

## Vertical migration and diel activity patterns of hydromedusae: studies in a large tank

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**Abstract.** Vertical distributions and swimming behaviors of 7 species of hydromedusae (*Aequorea victoria*, *Bougainvillia principis*, *Gonionemus vertens*, *Mitrocoma cellularia*, *Phialidium gregarium*, *Polyorchis penicillatus*, and *Stomatoca atra*) were observed over 24-h periods in a 2 m high, 1500 l transparent tank. In this tank, most species performed well-marked diel vertical migrations that were mediated by swimming. Manipulation of the light regime showed the diel swimming behaviors to be light-dependent rather than intrinsic, even in species that do not possess recognized photoreceptors. Correlations between vertical migration and spawning times for several species of medusae suggest that in cases when vertical migration reduces the distances between individuals (e.g., in mass movements to the surface) just prior to spawning, enhanced fertilization success may result from such movements.

### Introduction

Many species of hydromedusae are known to undergo diel vertical migrations. These migrations vary in magnitude from the 500 m travelled by *Solmissus albes-cens* (a Mediterranean species measuring only 25 mm in diameter) (Benović, 1973), to migrations of less than 50 m for some other species (Russell, 1925, 1928; Moreira, 1973; Thurston, 1977). Some species of hydromedusae apparently do not perform diel vertical migrations at all.

Hydromedusae are an often neglected, yet frequently conspicuous component of most marine plankton communities. In areas where they are abundant, these carnivores can be major consumers of copepods and other small crustaceans, as well as invertebrate larvae, fish larvae, and (in some cases) other hydromedusae (Lebour, 1923; McCormick, 1969; Zelickman *et al.*, 1969; Arai and Jacobs, 1980). Approximately 50 species of hydromedusae are present during the year in the Puget Sound—San Juan Archipelago—Strait of Georgia inland waters of Washington State, USA and British Columbia, Canada (Arai and Brinckmann-Voss, 1980; Mills, 1981a). At present, knowledge of the vertical distributions and vertical migrations of this assemblage of medusae is represented by only a brief study of one species (Arai and Fulton, 1973). Further examination of the diel behavior of hydromedusae will contribute to an understanding of their significance in the plankton and may at the same time shed light on some aspects of their complex life cycles.

In conjunction with a 2-year series of plankton tows designed to reveal the year-round vertical distributions and vertical migrations of hydromedusae in Saanich Inlet, Canada (Mills, 1982), the present study was undertaken in which several of the common species were observed at close range in a 1500 l transparent acrylic

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tank for periods of at least 24 h. In this tank, the diel behavior of various species (and of individual medusae) could be monitored at all times. It was my intention in these studies to record diel activity patterns and swimming behavior as they related to vertical migrations within the tank and in the field so as to better understand the natural biology of this group of planktonic predators.

### Materials and Methods

Medusae were collected individually in glass or plastic beakers from surface waters off the floating dock at the Friday Harbor Laboratories (FHL), Friday Harbor, Washington, USA. Healthy specimens were immediately transferred in a bucket to the experimental tank with the least possible disturbance. No visibly damaged medusae were used in the experiments. Depending on size and availability, 15–100 sexually mature medusae of one or two species were counted and placed at the same time in the tank. (Only in the case of *Bougainvillia principis* and *Mitrocomella polydiademata* (not described here) were 2 species placed together, and in this case no interspecific interactions were evident.) Each species was studied at a time when it was abundant in the plankton, so behavior as observed in the tank represents that of normal healthy adult individuals. All species reported in this paper have been observed for at least three 24-h periods. There were no apparent differences in behavior over a 24-h period in the tank between medusae collected during the day and medusae collected at night.

The tank is a transparent acrylic cylinder, made of 2 cm thick Plexiglas glued to a 4 cm thick transparent Plexiglas base. (It was originally built as part of the CEPEX bag flotation system.) The inside diameter of the tank is 106 cm; it is 194 cm tall and is filled with sea water to a depth of 170 or 180 cm. The tank is filled *via* a plastic hose from the FHL running sea water system. In addition to a drain in the base which is closed by a plastic valve, the tank has an overflow drain 185 cm up from the bottom. Salinity in the tank was measured using a salinity/conductivity meter (Yellow Springs Instruments). Water temperature was measured with a thermometer lowered to various levels in the tank.

The tank is enclosed by a plywood shed that has a 1 m by 1 m square opening in the roof above the tank through which daylight enters. The enclosure is shaded by a nearby building so that natural daytime lighting within the enclosure is subdued. A wooden lid can be placed over the top of the shed in order to darken it at any time. The structure is then light-tight. A light socket situated ~20 cm above the water surface accommodated either a 200 W frosted incandescent bulb or a 100 W red flood light during the experiments. The upper rim of the tank is covered with black tape to eliminate possible reflections from within the wall of the tank. The shed is large enough to allow an observer to move around the tank.

