THE SHADOW RESPONSE OF A HYDROMEDUSAN (*POLYORCHIS PENICILLATUS*): BEHAVIORAL MECHANISMS CONTROLLING DIEL AND ONTOGENIC VERTICAL MIGRATION

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ABSTRACT

A variety of photic stimuli were presented to the hydromedusan *Polyorchis penicillatus* under controlled conditions to characterize the photic responses of various sizes of *P. penicillatus* and to determine the role of these responses in its behavior. "Treadmill" experiments showed that for all but very small hydromedusae, swimming frequencies at different constant light intensities did not differ. Swimming frequency of *P. penicillatus* was, however, directly proportional to rates of decrease in light intensity. Slowly increasing light intensity caused an inhibition of swimming and "crumpling." Rapid, 100% shadows of various absolute magnitudes usually caused only a single swimming contraction. The maximal response to rapid shadows of monochromatic light occurred around 450–550 nm. These results suggest that the shadow response of *P. penicillatus* does not function in predator avoidance, but more likely contributes to nighttime upward movement in the water column. The inhibition of swimming during increasing light intensity may initiate dawn sinking. Most of the photic responses of *P. penicillatus* show size- (age) related differences which may result in ontogenic changes in distribution and feeding behavior.

INTRODUCTION

Many hydromedusae show distinct behavioral responses to changing light conditions. Some species of hydromedusae respond to rapidly decreasing light intensities with a few rapid swimming contractions. This behavior has been generally referred to as an "off response" (Singla, 1974), a "shadow response" (Tamasige and Yamaguchi, 1967), or a "shadow reflex" (Kikuchi, 1947). Although the function of this stereotypic behavior has never been demonstrated, traditionally it has been considered a predator avoidance mechanism. Many hydromedusae also respond to changes in light intensity as evidenced by their diel vertical migrations (Russell, 1925; Moreira, 1973; Mills, 1982). A few of these species, such as *Bougainvillia principis, Gonionemus sp., Polyorchis penicillatus, P. karafutoensis, Spirocodon saltatrix,* and *Stomotoca atra,* that have been shown to have a shadow response (Murbach, 1909; Kikuchi, 1947; Hisada, 1956; Tamasige and Yamaguchi, 1967; Singla, 1974; Mackie, 1975; Anderson and Mackie, 1977) also make distinct diel vertical migrations (Mills, 1982, 1983; Arkett, 1984). Even though rapidly changing light intensity at dawn and dusk is generally considered one of the most important cues used by zooplankters to initiate and regulate diel vertical migration (McNaught and Hasler, 1964; Ringelberg, 1964; Forward, 1976a; Buchanon and Haney, 1980; Stearns and Forward, 1984), the possibility of a causative relationship between the shadow response of hydromedusae and their diel vertical migration has not been considered previously.

Changing photic stimuli have been shown to alter the swimming activity of the hydromedusan, *Polyorchis penicillatus* (Anderson and Mackie, 1977). Anderson and Mackie (1977) showed that *P. penicillatus* responds to shadows with a burst of action potentials from the swimming motor neurons (SMNs—Spencer, 1979, 1981). Each action potential in the burst produces a contraction in the swimming muscles and hence one swimming contraction. This response to shadows is lost if the ocelli are removed, suggesting that the radially arranged ocelli are essential to the detection of shadows (Anderson and Mackie, 1977). Additionally, Anderson and Mackie (1977) found that the SMNs were directly photosensitive, that is, the membrane potential and the frequency of action potentials (and thus swimming frequency) of the SMNs were directly related to the ambient light intensity. From this finding, Anderson and Mackie (1977) suggested that diel vertical migration of medusae may be controlled by the effects of ambient light intensity on photosensitive swimming motor neurons. Thus, one might predict that *P. penicillatus* would show reverse diel vertical migration (*i.e.,* swimming up into the water column during daylight and sinking at night). However, Mills (1983) and Arkett (1984) have shown that *P. penicillatus* is a diel vertical migrator, occurring near the bottom during daytime and up in the water column at night. To reconcile this apparent contradiction, I have characterized the photic responses of various sizes, and thus ages, of *P. penicillatus.* Medusae were exposed to a variety of photic stimuli, simulating those produced by potential predators and those found during changing light conditions at various times of day, to determine the functions of the photic responses.

Although several laboratory studies have previously examined the photic behavior of medusae swimming freely in aquaria (Murbach, 1909; Mackie *et al.,* 1981; Mills, 1983), at least two aspects of these studies may bias their results. First, as medusae confined in aquaria collide with the walls, their swimming activity is altered. Swimming may be either inhibited by "crumpling" (Hyman, 1940) or increased by excitation of the tentacles upon contact with the tank walls. Secondly, with free-swimming medusae, it is difficult to control the lighting regime because the position of the medusa in the water column and the orientation of its ocelli with regard to light sources is constantly changing. I have eliminated these problems in this study by designing a "treadmill" which allows tethered swimming of medusae, eliminates wall effects, and maintains a constant orientation of ocelli to lighting.

Materials and Methods

Description of treadmill and lighting

Medusae of various sizes were suspended on the treadmill by fine (1 mm diameter) glass tubing (Fig. 1). Some very small individuals required suspension by finer wire. The tubing pierced the exumbrellar epithelial layer of the bell and passed through the thick mesogloea at the bell apex. Neither swimming musculature on the subumbrellar surface nor any nervous tissue was disrupted. Tubing ends rested on the sides of a 21 × 21 × 18 cm plexiglass tank and thus maintained the bell margin bearing the ocelli horizontal. Tentacles could not touch the sides or bottom of the tank. In this position, medusae could perform much of their behavior (*e.g.,* swimming, crumpling, feeding) without moving around the tank.

