Diversity of Swimming Behaviors in Hydromedusae as Related to Feeding and Utilization of Space

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Abstract

Feeding behaviors of the following 4 species of hydromedusae are described from field and laboratory observations: *Proboscidactyla flavicirrata, Stomotoca atra, Phialidium gregarium* and *Polyorchis penicillatus*. Feeding efficiency of medusae has previously been considered equivalent to fishing with a given amount (combined tentacle length) of adhesive "fishing line"; however, detailed observation shows that behavior of medusae greatly modifies the fishing capacity of each species. It is hypothesized that in addition to (1) tentacle number and length, the following factors strongly influence feeding efficiency: (2) tentacle posture, (3) velocity of tentacles moving through water, (4) swimming pattern of medusa, (5) streamlining effects of medusa bell on water flow, (6) diameter of prey, (7) swimming pattern and velocity of prey. Each species of hydromedusa utilizes the above factors in different combinations.

Introduction

Most hydromedusae are slightly negatively buoyant and must swim to maintain themselves in any preferred portion of the water column. Many hydromedusae have characteristic vertical locations which may change in diel patterns of vertical migration according to species (Russell, 1925; Kramp, 1959; Moreira, 1973; Mills, unpublished data).

It is generally believed that hydromedusae typically feed passively and randomly while swimming or floating with extended tentacles and depend on chance contacts with prey items (Hyman, 1940). If this were strictly true, then feeding efficiency of medusae would be a simple relationship of tentacle length, because prey is captured anywhere along the tentacles by nematocysts. It is shown in the present study, however, that swimming behavior of medusae greatly modifies the "fishing" capacity of each species. Previous studies on feeding by hydromedusae (e.g. Fraser, 1969) have noted differences in modes of prey capture, but have not recognised the importance of swimming patterns to feeding efficiency, presumably because the medusae were confined in small containers. Gladfelter's comprehensive study (1973) of skeletomuscular systems and swimming capabilities in a variety of medusae does not address swimming in terms of large-scale patterns.

In coastal waters of the Northeast Pacific Ocean, hydromedusae are conspicuous members of the zooplankton between April and November (Mills, in press), with over 40 species occurring in the Strait of Georgia and Puget Sound area (near the western Canada-USA boundary). Of these, I describe here the swimming behaviors of 4 common species. It is my purpose to show that, in spite of gross similarities in form, different species of hydromedusae have different swimming patterns. The characteristic pattern of each species is largely responsible for maintaining the medusae in specific portions of the water column and is also related to the unique feeding behavior and capability of the species. Prey selection is beyond the scope of the present study.

