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Nocturnalism in *Aplysia oculifera* (Adams & Reeve, 1850): An Avoidance Behavior Minimizing Exposure to Ultraviolet Radiation?

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**Abstract.** Circadian activity patterns and preferred location were recorded under experimental conditions in two groups of the sea hare *Aplysia oculifera*, one exposed to direct sunlight (group L) and the other placed in the shade (group S). Observations were made several times during the day and night for 20 days. Activities (resting, feeding, crawling, copulating and spawning) and locations (buried in the sand, under stones, on the substrate and on the algae) were recorded. Data were pooled into four time blocks (midnight to 06:00, 06:01 to 12:00, 12:01 to 18:00, and 18:01 to midnight). Sea hares of group L showed distinct nocturnal activity pattern, feeding at night when most of them were found on the algae, and resting during the day when they were located mostly under the stones. In group S no significant differences were detected between day and night activities or preferred location. The results show that the nocturnal activity pattern in the sea hare *A. oculifera* is governed by an external factor, probably direct sunlight, rather than an internal cue. It is suggested that *A. oculifera* is nocturnally active to avoid exposure to direct ultraviolet radiation.

**INTRODUCTION**

*Aplysia oculifera* (Adams & Reeve, 1850) is a widespread sea hare species, distributed in tropical and subtropical regions from the eastern coast of Africa, including the Red Sea, through the Indo-Pacific Ocean to the islands of Hawaii. *Aplysia oculifera* is a medium-sized sea hare (5–100 g live body weight), which dwells on shallow rocky shores, and feeds exclusively on macroalgae, mainly the green algae *Ulva* spp. and *Enteromorpha* spp (Plaut, 1993; Plaut et al., 1998).

Among sea hares of the genus *Aplysia*, some species are nocturnal and others diurnal (Susswein et al., 1984; Carefoot, 1987, 1989; Carefoot & Taylor, 1988). It is as yet unknown whether the cue for these patterns of activity is endogenous or exogenous, and what advantages sea hares gain by being either nocturnal or diurnal.

Carefoot & Taylor (1988) listed several possible reasons for nocturnalism in *A. dactylomela* Rang, 1828 (which ecologically resembles *A. oculifera*), such as avoiding predators, avoiding diurnal interspecific or conspecific competitors, and intolerance to light, particularly ultraviolet wavelengths. They strongly rejected avoidance of predation and competition as possible reasons because (1) *Aplysia* has few or no predators (Carefoot, 1987), and instances of predation known for *A. dactylomela* are isolated events of apparent opportunism involving only juveniles and eggs being eaten (Willan, 1979). In addition, the defensive repertoire of adult *Aplysia* includes purple ink and opaline gland secretions, unpalatable skin, and toxic digestive gland; (2) most interspecific competitors seem to show no effect on algal abundance or are nocturnal as well (e.g., Hobson, 1974); and (3) conspecific competition will not be avoided if the entire population is nocturnal. These same arguments apply also to *A. oculifera* in the Gulf of Eilat (Plaut, 1993). Carefoot & Taylor (1988), and Carefoot (1989) also rejected the avoidance of ultraviolet radiation as a possible reason because (1) light is unlikely to have operated as a primary force leading to the evolution of nocturnalism; (2) *Aplysia* makes no obvious attempt to protect its eggs from direct sunlight; and (3) other tropical and subtropical sea hares inhabiting shallow water are diurnal.

They suggested that there may be a metabolic advantage to splitting the day into two phases of activity (feeding and resting) but could not explain the advantage of nocturnalism versus diurnalism or vice versa.

Surveys conducted in the Gulf of Eilat (Aqaba) show that *A. oculifera* is mostly nocturnal (Plaut, 1993; Plaut et al., 1998). Its nighttime activities include feeding, crawling, copulating, and spawning. During the daytime, sea hares mostly rest either under stones or buried in the sand. Contrary to this general observation, in several cases, *A. oculifera* in the Gulf of Eilat was observed feeding, crawling, copulating, and spawning during daytime when algae were very abundant and when it was found at a depth below 2 m (Plaut, 1993).

In this study I examined the question of whether the nocturnalism of *A. oculifera* is a response to external cue, e.g., direct radiation (sunlight), or whether it is governed by internal cues. I followed the locations and activities of two groups of *A. oculifera* under outdoor experimental conditions.
conditions during daytime and nighttime, one exposed to
direct natural sunlight and the other under shade.