The light source for experiments was a Volpi AG Intralux fiber optic system equipped with a halogen lamp. Absolute light intensities were measured with a Licor LI-185 Quantum Sensor. Light intensity was altered by opening and closing an iris diaphragm located between the light source and fiber optic and by adjusting distances

FIGURE 1. Side view of *P. penicillatus* suspended on the "treadmill." Medusae were completely immersed and free from contact with sides and bottom of the tank. Individuals often assumed a typical "sink-fishing" posture shown here and could swim freely. Fiber optic lighting was suspended directly above the medusa. Distance between the marks on glass tubing is 1 cm. Bell height (measured from apex of bell to bell margin) was used as a measure of medusan size.

between the fiber optic head and bell margin. Specifics of lighting conditions for each experiment are given in their respective sections. All experiments were conducted in a darkened room, the light intensity of which was below that detectable by the Licor light meter (less than 0.1 microeinsteins/$m^2 \cdot s$). Seawater temperature in the treadmill ranged from 10–13°C. Treadmill seawater was changed after each medusa.

Individuals of *P. penicillatus* were collected by divers from Bamfield Inlet and Pachena Bay, Bamfield, British Columbia, Canada. Medusae were kept unfed in running seawater and were used within 3–4 days. All animals were kept under natural photoperiod prior to the experiments.

Medusa size/spontaneous swimming-frequency

In the field, *P. penicillatus* alternates from "maintenance swimming" at frequencies of about 5–15 swims per min (depending on size) to spontaneous extended swimming

bouts at higher frequencies (Arkett, 1984). This experiment was designed to examine the size/swimming-frequency relationship during these extended swimming bouts. Seventeen medusae of various sizes were placed singly on the treadmill and allowed to acclimate for 15 minutes. This time period was sufficient for medusae to relax tentacles and attain a sink-fishing posture. Under constant light conditions (ceiling fluorescent lights), the total number of swimming contractions during spontaneous extended swimming bouts was counted. Three to five separate bouts were observed for each medusa. The mean number of swimming contractions per minute was plotted as a function of bell height.

Swimming frequency/different constant light intensities

In these experiments, *P. penicillatus* was illuminated with two different light intensities, representative of those found in daytime surface or bottom waters of Bamfield Inlet, to examine photokinetic effects on swimming frequency. Twenty-nine medusae were placed singly on the treadmill and they were allowed to acclimate for 15 minutes at LOW (9.7 microeinsteins/$m^2 \cdot$ s) light intensity. At the start of the experiment, the diaphragm was opened over 15 seconds to create the HIGH (280.7 microeinsteins/ $m^2 \cdot$ s) light intensity. The number of swimming contractions was counted for a total of 15 minutes (beginning 15 seconds after opening the diaphragm) with the first 2 minutes divided into 15 s intervals (8 time periods). After 2 minutes, the number of swimming contractions was counted for each of the remaining thirteen 1 minute intervals. At the end of the 15 minute trial period, the diaphragm was closed over 15 s to create the LOW light intensity and swimming contractions were counted as before. This procedure was followed by one more HIGH light and one more LOW light intensity trial, totalling two LOW and two HIGH light intensity trials per medusa. A two-way ANOVA (Sokal and Rohlf, 1969) was performed on log (x + 1) transformed values (x = calculated number of swimming contractions per s) comparing differences in swimming frequency at the 2 light intensities and 21 time periods. The total number of individuals was separated into three arbitrary size classes, those with bell heights less than 1 cm, 1–2 cm, and greater than 2.0 cm. Since replicate trials for one medusa were not independent in this and the remaining experiments, the degrees of freedom for all statistical tests are based on the number of individual medusae and not on the total number of trials.

Shadow response/rapid 100% shadows

Rapid shadows of different absolute light intensity change, but of the same relative change, were presented to determine whether the shadow response was affected by the absolute light intensity change. Nine medusae of various sizes were placed singly on the treadmill and were allowed to acclimate in the dark for 15 minutes. Four light intensities (280.7, 65.8, 9.7, 2.4 microeinsteins/$m^2 \cdot$ s) were separately presented for 2 minutes and then a rapid, OFF-ON 100% shadow was made by passing a card between the fiber optic head and the medusa. The duration of the OFF period was approximately 0.5 s. The percent change in light intensity was determined by $(I_0 - I_1)/I_0$ where I_0 = initial absolute light intensity and I_1 = light intensity after 0.5 s (in this case approximately 0 microeinsteins/$m^2 \cdot$ s). During the two minute pre-shadow period, the number of swimming contractions per minute was counted. After the shadow, the number of swimming contractions in five seconds was recorded. The shadow response, as indicated by the number of swimming contractions per minute following the stimulus, was determined by subtracting the pre-shadow swimming frequency from the

post-shadow swimming frequency. Four trials per individual were made at each of the four light intensities in random order. Comparisons of the mean swimming frequency [after log (x + 1) transform] of the shadow response at the four different absolute light intensities were made by a one-way ANOVA (Sokal and Rohlf, 1969).

