

Activity pattern of the brittlestar *Ophiocoma echinata* (Echinodermata: Ophiuroidea) and its relationship to foraging and predation potential

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ABSTRACT

The evolution of activity patterns is influenced by a number of selective pressures, including predation risk and food availability. We documented the activity patterns of *Ophiocoma echinata* (Lamarck) at San Salvador Island, Bahamas. Brittlestars were most active at night with decreasing activity at dawn and dusk. To better understand the ecological factors that influence this pattern of activity, we investigated the gut contents and potential predation risk of brittlestars. There was a significant positive correlation between normalized dry weight of gut contents and the time of day; however, there was no significant difference across time periods in the percent of organic matter in these gut contents. This suggests that the amount of food in brittlestar guts does not change during daylight hours. Through tethering experiments, we found that predation potential was higher during the daylight hours than during nighttime. Our data suggest that predation is probably much more important than food gathering for the patterns of activity of *O. echinata* at our study site.

key words: predator avoidance, foraging behavior

The evolution of activity patterns in animals is influenced by a number of selective pressures, including the availability of food and the activity patterns of predators.

Predation in particular is an important feature of life in the inshore waters inhabited by many benthic marine organisms (e.g. Vermeij 1987). Fish predation of brittlestars can be intense. In the Caribbean, fish predators of brittlestars are mainly members of the Labridae, Haemulidae, and Labrisomidae (Randall 1967; Shirley 1982; Aronson 1988). Most of the fish that prey on brittlestars are diurnal (Randall 1967); thus the nocturnal lifestyle of brittlestars and many other small invertebrates is probably influenced by the activity of their predators (Hendler 1984a; Aronson 1998). In fact, low predation is thought to allow the formation of dense brittlestar beds found in some locations (Aronson & Harms 1985; Aronson 1989; Fujita 2003).

Food availability also can influence activity patterns of animals, even under predation threat (Metcalf et al. 1999). Most studies of brittlestar activity have not focused on the possibility that foraging requirements might influence activity patterns in brittlestars. Little is known about diel patterns of food acquisition in brittlestars; with few exceptions (Singletary 1980;

Hendler 1984b), most studies of brittlestar diets have not correlated gut contents with time of day.

To better understand the factors that influence activity patterns of brittlestars, we studied *O. echinata* in coral rubble habitat in the near shore waters of San Salvador Island, Bahamas. We assessed activity patterns of free-living brittlestars in natural habitats, documented foraging activity of brittlestars by analyzing gut contents of individuals, and estimated the potential for predation of brittlestars by fishes with a tethering experiment.

METHODS

We conducted field studies of *O. echinata* at San Salvador Island, Bahamas. We recorded the activity of brittlestars at a site along the north coast of the island ("Dump Reef") just before sunrise and into the early morning (0515 – 0630) and just before sunset and into the evening (1900 – 2045) between 12 and 16 June 1999. At 15 min intervals, we conducted a scan sample and recorded the number of arms exposed for all specimens in two 3m x 3m quadrats. We calculated activity as a percentage of the maximum number of individuals observed during any scan sample.

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We obtained brittlestars for gut contents at different times of day from three sites on the northern end of the island: Dump Reef (1830, in a location outside of our study area for activity patterns), Sand Dollar Bay (1015), and Graham's Harbor (0615, 0830, 1430, and 2200). We submerged specimens ($N = 23$) in a dilute $MgCl_2$ solution, thoroughly flushed the stomach cavity with a syringe containing filtered seawater, and collected the contents in a dissection pan. We dissected most of the specimens and, if necessary, retrieved any remaining gut matter. A measured aliquot of the water containing the flushed gut contents was filtered onto pre-combusted, pre-weighed 25mm GF/C filters. To identify particles found in the gut, we filtered a smaller measured aliquot onto Millipore 0.45 μ m cellulose acetate filters. These filters were placed on microscope slides and cleared with immersion oil.