Between experiments, the tank was continuously flushed with running sea water. Just prior to adding medusae, the water flow was turned off and the tank drained a few cm below the overflow drain. (For most species of medusae, any flow was sufficient to waft the medusae throughout the water column, obscuring any diel distribution patterns.) Because of the large volume of water and relatively cool outdoor temperatures (usually 12–20°C), the water temperature remained constant within a few degrees for several days. Growth of periphyton on

surface observations at Friday Harbor and on a 2-year series of 650 stratified plankton tows in Saanich Inlet, British Columbia, Canada.

## Results and Discussion

The tank was a convenient and relatively uniform environment for observations of hydromedusae. Salinity in the tank remained between 28 and 30‰ during the study. Temperature in the tank fluctuated most severely on warm mid-summer days when a rise of 2–3°C per day was not unusual; on cool days the temperature remained constant or rose less than 1°C per day.

In the present study, seven species of hydromedusae were placed in the tank at various times for observations of swimming behavior and diel activity pattern. In general, the medusae appeared to be relatively uninhibited in the tank and they displayed reproducible diel swimming patterns. The behaviors of these species are reported below together with their spawning times and a brief synopsis of the known field biology of each. The behavior of each species in the tank is illustrated by a record of one representative 24-h period (Figure 1–7).

### *Aequorea victoria* (Murbach and Shearer, 1902)

*Aequorea victoria* is one of the most abundant hydromedusae in the inland waters of Washington State and British Columbia. Its large size at maturity (up to 120 mm in bell diameter) makes it especially conspicuous. Although a few *A. victoria* medusae may be seen all winter, the typical annual cycle is for the population of medusae to be present from February or March until autumn. *A. victoria* is a major predator on other species of hydromedusae in the plankton. Up to 200,000 *A. victoria* medusae are harvested annually in Friday Harbor for the isolation of aequorin, a calcium-activated luminescent protein used in biomedical research. *A. victoria* medusae do not possess ocelli or any other conventional photoreceptors.

In the tank, *A. victoria* showed little change in its vertical distribution over a 24-h period; it was the species of medusa least responsive to variation in light (Figure 1). At all times, 25–50% of the medusae were pulsating against the bottom, the remainder were swimming or slowly sinking throughout the tank (*A. victoria* is slightly negatively buoyant). Consistently, however, a small increase in the number of *A. victoria* in the tank's water column in mid-morning was accentuated by a substantial increase in the number of near-surface individuals at this time. Such a morning increase in near-surface *A. victoria* medusae in the field is well known by *Aequorea* harvesters.

*A. victoria* spawns in the mid- to late morning (~4 h after dawn); the duration of spawning may be extended longer than in other hydromedusan species. A female *A. victoria* may release eggs for 10–40 min, although the majority of these eggs are released in the first 15 min. The spawning time for *A. victoria* corresponds to that time of day in which a significantly increased proportion of the population may be found near the surface. This concentration of *A. victoria* may help to promote fertilization by bringing freely spawned eggs and sperm closer together.

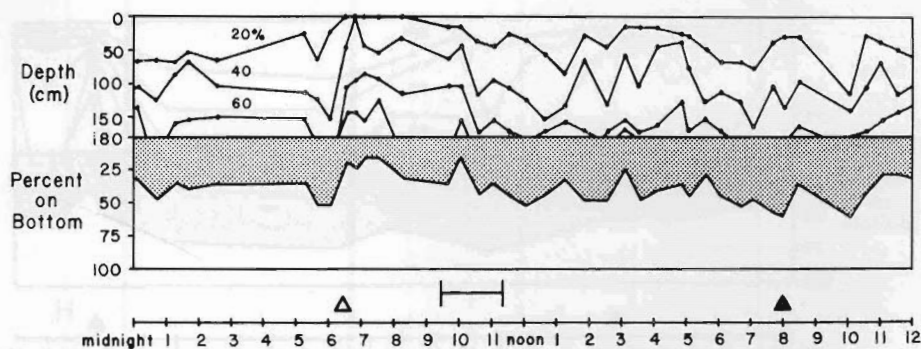


Fig. 1. Vertical positions of 26 *A. victoria* medusae in the tank over a 24-h period (September 11–12, 1978) recorded by visual observation. The upper half of the figure represents a depth profile of the tank with locations of selected proportions (labelled) of individuals above and below each line plotted against time. The shaded area in the lower half of the figure represents the proportion of the total number of medusae that were on the bottom throughout the experiment. On the time line below the figure are shown dawn ( $\triangle$ ), dusk ( $\blacktriangle$ ), and the time of daily spawning for this species (—).