Materials and Methods

Medusae of *Proboscidactyla flavicirrata, Stomotoca atra, Phialidium gregarium* and *Polyorchis penicillatus* were observed at the Friday Harbor Laboratories, Friday Harbor, Washington (USA), from a floating dock either during the day or at night by an underwater lamp. Medusae were also hand-collected in plastic beakers from surface waters (obviously damaged individuals were discarded). Captured specimens were observed in a cylindrical transparent Plexiglas tank (approximately 2 m high and 1 m in diameter) filled with natural sea
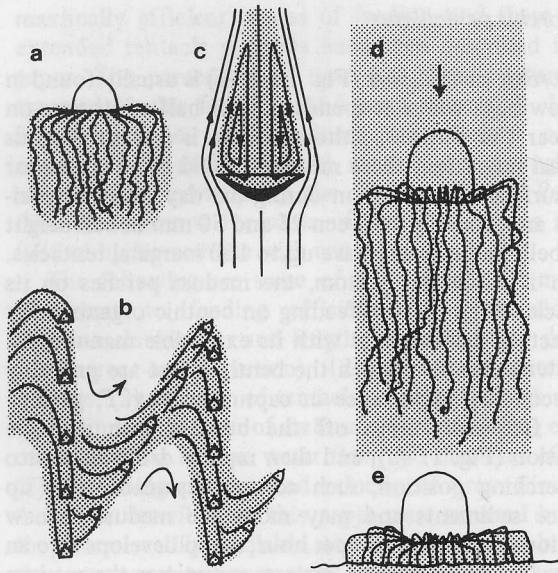
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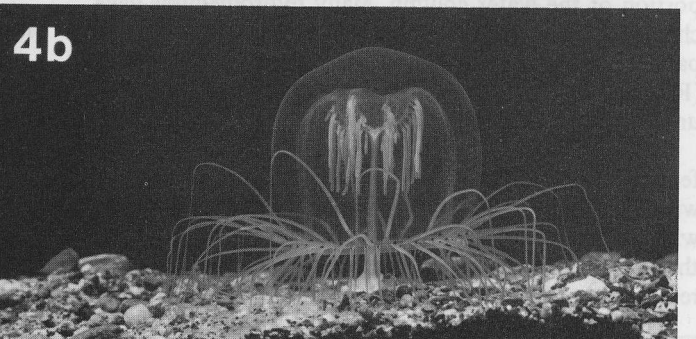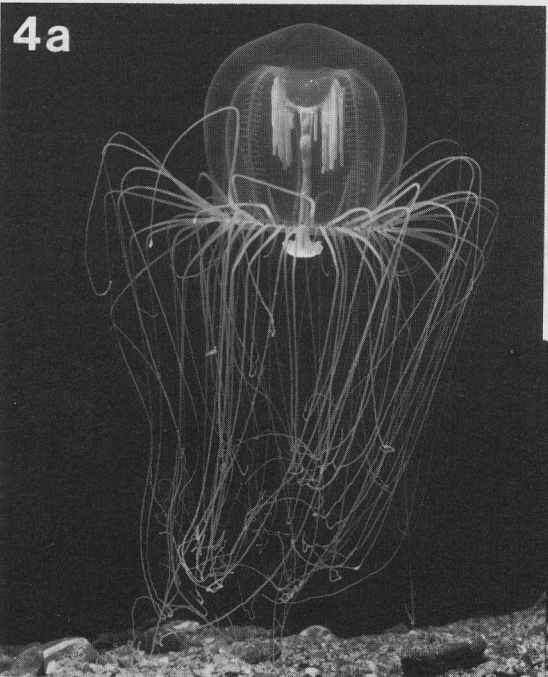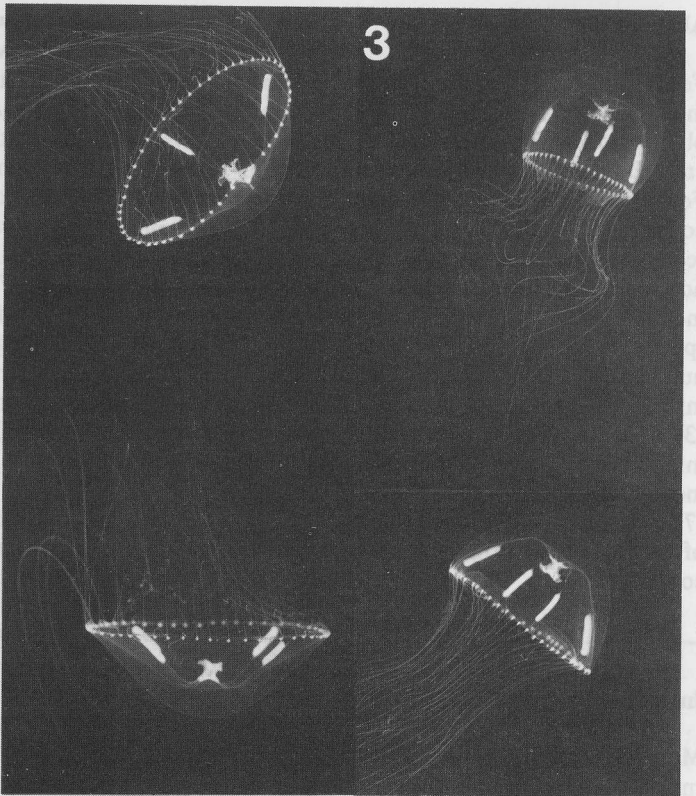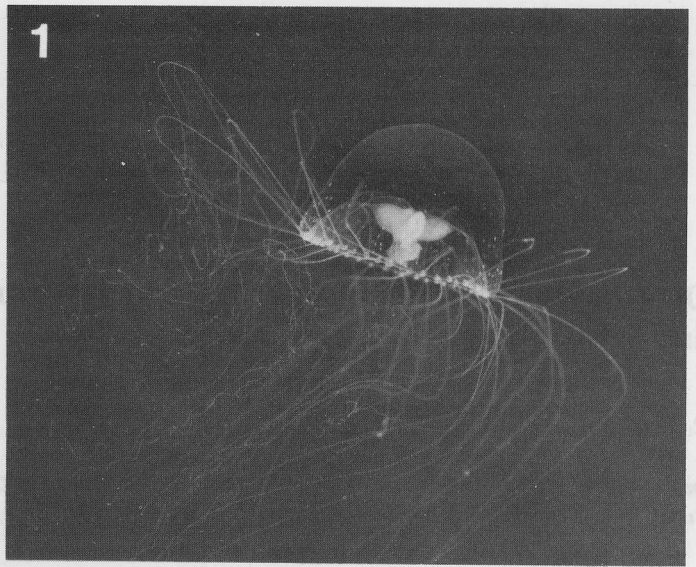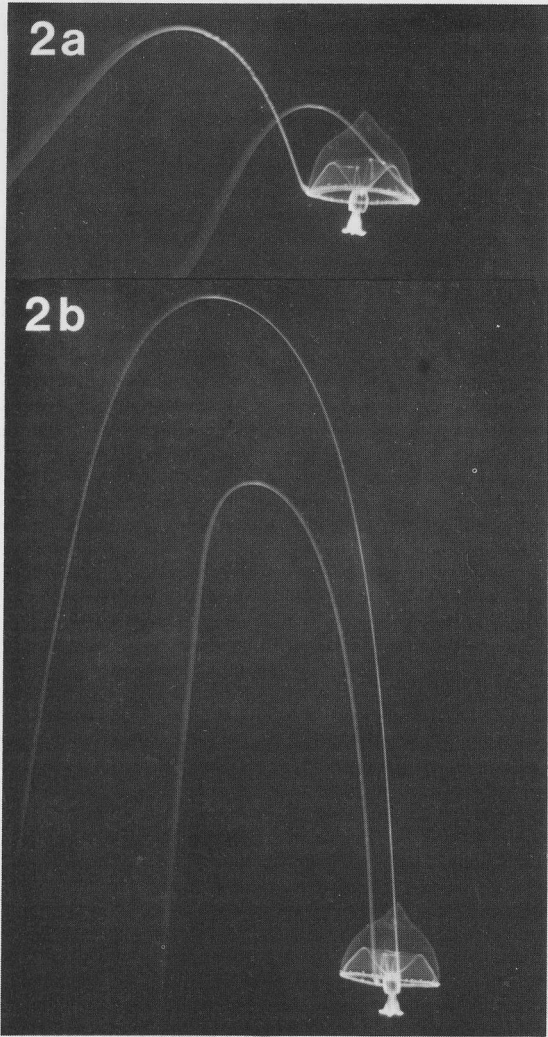
Fig. 2. *Proboscidactyla flavicirrata, Stomotoca atra, Phialidium gregarium* and *Polyorchis penicillatus*. Shaded areas indicate feeding spaces of each species. (a) *Proboscidactyla flavicirrata* remains motionless for long periods, relying on the motion of prey to bring food within the approximately spherical space defined by the tentacles. (b) The swimming-sinking search pattern of *S. atra* traces a sine wave with an amplitude of 1 to 2 m; the 2 tentacles drag through a plane with frontal height of about 1 m, sweeping a much larger volume than is contracted by the medusa bell. (c) Streamlines past a sinking medusa of *Phialidium gregarium* create a dead water space above the bell in which 1 or 2 vortices are set up and rotate past the tentacles and mouth; the sinking medusa thus has access to point samples of plankton after each brief upward swim, when the dead water space is established just prior to the sinking interval. (d) *Polyorchis penicillatus* spends part of the time in the plankton, fishing as it sinks through a cylindrical space. (e) Much of the time, *P. penicillatus* is more or less stationary on the bottom, perching on its tentacles and using its manubrium to capture prey directly beneath the bell

