



## FAU Institutional Repository

<http://purl.fcla.edu/fau/fauir>

This paper was submitted by the faculty of [FAU's Harbor Branch Oceanographic Institute](#).

Notice: ©1988 Academic Press Inc. (London) Limited in association with the Estuarine and Brackish-water Sciences Association. The final published version of this manuscript is available at <http://www.sciencedirect.com/science/journal/02727714> and may be cited as: Larson, R. J. (1988). Feeding and Functional Morphology of the Lobate Ctenophore *Mnemiopsis mccradyi*. *Estuarine, Coastal and Shelf Science*, 27(5), 495-502. doi:10.1016/0272-7714(88)90080-7

## Feeding and Functional Morphology of the Lobate Ctenophore *Mnemiopsis mccradyi*

**R. J. Larson**

Harbor Branch Institution, 5600 Old Dixie Highway, Fort Pierce, FL 34946, U.S.A.

---

**Keywords:** Ctenophora; feeding

In the laboratory, specimens of *Mnemiopsis mccradyi* caught prey during vertical foraging when their preoral lobes were expanded. The site of prey entrapment depended mostly on prey size and activity. Relatively small (0.2–0.5 mm) inactive nauplii were caught mostly by the tentacles which number in the thousands. Larger (1–2 mm) more active copepods were caught on the inner surfaces of the expansive preoral lobes by viscous mucus. The lobes generally closed in response to contact by active copepod prey, thus reducing the possibility of escape. Prey were transported from the lobes, by cilia, directly to the mouth, or to the labial grooves and then to the mouth. By having two different prey-capturing mechanisms, *Mnemiopsis* can feed on a greater range of prey sizes than if it had only one mechanism.

### Introduction

Lobate ctenophores of the genus *Mnemiopsis*, *M. mccradyi* and *M. leidyi*, may be the major predators of mesozooplankton (e.g., bivalve larvae, barnacle nauplii, copepods) in inshore waters between Rhode Island and Florida (Miller, 1970; Reeve & Baker, 1975; Burrell & Van Engel, 1976; Kremer, 1976, 1979; Deason, 1982; Larson, 1987). Although many aspects of the trophic biology of these ctenophores have been investigated (see Reeve & Walter, 1978), no detailed behavioural studies have been made on prey capture or on the functional morphology of the feeding structures. Furthermore, despite the fact that prey are caught by both the preoral lobes and tentacles (Main, 1928; Reeve & Walter, 1978), it is not known whether these structures are equally important or whether they exhibit prey selection. Therefore, a study was made of the feeding behaviour of *Mnemiopsis mccradyi* (an abundant, nearshore ctenophore along the coast of Florida). The results of this investigation are compared with those of previous studies.

Some aspects of the morphology and behaviour of *Mnemiopsis* are presented in Mayer (1912), Main (1928), and Reeve and Walter (1978). Additional descriptions of lobate morphology and behaviour appear in Harbison *et al.* (1978), Schulze-Robbecke (1984), and Matsumoto and Hamner (1988). This study deals only with the functional morphology and behaviour of the lobate stage of *M. mccradyi*.

## Methods

Specimens of *Mnemiopsis mccradyi* were collected during April 1986 at Link Port, an artificial harbour 10 km north of Fort Pierce, Florida, on the Indian River estuary. Here, ctenophores were very abundant in the upper 1 m, reaching a displacement volume of  $300 \text{ ml m}^{-3}$  during the second week of April. Animals were dipped from the surface using a beaker, and within 15 min were transported to the laboratory where they were maintained in filtered seawater at a temperature of 22–23 °C. In situ water temperatures ranged from 22 °C to 25 °C. Zooplankton prey were collected daily using a 0.2 mm mesh plankton net. Prey consisted mostly of adult *Acartia tonsa*, nauplii of barnacles, and unidentified fish eggs and larvae. In addition, *Artemia* sp nauplii were also presented to the ctenophores.

Trophic interactions were observed by placing ctenophores in a cylindrical, glass aquarium (40 cm high  $\times$  30 cm in diameter). Horizontal lines placed at depth intervals of 5 cm on the back of the aquarium allowed for determination of the vertical positions of the ctenophores. Approximate ctenophore vertical swimming velocities were determined with the aid of a stopwatch. The tank was placed in a dimly lit room, backlit with diffuse skylight. This backlighting and the magnification caused by the curvature of the tank allowed for detailed observations of the ctenophores and prey, even small barnacle nauplii (0.3 mm in length) could be readily seen. Observations of tentacle and labial ridge behaviour were made with the aid of a dissecting microscope.