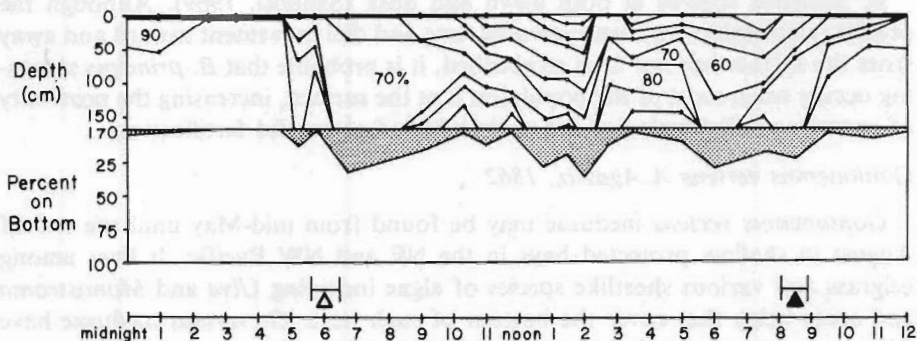


Fig. 2. Vertical positions of 30 *B. principis* medusae in the tank over a 24-h period (May 22–23, 1979) recorded by visual observation. (See Figure 1 for explanation of format.)

### *Bougainvillia principis* (Steenstrup, 1850)

*Bougainvillia principis* medusae may be common in the surface waters of the San Juan Archipelago between late April and early June. Sexually mature *B. principis* measuring 6–10 mm in bell diameter may be found from mid-May into June. *B. principis* feeds on small crustaceans, especially barnacle nauplii. These medusae have up to 120 marginal tentacles, each with an ocellus at the base.

*B. principis* is generally a quiescent medusa, spending most of its time with tentacles extended, hanging motionless and neutrally buoyant in the water. It demonstrated a short-range vertical migration in the tank (Figure 2). During the day, individuals were distributed fairly evenly throughout the tank; only a few were on the bottom. At dusk, most *B. principis* move to the surface. They remain suspended within a few cm of the surface at night and then move down again at dawn. Since at least 65% of the medusae remain above the bottom of the tank,

Murbach (1909) and Zelickman (1976) have also described periodic daytime bouts of swimming in *Gonionemus*. Murbach (1909) details a rather elaborate set of experiments in which it is determined that changes in daytime light intensity (as might be experienced by shifting of the algae or eelgrass near *Gonionemus*) stimulate swimming and turning activity of this medusa. Murbach (1895) also observed that whereas *Gonionemus* is rather quiet during the day unless disturbed, it becomes very active as darkness sets in.

*G. vertens* feeds on a variety of prey including harpacticoid copepods and amphipods. The diel migration of *G. vertens* may enable this medusa to feed on a diet of the same demersal organisms both during the day and at night. Investigation of the effect of vertical migration on diet of *G. vertens* is now in progress (Mills, unpublished results).

The pattern of migration from the bottom during the day to a position high in the water column at night has been observed in the field by SCUBA divers (personal communication R. Shimek and J. von Carolsfeld). Diel behavior in the field is apparently complicated by a pronounced response of *G. vertens* to the tidal cycle. This medusa is rarely seen in the water column when the tide is running, regardless of the time of day. The influence of tidal currents on *G. vertens* behavior has not been carefully analyzed.

*G. vertens* spawns 45–65 min after dark and the spawning process takes <15 min. At the time of spawning, most of the population has moved near the surface. Such behavior probably enhances reproductive success in several ways. Although *G. vertens* eggs are sticky and negatively buoyant, they will tend to disperse before they become fixed to the bottom. Thus the eggs are ensured of a wider distribution and probably a better chance of fertilization than would be possible if *G. vertens* medusae spawned at a time when most of the population was near the bottom clinging to eelgrass or algae. Once a *G. vertens* egg has settled to the bottom, it may have no further opportunity for substrate selection prior to growth of the hydroid stage. *G. vertens* embryos may or may not become swimming planulae (Murbach, 1895; Mills, unpublished data). Non-swimming embryos appear to remain as relatively undifferentiated masses of cells that loosely adhere to the bottom and metamorphose in place into the solitary *G. vertens* polyps. *G. vertens* polyps are apparently quite non-specific in substrate; in nature they have been found on rock, shell and wood.

#### *Mitrocoma cellularia* (A. Agassiz, 1865)

*Mitrocoma cellularia* is a common medusa in the inland waters of Washington State and British Columbia. It may be found between April and December in surface waters. Sexually mature *M. cellularia* medusae are usually 40–100 mm in bell diameter. Field observations suggest that *M. cellularia* is a favorite food item of the hydromedusa *Aequorea victoria*. *M. cellularia* medusae do not possess ocelli or any other conventional photoreceptors.