water at 10° to 14 °C and provided with indirect daylight from above. Information about the vertical distribution of medusae was obtained from over 600 plankton tows taken with a closing net in nearby Saanich Inlet, British Columbia, Canada, in the following intervals: 0 to 25 m, 25 to 50 m, 50 to 75 m, 75 to 130 m, and 130 to 180 m. Saanich Inlet is approximately 200 m deep at the sampling location.

Results

Described below are the swimming and feeding behaviors of 4 species of hydromedusae. These medusae vary widely in the importance of tentacle geometry, bell morphology, and swimming patterns to spatial exploitation and putative feeding efficiency in the plankton.

Proboscidactyla flavicirrata

Proboscidactyla flavicirrata (Fig 1: *1*) is neutrally buoyant and reaches a maximum size of 10 mm in bell height and bell diameter. The bell with its thick jelly, always rests with its apex uppermost. This species is a short-range vertical migrator (Mills, unpublished data), and it usually remains in the surface 25 m of the water column. The medusa often remains motionless in the water for periods on the order of 1 h, while the tentacles extend outward and curve down distally. Mature medusae have 40 to 80 tentacles each, extending to a maximum length of 30 mm; thus, the cumulative length of the tentacles is 120 to 240 cm, defining a more or less spherical space of about 25 mm diameter. The static feeding posture of the medusa (Fig. 2a) depends on "random" movements of zooplankton to bring prey into the domain of the extended tentacles. These neutrally buoyant medusae need not swim to maintain themselves in the water column. Thus, in *P. flavicirrata* feeding efficiency is dependent on prey concentrations in the water and on how often a medusa swims to a new location.

Stomotoca atra

Stomtoca atra (Fig. 1: *2a,b*) inhabits surface waters and is also a short-range vertical migrator, maintaining itself near the surface at night. This medusa reaches a maximum size of about 25 mm in bell height and bell diameter and is negatively buoyant, sinking at a rate of approximately 65 cm min^{-1}. Each medusa alternately swims upward at an angle of roughly 30° at a rate of 40 to 90 cm min^{-1}, and sinks passively, its bell tracing a sine wave path of 1 to 2 m amplitude and approximately 2 to 3 min frequency (Fig. 2b). Although this species has no intrinsic ability to steer, its very low center of gravity

◄**Fig. 1.** *1*: *Proboscidactyla flavicirrata*; neutrally buoyant medusa in its typical feeding posture, floating motionless; bell diameter is 7 mm. *2*: *Stomotoca atra*; medusa showing a portion of its swimming sequence (full sequence sketched in Fig. 2); (a) medusa at the peak of an upward swim, just beginning to sink; (b) medusa sinking; bell diameter is 20 mm. *3*: *Phialidium gregarium*; swimming sequence – medusa swims up, turns over and sinks in a bell-downward position, then asymmetric pulsations turn the bell over, it swims up again and repeats sequence; bell diameter is 18 mm. *4*: *Polyorchis penicillatus*; (a) medusa that has momentarily left the benthos by making one bell contraction (in most cases it will return to the bottom immediately, but on occasion it may continue swimming up as far as the surface); (b) medusa in characteristic benthic posture (note manubrium hanging on the substrate for feeding); bell diameter is 30 mm