## Results

### *Functional morphology*

The main prey-catching structures of *Mnemiopsis mccradyi*, in the lobate stage, are the preoral lobes and the secondary tentacles (Figure 1). The inner surfaces of the paired, convex, paddle-shaped lobes are highly muscular, with numerous muscle fibres forming a rectangular quiltwork. During prey capture the contraction of these muscles causes the lobes to close tightly (Plate 1). The lobes are well ciliated and produce copious amounts of apparently sticky and viscous mucus. In the foraging posture the lobes are expanded, by muscles, forming a cylindrical preoral cavity anterior to the mouth (Figure 1 and Plate 1).

Between the preoral lobes and on either side of the mouth are two pairs of triangular auricles (Figure 1). Ciliary bands, on the lateral margins of the auricles, produce a water current that moves water and contained prey through the preoral chamber. The outer (abaxial) ciliary bands continue along the body, opposite the tentacles, to the level of the posterior gut. They produce a vortex that moves particles in a spiral of decreasing diameter posteriorly. This swirling motion draws the tentacles out and may increase the probability that prey will impact onto the tentacles.

On each side of the large, laterally flattened mouth, and extending posteriorly in a broad arch, are the four labial ridges which are formed by four shelf-like extensions of the lips (0.3–0.6 mm broad) (Figure 1). The ridges also extend abaxially past the corners of the mouth and meet near the midline adjacent to the sheaths of the degenerated primary tentacles.

On each side of the ridges are grooves. On the abaxial sides are the labial gooves, extending about two-thirds the total length of an animal. The grooves are ciliated and transport prey from the tentacles and posterior part of the preoral lobes to the mouth. Adaxial to the labial ridges are four grooves containing the numerous, but small secondary tentacles (10–20  $\mu\text{m}$  in diameter and 2–5 mm long) which are contractile and which are covered with numerous colloblasts.

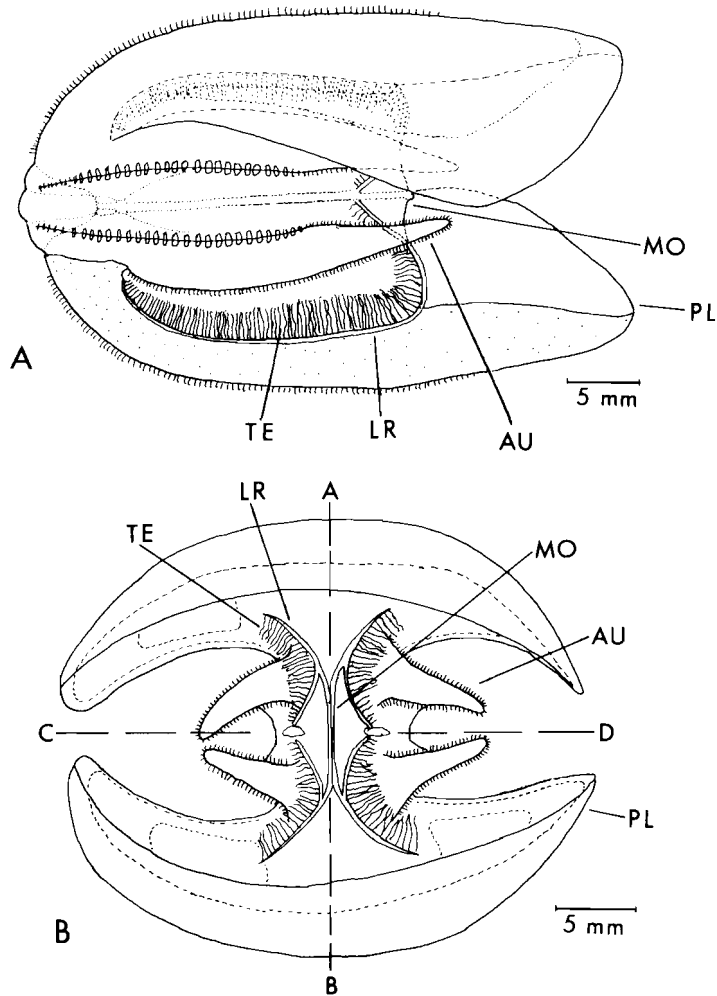


Figure 1. Morphology of *Mnemiopsis mccradyi*. (A) Diagrammatic side-view (of the oral plane). Note: part of the right preoral lobe is removed to show labial ridge and tentacles. AU = auricle; LR = labial ridge; MO = mouth; PL = preoral lobe; TE = tentacles. (B) Diagrammatic frontal view of *Mnemiopsis* in foraging position showing preoral chamber. Dashed lines: AB = oral plane; CD = auricular plane.