In the tank, most *M. cellularia* remain on the bottom during the day where they pulsate with tentacles contracted, apex down, for hours (Figure 4). Only rarely do individual medusae swim up into the water column during the day and these excursions are usually restricted to the lower quarter of the tank. At dusk, some in-

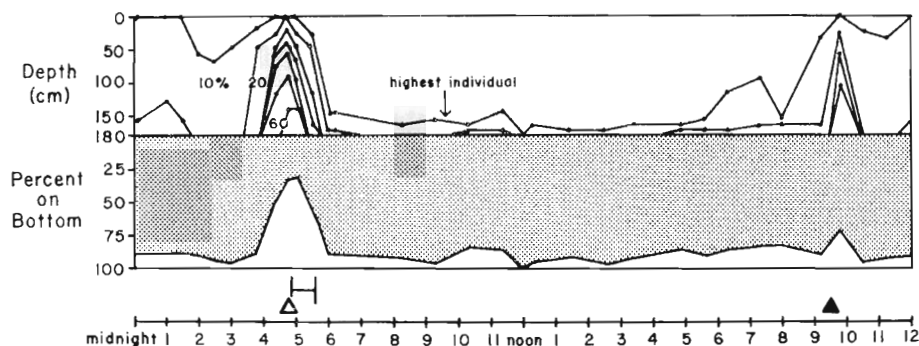


Fig. 4. Vertical positions of 40 *M. cellularia* medusae in the tank over a 24-h period (July 13–14, 1978) recorded by visual observation. (See Figure 1 for explanation of format.)

dividuals leave the bottom and swim throughout the tank. During the night, a few *M. cellularia* medusae are usually seen slowly pulsating through the water or sinking quiescently with their tentacles expanded, but vigorous swimming is not seen. At first light, nearly all *M. cellularia* medusae leave the bottom and swim throughout the tank for ~1 h (Figure 8). Their return to the bottom as the light increases is gradual and rather subtle; individuals simply cease active pulsations and eventually sink out of the water column (they are slightly negatively buoyant). I cannot distinguish whether this activity is in response to an absolute level or to a changing level of light.

*M. cellularia* spawns at dawn, at the same time that it is seen actively swimming in the tank. The relationship between these two events is not yet known.

Little information has been obtained about vertical distribution of *M. cellularia* in the field. The medusa is common both during the day and at night in surface waters off the FHL floating dock. Tidal currents in that region are strong enough to mix the water column to the extent that hydromedusae, which are easily wafted about even by gentle currents, are probably unable to maintain a preferred vertical position. The vertical position of *M. cellularia* in less disrupted waters is not known.

#### *Phialidium gregarium* (A. Agassiz, 1862)

*Phialidium gregarium* medusae are abundant in many NE Pacific nearshore areas between March and November. They are characteristic of surface waters; in Saanich Inlet, B.C., most *P. gregarium* occur in the upper 25 m. Sexually mature *P. gregarium* are usually ~20 mm in bell diameter and are slightly negatively buoyant. They feed primarily on small planktonic crustaceans as well as on miscellaneous invertebrate larvae and eggs (McCormick, 1969). *P. gregarium* medusae do not possess ocelli or any other conventional photoreceptors.

In the tank, *P. gregarium* performs a reverse vertical migration (Figure 5). During the day, individual medusae move throughout the tank in a cyclical sink/swim pattern (Mills, 1981b); less than one-half of the medusae are generally on the bottom at any one time. Soon after dusk, nearly all of the medusae are on the bottom of the tank, either pulsating apex down, or quiescent. After a few hours in the



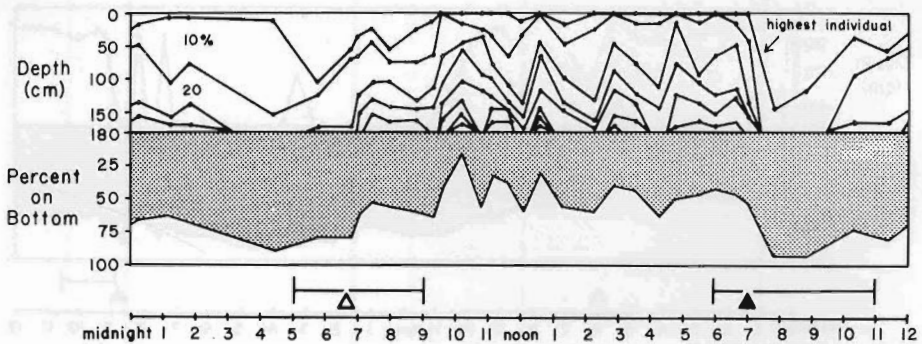


Fig. 5. Vertical positions of 30 *P. gregarium* medusae in the tank over a 24-h period (September 26–27, 1978) recorded by visual observation. (See Figure 1 for explanation of format.)

dark, a small number (~25%) return to the water column; most of these remain in the lower portion of the tank. Shortly after dawn, medusae gradually rise in the water column, although a well-synchronized upward movement of medusae does not occur.

Plankton tows in Saanich Inlet confirm that a small percentage of the *P. gregarium* population in the field reverse-migrate (downward) as much as 25–50 m at night. The majority of the *P. gregarium* population in Saanich Inlet remain above 25 m at all times and any migratory behavior within this upper layer has not yet been documented in the field.

Most *P. gregarium* medusae spawn twice daily, at approximately dawn and dusk (Roosen-Runge, 1962). The morning spawning may occur anytime from 1.75 h before sunrise to 2.75 h after sunrise, and the evening spawning may occur from 1 h before sunset to 4 h after sunset. Spawning takes 10–15 min for each individual; the majority of eggs are released in <5 min. The animals apparently spawn during their migratory swimming periods, both at dawn and dusk and the advantages of such timing is not clear.