Shadow response/spectral sensitivity

The spectral sensitivity of the shadow response was determined in experiments similar to the preceding ones, but with monochromatic light. Seventeen medusae of various sizes were placed singly on the treadmill and they were allowed to acclimate in the dark for 15 minutes. Medusae were then exposed to 25 nm increments of monochromatic light ranging from 425 to 700 nm. Monochromatic light was produced by shining the fiber optic light source into a Bausch and Lomb Monochrometer (band pass width 19.2 μm; dispersion 6.4 μm/mm; first order range 350–800 nm). All light intensities were adjusted to 0.7 microeinsteins/m^2·s, the greatest light intensity attainable for all wavelengths. Medusae were illuminated with monochromatic light for 2 minutes and then given a rapid (0.5 s duration), OFF-ON 100% shadow as described previously. If a swimming contraction followed the shadow within 1 s, I considered that the individual was able to respond to that wavelength and assigned a value of 1 to that trial. Additional swimming contractions after 1 s were judged to be not due to the shadow and were not counted. If the medusa did not respond, I assigned a value of 0. Four such trials for each individual were conducted at each wavelength increment in random order. The spectral sensitivity of the shadow response is reported as a percent of the maximum possible number of responses for each wavelength increment.

Shadow response/continuous changes in light intensity

Continuous decreasing and increasing light intensities were presented to *P. penicillatus* to determine how its response to continuous changes in light intensity differs from its response to rapid OFF-ON shadows. Eleven medusae of various sizes were placed singly on the treadmill and allowed to acclimate in the dark for 15 minutes. Medusae were then presented with four different rates of light intensity change and the observed swimming frequency was recorded. Changing light conditions were produced by manually opening and closing an iris diaphragm located between the fiber optic and the light source. The light intensity at the bell margin ranged from 280.7 microeinsteins/m · s (diaphragm fully open, HIGH) to 9.7 microeinsteins/m^2 · s (LOW). The light intensity changes produced by opening and closing the diaphragm were not linear (Fig. 2). Changes in diaphragm position (HIGH to LOW and LOW to HIGH) were made over four time periods (1, 15, 30, 60 s) and corresponded to the log of the mean percent change in light intensity per s ($\Delta I_{\bar{x}}$) of -0.015, -0.914, -1.123, -1.344, respectively. Although the rates at which the diaphragm was opened and closed were identical for both increasing and decreasing light intensity trials, these values were calculated from decreasing light intensity only.

Medusae were exposed to LOW light for 15 minutes after which the diaphragm was opened to HIGH, followed by a change from HIGH to LOW. A 2-minute interval separated each change and 5 such increasing and 5 decreasing light intensity trials were given to each individual for each of the four rates of change. The total number of swimming contractions during these periods of light intensity change was counted and the mean number of swimming contractions per minute was calculated. Medusae were divided into two arbitrary size classes (<2.0 cm and >2.0 cm bell heights). Com-
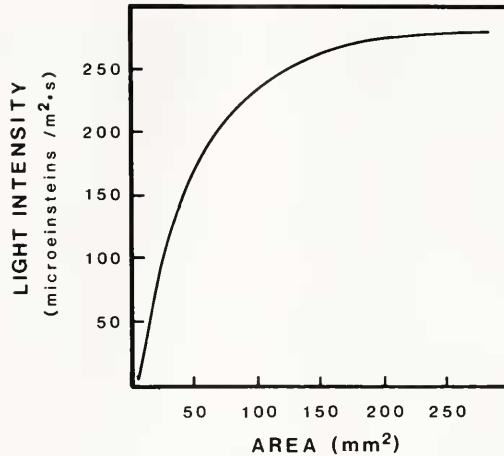
FIGURE 2. Stimulus curve for continuous changes in light intensity showing the area of iris diaphragm aperture and light intensity of the fiber optic at a distance of 10 cm. A logarithmic curve ($Y = -121.17 + 73.62 \ln x$, $r = 0.977$) has been fitted to the measured values. The curve was divided into 1, 15, 30, 60 second intervals and the absolute light intensity change per s was calculated for each of the four time intervals. The mean rate of percent change in light intensity per s ($\Delta I_{\bar{x}}$) was determined for each of the four time intervals by $(I_0 - I_1)/I_0$ where I_0 = initial absolute light intensity and I_1 is the light intensity after 1 s.

parisons between the mean swimming frequency at each rate of light intensity change were made by one-way ANOVA (Sokal and Rohlf, 1969).

RESULTS

Medusa size/spontaneous swimming frequency

Individual swimming bout durations ranged from as short as fifteen seconds to longer than five minutes. Swimming frequency during each bout was usually very regular. Quiescent periods of sink-fishing or an occasional crumple separated bouts. The mean swimming frequency of *P. penicillatus* during extended swimming bouts increased exponentially with decreasing bell height (Fig. 3). In the field, *P. penicillatus* usually swims in an arc at frequencies close to those seen in Figure 3 (Arkett, 1984).

Swimming frequency/different constant light intensities

Small medusae swam at a greater frequency under constant HIGH light intensity than under LOW light intensity; large medusae swam at nearly the same frequency regardless of the light intensity (Fig. 4). A two-way ANOVA comparing the mean number of swimming contractions per second at two light intensities and 21 time increments showed that medusae with bell heights less than 1.0 cm swam at significantly ($0.05 > P > 0.01$) greater frequency under HIGH than under LOW light intensity. For the two groups of medusae with bell heights greater than 1.0 cm, there was no significant ($P > 0.05$) difference in swimming frequency under the two light intensities. Although the group of smallest medusae showed an initial reduction in swimming frequency under HIGH light intensity, suggesting some adaptation to the light intensity, none of the groups showed a significant ($P > 0.05$) difference in swimming frequency over the 15 minute period.
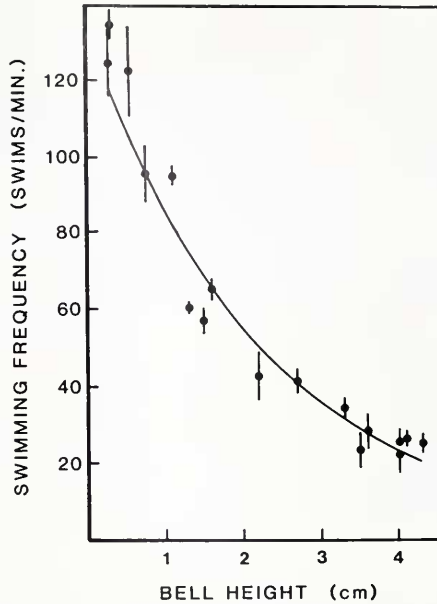
FIGURE 3. Mean (±1 SE) number of swimming contractions per minute of various sizes of *P. penicillatus* observed during spontaneous extended swimming bouts on the treadmill. An exponential curve (Y = 132.65 $e^{-0.43x}$; r = 0.96) has been fitted to the mean swimming frequencies. The smallest individuals used were early eight and sixteen tentacle stages. Each mean represents a single individual.