We quantified predation potential of *O. echinata* at Dump Reef with a tethering experiment. Predation potential is not a measure of actual predation rates in the field, but allows us to assess the potential for predation of brittlestars (Aronson 1989). Each field trial consisted of two weighted 6 m lines deployed 25 and 30 m from the shore (water depth approximately 1-2.5 m). Five brittlestars were tethered to each line at 1 m intervals by passing 20 to 30 mm of upholstery thread through the mouth and out the aboral disk of each animal. Predation of the animals tethered to the line was scored every 30 min for 2 h. Between observations, we moved 10-15 m from the line to reduce observer effects on the activity of predators. Each morning, we moved both lines 4 m to either the right or left. Between 28 May to 9 June 2000, we conducted five field trials immediately after dusk (2 transects/day for 5 days for a total of 10 nighttime trials) and five immediately after dawn (2 transects/day for 5 days for a total of 10 daytime trials).

To ensure that individuals could not escape their tethers, we used two control procedures. In a wet lab at Gerace Research Station on San Salvador Island, we tethered 16 test animals and observed them every 30 min for 2 h. For each trial in the field, one of the tethered animals was placed inside a cage made of fine plastic mesh that allowed the flow of water through the cage, but excluded predators and prevented the brittlestar from escaping.

We quantified and identified gut material in laboratories at Hood College, Maryland, USA. To obtain dry weights of gut contents, we dried GF/C filters ($N = 23$) containing gut material for 24 h at 90°C. For six of these samples we determined the organic content of the gut material by firing the filters in a muffle furnace at 500°C for 3 h. All weights were corrected for the volume of water used to filter the sample.

We identified contents of the brittlestar guts filtered on to the cleared cellulose-acetate filters using a Nikon

microscope (model Alphaphot-2 YS2) connected to a color CCD camera (Sanyo model VDC-2972) and projected on a 550 mm by 410 mm (27 inch) television monitor. For each gut examined ($N = 23$), we identified individual items in 80 (37 for two specimens) different randomly chosen fields of view. Each particle type was categorized into one of four categories: detritus, filamentous algae, inorganic particles, or invertebrates. We measured the area of the particle closest to the center of the screen. We treated each particle as a rectangle: length measurements were taken along the longest axis of the particle, width measurements were made perpendicular to this axis across the widest point of the particle. All measurements were corrected for the level of magnification of the particle. To reduce measurement error from distortion at the periphery of the monitor, we measured only those particles that fell entirely within a 203 mm by 254 mm rectangle superimposed on the center of the television screen.

We performed Spearman rank correlations to detect any effects of collection time on normalized dry weight or percent organic matter. We normalized the dry weight of gut contents for the size of the brittlestar by dividing each weight by the disk diameter of the specimen.

To compare daytime and nighttime predation on tethered *O. echinata* we treated each transect as a unit of replication (daytime $N = 10$, nighttime $N = 10$). Individual brittlestars on each transect were scored on a scale of 0-1 for predation (0 = no predation, 0.5 = partial predation, 1.0 = total predation) and this total was divided by the number of experimental animals tethered to that transect (4 or 5 animals, depending on if the transect line included a caged control) to provide a predation index for each transect. This predation index score thus ranged from 0 (no animals predated on the transect) to 1.0 (complete predation of all animals on the transect). We arcsin transformed all predation index scores and performed a two-sample t-test to compare predation indices of daytime and nighttime transects.

RESULTS

Ophiocoma echinata were exposed, either partially or completely, only after dark and before dawn (Figure 1). Only rarely did brittlestars emerge completely from cover, even at night. Animals were never seen exposed during the daytime in over 170 person-hours of additional informal observation.