MATERIALS AND METHODS

Newly recruited (>1 g live body weight at the beginning
of the settlement season) sea hares were collected at sev-
eral sites in the northern Gulf of Eilat (Aqaba) in Feb-
uary 1990. They were kept at the Interuniversity Institute
for Marine Sciences of Eilat in an open circulated sea-
water system. Experiments were initiated within 1–2 days
after collection. Two groups of 20 individuals of similar
size (0.8–1.9 g body live mass) were reared in two un-
covered 30 L glass aquaria (50 × 25 × 25 cm length,
width, and height, respectively). Both aquaria were
placed outdoors. One was in the shade (group S), under
a roof and with one of its sides a wall facing west, and
the other three sides left open; the other was under direct
natural sunlight (group L). Each aquarium was supplied
with continuous water flow (2–3 L min⁻¹) to maintain
similar temperatures (day water temperature, 26 ± 1 °C
and night temperature 22 ± 1 °C with no significant
differences between the two aquaria). Each aquarium con-
tained a layer of 3–4 cm sand from the sea hares’ natural
habitat, and two stones, 10–13 cm in diameter, that were
placed as shelters for the sea hares. Food (Ulva sp.) was
provided in amounts sufficient for ad libitum feeding, but
at small rations and in small pieces so as to prevent sea
hares from using them as shelters against sunlight.
Location of the sea hares and their activities were recorded
randomly four to six times daily (day and night) during
20 days. Four areas were defined in the aquaria for the
location of the sea hares: (1) under stone; (2) buried
in the sand; (3) on the substrate (including sand, stone,
and aquarium walls); and (4) on the algae. Five different
activities were defined (after Carefoot, 1989): (1) resting
(inactive); (2) feeding (biting or chewing); (3) crawling
(moving around without feeding, spawning or copulating);
(4) spawning (laying eggs); and (5) copulating. In sev-
eral cases, when sea hares were observed conducting
more than one type of activity simultaneously, (e.g., feed-
ing and copulating, copulating and spawning), all activ-
ities were recorded for each individual. The results were
treated for each location or activity as percentages of all
the sea hares in the aquarium.

Although the objective of this study was to detect
whether sea hares show different patterns of activities and
locations during the day and the night, the results were
pooled to four 6 hr time blocks. This was done to refine
the detection and to obtain results comparable to those of
Carefoot (1989). Times blocks were: (1) from 00:00
to 06:00; (2) 06:00 to 12:00; (3) 12:00 to 18:00; and (4)
18:00 to 24:00. The experiment lasted 20 days.

Statistical analyses of the results were made after
square root transformation of the percentages, and in-
cluded two-way ANOVA between day and night and be-
tween treatments and Tukey tests between time blocks
and between treatments for each location and for each
type of activity. Analyses were performed with Systat
5.04 for Windows (Wilkinson, 1990). Significant dif-
ferences were declared when $P < 0.05$.

RESULTS

In order to compare general patterns of location and ac-
tivities between sea hares in the light and those in the
shade, data were pooled for each treatment for the whole
day (24 hr). This comparison shows that sea hares in
group L were significantly more likely to be found buried
and under stones and significantly less on the algae.
Moreover, they rested more and fed and copulated less
than sea hares in group S (Figures 1, 2, $P < 0.0001$).

Dividing the day into four blocks of 6 hours each dem-
onstrated more clearly the circadian patterns of sea hares’
location (Figure 1) and activities (Figure 2).

Aplysia oculifera were rarely found buried in this ex-
periment. However most of the records of buried sea
hares were collected in group L during daytime (7.1 ±
1.4% and 7.1 ± 1.8% from 06:00 to 12:00 hr and 12:00
to 18:00 hr, respectively). At these time blocks they bur-
rowed significantly more than during night hours (0% dur-
ing the night), and significantly more than the sea
hares in group S (1.8 ± 0.7% between 18:00 to 24:00 h
and 0% in the other time blocks).

The preferred location of resting sea hares was under
the stone; sea hares were found under stones mainly in
group L during the day (58.6 ± 3.4% from 06:00 to 12:
00 hr and 56.4 ± 2.3% from 12:00 to 18:00 hr), signif-
ically more than in the same group at night (less than
5.8%) and significantly more than in group S during all
24 hr (2.1 ± 1.4% between 06:00 and 12:00 hr and 0%
in the rest of the day).

Sea hares were found on the substrate during all times
and activities. In group L, 35.0 ± 2.0% of the sea hares
were on the substrate between 00:00 and 06:00 hr, sig-
ificantly more than at all other times and more than
group S which spent only about 25% on the substrate.