Shadow response/rapid 100% shadows

Medusae of all sizes tested (0.9–3.3 cm bell height) usually responded to rapid 100% shadows with one rapid swimming contraction, regardless of the absolute magnitude of the light intensity change (Table I). During the two minute pre-shadow period, most of the individuals did not swim and remained nearly motionless in the sink-fishing posture. Immediately after the brief shadow was presented, nearly all of these medusae responded with one swimming contraction. This single swimming contraction did not lead to extended swimming bouts and medusae returned to their sink-fishing posture. For those medusae that were swimming during the pre-shadow period, the response to the shadow was one additional swimming contraction in its pre-shadow swimming frequency. There were no size-related differences in the response to the rapid shadows.

Shadow response/spectral sensitivity

All medusae consistently responded to shadows of monochromatic light between 450–575 nm (Fig. 5). Small medusae responded to a broad range of wavelengths with a peak response at 450 nm while the response range of larger medusae was compressed (failing to respond at 675 nm) and the peak response shifted to a slightly longer (550 nm) wavelength. These peaks and spectral distribution of the shadow response is similar to the spectral response of the electroretinogram (ERG) of *P. penicillatus* found by Weber (1982). Smaller individuals were generally more responsive to all wavelengths as indicated by the higher overall percentage of responses.
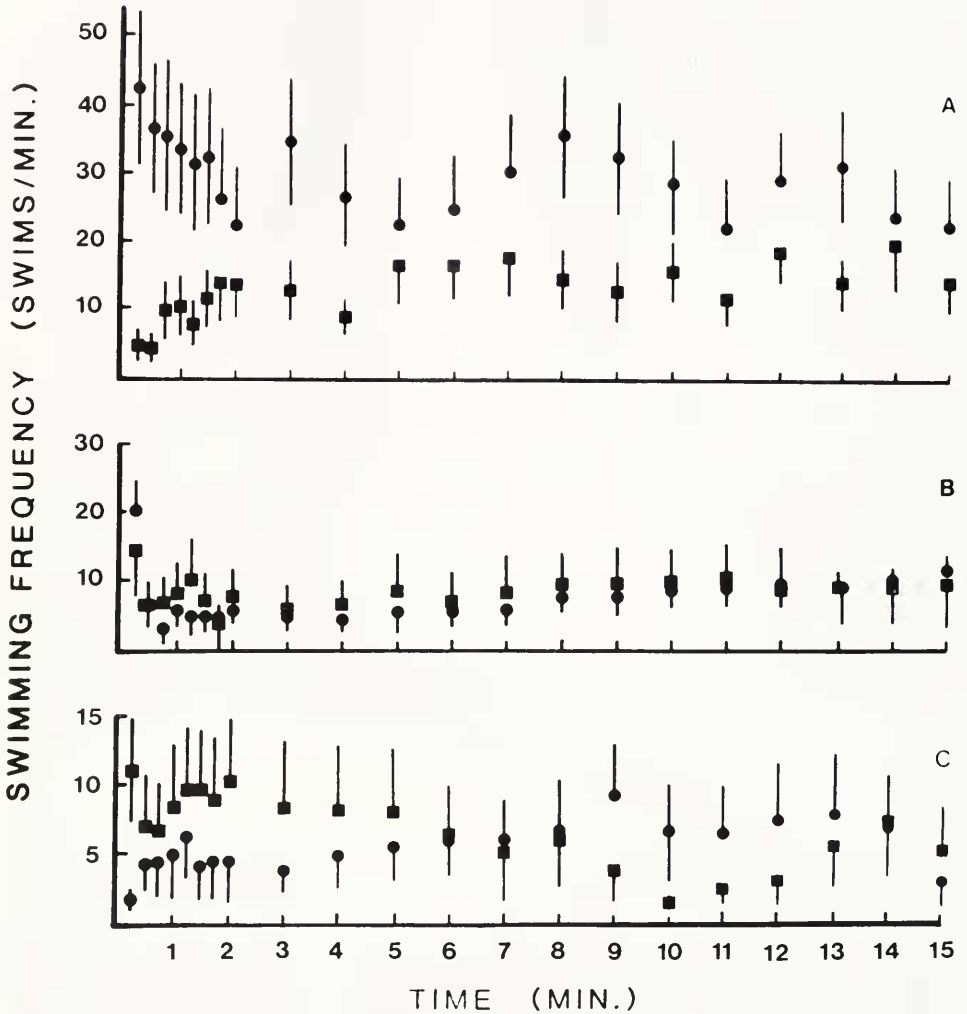
FIGURE 4. Mean (±1 SE) number of swimming contractions per minute by *P. penicillatus* on the treadmill over 15 min periods at HIGH (● 280.7 microeinsteins/m² · s) and LOW (■ 9.7 microeinsteins/m² · s) light intensity. (A) Swimming frequency of individuals with bell heights less than 1.0 cm (range 0.3–0.7 cm, n = 24, 12 individuals); (B) swimming frequency of individuals with bell heights between 1–2 cm (range 1.2–1.8 cm, n = 16, 8 individuals); (C) swimming frequency of individuals with bell heights greater than 2.0 cm (range 2.1–3.4 cm, n = 18, 9 individuals). Notice the size class differences in overall swimming frequency with smaller medusae swimming at a much higher frequency than larger individuals. *N.B.*, the means and SE presented here are from raw data and are not antilogarithms of the log (x + 1) transformed data.