determines the upward direction of swimming (Mackie and Singla, 1975). There are only two long tentacles, which trail during this repeating swim-sink cycle, fishing through a plane with a projected frontal height of about 1 m. *S. atra* feeds primarily on other medusae, especially *Phialidium gregarium*, which are often 10 to 20 mm in diameter. The comparatively large size of such prey gives the tentacles of *S. atra* effective diameters much greater than their actual widths, as they will contact all prey within one-half of the prey's bell diameter. Effective tentacle diameter therefore becomes 10 to 20 mm, and the maximum extension for both tentacles combined is 2 m. Thus, the search pattern of *S. atra* enables the long tentacles to drag through a much larger volume of water than is contacted by the swimming bell, so that the tentacles fish a planar rather than linear path.

Phialidium gregarium

Phialidium gregarium (Fig 1: *3*) is usually found in the upper 25 m of the water column, where it apparently undergoes a short-range reverse vertical migration. (In a large tank, these medusae always maintain themselves lower in the water column at night than during the day.) This species is somewhat flattened, having a maximum bell diameter of approximately 20 mm and bell height about one-half the diameter. The medusa is usually slightly negatively buoyant and sinks upside down, with the bell preceding the tentacles at a rate of about 120 cm min^{-1}; by some mechanism that is not understood, the medusa may become nearly neutrally buoyant at times. Like *Stomotoca atra*, *P. gregarium* repeatedly sinks and swims back up, but this behavior does not result in the systematic type of searching accomplished by *S. atra*. In a large tank, *P. gregarium* sinks upside down for 1 to 2 min, then turns over by asymmetric pulsations of the bell, and rapidly swims upward at about 180 cm min^{-1} for distances up to 2 m before again turning upside down passively and beginning to sink. The trailing tentacles presumably provide stability so that sinking occurs without wobble. Each time the medusa turns over to begin sinking, a pocket of water is established in the dead space behind the bell that is created by streamlining. Hydrodynamic theory predicts that the slow falling of the medusa sets up 1 or 2 gentle vortices in this dead water space that will circulate this water past the tentacles (Fig. 2c). With its tentacles remaining primarily within the dead space, *P. gregarium* presumably exhausts a small volume of water of its prey. Intermittent upward excursions of the medusa both establish new static feeding spaces and maintain the negatively buoyant medusa in surface waters. Since this species sinks more slowly than it swims, it spends most of its time upside down, as has been observed by SCUBA divers near Friday Harbor. The maximal tentacle extension is 3 cm; with 60 tentacles, a mature medusa has 1.8 m total tentacle length, but the streamlining effects of falling upside down appear to be more relevant than tentacle length in determining feeding efficiency.

Polyorchis penicillatus

Polyorchis penicillatus (Fig. 1: *4a, b*) is usually found in shallow bays where it spends at least half of its time on or near the bottom; although there is not an obvious vertical migration, these medusae spend more time near the surface at night than during the day. Mature specimens are generally between 25 and 50 mm in bell height and bell diameter and have up to 160 marginal tentacles. When it is on the bottom, the medusa perches on its tentacles (Fig. 1: *4b*), feeding on benthic organisms by contacting the sediment with its extensible manubrium. The tentacles also touch the benthos, but are probably of secondary importance in capturing prey. *P. penicillatus* frequently hops off the bottom with a single pulsation (Fig. 1: *4a*), and then rapidly drops back into its perching position; such action presumably stirs up surface sediments and may move the medusa to new locations. Several times per hour, a hop develops into an upward swim of several meters; sometimes the medusa swims all the way to the surface (1 to 5 m above) at a rate of 100 to 180 cm min^{-1}. From the surface, it then slowly drifts back down with its tentacles in advance, evidently capturing planktonic prey. *P. penicillatus* falls at a minimum speed of 15 to 20 cm min^{-1} when its tentacles, which have considerable drag, are fully extended. Partially contracted tentacles proportionately increase the sinking rate and medusae with fully contracted tentacles may sink at 35 cm min^{-1}. While sinking, these medusae generally pulsate once or twice about every 30 s. This activity repositions the bell (which tends to sink more rapidly then the tentacles) for what is presumably the most efficient feeding posture. Maximal tentacle extension is approximately 150 mm; with 160 tentacles, this species has 22.5 m of total tentacle length. As it sinks, *P. penicillatus* fishes in a cylindrical path about 10 cm in diameter (Fig. 2d). Since the tentacles fall ahead of the bell, streamlining effects of the bell are not important for food capture. Individual medusae of *P. penicillatus* in the large tank spend approximately 65% of the time at the bottom and 35% of the time in the water column (Fig. 2d, e); for this species, calculations of feeding capacity must take into account both the benthic and the planktonic modes of feeding.