#### *Polyorchis penicillatus* (Eschscholtz, 1829)

Like *G. vertens*, the medusae of *Polyorchis penicillatus* usually live in shallow protected bays in the NE Pacific in association with eelgrass. *P. penicillatus* is also found in some deeper bays on the exposed outer coast. This medusa is most often seen between May and November, although in some areas it can be found year-round. *P. penicillatus* spends a large percentage of its time on the bottom; the negatively buoyant medusa perches on its tentacles (which do not have any specialized adhesive portions), maintaining its bell margin a few mm off the sediments. Sexually mature *P. penicillatus* medusae are usually between 25 and 50 mm in bell height, and have up to 120 marginal tentacles, each with an ocellus at the base.

During the day, *P. penicillatus* medusae in the tank characteristically perched on the bottom. (In the field they feed in this posture on superficial benthic organisms and shallow infauna.) Each medusa made frequent hops consisting of a single pulsation off the bottom; several times per hour each swam further up in-

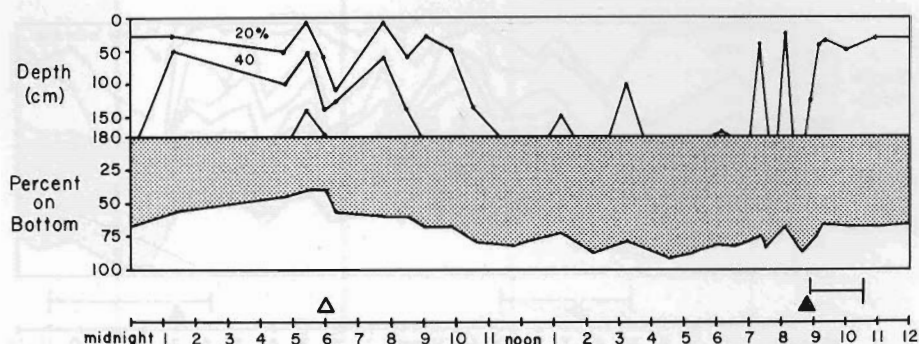


Fig. 6. Vertical positions of 25 *P. penicillatus* medusae in the tank over a 24-h period (August 10–11, 1978) recorded by visual observation. (See Figure 1 for explanation of format.)

to the water column. Hourly observations of *P. penicillatus* in the tank showed a decrease in the number of medusae on the bottom between dusk and dawn (Figure 6), although no distinct change in individual behavior was discernible. More medusae were in the water column at any given time of night than during the day, but no general accumulation of medusae near the surface occurred at night. The laser transect record (Figure 8) shows a marked increase in near-surface activity at night which simply reflects an increase in swimming activity throughout the tank that begins shortly after dusk and falls off at dawn. The increased number of swims to the surface at night presumably facilitates feeding in the plankton and may result in a diet based on demersal organisms that are in the plankton at night and benthic during the day.

*P. penicillatus* spawns in the hour immediately following darkness; the spawning process for each individual taking <10 min. Although *P. penicillatus* are more likely to be swimming after dusk when they spawn, there does not appear to be any net concentration of these medusae at the time of fertilization such as occurs with *Aequorea victoria*, *Gonionemus vertens*, and perhaps *Bougainvillea principis* when these species move toward the surface at dusk just prior to spawning.

Although *P. penicillatus* demonstrates a relatively well-defined light-induced diel activity pattern in the tank, daytime light conditions were relatively constant in this environment. In the field, *P. penicillatus* is subject to less uniform lighting (e.g., on bright sunny days shadows are produced by waving eelgrass or by clouds passing in front of the sun). *P. penicillatus* exhibits some rather complicated light responses that presumably temper its behavior in the field so that the above-described diel pattern is not so obvious. *P. penicillatus* has a strong shadow response; that is, when a shadow passes over a quiescent medusa, or the room lights are turned off in the laboratory, the medusa swims up temporarily, soon returning to its resting position. The ocelli appear to be the receptors for this response (Anderson and Mackie, 1977). Anderson and Mackie (1977) have demonstrated that in addition to its ocelli, the swimming neurons of *P. penicillatus* are directly light sensitive, and an increase in light intensity causes this medusa to swim. Indeed, on calm sunny days, many *P. penicillatus* medusae