The tentacular grooves extend anteriorly to the tentacular sheaths of the resorbed primary tentacles. Along the anterior part of the groove there are few tentacles ( $1\text{--}5\text{ mm}^{-1}$ ), but posteriorly they become more numerous ( $25\text{--}50\text{ mm}^{-1}$ ). A 3-cm long ctenophore has about 500 tentacles per groove (about 2000 tentacles total); a 6-cm animal has about double this number.

#### *Foraging behaviour*

In the laboratory the foraging behaviour of *Mnemiopsis* consisted either of swimming (with the mouth forward) or of stationary hovering (with the mouth downward). During

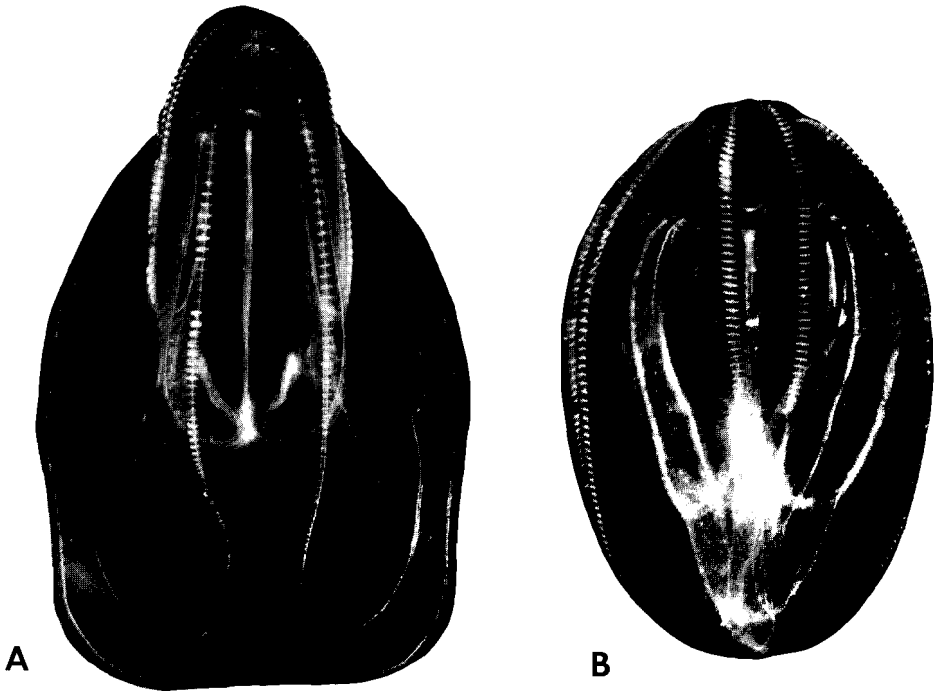


Plate 1. In-life photos of *Mnemiopsis mccradyi*. (A) Side-view (auricular plane) of a 5 cm long specimen in the foraging position with the preoral lobes fully open. (B) Side-view (oral plane) of a 4 cm long specimen which has closed its preoral lobes in response to a copepod.

either manoeuvre, the preoral lobes were widely spread in a prey-capture position (Figure 1), being held open by the muscles and by the elasticity of the mesogloea.

*Mnemiopsis* foraged mostly vertically, only a small fraction ( $< 2\%$ ) of the total foraging time being spent swimming horizontally—when an animal was tangential to, or parallel to, the water surface. Most of the time the ctenophores were oriented vertically: (1) swimming up or down, (2) hovering in the water column, or (3) swimming against the water–air interface or against the bottom. Some animals (15% of 52) did not forage at all, but instead swam downward against the bottom. Other specimens swam upwards at the surface. Of the time that was spent in the water column, hovering occupied 8% of the time and vertical swimming 92%.

Hovering behaviour (with the mouth usually orientated downward) apparently occurred when a slow forward motion of the ctenophore, produced by the auricles, was offset by rearward propulsion from the eight locomotory ciliary bands. Such posturing resulted in the formation of a weak inflowing current which drew water and prey into the preoral cavity. Ctenophores that had become inactive due to starvation spent most of their time hovering, suggesting that it may be an energy-conserving form of behaviour.

