full moon phase (97–100% lunar illumination). When fixed, each goniadid epitoke fully everted its proboscis, on which there was no evidence of jaws, micrognaths, macrognaths or chevrons, features generally used for species identification in this family. The phyllodocid epitokes (Figure 4D) appeared only during the darkest phases of the moon (waning crescent and new moon), when the lunar illumination was 0.1–2.4% (Table 1).

Epitokes from three other families (Amphinomidae, Dorvilleidae, and Scalibregmatidae) occurred only occasionally during the waning or waxing lunar phases (Table 1). When the amphinomid, *Notopygos crinita* Grube, 1855 swarmed, the abundant epitokes were bright red and bore many natatory chaetae (Figure 5A). The dorvilleid epitokes were all females, harboring bright purple eggs (Figure 5B). Only one scalibregmatid epitoke was observed, and occurred on the night of a first quarter moon. Packed with eggs, this female had two parallel bands of red eyes and long natatory chaetae (Figure 5C–D).

Other planktonic fauna caught along with the polychaete epitokes included tiny cnidarians, chaetognaths, crab zoea, spiny lobster larvae, copepods, barnacle cyprid larvae, cumaceans, isopods, and assorted larvae of sipunculids, cephalopods (squid & octopus), echinoderms, and fish.

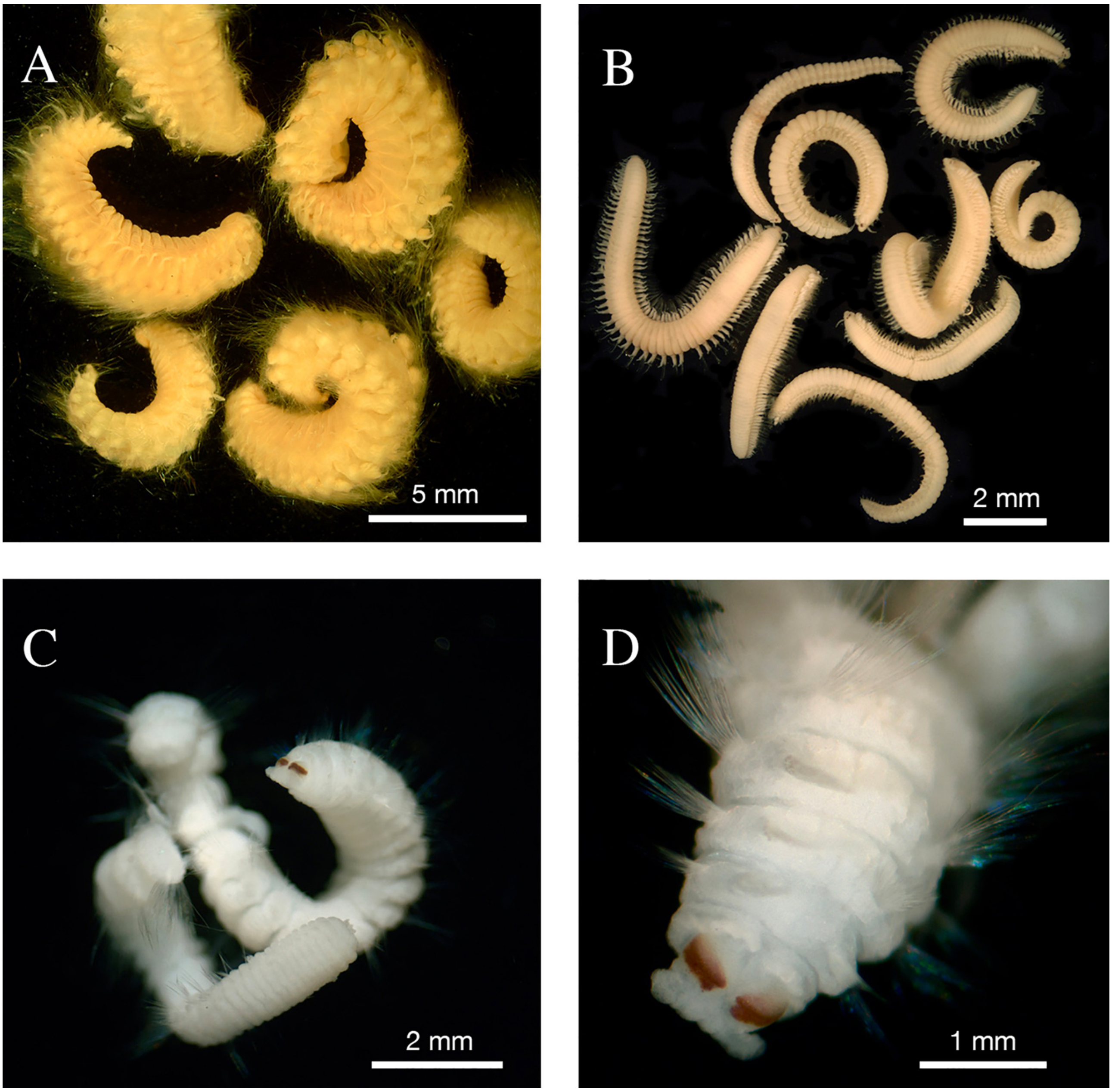

FIGURE 5. A. *Notopygos crinita* (Amphinomidae). **B.** Dorvilleids. **C.** A scalibregmatid (one individual, broken in the middle). **D.** The anterior end of the scalibregmatid individual shown in Fig. 5C.

Discussion

For over a century, there have been many accounts in the polychaete literature of nocturnally swarming polychaetes, especially those forming large epitokal swarms comprised of species from the families Eunicidae, Nereididae, and Syllidae (Browne 1900; Horst 1904; Mayer 1908; Moore 1908; Clark 1961; Bentley *et al.* 1999; Pamungkas and Glasby 2015). Epitokes have also been recorded in the families Amphinomidae, Dorvilleidae, Glyceridae, Goniadidae, Ophelleidae, Phyllodocidae, and Scalibregmatidae (Chamberlain 1919; Allen 1957; Clark 1954; Glasby *et al.* 2000; Pleijel & Rouse 2006). Some polychaete species, such as the syllid "fireworm" (*Odontosyllis enopla*) and the Palolo worm (*Eunice viridis*) swarm during very specific lunar phases and times of the year (Fischer & Fischer 1995; Pamungkas & Glasby 2015); during these times, one can expect to see massive swarming events. For other polychaete families (e.g. Scalibregmatidae), epitoke emergence is less predictable and the swarms are smaller overall (Clark 1954).