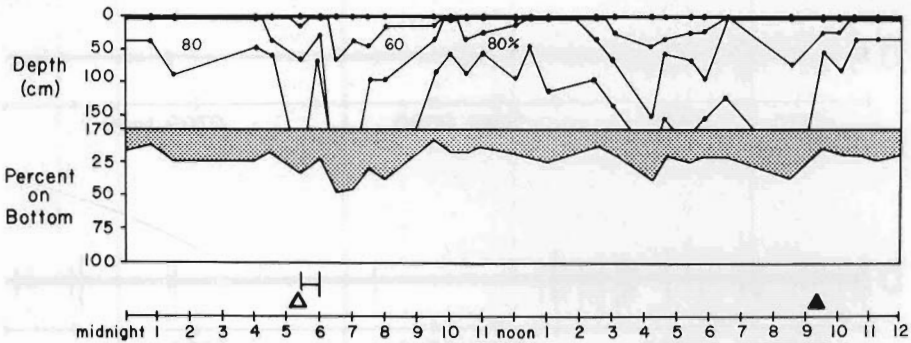


Fig. 7. Vertical positions of 25 *S. atra* medusae in the tank over a 24-h period (July 7–8, 1980) recorded by visual observation. (See Figure 1 for explanation of format.)

are seen at the surface in the field. For a large number of these animals, swimming near the surface appears to be behavioral, but some of the *P. penicillatus* at the surface seem to be held there by small gas bubbles trapped inside their bells. Such bubbles are produced by the photosynthesizing eelgrass. There is still no comprehensive understanding of the light-related behavior of *P. penicillatus*.

#### *Stomatoca atra* A. Agassiz, 1862

*Stomatoca atra* is found in surface waters of the San Juan Archipelago between April and November; it may be very common during the summer. These negatively buoyant medusae have bell diameters between 15 and 25 mm at sexual maturity. *S. atra* feeds on other small hydromedusae, especially *Phialidium gregarium*. *S. atra* medusae do not possess ocelli or any other conventional photoreceptors.

*S. atra* medusae demonstrate a short-range vertical migration in the tank (Figure 7). During the day *S. atra* are seen throughout the tank where they perform a repeating sinusoidal sink/swim behavior which also constitutes a search pattern for feeding (Mills, 1981b). Approximately 25% of the medusae are on the bottom at most times. At dusk, most of the medusae in the water column move toward the surface. They maintain their position near the surface by swimming more or less continuously during the night. At dawn, these medusae drop lower in the tank and resume their sinusoidal sink/swim pattern; individuals periodically 'rest' on the bottom.

In addition to the above-described diel vertical migration, and perhaps overriding it, *S. atra* apparently move up to the surface in bright sunlight. Such behavior has been observed both in the tank and in the field, and may indicate that diel migrations are of rather short range in the field. *S. atra* spawns at dawn. No ecological advantages of such timing are yet apparent.

#### *Relationships between vertical migration and light*

As described above, the behavior of many species of hydromedusae includes a vertical migration whose timing corresponds to natural light cycles. Natural lighting was easily overcome by darkening the tank shed and establishing arti-

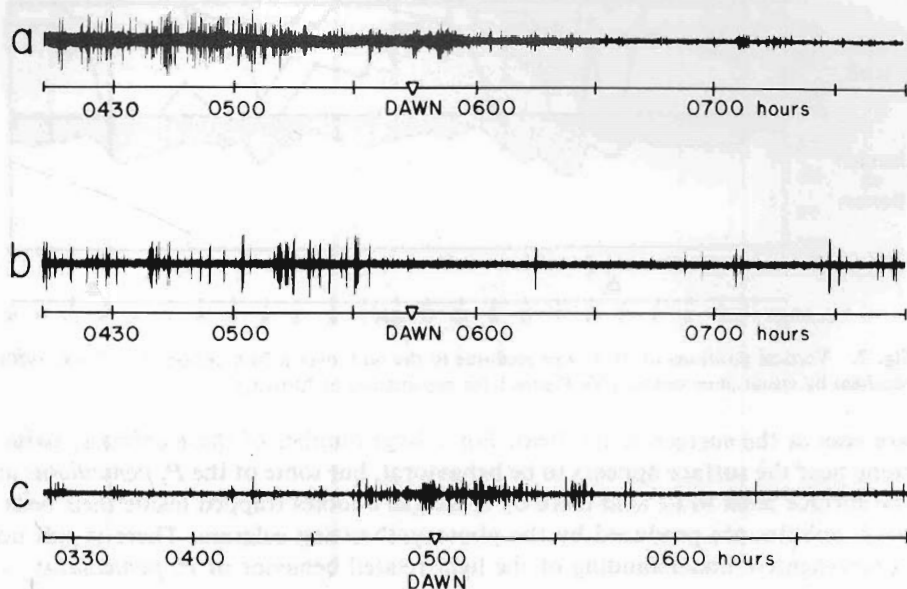


Fig. 8. Changes in swimming activity near the tank surface associated with dawn (recorded by the laser monitoring system described in text). A spike was produced whenever a medusa swam through the laser beam, momentarily interrupting the electrical continuity. (a) 50 *G. vertens*, (b) 25 *P. penicillatus*, (c) 40 *M. cellularia*.