Ctenophore swimming velocities were highly variable, depending on the size of the ctenophore and its physiological state. Maximum cruising velocities of foraging *Mnemiopsis* ranged from 0.2 to 1.2 cm s<sup>-1</sup>, depending on size, and within the spatial constraints of the tank. The highest swimming speed (2 cm s<sup>-1</sup>) was measured for a

non-foraging animal (6 cm long) apparently in a disturbed state, since its lobes were tightly closed.

### Prey Capture

Zooplankton prey of foraging *Mnemiopsis mccradyi* were captured either by the preoral lobes or by the tentacles, depending on size and behaviour of the prey. Active prey (e.g. copepods) were readily caught by either structure, whereas relatively inactive and usually smaller prey (e.g. nauplii, fish eggs) were captured mostly by the tentacles.

Observations of trophic interactions (observed interactions = > 165) between foraging ctenophores and cruising copepods (i.e. *Acartia tonsa* adults, 1 mm total length) revealed that when the copepods were within 0.5–1 cm of the lobes or auricles they generally showed an increase in swimming speed, possibly because they sensed the presence the current created by the auricles. The copepods then: (1) escaped by swimming in front of the ctenophore, (2) impacted the lobes and were caught, (3) escaped between the lobes after impact, and/or (4) contacted a lobe and temporarily escaped but then became entangled in the tentacles.

Of 165 observed physical contacts between ctenophores and copepods, 62% occurred on the lobes and 26% on the tentacles; 12% were of undeterminable location. Observed interactions ( $n=117$ ) between ctenophores and *Artemia* nauplii (0.5 mm TL), which showed no obvious escape response and swam at a relatively low velocity, revealed that the *Artemia* were captured mostly by the tentacles (74%). However, if the nauplii contacted the inside margin of a lobe they were often trapped by the infolding of the margin (16%) or, more rarely, on other parts of the lobe (10%). Barnacle nauplii (0.1–0.3 mm) (observations,  $n=16$ ) were also captured mostly by the tentacles. Apparently neither the *Artemia* nor the barnacle nauplii contacted the lobes with sufficient impact to produce lobe closure. Instead, they often passed between the auricles and escaped. (Note: 66% of those nauplii that entered the preoral chamber escaped.) Unidentified fish eggs (0.3 mm) (observations,  $n=9$ ) were either caught on the tentacles or else passed between the auricles and were not captured. Unidentified fish larvae (5–8 mm long) (observations,  $n=12$ ) were caught either by the tentacles or by the lip-like margins of the lobes. Although most of the larvae contacted the lobes, none adhered to the mucus.

The auricles performed an active, although minor, role in prey capture by deflecting passing prey inward. For instance, *Artemia* that had contacted an auricle caused it to bend inward slightly, moving the nauplii adaxially toward the tentacles.

The lobes responded mainly to impinging copepods. If contact was made near the lip-like margin of the lobe, the margin rapidly curled inward, enfolding and thus trapping the prey. If contact was made elsewhere, the lobes rapidly moved together, their margins bending inwards (approximately perpendicular to the longitudinal axis) and coming together, effectively closing the preoral cavity. This trapping behaviour was rapid (lasting only 2–5 s), after which time the lobes reopened in a foraging position. *Mnemiopsis* were very sensitive to tactile stimulation, and showed this closing behaviour in reaction to most physical disturbances.

Copepods that impinged on the lobes became entangled in the surface layer of mucus. Apparently the momentum produced by the relatively rapid escape velocity of the copepods causes them to penetrate the mucus (which probably has considerable surface tension) and become embedded within it. The apparently high viscosity of the mucus effectively immobilizes small crustacean prey. There was no evidence that colloblasts played any role in prey capture by the preoral lobes; indeed, I could not find colloblasts on the lobes.

Smaller prey (e.g., nauplii) generally did not impinge on the lobes, possibly because flow over their surfaces is laminar (Reynolds number = 200–300). Additionally, these smaller prey probably lack the momentum necessary to penetrate into the mucus.

The tentacles, when viewed under magnification, were also highly responsive to tactile stimulation, and showed continuous spontaneous twitching in addition to complete contracting activity.