There was a significant relationship between the time the brittlestar was collected and normalized dry weight of gut contents ($r^2 = 0.253$, $P=0.014$, $N=23$, Figure 2), but not the proportion that was organic matter ($r^2 = 0.004$, $P = 0.78$, $N = 23$, data not shown). Organic matter comprised about 45% of the gut contents on

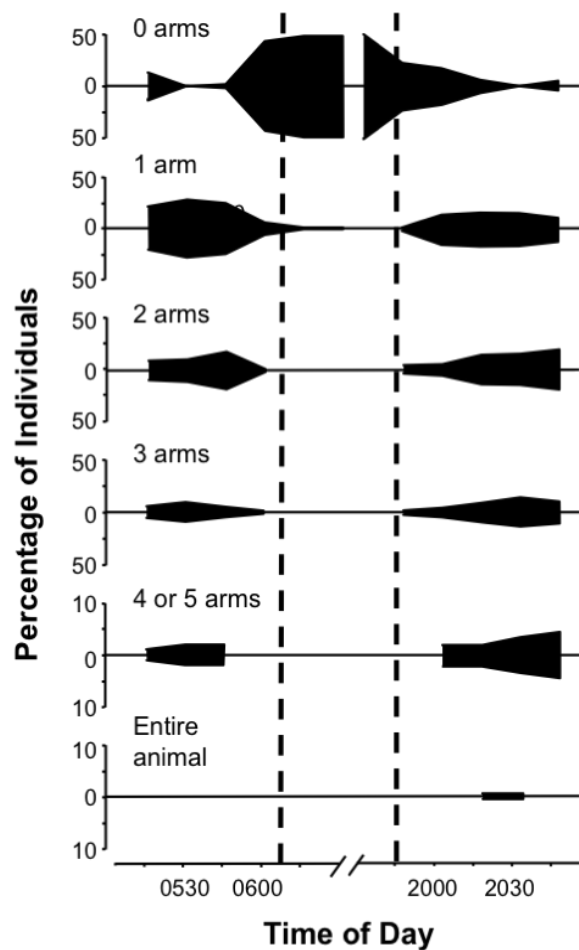


Figure 1. Activity patterns, measured as levels of exposure, of *O. echinata* in coral rubble at Dump Reef, San Salvador Island, Bahamas. The dashed lines indicate sunrise (608) and sunset (1945).

average. The four food categories were not equally represented in brittlestar guts. Visual inspection of the data revealed that there tended to be more detritus and filamentous algae in the guts than inorganic matter or invertebrates (Figure 3a). The average particle size of filamentous algae was larger than particles of detritus, invertebrate, or inorganic food items, which were all similarly sized (Figure 3b).

During the course of the tethering experiment, none of the brittle stars in the control cages escaped their tethers; likewise, none of the animals tethered in the wet lab at Gerace Research Station escaped. Thus all animals missing from the transect lines were removed by predators. The average predation index (± 1 SE) for brittlestars tethered after sunrise was 0.95 ± 0.05 ; the average predation index for brittlestars tethered after sunset was 0.05 ± 0.05 . Thus, brittlestars tethered after sunrise were significantly more likely to be eaten than those tethered after sunset (two-sample t-test: $t_{18} = 12.08$, $P < 0.001$).

We did not systematically collect data on the predators

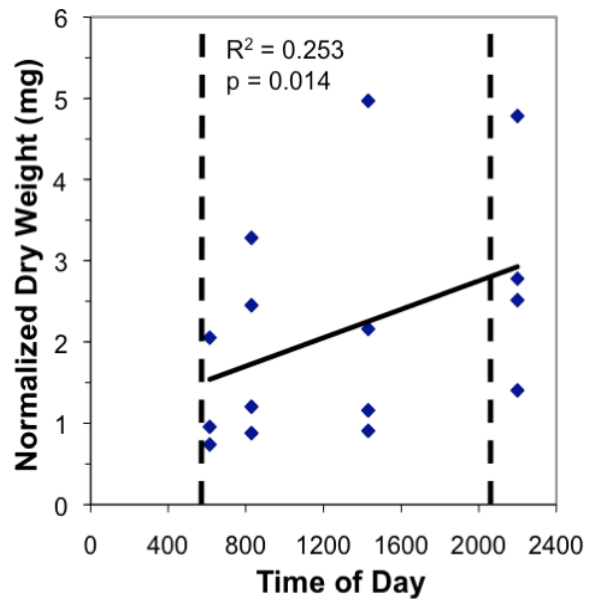


Figure 2. Relationship between collection time and normalized dry weight of gut contents of brittlestars collected at Graham's Harbor, San Salvador Island, Bahamas. Each point represents one individual. The dashed lines represent sunrise and sunset.