ficial light cycles within the shed. In this case, the vertical distributions of species that clearly responded to light (all but *Aequorea victoria* in the present study) were easily manipulated by a change in ambient lighting. For example (Figure 9), *Gonionemus vertens* showed a diel vertical migration in natural light, but it remained near the surface indefinitely if the tank was covered at night and remained dark during the following day. Conversely, if a 200 W frosted incandescent light was turned on above the tank at night (to simulate daylight), most *G. vertens* remained attached to the bottom and sides of the tank. Similarly, *Mitrocoma cellularia* medusae normally displayed a marked period of swimming activity at dawn, and at other times generally were pulsating against the bottom of the tank. However, *M. cellularia* that were kept in an artificially darkened tank during the daytime underwent this active period of swimming when the tank was uncovered in the waning light of evening, presumably in response to the low level of light following darkness. All species of medusae that were kept in continuous light or continuous dark for 48 h behaved accordingly, showing no intrinsic rhythms, although some deterioration of the animals was evident over such long periods without food. These data as discussed above are inconsistent with the existence of an endogenous migratory rhythm in hydromedusae. It is concluded that the diel swimming behaviors which constitute vertical migration and other activities are light-related and that hydromedusae apparently do not possess internal clocks governing such behavior. A similar conclusion was reached by Mackie *et al.* (1981)

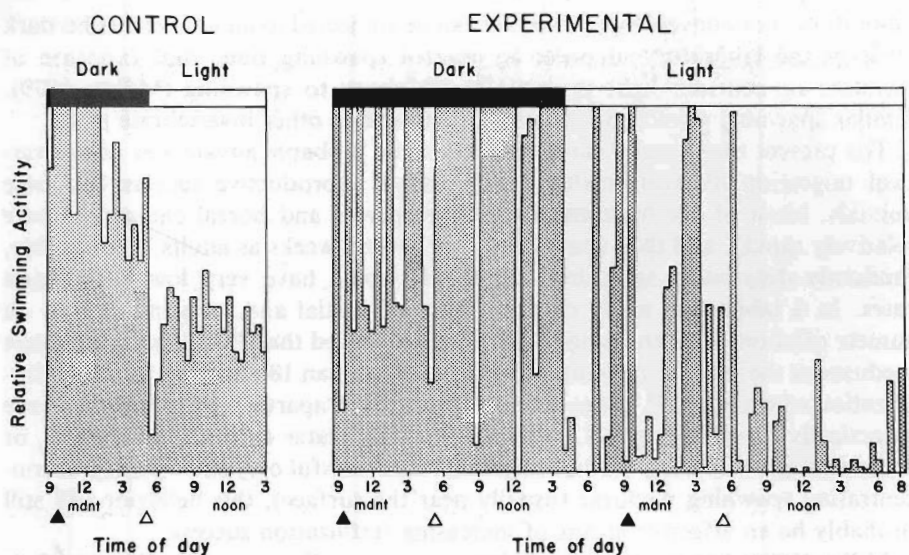


Fig. 9. Manipulation by light of the swimming activity of *G. vertens*. The histograms are derived by counting electronic spikes produced by medusae swimming through a laser beam near the tank surface (see Figure 8). In the control situation, the tank received natural lighting. In the experimental situation, the tank was artificially darkened from the first evening until early afternoon of the following day and then was artificially illuminated for 28 h. Natural dawn ( $\Delta$ ) and dusk ( $\blacktriangle$ ) are indicated on the time scales.

in a recent study of vertical migration in captive scyphomedusae (*Aurelia aurita*). Passano (1973) also found no light-independent circadian rhythms in hydromedusae during laboratory investigations of their nervous systems and swimming behavior.

It is somewhat enigmatic that many hydromedusae which vertically migrate lack conventional photoreceptors. This fact has been noted by Moreira (1973) and Benović (1973) for species of hydromedusae with widely varying depth ranges. There can be little question, however, that such species indeed perceive light. In the present study, *Gonionemus vertens*, *Mitrocoma cellularia*, *Phialidium gregarium* and *Stomatoca atra* all lack known photoreceptors, yet their diel behavior is motivated by light no less than that of *Bougainvillia principis* or *Polyorchis penicillatus*, which have ocelli. The discovery of photosensitive swimming neurons (in addition to ocelli) in *P. penicillatus* (Anderson and Mackie, 1977) offers one of many possible solutions to this enigma. That other cell types in hydromedusae may be photoreceptors seems quite probable.

#### *Relationships between vertical migration and spawning*

Ovulation and sperm release in hydromedusae are regulated within limits by light (Roosen-Runge, 1962; Miller, 1979). Spawning occurs after transitions from light to dark, dark to light, or both. Time after the light cue is species-specific and reproducible; it may be minutes as in the case of *Polyorchis penicillatus*, or hours as in the case of *Aequorea victoria*, but it is effective both in the field and in the

laboratory. For convenience, medusae can be subjected to an artificial light/dark cycle in the laboratory in order to control spawning time, and exposure of medusae to constant light is partially inhibitory to spawning (Miller, 1979). Similar spawning photosensitivity occurs in several other invertebrate phyla.