Shadow response/continuous changes in light intensity

The swimming frequency of *P. penicillatus* decreased markedly as the rate of decrease in light intensity decreased (Fig. 6). Medusae swam almost continuously throughout the period of decreasing light intensity. Thus, the greatest total number of swimming contractions occurred during the slowest rate of decrease in light intensity

TABLE I

Mean (±1 SE, n = 36) number of swimming contractions in the 5 s period after a rapid 100% shadow of four different absolute light intensity changes. Comparisons of the mean shadow response frequency at four absolute light intensity changes by one-way ANOVA showed no significant (P > 0.05) difference in the responses

Light intensity (microeinsteins/m² · s)			
2.4	9.2	65.8	280.7
0.84 (0.08)	1.08 (0.09)	1.01 (0.13)	0.98 (0.02)

(Table II). The highest swimming frequency was observed during the most rapid light intensity reductions, but the total number of swimming contractions in the response was small (Table II). Smaller medusae showed a greater overall swimming frequency and were more responsive to rapid shadows (*i.e.,* exhibited greater swimming frequency than larger medusae). For slower shadows, however, larger medusae showed a greater swimming frequency.

During increasing light intensity, medusae rarely swam and often crumpled, resulting in marked differences in swimming frequencies from those seen during decreasing light intensity (Fig. 6). Crumpling behavior was most obvious during the slower light intensity increases and consisted of progressive tentacle contractions, bell margin involutions, and radial muscle contractions. Once fully crumpled, medusae often remained so for several minutes. If a medusa was in the crumpled position at the start of a successive decreasing light intensity trial, it usually relaxed the severe contractions, responded to the shadow with a swimming contraction, and began to swim at a frequency proportional to the rate of light intensity decrease. There were
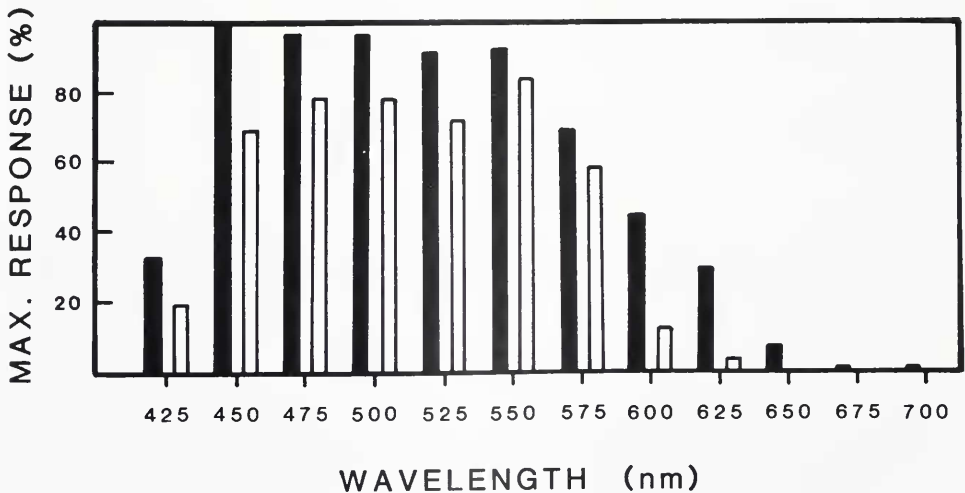

FIGURE 5. Percent of the maximum possible number of shadow responses to rapid shadows of monochromatic light. Solid columns indicate individuals with bell heights less than 2.0 cm (10 individuals), open columns indicate individuals with bell heights greater than 2.0 cm (7 individuals). The light intensity has been adjusted to 0.7 microeinsteins/m² · s for each wavelength.
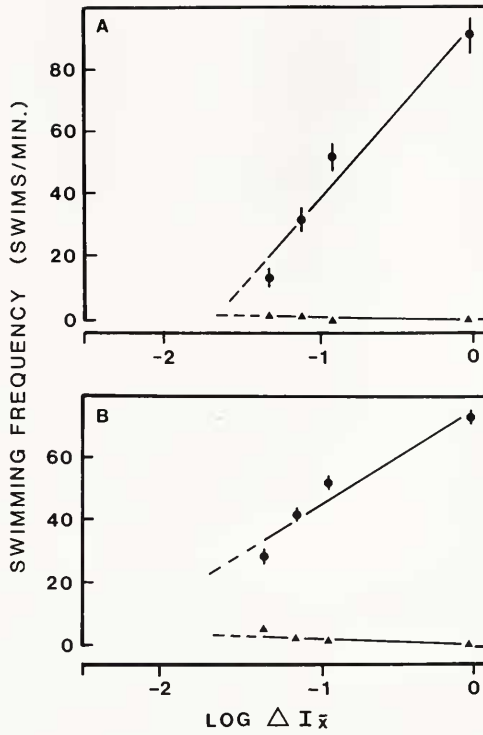
FIGURE 6.   Mean (±1 SE) number of swimming contractions per minute by *P. penicillatus* in response to four mean rates of percent change in light intensity per s (Δ I$_{\bar{x}}$). (A) Responses of medusae with bell heights less than 2.0 cm (range 0.7–1.9 cm, 6 individuals). There was a significant ($P < 0.001$) difference between the four mean swimming frequencies and a significant ($0.05 > P > 0.01$) linear regression (Y = 94.42 + 56.77 X) for decreasing (●) light intensity. No significant ($P > 0.05$) difference between the mean swimming frequencies or regression (Y = −0.16 − 0.52 X) for increasing (▲) light intensity. (B) Responses of medusae with bell heights greater than 2.0 cm (range 2.4–2.8 cm, 5 individuals). There was a significant ($P < 0.001$) difference between the four mean swimming frequencies and a significant ($0.05 > P > 0.01$) linear regression (Y = 75.40 + 31.09 X) for decreasing light intensity. For increasing light intensity, there was no significant ($P > 0.05$) difference between the four means. Linear regression (Y = 0.43 − 2.49 X) is not significant ($P > 0.05$). For both size classes, swimming frequencies at the greatest rate of percentage decrease is probably close to the maximum swimming frequency. Dashed lines show predicted swimming frequencies for other rates of light intensity changes.