Whether caught on the tentacles or on the lobe, prey were transported via cilia to the mouth. Prey were transported to the stomach within minutes of capture. Those trapped on the lobes in front of the mouth were swept (at velocities of 0.1–0.3 mm s<sup>-1</sup>) directly to the mouth. Those prey caught on the lobes posterior to the mouth, or on the tentacles, were moved to the labial grooves (at velocities of 0.1–0.2 mm s<sup>-1</sup> in the posterior portion, and at 0.5–0.7 mm s<sup>-1</sup> in the anterior portion), and then transported to the mouth. The cilia apparently always beat in the same direction: those that covered the inner surfaces of the anterior lobes and the labial grooves always beat toward the mouth; those that covered the posterior lobes always beat toward the labial grooves. Many prey can be caught simultaneously and moved to the stomach.

Particle selection (separation of food from non-food) was done by the lip-like folds of the grooves and by the lips of the mouth (which are continuous with one another). This ensures that only food enters the grooves and the mouth. Nonetheless, some non-food items, mixed with the mucus surrounding prey, do enter the stomach.

### Discussion

The feeding mechanisms of adult lobate ctenophores are highly evolved and fall into two categories. In one category prey are caught on preoral lobes only, while in the other category both lobes and secondary tentacles capture prey (Harbison *et al.*, 1978; Reeve & Walter, 1978). In most species, including *Mnemiopsis*, the feeding mechanism is of the second type. The relative importance of the lobes *vs.* the tentacles apparently depends on the swimming ability and size of the prey. Active and relatively large prey, e.g., copepods, are trapped mostly by the lobes because they impact with sufficient speed to become entangled in the mucus and/or cause lobe closure or curling. Relatively inactive prey, e.g., nauplii and eggs, bypass the lobes and are swept into the tentacles where they are trapped. By using both prey-capture mechanisms, *Mnemiopsis* is able to feed on a greater variety of prey than if it used only one mechanism.

Are these mechanisms consistent with encounter theory? To increase the rate at which prey are encountered, a contact predator can (1) increase its feeding surface area, (2) increase its velocity, and/or (3) feed on larger and faster prey (Gerritsen & Strickler, 1977). Probably because of energy constraints, lobates apparently have not adopted a fast swimming mode; however, they have utilized the other two strategies.

If the relative development of tentacles *vs.* preoral lobes in lobates is a function of the availability of prey of different sizes, then it would be expected that lobate morphology would vary with prey size. This seems to be the case. Where small prey predominate (inshore waters) tentacles should be important (e.g. *Mnemiopsis*), whereas where prey are generally larger (offshore waters) the lobes would be more significant (e.g. *Ocyropsis*, where tentacles are absent). In fact, lobate ctenophores that depend only on lobes for prey capture are limited to oceanic species.

As pointed out by Schulze-Robbecke (1984), the morphology and behaviour of the secondary tentacles is unclear in the literature. In *Mnemiopsis* the numerous tentacles are

separate from one another. The possibility that they function primarily as chemosensory structures in *Bolinopsis* because of their fragility (Schulze-Robbecke, 1984) is doubtful, since Nagabhushanam (1959) reported that the tentacles do capture prey. In *Mnemiopsis* the tentacles are also fragile, but this is probably necessary for the capture of small prey, e.g. copepod nauplii. Functionally the tentacles act as filters which remove prey particles from the water by direct interception and inertial impaction (Rubenstein & Koehl, 1977).

The importance of the preoral lobes as enlarged prey-capturing surfaces has been noted previously (Harbison *et al.*, 1978; Reeve & Walter, 1978; Schulze-Robbecke, 1984; Matsumoto & Hamner, 1988). Additionally, they also serve as a funnel to direct water (pulled by the auricles) into the preoral cavity. This probably reduces the escape of prey by ensuring that they are nearly surrounded by the lobes before they can detect the ctenophore.

The ability of *Mnemiopsis* and some other lobates to ingest food almost continuously, even at very high prey densities (Reeve *et al.*, 1978; Kremer, 1979), suggests that they might be adapted to environments where prey densities may sometimes become high. However, for *Mnemiopsis* and *Bolinopsis*, available data on gut contents ( $n$ =several hundred) (Walter, 1976; Kremer *et al.*, 1986; Larson, 1987), suggest that ingestion rates are generally low, averaging about 1–2 prey  $\text{min}^{-1}$  for *Mnemiopsis mccradyi* and even less for *Bolinopsis vitrea*. The lack of evidence from field studies for high rates of ingestion suggests that the ability of *Mnemiopsis* and *Bolinopsis* to feed continuously is only a secondary result of their feeding method rather than its primary purpose. No doubt rapid ingestion of many prey by lobates does take place, as is suggested by the large gut size capable of holding hundreds of prey in adult *Mnemiopsis*; however, this is yet to be documented. Hamner *et al.* (1987) however, present some interesting data on gut contents which suggest that *Leucothea* may have high ingestion rates in situ, but data are lacking on actual rates.