In this study, nocturnally swarming polychaetes were collected in Great Lameshur Bay (St. John, USVI), during different lunar phases and months, over a span of 10 years. No two nights were alike, and the biodiversity of all plankton fauna varied greatly, depending on the lunar phase and cloud cover. Greater numbers of polychaete epitokes emerged on darker nights (late moon rise or overcast skies) as did more zooplankton of all types: crustaceans, larval molluscs, echinoderms, and fish larvae. During bright nights, following moonrise (especially around the full moon), the overall plankton abundance appeared low and very few polychaetes were visible.

Polychaetes were collected from most of the above-listed families, with the exception of Eunicidae, members of which were notably absent from the samples. The absence of eunicid epitokes is interesting, since many species within this family are known to form huge swarms (Pamungkas & Glasby 2015). In Puerto Rico, Allen (1957) collected two eunicid species (*Eunice* sp. and *Lysidice* sp.), but she noted they were few in number. In Great Lameshur Bay, the benthic environment in the immediate vicinity of the collecting site (NPS dock), may not have provided suitable habitat for epitoke-forming eunicids. Yet some eunicid species are common in Great Lameshur Bay, where the species *Eunice vittata* (Dell Chiaje, 1828) and *Lysidice unicornis* (Grube, 1840) were collected from benthic vase sponges and coarse sand (Prentiss & Harris 2011). The author also collected many specimens of the "Atlantic Palola worm" (*Eunice fucata* Ehlers, 1887) from dead coral rubble and benthic fouling matter near the Great Lameshur Bay NPS dock. This eunicid has been reported to swarm elsewhere: Mayer (1908) documented large swarms of *E. fucata* in Tortugas, Florida, "within three days of the last quarter of the moon" of the lunar cycle at the end of June and July. He noted that *E. fucata* was widely and abundantly distributed throughout the Bahamas and West Indies, but that swarms apparently occurred only in Tortugas. Despite many searches for such swarms in other locations in different years, he never observed *E. fucata* swarming behavior outside of Tortugas (Mayer 1908).