no obvious differences in the response to increasing light intensity between the different sizes of *P. penicillatus* (Fig. 6); nearly all individuals, regardless of size, showed at least partial crumpling. Similar results were observed when the absolute light intensity for

TABLE II

Mean (±1 SE) total number of swimming contractions duringn four different rates of percentage change in light intensity ($\Delta I_{\bar{x}}$). Values are for decreasing light intensity only. (1) For individuals with bell heights less than 2.0 cm, n = 30. (2) For individuals with bell heights greater than 2.0 cm, n = 25

	LOG $\Delta I_{\bar{x}}$			
	−0.015	−0.914	−1.123	−1.344
(1)	1.51 (0.12)	12.73 (1.17)	15.53 (2.02)	12.17 (2.83)
(2)	1.22 (0.03)	13.08 (0.52)	21.00 (1.03)	28.76 (2.73)

HIGH was 9.4 microeinsteins/m$^2 \cdot$s and LOW was 0.2 microeinsteins/m$^2 \cdot$s at the same rates of percent change in light intensity.

DISCUSSION

Results from this study indicate that predator avoidance is an unlikely function of the shadow response of *P. penicillatus,* although the shadow response of some medusae (Singla, 1974; Anderson and Mackie, 1977) and other animals (Gwilliam, 1963, 1965; Forward, 1976b; Forward, 1977; Moore and Cobb, 1985) traditionally has been considered to function as such. A typical shadow generated by some cruising predator, such as a fish, might be a rapid OFF-ON shadow of a duration similar to that used in the experiments shown in Table I, although a predator-generated shadow would probably be less than a 100% decrease in light intensity. *P. penicillatus* responds to such rapid shadows with 1–2 additional swimming contractions (Table I). These swimming contractions would not propel the medusa far or fast enough to escape rapidly swimming predators because distances travelled are negligible until the medusa reaches maximum velocity, which usually occurs after 1–2 swimming contractions (Gladfelter, 1972; Daniel, 1983). Furthermore, the subsequent increase in light intensity following the shadow would inhibit further swimming contractions (Table I, Fig. 6). Some medusae eat other medusae (Plotnikova, 1961; Zelikman, 1969; Fraser, 1969; Arai, 1980) and predatory medusae might produce slow, long duration shadows causing extended upward swimming (Fig. 6). These movements might result in escape from these relatively slow moving predators. However, even if *P. penicillatus* does respond to predator-generated shadows, it seems unlikely that the resultant movement would yield any advantage to the medusae. Rather, because the potential predator creating the shadow would necessarily be positioned above the medusa (ocelli are oriented upward on the abaxial surface of each tentacle base), the upward swimming in response to such a shadow would only increase the probability of detection and capture as the medusa moves closer to the predator. Furthermore, known predators of *P. penicillatus* in Bamfield Inlet (pers. obs.) are benthic and would not produce shadows. *P. penicillatus* is occasionally found in the tentacles of and in the pharynx of sea anemones (*e.g., Urticina* sp., *Pachycerianthus* sp.) and in the chelipeds of crabs (*e.g., Cancer productus*). These benthic predators capture *P. penicillatus* because this hydromedusan spends much of its time near the bottom (Arkett, 1984).

The swimming frequency of *P. penicillatus* observed under constant light (Fig. 4) is similar to the "maintenance swimming" frequency observed in the field (Arkett, 1984). Constant light intensities of different absolute magnitudes do not cause differences in these swimming frequencies, at least for larger medusae. Net vertical movement during maintenance swimming is neglible because swimming contractions and upward movements are separated by short sinking periods. However, any increase or decrease in this swimming frequency over extended periods of time should result in a change in the position in the water column. Marked differences in maintenance swimming frequency have been observed in the field during extended swimming bouts, as *P. penicillatus* usually swims in an arc at frequencies close to those seen in Figure 3 (Arkett, 1984). Even though the swimming frequency and the duration of these bouts are sufficient to displace the medusae appreciable distances, the bouts are transient, apparently spontaneous, and are probably not a direct result of changing light conditions. That swimming frequency for large medusae does not increase with constant higher light intensities would explain why *P. penicillatus* is not found up in the water column during the daytime (Mills, 1983; Arkett, 1984). The lack of a direct relationship between swimming frequency and ambient light intensity are contrary to the findings of Anderson and Mackie (1977) and are contrary to predictions of swimming activity

and hence water column position. However, there is more recent electrophysiological evidence that the SMNs are not directly photosensitive (Arkett and Spencer, in prep.). Therefore, swimming frequency and water column position are not a direct function of ambient light intensity.

