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OBSERVATIONS ON THE LIGHT-INHIBITED ACTIVITY CYCLE AND FEEDING BEHAVIOR OF THE HYDROMEDUSA OLINDIAS TENUIS

by

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ABSTRACT

Olindias tenuis is a shallow-water hydromedusa from the Caribbean that during the day is cryptic, residing among seagrass and algae, and after sunset swims into the water column. The medusae forage by swimming towards the surface, and then slowly drifting downwards with the exumbrella uppermost and the long primary tentacles hanging below. Positive buoyancy of the umbrella reduces the sinking rate. Both the activity cycle and buoyancy appear to be regulated by light, since the intensity of light alters the normal activity cycle both day and night. Feeding occurs once the medusae have entered the water column. At Puerto Rico, *Olindias* fed mostly on calanoid copepods; but chaetognaths, polychaetes, fish larvae, and amphipods are also consumed. Possible "lures" on the tips of the long, primary tentacles may offer both visual and vibratory stimuli to prey. The nocturnal emergence of *Olindias* may be adaptive for feeding on nocturnal, demersal plankton and for avoiding diurnal, visual predators.

INTRODUCTION

The Olindiadidae are a somewhat aberrant group of neritic hydromedusae. they occur in shallow temperate and tropical waters and are partially epibenthic. The first note on the behavior of this group dealt with the swimming cycle of *Gonionemus,* whereby individuals rapidly swam to the surface, turned over, and then sank downwards with tentacles extended (AGASSIZ, 1865). Once at the bottom, the medusae attached themselves to

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algae, with their tentacles still extended. This cycle was repeated at intervals. Other workers (MURBACH, 1909; ZELICKMAN, 1976; and MILLS, 1983) found that *Gonionemus* was most active at night. MILLS (1982) speculated that this behavior may enable *Gonionemus* to feed on demersal plankton, both day and night.

The diel activity cycle of *Olindias tenuis* was first described by BREDER (1956). In the Bahamas, medusae were observed drifting near the surface at night, however during the day, no medusae were seen. In an aquarium, the medusae were crumpled and hidden in bottom debris by day. But at dusk, the medusae would swim off the bottom and begin drifting with the bell aboral side upwards and the tentacles extended downwards. BREDER did not determine what regulated this activity cycle.

Interest in the diel behavior of *Olindias tenuis* was generated when students at the marine station on Magueyes Island, Puerto Rico, complained of being stung while swimming at night in shallow water. The cubomedusa, *Carybdea marsupialis,* which although common around the island, was not abundant enough to explain the high incidence of reported stings. The only other possible planktonic cnidarian was the hydromedusa *Olindias tenuis,* which was more abundant. It was observed that physical contact with a tentacle of *O. tenuis* could result in a painful sting; the welt lasting for a week!

In this paper, I describe the light-regulated diel swimming and feeding behavior of *Olindias tenuis.*

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METHODS AND MATERIALS

Olindias tenuis medusae were observed at night as they drifted below a 100-watt nightlight located at the end of the pier on the west side of Magueyes Island, near La Parguera, P.R. (18°08′ N 67°02′ W). Medusae were collected between 1845 and 2200 h by carefully dipping them from the water with a small net. About 100 medusae were fixed immediately in 5% formalin for later gut contents analyses; other medusae ($n = 20$) were maintained in a 50 L aquarium (27–29°C) in good health for a week or more by feeding them *Acartia* copepods. The aquarium was placed where indirect skylight reached it.

In order to determine when the medusae entered the water column, 4 net tows were made between 1845 and 2015 h on 15 Dec. 1976 at La Parguera. The net used resembled a floating beam trawl, 3 × 0.5 m, with 5 mm mesh size. The net was towed for a measured distance of 500 m (~750 m^3 sampled per tow) over a 3–4 m depth area covered mostly by *Thalassia* seagrass.

RESULTS

Laboratory Observations

During the day, the medusae (n = 20) remained at the bottom, crumpled with the bell folded inhalf. The medusae were attached to seagrass, with their tentacles fully contracted in helical coils. Slight bell pulsation and spontaneous tentacle contractions occurred at irregular intervals, but there was no swimming activity. When only skylight illuminated the aquarium, the medusae became active at dusk (1845–1900 h local time, 15–17 Dec., sunset = 1845). At first, a few medusae would swim briefly, with their tentacles contracted, and then sink to the bottom. However, as the illumination decreased, the swimming activity increased. By 2000 h all the medusae in the aquarium were either swimming or drifting upright (exumbrella upwards), with their tentacles fully extended downward (Fig. 1) (just as they appeared *in situ* below the nightlight).

The next day when a 100-watt incandescent light was placed 20 cm above the aquarium, there was some weak swimming activity between 1800 and 2000 h; but no prolonged swimming occurred until the light was switched off at 2200 h.