Discussion

Feeding efficiency of hydromedusae is not clearly related to any single parameter such as size of medusa or tentacle number. Certainly the total tentacle length is important, yet tentacle extension is controlled by the medusa according to circumstances that are not well understood. In the field, medusae near the surface often have their tentacles either partially or wholly contracted during the day or night. In the large tank, after several days without food, most medusae have their tentacles extended, often to lengths rarely seen in the field. Presumably starvation causes medusae to assume their

maximally efficient modes of feeding, and these fully-extended tentacle postures have been described in this paper. The percentage of time that these postures are assumed in the field is not known at present. Unlike Scyphomedusae, hydromedusae cannot feed continuously. Indigestible material must leave through the mouth, thus interrupting the feeding process. Perhaps this fact accounts for some of the observations in the field of hydromedusae with contracted tentacles.

The following are some of the factors that may be important to feeding efficiency in hydromedusae: (1) tentacle number and length (extension may depend on degree on starvation), (2) geometry of tentacle posture, (3) velocity of tentacles moving through water, (4) swimming pattern of medusa, (5) streamlining effects of the medusa bell on water flow, (6) diameter of prey, (7) swimming pattern and velocity of prey. Since the 4 species described in this paper were selected because they were readily available, and not necessarily because they represent extreme cases of difference, it can be assumed that further studies on feeding or plankton-clearing rates involving medusae must include a detailed understanding of the species involved. Each species of hydromedusa evidently utilizes the above-mentioned factors in different combinations, resulting in unique patterns of spatial exploitation in feeding.

Hydromedusae have simple nervous systems, composed of interconnected differentially concentrated nerve nets that interact with conducting epithelia. Although a brain and large ganglia are absent, there are concentrations of nerves that generate endogenous rhythms such as the pulsation pacemaker. This type of nervous system permits only a very limited behavioral repertoire. The wide range of feeding and swimming behaviors of hydromedusae which result in such varying types of spatial utilization are simply the product of different medusa morphologies and different pulsation patterns driven by a pacemaker.

Haury and Weihs (1976) have analyzed and compared the energetics of "hop and sink" swimming with hovering for negatively buoyant zooplankton. The oscillating swimming patterns of Stomotoca atra and Phialidium gregarium might be considered to be hop and sink behaviors, but a comparison of cost with hovering would be difficult for medusae. Medusae that hover (e.g. Proboscidactyla flavicirrata), generally do so by neutral buoyancy rather than by continuously swimming ("treading water"). Probably all pelagic Cnidaria and Ctenophora (Denton and Shaw, 1962; Mackay, 1969; Bidigare and Biggs, 1980; Mills, unpublished data) offset some of the weight of their proteinaceous tissues by an epithelial active transport system excluding relatively heavy sulphate ions from the mesogloea. Different species of hydromedusae vary in the concentration of sulphate in their mesogloea (from 8 to 85% of the sulphate in seawater: Mills, unpublished data). This, coupled with other chemical or morphological buoyancy systems, results in different degrees of buoyancy and differentiation of habitats for each species. The energetic demand of molecular regulation of buoyancy has not been measured.

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