Sea hares were usually located on the algae while feed-
ing or copulating. In group S no significant difference
between the four time blocks was detected (values ranged
between 69.6 and 77.7%). These values were similar to
those of group L during the night (61.5 ± 1.4 and 71.9
± 2.0% from 18:00 to 24:00 hr and from 00:00 to 06:00
hr, respectively). However, during the day, only 11.8 ±
2.6% (06:00 to 12:00 hr) and 17.9 ± 1.6% (12:00 to 18:
00 hr) of the sea hares in group L were found on the
algae, significantly less than the above.

Patterns of activities within the groups were somewhat
more complex. Sea hares were observed resting mostly
in group L during the day (more than 60%), significantly
more than in the same group at night (about 3%), and
more than in group S (< 5.9% during day and night).
Locations of sea hares *Aplysia oculifera* from the Gulf of Eilat, Red Sea, under natural photoperiod (group L, clear bars) and in the shade (group S, shaded bars) in the aquaria at four time blocks of the day. Bars indicate mean ± SD percentage of sea hares in each group in each location.

Feeding showed almost the opposite pattern. In group L only 13.2 ± 2.1% (06:00–12:00 hr) and 19.3 ± 2.2% (12:00–18:00 hr) were found feeding during the day, significantly less than during the night (58.8 ± 3.1 [18:00–24:00 hr] and 60.0 ± 2.8% [00:00–06:00 hr]). In group S significantly higher percentages of feeding sea hares were recorded throughout the 24 hr than in group L during daytime. Percentages of feeding sea hares were similar in both groups during the night. From 06:00–12:00 hr only 53.8 ± 2.6% of the sea hares in group S were feeding (significantly less than during 18:00–06:00 hr in both groups) and 70.4 ± 1.5% between 18:00–24:00 hr, significantly more than all other time blocks in both groups.

Crawling activity was sometimes observed coupled with some other activity (feeding, copulating, or spawning). It did not show a distinct nocturnal pattern. In group L, crawling was observed significantly more during the night (16.2 ± 1.7% at 18:00–24:00 and 11.9 ± 2.1% at 00:00–06:00) than in the daytime (6.8 ± 1.4% at 06:00–
12:00 and 8.2 ± 1.3% at 12:00–18:00). In group S crawling was observed most frequently at 12:00–18:00 (18.9 ± 2.8%), significantly more than at night (8.8 ± 1.7%, and 5.0 ± 1.0% at 18:00–24:00 hr and 00:00–06:00 hr, respectively). During the 06:00–12:00 time block, sea hares from group S crawled significantly less than in all other time blocks (1.4 ± 0.7%).

Sea hares in group L showed significant differences between day and night in the frequency of copulation. During the daytime, only 14.3 ± 3.8% and 11.4 ± 3.0% (at 06:00–12:00 hr and 12:00–18:00 hr, respectively) were copulating, significantly lower than at night (29.9 ± 1.9% and 28.8 ± 2.7% at 18:00–24:00 hr and 00:00–06:00 hr, respectively). In group S copulation activity was similarly high during the night and the first part of the day (35.4 ± 2.2%, 42.1 ± 4.3% and 23.1 ± 3.5% at 00:00–06:00 hr, 06:00–12:00 hr and 18:00–24:00 hr, respectively) and significantly lower in the second part of daytime (18.6 ± 2.7% at 12:00–18:00 hr).

Unlike all other activities, sea hares in both groups spawned only at the second part of the night (00:00–06:00 hr, 1.5 ± 0.7% and 2.3 ± 0.8% in group L and group S, respectively) and the first part of the day (06:00–12:00 hr, 3.2 ± 0.9% and 4.5 ± 0.9% in group L and group S, respectively). Group L continued to spawn in the second part of the day (12:00–18:00 hr, 1.4 ± 0.7%), significantly less than in the other time blocks. During the 18:00–24:00 hr time block, no spawning was observed.

**DISCUSSION**

The main finding of this study is that *A. oculifera* demonstrates a nocturnal activity pattern only when exposed to direct sunlight during the day. It has been clearly shown that when under direct sunlight *A. oculifera* was quiescent during the day and active at night. When under the shade, exposed to indirect light of natural photoperiod, where there were, at least, potential light-related cues as to the time of the day, they showed no pattern of nocturnalism, and were active throughout the whole day and night.