The following day, 5 medusae were isolated in a 2 L aquarium. This aquarium was moved into a darkroom with only a dim red light for illumination. Within 5 min. the medusae were actively swimming. A 100-watt incandescent light was then directed on the aquarium; swimming ceased and the medusae became crumpled and attached themselves to the bottom of the aquarium and remained there. The light was then switched off, and again the medusae became active. This was repeated several more times with the same results.

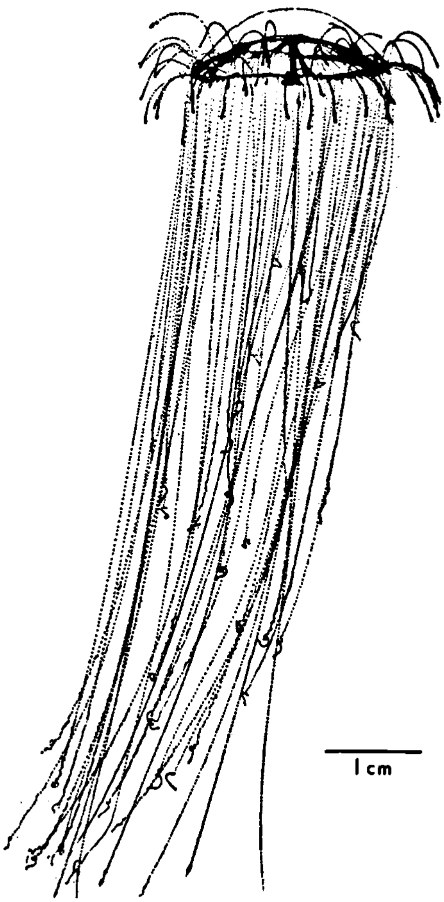

FIGURE 1. Drifting posture of *Olindias tenuis*. — This medusa (20 mm bell diameter) is neutrally bouyant, resting with its primary tentacle tips on the bottom of an aquarium. Note the J-shaped, tentacle tip "lures" and the arched secondary tentacles (around bell margin) which possibly have a defense function.

In Situ Observations

The results of the quantitative net hauls showed that the number of medusae in the water column increased after sunset (Table 1). To provide further evidence of when *Olindias* medusae appeared in the water column,

Table 1

Results of quantitative net hauls

Time (h)

Time	1845–1900	1910–1925	1935–1950	2000–2015
No. Medusae 100 m^{-3}	0	0.93	2.1	3.5

Note: ~750 m^3 sampled per tow.

medusae were collected below the nightlight at different times from 1830 to 2100 h and preserved for gut contents analyses. The results showed that only 6% of the medusae (n = 32) collected between 1830 and 1900 h contained prey; whereas between 1900 and 2100 h 80% (n = 64) contained prey (Table 2). Thus, *Olindias* appear in the water column following sunset. Feeding begins once the medusae become planktonic.

To corroborate lab observations, a search for *Olindias* medusae was made during the day in the *Thalassia* off the west side of Magueyes Island. No specimens were seen, either swimming, or on the bottom. However, when 10 medusae were kept overnight in a 0.5 m^3 wire cage (with an open bottom) placed over *Thalassia*, they were seen the next morning hidden among the seagrass blades and macroalgae. Their umbrellas were crumpled and their tentacles contracted. That night, the medusae were seen swimming in the cage at 2000 h,

TABLE 2

RESULTS OF GUT CONTENTS ANALYSES

No. prey per medusa (mean and range)

Time (h)	N	Chaetognaths	Copepods	Decapod larvae	Gammarids	Fish larvae
1830–1900	32	0	0.1(0–1)0	0	0	0
1900–2100	64	0.2(0–2)	6.7(0–30)	0.2(0–2)	<0.1(0–1)	0.2(0–2)

FEEDING BEHAVIOR AND TENTACLE POSTURE

Observations of *Olindias* below a light at night suggested that the medusae spent much of their time drifting, with tentacles fully extended. Medusae brought into the lab and observed at night, with a red light, went through a cycle of rapid swimming toward the surface and then slow sinking (with umbrella aboral side upwards). Sinking is reduced by the positive buoyancy of the umbrella. This was substantiated by observations of medusae in the aquarium which showed that they sink only until the tentacles touch the substratum. When the tentacles of one medusa were removed, the umbrella remained at the surface due to its buoyancy. However, during the day, medusae remain on the bottom suggesting that they were negatively buoyant.