of tethered brittlestars, but when we observed predation, we noted the species of the attacker. All predators that we observed were fish. *Lactophrys trigonus* and *L. triqueter* (Ostraciidae), and *Balistes vetula* (Balistidae) consumed entire tethered brittlestars on numerous occasions. They attacked the central disk first, tore the arms off the brittlestars, and then consumed the arms they removed. Less commonly encountered predators included scarid (female *Sparisoma rubripinne*) and labrid fishes (*Thalassoma bifasciatum*, *Halichoeres bivittatus*, and *Clepticus parrae*). Labrid fish predators did not consume entire animals, but bit off arm tips and pieces of the central disk until as a group they consumed nearly all of the tethered brittlestar.

DISCUSSION

The number of arms that a brittlestar extended from cover increased markedly at dusk and decreased markedly at dawn. These data suggest that *O. echinata* are active during nighttime hours and support previous observations of brittlestar activity patterns (Hendler 1984a, b; Rosenberg & Lundberg 2004). Brittlestars tethered for the predation experiment mirrored this activity pattern: at night they extended their arms as if to feed and in the day they withdrew their arms and tried to cover themselves with sand.

Surprisingly, we found that the dry weight of gut contents increased over the day. However, most of this increase probably resulted from the ingestion of inorganic material because there was no relationship

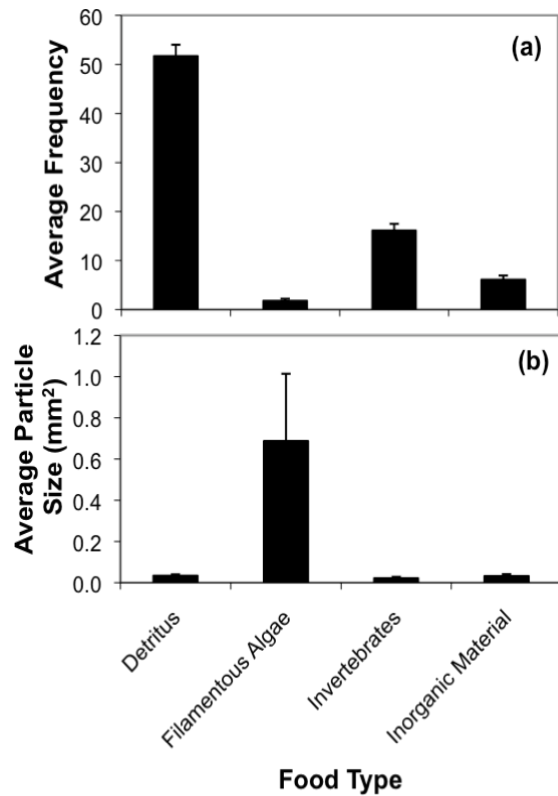


Figure 3. Gut contents of *Ophiocoma echinata*. N = 23, error bars = 1 SE. (a) Frequency of different food types averaged over all individuals. (b) Particle size of different food types averaged over all individuals.

between time of day and the proportion of organic matter in guts. Other studies have found periodicity in gut contents of brittlestars. *Amphioplus coniertodes*, *Ophionephys limicola*, and *Micropholus gracillima* consumed more in the daytime than at night, at least in laboratory experiments (Singletary 1980). On the other hand, *Ophiothrix lineata* fed more often at night than in the day and their stomach contents reflected this bias (Hendler 1984b).