More observations are needed on the behaviour of lobates. Most previous laboratory studies on feeding have not examined feeding behaviour but have mostly quantified feeding by measured changes in prey densities. Field data are few. The probable significance of lobates as consumers of zooplankton in a variety of environments is such that a better understanding of their functional morphology, behaviour, and possible evolution are needed.

### Acknowledgements

I would like to thank G. R. Harbison and K. S. Larson for providing helpful comments on manuscript. Harbor Branch Institution provided financial support. This is contribution no. 633 of Harbor Branch Oceanographic Institution.

### References

- Burrell, V. G. & Van Engel, W. A. 1976 Predation by and distribution of a ctenophore *Mnemiopsis leidyi* A. Agassiz, in the York River. *Estuarine, Coastal and Shelf Science* **4**, 235–242.
- Deason, E. E. 1982 *Mnemiopsis mccradyi* in Narragansett Bay, 1975–1979: abundance, size composition, and estimation of grazing. *Estuarine, Coastal and Shelf Science* **15**, 121–134.
- Gerritsen, H. & Strickler, J. R. 1977 Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of the Fisheries Research board of Canada* **34**, 73–82.
- Hamner, W. M., Strand, S. W., Matsumoto, G. I. & Hamner, P. P. 1987 Ethological observations on the foraging behavior of the ctenophore *Leucothoe* sp. in the open sea. *Limnology and Oceanography* **32**, 645–652.



- Harbison, G. R., Madin, L. P. & Swanberg, N. R. 1978 On the natural history and distribution of oceanic ctenophores. *Deep-Sea Research* **25**, 233–256.
- Kremer, P. 1976 Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. In *Estuarine Processes* (Wiley, M. L., ed.), Vol. 1. Academic Press, NY, pp. 197–215.
- Kremer, P. 1979 Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Estuaries* **2**, 97–105.
- Kremer, P., Reeve, M. R. & Syms, M. A. 1986 The nutritional ecology of the ctenophore *Bolinopsis vitrea*: comparisons with *Mnemiopsis mccradyi* from the same region. *Journal of Plankton Research* **8**, 1197–1208.
- Larson, R. J. 1987 In situ feeding rates of the lobate ctenophore *Mnemiopsis mccradyi*. *Estuaries* **10**, 87–91.
- Main, R. J. 1928 Observations of the feeding mechanism of the ctenophore, *Mnemiopsis leidyi*. *Biological Bulletin* **55**, 69–78.
- Matsumoto, G. I. & Hamner, W. M. 1988 Modes of water manipulation by the lobate ctenophore *Leucothoe* sp. *Marine Biology* **97**, 551–558.
- Mayer, A. G. 1912 *Ctenophores of the Atlantic Coast of North America*. Carnegie Institute, Washington DC. 58 pp.
- Miller, R. J. 1970 Distribution and energetics of an estuarine population of the ctenophore, *Mnemiopsis leidyi*. PhD Thesis, North Carolina State University. 85 pp.
- Nagabhushanam, A. K. 1959 Feeding of a ctenophore, *Bolinopsis infundibulum* (O. F. Müller). *Nature* **4689**, 829.
- Reeve, M. R. & Baker, L. D. 1975 Production of two planktonic carnivores (chaetognath and ctenophore) in south Florida inshore waters. *Fishery Bulletin* **73**, 238–247.
- Reeve, M. R. & Walter, M. A. 1978 Nutritional ecology of ctenophores—a review of recent research. *Advances in Marine Biology* **15**, 249–287.
- Reeve, M. R., Walter, M. A. & Ikeda, T. 1978 Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. *Limnology and Oceanography* **23**, 740–751.
- Rubenstein, D. I. & Koehl, M. A. R. 1977 The mechanisms of filter feeding: some theoretical considerations. *American Naturalist* **111**, 981–994.
- Schulze-Robbecke, A. C. 1984 Functional morphology of *Bolinopsis infundibulum* (Ctenophora). *Helgolander Meeresuntersuchungen* **38**, 47–64.
- Walter, M. A. 1976 Quantitative observations on the nutritional ecology of ctenophores with special references to *Mnemiopsis mccradyi*. MS Thesis, University of Miami. 70 pp.