Plaut et al. (1996) showed that under shade *A. oculifera* grew somewhat faster than under direct sunlight. The fact that more than 60% of the *A. oculifera* individuals under shade were observed feeding throughout the day (Figure 2) makes it doubtful that there is any energetic advantage for *A. oculifera* being quiescent for more than about 30% of the day, as was suggested by Carefoot & Taylor (1988). Moreover, under direct sunlight, more than 70% of the sea hares were inactive and were located in the shade (under stone or buried). About 20% of the sea hares were on the algae, possibly in partial shade. In addition, *A. oculifera* under natural photoperiod of direct sunlight grew at a rate somewhat slower, although not significantly different than under shade (Plaut et al., 1996). The slower growth rate of sea hares, coupled with greater egg production under direct sunlight (Plaut et al., 1996) suggests that they may have been feeding less and were under suboptimal conditions of restricted feeding (Plaut et al., 1996). Thus, no energetic advantage of being quiescent for part of the day can be claimed in this case.

The fact that sea hares under shade showed neither a nocturnal nor a diurnal pattern of activity suggests that the cue for nocturnalism of sea hares in their natural habitat is exogenous. It seems that in this case, as reported previously (Jacklet, 1976; Carefoot & Taylor, 1988; Carefoot, 1989) direct sunlight is the cue for this pattern. Sunlight containing ultraviolet wavelengths has been found to directly harm tropical shallow-water organisms. Damage may include decrease in respiration, growth rates, and calcification rates, and death (Shick et al., 1996). Indirectly, ultraviolet radiation may damage shallow-water organisms via photochemical reactions that produce reactive oxygen molecules like H2O2 (Shick et al., 1996). The natural concentration of stratospheric ozone, generally less near the Equator than at higher latitudes (Cutliss, 1982), together with the lower solar zenith angle in tropical regions, means that the tropics receive more ultraviolet radiation. Thus, tropical ecosystems have an evolutionary history of exposure to high fluxes of ultraviolet radiation (Green et al., 1974; Frederick et al., 1989). The transparency of tropical seawater allows penetration of ultraviolet radiation in shallow-water habitats (Kirk, 1994). Thus, if ultraviolet radiation may harm sea hares, as it does other organisms in tropical shallow water, an evolution toward avoidance of being exposed to this radiation is highly probable.

Carefoot & Taylor (1988) and Carefoot (1989) considered avoidance of light, particularly ultraviolet wavelengths, as a possible advantage of nocturnality in shallow-water populations of tropical *Aplysia*. However, they raised three arguments against this hypothesis. First, “light is unlikely to have operated as a primary force leading to the evolution of nocturnalism.” Second, *A. dactylohomela*, as *A. oculifera* (Plaut, 1993) makes no obvious attempt to protect its eggs from the sun’s rays. Finally, many other species of tropical and subtropical sea hares are active during the day in shallow water.

As for Carefoot & Taylor’s (1988) first argument, it is a general statement, not supported by any explanation and thus it remains unclear.

Regarding the argument about unprotected egg masses, *A. oculifera*, like other sea hares, lays its egg masses during day and night (Figure 2) wherever it happens to be located while spawning, either exposed to (Carefoot & Taylor, 1988) or hidden from sunlight (Plaut, personal observation). Rawlings (1996) stated that many benthic marine invertebrates, living in tidal and subtidal habitats, including Mollusca, shield their embryos from direct exposure to ultraviolet radiation by a capsule wall which effectively filters ultraviolet radiation, as in the caenogastropod, *Nucella emarginata* (Deshayes, 1839). Re-
cently, Carefoot et al. (1998) also suggested possible UV protection in eggs of the sea hare, A. dactylomela. This may be also the case in the egg masses of Aplysia oculifera, indicating evolutionary adaptation of UV avoidance.

The fact that there are populations of sea hares that do not show a nocturnal pattern of activity should be tested for each population individually. Plaut (1993) reported diurnal activity of A. oculifera in several cases, in all of which sea hares were, at least partially, protected from direct sunlight, either by high amounts of algae, or by being in relatively deep water (> 2 m). The same may apply to other populations of sea hares observed to be active diurnally, thus strengthening the assumption that nocturnalism in sea hares is a form of an opportunistic behavior, directly aimed at avoiding exposure to ultraviolet radiation.

The only activity that showed a constant circadian pattern in both groups was spawning, which occurred only between midnight and noon. This pattern may be related to avoidance of egg predators before the egg capsules are fully developed. However, results are insufficient to examine this hypothesis.

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LITERATURE CITED