Slow, continuous reductions in light intensity cause nearly continuous swimming of *P. penicillatus* at frequencies above maintenance swimming frequency and for extended periods (Fig. 6). These recurring shadow responses should displace individuals significant distances and result in upward movements. Whether recurring shadow responses in response to continuously decreasing light intensity contribute to the diel vertical migration of *P. penicillatus* depends upon the rate of change in light intensity under field conditions. In one of the few field studies that has recorded rates of change in light intensity, Munz and McFarland (1973) showed that the greatest rate of light intensity decrease does not occur until after sunset and for about 40 minutes after that time. During this period the mean rate of percent decrease in light intensity (over a selected period) was approximately 88% in 7 min (=0.21%/s; =0.0021/s, log x = −2.67) (Munz and McFarland, 1973). Stearns and Forward's (1984) study in estuarine coastal waters showed that the mean rate of percent decrease in light intensity (over a single 10 min interval from between sunset and about 50 min after sunset) was approximately 0.16%/s. Attempts were made to measure the rate of percent change in light intensity every 10 minutes before and during sunset in Bamfield Inlet on several days in May 1983. The greatest rate of decrease in light intensity that could be recorded before light intensity fell below the sensitivity of the light meter was 90% in 10 minutes (=0.15%/s). These rates are about 10 times slower than the slowest rates that could be produced in my experiments (Fig. 6). However, the predicted swimming frequency of large medusae (greater than 2.0 cm bell height, Fig. 6) for such rates of change in light intensity are close to, or slightly greater than, those found during constant light intensity experiments (Fig. 4) and the maintenance swimming frequency found in the field (5–10 swims/min; Arkett, 1984). This small increase in swimming frequency may then contribute to the initiation of upward movement at sunset and the diel vertical migration of *P. penicillatus*. However, for small medusae, (less than 2.0 cm bell height, Fig. 6) predicted swimming frequency for rates of decrease in light intensity at sunset is well below that of their maintenance swimming frequency (10–15 swims/min; Arkett, 1984) and their swimming frequency in constant light intensities (Fig. 4). It thus remains unclear whether slow reductions in light intensity initiate diel vertical movement in young medusae.

The timing of the initiation of the upward movement in most plankters appears to be governed by the threshold rate of light intensity decrease necessary to elicit the shadow response. The swimming reaction of *Daphnia magna* is not initiated until the rate of percent decrease reaches 0.17%/s, even though the rate of decrease in light intensity at dusk ranged from 0.13%/s to 0.24%/s (Ringelberg, 1964). Stearns and Forward (1984) also found that the copepod *Acartia tonsa* did not move upward in the water column in appreciable numbers until about 30–40 minutes after sunset. Pre-sunset rates of decrease in light intensity (approximately 20% over a 3 min interval) did not cause pronounced upward movement (Stearns and Forward, 1984). Munz and McFarland (1973) found that the "quiet period" in coral reef fishes also occurs only during the most rapid changes in light intensity: after sunset. Although the threshold rate of change in light intensity for the shadow response in *P. penicillatus* was not determined, predicted swimming frequencies (Fig. 6) at rates comparable to those of Stearns and Forward (1984) and Munz and McFarland (1973) and those recorded near the bottom of Bamfield Inlet 10–30 min prior to sunset (*e.g.,* 0.03%–0.05%/s) would be well below maintenance swimming frequency and below the swimming

frequencies found at constant light intensities (Fig. 4). Thus, only when light intensity is rapidly decreasing near and after sunset (Rosenberg, 1966) would recurring shadow responses be elicited and swimming frequencies above maintenance swimming be reached. Only then could net upward movement result. Slower rates of decrease in light intensity, which occur late in the day and early evening, would probably not cause recurring shadow responses and net upward movement. This reasoning may explain why *P. penicillatus* begins to appear off the bottom and in the water column only after sunset and does not occur in large numbers up in the water column until several hours later (Mills, 1983; Arkett, 1984). Recurring shadow responses could, however, only initiate upward movement at sunset; they cannot explain the sustained nighttime position up in the water column. Sweatt and Forward (1985) found that the chaetognath *Sagitta hispida* continues upward swimming even in darkness. Although this continuous upward swimming may account for the sustained shallower water column position of *S. hispida,* this explanation does not appear to hold for *P. penicillatus.* Swimming in response to decreasing light intensity usually stops as soon as the rate of change in light intensity goes to zero. It is unknown how *P. penicillatus* maintains the nighttime water column position because it shows neither diel changes in ionic concentration (Mills and Vogt, 1984), which may contribute to buoyancy changes, nor intrinsic circadian rhythms (Mills, 1983).

The marked decrease in swimming frequency during increasing light intensity (Fig. 6) may explain why *P. penicillatus* moves downward and aggregates near the bottom just after dawn (Mills, 1983; Arkett, 1984). At rates of increasing light intensity representative of field conditions, the predicted swimming frequency falls well below that of maintenance swimming (Fig. 6). This alone should account for a net downward movement near dawn since *P. penicillatus* is usually negatively buoyant (Mills, 1984), sinking at rates of between 15–35 cm per min (depending on its tentacle extension, Mills, 1981). Even more important than a reduction in swimming frequency is the fact that during increasing light intensity, severe crumpling occurs. This behavior is common to many medusae and it is often a response to noxious stimuli. Because this behavior increases normal sinking rates, it has usually been considered an escape mechanism; rapidly sinking to avoid predators (Hyman, 1940). However, the progressive, sustained crumpling and resultant rapid passive sinking in response to increasing light intensity suggests that this behavior causes dawn downward movement. The rate of light intensity increase necessary to elicit the inhibition of swimming also appears to ensure the timing of the pre-dawn sinking of *P. penicillatus* (Mills, 1983; Arkett, 1984). As the rate of percent increase in light intensity is most rapid before sunrise (McNaught and Hasler, 1964), the initiation of sinking due to the inhibition of swimming should occur just before sunrise. Because the sustained crumpling often lasts the duration of the increasing light intensity period (Fig. 6), medusae should be found in deeper water during and just after sunrise.