The present experiments have revealed some probable advantages of the vertical migration of hydromedusae in terms of reproductive success for these animals. Most of the hydromedusae in temperate and boreal climates mature relatively rapidly and then spawn daily for several weeks as adults. Presumably, randomly distributed spawning individuals would have very low fertilization rates. In a laboratory study on the effects of spatial and temporal factors on gamete dilution, Roosen-Runge (1962) has concluded that *Phialidium gregarium* medusae at the time of spawning must be no more than 18 cm apart for 100% fertilization of the eggs. *P. gregarium* medusae 69 cm apart were predicted to have 'practically no offspring'. If, because of strong water currents, full moon, or other disruptive factors, vertical migration is successful only infrequently in concentrating spawning medusae (usually near the surface), this behavior will still probably be an effective means of increasing fertilization success.

Miller (1979) has demonstrated that species-specific egg-sperm chemotaxis is very common, if not virtually universal, in hydromedusae. The eggs of hydromedusae produce a diffusible 'attractant' which is detected by sperm located some distance away, and which serves to direct sperm to swim toward the egg. Such chemotaxis may further enhance fertilization by preventing near misses of much diluted eggs and sperm.

#### *Usefulness of large tank studies*

Jellyfish are well suited to visual observation in large tanks because of their relatively large size. Medusae smaller than 5 mm in bell diameter proved to be difficult to locate in the tank. It may be noted that this minimum convenient size is greater than that of many planktonic organisms, and thereby may limit the value of the present technique.

Previous studies have demonstrated the usefulness of large-scale tower tanks in experimental studies of vertical migration for a variety of organisms including motile phytoplankton (Kamykowski and Zentara, 1977), various zooplankton (Balch *et al.*, 1978; Conover and Paranjape, 1977), pelagic cephalopods (Palmer, 1978; Gould, 1979), and scyphomedusae (Mackie *et al.*, 1981). Tower tanks have the disadvantage of being largely opaque — observations must be made *via* port-holes which provide rather limited fields of view.

The present tank, much smaller than a tower tank, is easily managed by a single person and has the additional advantage that the activities of individual medusae as well as the entire population of medusae can be easily observed at all times through the transparent sides. The 1500 l tank is portable and can be set up very near the collecting site in order to minimize damage incurred by transportation of the animals.

The 1500 l tank proved useful for studying vertical migration of medusae. Intuitively, it was probably most appropriate as a habitat for *G. vertens* and *P. penicillatus*, both of which occur in bays that may be only 1–5 m deep, depen-

ding on the tide. These medusae had the opportunity for nearly as much vertical movement in the tank as is possible in the field. The diel behavior of *G. vertens* in the tank has been corroborated by the observations of SCUBA divers in the field. In the case of medusae that normally occur in deeper water and vertically migrate distances measured in tens of meters, the tank obviously severely limited their vertical movements. Species such as *A. victoria*, *M. cellularia* and *P. gregarium* that spent large amounts of time pulsating against the bottom of the tank would presumably have been moving through the water column for some or all of this time. However, the vertical movements and diel activity patterns demonstrated by these species in the tank appear to be indicative of field behaviors. It is reassuring to note, for instance, that behavior of *A. victoria* in the tank appears to correspond to a known pattern of rising to the surface of the sea in mid-morning, and that plankton tows (Mills, 1982) and underwater observations from a submersible (Mills, unpublished results) in nearby Saanich Inlet, B.C. suggest a reverse vertical migration of *P. gregarium* similar to that seen in the tank.

That the actual process of vertical migration has been observed in the tank is significant. Active swimming of medusae toward the surface in the evening and continuous swimming to maintain themselves high in the water column at night is rather convincing evidence that vertical migration of medusae is an active process rather than a passive one. The possible role of buoyancy regulation in vertical migration of planktonic coelenterates has been suggested several times (Mackie, 1974; Leonard, 1980; Mackie *et al.*, 1981). Although partial exclusion of sulphate ion from the mesogloea fluid may provide buoyancy for medusae (Robertson, 1949; Denton and Shaw, 1962; Mackay, 1969), it has been recently demonstrated that the concentrations of sulphate and other major ions in hydromedusae do not vary on a day/night schedule and therefore that ionic regulation of buoyancy probably does not drive or enhance vertical migration in hydromedusae (Mills, 1982).

By providing a relatively unrestricted environment for captive medusae, the 1500 l tank has been extremely useful for discovering ecological differences between apparently co-occurring species. As described in this paper and is evident from plankton tows, different species may, by preference, occupy different parts of the water column at any one time. Furthermore, each species has a unique small-scale pattern of swimming that both serves to retain that species at its desired vertical position in the water column and determines its feeding behavior and capabilities (Mills, 1981b). Additionally, it was noted that medusae which pulsate apex-down on the bottom may subsequently carry benthic debris on their bells for a while after re-entering the water column. Medusae in this condition are frequently seen in the field and have previously been assumed to be moribund. The possibility of frequent and substantial contacts between medusae and the benthos (at least in shallow waters) and the concomitant effect of medusae as alien predators in benthic communities have not previously been seriously considered.

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