For the entire year of 1955, Allen (1957) collected planktonic polychaetes from a laboratory dock and coral reef on the island of Magüeyes, Parguera, Puerto Rico. Using an electrically-powered reflector bulb, she created a bright light above the water to attract nocturnal plankton, which she collected with a dip net. In addition to collecting some eunicids, Allen (1957) also collected epitokes of Syllidae, Nereididae, Glyceridae, and Amphinomidae. During the full moon in October, 1955, Allen (1957) reported a one-time collection of "*Glycera* ? *sphyrabrancha*", after which the elongated (23–28 cm) male and female epitokes self-fragmented and released gametes. The epitokes of some glycerids can be difficult to identify since epigamous metamorphosis may cause an atrophy or degeneration of the proboscis and associated jaws (Simpson 1962; Pettibone 1963). *Glycera* was collected from benthic substrates in Great Lameshur Bay (Prentiss & Harris 2011), however no epitokous glycerids were ever collected in nocturnal plankton samples. The goniadid epitokes collected in this study also appeared on several nights around the full moon phase. There are reports of goniadid swarming for many species (Böggemann 2005), but there is relatively little information regarding links between spawning and lunar phases. It is suggested by some authors (Rouse & Pleijel 2001) that the glycerids and goniadids (both in the suborder Glyceriformia) should be considered as a single family, as the two groups are sister taxa. Glycerids and goniadids may exhibit similar behavioral reproductive behaviors in terms of synchronizing spawns during the full moon.

Syllid and nereidid epitokes of many different species comprised the bulk of swarming polychaetes collected over the study period. Likewise, Allen (1957) noted that her Puerto Rican collections yielded mostly syllids and nereidids. She reported that *Autolytus ornatus* (Verrill, 1873) was most abundant in summer months, while *Nereis riisei* (Grube, 1857) was found year-round. In Puerto Rico, Allen (1957) collected three specimens of the amphinomid, *Notopygos crinita*, swarming over the reef just before the third quarter moon in May, 1955. This was the only time the species was seen. The current St. John study likewise documented the swarming of *N. crinita* in May (and June) of 2008, also around the third quarter moon, or during waning gibbous or crescent moons, but the swarms were comprised of hundreds of epitokes.

The ubiquitous opheliid *Polyophthalmus pictus* frequently swarmed, yet there was no evidence of gametes in these animals even when dissected, and the swarmers looked identical to non-swarming forms found in benthic samples (Prentiss & Harris 2011). These *Polyophthalmus* swarmers may have been atokes that were attracted to the lights, but possibly they were male epitokes that had already shed their sperm. Regarding the dorvilleids, phyllodocids, and scalibregmatids, relatively few epitokes were collected over a 10-year period, but it is probable that very small individuals escaped through the coarse weave of the dip nets. While spawning events have been reported for these families, there are fewer accounts relative to those recorded for the eunicids, nereidids, and syllids.

Over the years, this project provided opportunities for incorporating citizen science into polychaete research, and many young campers from the U.S. Virgin Islands developed a new appreciation for learning about marine life in their own waters. Improving the methodology for collecting plankton (e.g. using brighter underwater lights and larger plankton nets with smaller mesh size), would yield a greater biodiversity of polychaete epitokes, and quantitative sampling during all lunar cycles over the course of a year would facilitate a broader understanding of the life cycles in epitokous polychaetes. The accurate identification of these polychaetes requires more regional taxonomic literature, such as that describing the nereidid epitokes of Indonesia (Pamungkas & Glasby 2015). Additional focused research on swarming polychaetes would increase the overall understanding of polychaete reproduction, as well as the dynamic roles these meroplankton play in the complex trophic network of the Caribbean Sea.

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