Passive sinking in response to increases in light intensity at dawn also appears to be a common behavior among other zooplankters (*e.g.,* cladocerans, copepods, brachyuran larvae) (Daan and Ringelberg, 1969; Forward *et al.,* 1984; Stearns and Forward, 1984; Sulkin, 1984). This response, in addition to causing dawn sinking, has also been suggested to regulate daytime depths. Light intensity increases, encountered by plankters during the day, act as a barrier against upward movements (Pearre, 1973; Forward *et al.,* 1984). The deep daytime position of *P. penicillatus* is probably maintained similarly. This explanation is supported by the observation that the continuous swimming, observed during slow decreasing light intensity, can be stopped by interposed light intensity increases. Even if rapid shadows of sufficient magnitude to elicit a response do occur during the daytime, due to waves, clouds, or eel grass, net upward

movement would not result because subsequent increases in light intensity would inhibit swimming. However, Ohtsu (1983) has suggested another mechanism by which the deep daytime position of the hydromedusan *Spirocodon saltatrix* may be regulated. He found that ultraviolet (UV, 350 nm) light hyperpolarizes the swimming motor neurons and thereby inhibits swimming. Ohtsu (1983) suggested that as medusae swim upward in the water column toward the surface, they encounter increasingly greater intensities of UV light, which should inhibit swimming and eventually cause sinking. It is conceivable that Ohtsu's explanation of sinking upon approach to surface waters may apply to *P. penicillatus*, but because the effect of UV light was not examined with *P. penicillatus*, no conclusions can be made at this time. However, this explanation seems unlikely because many young medusae are often found in surface waters (see below).

In addition to changes in light intensity the spectral shift in light penetrating the water during sunrise and sunset may influence the shadow response. During sunset, the underwater spectrum tends to shift toward shorter wavelengths (450–500 nm, blue) (Munz and McFarland, 1973). However, the large amount of detrital matter or "yellow substance" in coastal waters (Jerlov, 1966) would tend to absorb blue light, shifting maximum transmission to green (500–550 nm). The spectral quality of the water in Bamfield Inlet is unknown, but the large amount of detritus present probably shifts maximum transmission to green, which is close to the maximal shadow response for larger medusae (Fig. 5). It is unknown whether spectral shifts at sunset and sunrise alter the sensitivity of the response to continuous changes in light intensity.

Ontogenic changes in photosensitivity in planktonic invertebrates are common (Thorson, 1964; Pearre, 1979) and these changes affect the vertical distribution and feeding behavior of later stages and adults (Pearre, 1973; Buchanan and Haney, 1980; Forward and Costlow, 1974; Cronin, 1982). Differences in the responses of various sizes of medusae to light stimuli found in this study suggest that *P. penicillatus* also undergoes ontogenic changes in its photic behavior. Smaller medusae showed: (1) a distinct photokinetic effect with swimming frequency (Fig. 4); (2) a slightly broader spectral sensitivity of the shadow response with its peak shifted toward shorter wavelength (Fig. 5); and (3) a more acute response to continuous changes in light intensity (Fig. 6). This last finding in particular suggests that small medusae do not use the slow decrease in light intensity at sunset to initiate upward movements since their predicted swimming frequency at these rates of change in light intensity is far too low. These findings, in addition to (1) the observed higher maximum swimming frequency during extended swimming bouts (Fig. 2); (2) greater maintenance swimming frequency (Arkett, 1984); and (3) a greater maximum velocity gain per swimming cycle (relative to their size) (Gladfelter, 1972), all suggest that smaller and presumably younger medusae are more truly planktonic and occupy shallower waters than older medusae. These characteristics should maintain newly budded and young stages of medusae in surface waters, thereby facilitating dispersal. The small number and size of the tentacles in these young medusae may limit them to capturing and eating smaller plankters. Indeed, large numbers of very small individuals are often observed in the surface waters near Bamfield Inlet. As medusae age, many of the juvenile photic traits appear to be altered, although the mechanisms by which these apparent ontogenic changes occur are unknown. Larger individuals do not show photokinetic differences (Fig. 4), have a narrower spectral sensitivity of the shadow response (Fig. 5), and show a less acute response to continuous changes in light intensity (Fig. 6). As already discussed, this last characteristic may explain the initiation of diel vertical migration of *P. penicillatus*. Furthermore, the lower swimming frequency during extended swimming bouts (Fig. 2), and lower "maintenance swimming" frequency (Arkett, 1984) suggests that they spend more time in deeper water. In shallow inlets, where *P. penicillatus* is commonly found,

they assume a demersal existence, feeding on large demersal zooplankters (Arkett, 1984). Synchronized upward movement at night and concomitant spawning of these older reproductive individuals (Mills, 1983) may also ensure higher rates of fertilization.

In summary, *P. penicillatus* is most responsive to the rate of change in light intensity. In older medusae, the shadow response probably initiates diel vertical migration and does not function in predator avoidance. The function of the shadow response in young medusae remains unclear. That the shadow response of other hydromedusae (*e.g., G. vertens, S. atra, B. principis*) may function in the same way is suggested by their rapid upward movement during sunset (Mills, 1983). Additionally, the rapid downward movement of *P. penicillatus* and these other hydromedusae may be due to inhibition of swimming and to crumpling during sunrise. These movements are likely due to changes in the normal or "maintenance swimming" frequency alone.

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