Olindias has two types of tentacles. Short, stiff, secondary tentacles (~40 in number in large medusae), about equal in length to the bell radius, surround the umbrella margin; they extend upwards and arch outwards from the umbrella (Fig. 1). These tentacles may protect the umbrella from potential predators. Longer, contractile, primary tentacles (~90 in number), about 10 times the bell radius in length, hang from the margin. These tentacles have numerous ring-like nematocyst warts and terminal capitate tips (~0.3 mm in diameter) which are of a conspicuous white color. The ends of the primary tentacles curve upwards, and are J-shaped for about 2–3 mm (Fig. 1). This portion of the tentacle rapidly vibrates the capitate tip up and down. Although this may serve as a visual and/or vibratory lure, no observations were made to substantiate their function.

Gut Contents

The gut contents of *Olindias tenuis* ($n = 98$), collected between 1830 and 2100 h, as they drifted below a nightlight, were examined. Medusae ranged in size from 12 to 30 mm in bell diameter (preserved). From medusae collected after 1900 h, copepods, mostly *Acartia* spp., were most numerous (mean = 7/medusa); *Sagitta* sp., heteronereid polychaetes, and decapod larvae were next in importance (mean = 0.2/medusa); least abundant were gammarid amphipods and fish larvae (mean = <0.1/medusa) (Table 2).

DISCUSSION

The observations herein agree with those of Breder (1956) in that *Olindias tenuis* is nocturnal, and is hidden and attached to seagrass or algae during the day. Cleland & Southcott (1965) remarked that in waters off eastern Australia, *Olindias singularis* commonly stings bathers at night.

Light appears to be the primary factor that regulates the diel behavioral cycle of *Olindias*, since medusae will swim during the day if the light intensity is sufficiently reduced and will not swim at night if illuminated sufficiently. The response is apparently graded, rather than all-or-none, since at night partial swimming occurs in weak light intensity. However, the presence of a circadian rhythm initially set by light cannot be discounted. The wavelengths or intensities of light that inhibit activity are not known. *Olindias* lacks ocelli; but in other hydromedusae, light-sensitive neurons control swimming (Anderson & Mackie, 1977).

Light may also regulate buoyancy in *Olindias*, since sinking rates are much reduced at night. Buoyancy in medusae is mostly achieved by ionic regulation (Denton & Shaw, 1962; Bidigare & Biggs, 1980; Mills & Vogt, 1984). However, Mills & Vogt (1984) were unable to find diel differences in ion concentration for a number of hydromedusae. Yet none of the species that they examined exhibited such a pronounced diel activity pattern as that of *O. tenuis*.

Nocturnal emergence behavior has been reported for other demersal medusae. Mills (1983) showed that *Gonionemus vertens* and *Polyorchis* *penicillatus* most actively swim after dark. ARKETT (1984) examined the *in situ* behavior of *P. penicillatus* in more detail and concluded that such behavior was adaptive because the medusa fed mostly on demersal plankton. A similar conclusion can be made for *Olindias*. Demersal behavior is common in shallow water tropical zooplankton (ALLDREDGE & KING, 1980).

However, *Olindias* is different from *Gonionemus* and *Polyorchis* because it does not feed during the day, and in fact, is cryptic, residing among seagrass and macroalgae with its tentacles contracted. Possibly in the tropics, with a greater variety of diurnal predators, especially fishes, it may be more advantageous for *Olindias* to remain hidden by day than to gain a small amount of energy by foraging. At night the increased abundance of zooplankton might offset predation losses by nocturnal predators. Actually, in the tropics, many, if not most, shallow water cnidarians (e.g., actiniarians, alcyonarians, cerianthids, corallimorpharians, and corals) are nocturnal feeders (unpublished observations).

The diet of *Olindias tenuis* at La Parguera consisted mostly of calcanoid copepods and some larger prey (e.g., *Sagitta,* polychaetes, decapod larvae). BREDER (1956) found that this medusa in an aquarium would capture small fishes. Another larger *Olindias* from Argentina, *O. sambaquiensis,* which reaches 75 mm in diameter, feeds on small fish and mysids (ZAMPONI & MIANZAN, in press). This species is also known to sting bathers (VANNUCCI, 1966). The virulent nematocysts of *Olindias* spp. are used to capture small fishes and other relatively large prey and to repel potential predators.

The tentacle tip "lure" of *Olindias* may serve to attract visual predators, e.g. small fish, or *Sagitta* which are attracted by vibrations (FEIGENBAUM & MARIS, 1984). Another olindiad, *Gossea corynetes* (Gosse), undergoes tentacle tip twitching at intervals of one second or longer (RUSSELL, 1953). This may be a more primitive type of "lure" than the suspected vibrational type of *O. tenuis*. Possible "lures" have been described for siphonophores (PURCELL, 1980).

A number of aspects of the biology of *Olindias tenuis* require further examination, i.e., photoreceptor location and structure and how they inhibit swimming and their possible role in regulating buoyancy, and the buoyancy mechanism.

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