Ophiocoma echinata must ingest inorganic material while under cover objects because the dry weight of gut contents increased throughout the day but they did not extend arms during the day. A number of brittlestars feed on deposits while under cover objects or while in burrows (Woodley 1975; Singletary 1980; Loo et al. 1996), including *O. echinata* (Sides & Woodley 1985). This species is both a suspension and deposit feeder (Sides & Woodley 1985) and it would need to emerge, at least partially, from burrows to feed on suspended material. If prey obtained through suspension feeding is digested quickly in the gut, our analysis of gut contents could have underestimated the importance of suspension feeding. Thus, the data available now suggest that *O. echinata* feed both during the day (while under cover) as well as at night.

Ophiocoma echinata are reported to eat a wide variety of food types, including plant and animal matter and detritus (Hendler & Meyer 1982) and our data support this observation. Gut contents of *O. echinata* at San Salvador were different from those reported for this species in Jamaica (Sides & Woodley 1985). Jamaican populations contained sand (what we called inorganic matter) as the predominant food item, whereas in our population detritus and filamentous algae were most abundant. Differences in diet between these populations might reflect differences in food availability between San Salvador and Jamaica.

Predation of tethered brittlestars was highest in the daytime. This indicates that if brittlestars were available to predators in the daytime, they probably would be eaten quickly. Tethering experiments of *Ophiothrix orstedii* at other Caribbean sites found the same pattern: lower predation of tethered animals in the night than in the day even in locations with reduced fish populations (Aronson 1998). In locations with high predation risk at night, *O. orstedii* expose only one or a few arms at night to feed (Aronson & Harms 1985, Aronson 1989), much as *O. echinata* did in this study. The evidence is strong that, in the absence of other defenses against predators, natural selection should favor those animals that are hidden in the day and emerge at night.

Tethering experiments measure predation potential, the propensity of predators to consume prey, rather than actual predation rate (Aronson 1989), a distinction that should not be ignored. For example, tethering experiments can allow predation by otherwise unlikely predators. We observed *Balistes vetula* and *Clepticus parrae* eating tethered brittlestars during our experiment, even though brittlestars are not important food for *B. vetula* (Randall 1967; Reinthal et al. 1984) and perhaps not for *C. parrae*. However, we also observed several known brittlestar predators eating tethered animals, including wrasses (*T. bifasciatum* and *H. bivittatus*) and trunkfish (*Lactophrys* spp.) (Randall 1967; Shirley 1982; Hendler 1984a; Aronson & Harms 1985, Aronson 1988; Wainwright 1988). Thus our experimental measurements of predation potential do reflect general patterns of predation risk, albeit imperfectly.

Why don't nocturnal predators eat brittlestars? Experiments to document the sensory cues used by foragers to find brittlestars would help to answer this question. *Ophiocoma echinata* might not emit substantial chemical or olfactory cues, even when tethered (Aronson & Heck 1995), although Aronson (1988) observed fish investigating empty hooks that had previously held brittlestars. Nevertheless, it appears that visual cues are most important to fish searching for brittlestar prey. At night, of course, low light conditions probably make visual location of prey difficult. For

example, dwarf scorpion fish (*Scorpaena papillosus*), a nocturnal predator of brittlestars, can locate prey visually only at dusk and dawn. At night, they rely solely on tactile cues to find brittlestars (Montgomery & Hamilton 1997).

Our data suggest that *O. echinata* are active at night to avoid predation rather than to forage, as shown by other studies of brittlestars and their predators. The question of why brittlestars emerge at all from their refuges remains to be answered. We suggest that *O. echinata* are not limited to foraging at night as food quantity does not appear to differ between night and day. However food quality might. Detailed studies of how gut contents vary with time of day would help us understand the role that food gathering has in brittlestar behavior. In addition, we know little of social behavior in brittlestars; it is possible that mating behavior or other social behaviors are involved in regulating diel activity patterns in brittlestars.

Acknowledgements

We wish to thank Gerace Research Center in San Salvador for logistical support and Ronald Albaugh for help with the tethering experiments. Funding for this project was provided by the Second Century Foundation, Graduate Student Research Fund, and the Faculty Development Travel Fund of Hood College. This research was reviewed and approved by the Gerace Research Center.

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