

## The nutritional ecology of the ctenophore *Bolinopsis vitrea*: comparisons with *Mnemiopsis mccradyi* from the same region

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**Abstract.** *Bolinopsis vitrea* is a warm water lobate ctenophore which does not overlap in its distribution with *Mnemiopsis mccradyi* in contiguous waters. We examined its feeding ecology on a series of cruises. *B. vitrea* ingested increasingly more prey at higher food concentrations ( $2-100$  prey  $l^{-1}$ ) but feeding effort (clearance rate) decreased with increasing food availability. On a dry weight basis, smaller tentaculate *Bolinopsis* ingested several times more than larger lobates, but based on carbon weight, specific ingestion was fairly uniform over the entire size range investigated ( $6-60$  mm total length). *Bolinopsis* collected during the daytime in the Bahamas rarely had more than three prey items in their guts. These results and laboratory measurements of digestion times (av. = 1.9 h) allowed computation of daily rations, which could not account for the metabolic requirement as measured on the same cruises. Results of feeding experiments, however, implied that prey densities in excess of  $1 l^{-1}$  were sufficient to sustain a growing population of *Bolinopsis*. Prey concentrations about an order of magnitude higher were required for *M. mccradyi* based on similar experiments. These results were in general agreement with observed densities and distributions of ctenophores and their zooplankton prey in the Bahamas and coastal South Florida.

### Introduction

*Bolinopsis vitrea* was considered by Mayer (1912) to be the commonest ctenophore in Florida – Bahamian waters. Its close relative, *Mnemiopsis mccradyi*, which is similar in size and physical appearance is also found in this general region. Though both occur typically in shallow neritic waters, we have never known their habitats to overlap in over 10 years of observations of south Florida and Bahamian waters. *Bolinopsis* generally occurs in clearer, more open waters, which are presumably less productive and which vary less seasonally in temperature and salinity. These include the reef environments outside Biscayne Bay, along the Florida Keys to the Dry Tortugas, and at several locations in the Bahamas. *Mnemiopsis* is commonly found in the more turbid, relatively eutrophic waters of Biscayne Bay and other estuaries of the Southeast United States. Mayer (1912) mentioned *Mnemiopsis* as occurring in Charleston Harbor, South Carolina, and Kingston Harbor, Jamaica.

*B. vitrea* is a fragile species, and although we have maintained it and its spawned larvae for several days in the laboratory, it cannot tolerate frequent handling. *M. mccradyi*, on the other hand, by virtue of 'the extraordinary rigidity of its gelatinous substance' (Mayer, 1912), is easily cultured in the laboratory over long periods, whether in water from its own habitat or from that of *Bolinopsis*. Both these species of lobate ctenophores sometimes occur in dense patches and both are prey for the predatory ctenophore *Beroë ovata* (Swanberg, 1974; personal observation).

During the past several years we have accumulated a large body of information on

the ecology of *Mnemiopsis* spp., both experimentally and in the environment. These studies include data on abundance and production (Reeve and Baker, 1975; Kremer and Nixon, 1976), nutritional ecology (Reeve *et al.*, 1978; Kremer, 1979; Reeve, 1980b; Stanlaw *et al.*, 1981), and metabolism (Kremer, 1977, 1982). We subsequently became interested in the nutritional ecology and metabolism of *B. vitrea*, a neritic but not estuarine species. Because of its delicate nature, hand collection, and shipboard experimentation, were the only practical methods for *Bolinopsis*. We made a series of Fall and Spring cruises to the Bahamas and Florida Keys during 1982–85, aboard O.R.V. *Calanus*, a small ship designed for shallow water research. Inevitably, the range of the measurements and experiments for *Bolinopsis* were not as great as for *Mnemiopsis*, but the experimental approach was similar.

The emphasis of this paper is the nutritional ecology of *B. vitrea*, and where appropriate, comparison with *M. mccradyi*. The detailed results of concurrent metabolic studies on *B. vitrea* are presented elsewhere (Kremer *et al.* 1986).

## Methods

*Bolinopsis* were collected in hand-held plastic jars. The methods and procedures used for feeding experiments in this study were similar to those used previously (Reeve *et al.*, 1978). Ingestion rates were measured from the difference in the number of copepods in experimental and control tanks. The prey (200–330  $\mu\text{m}$  screened size fraction) was typical of what was observed to be ingested by the ctenophores and was an intermediate size of the zooplankton available as prey. Tank volumes ranged from 20 to 50 l and experimental prey concentrations from 2 to 200  $\text{l}^{-1}$ . Numbers of ctenophores and feeding times were varied for the experiments in order to produce measurable changes in the prey, but were usually 4–12 h. For prey concentrations of 20 copepods  $\text{l}^{-1}$  and less, prey organisms were counted out individually. For higher prey densities, appropriate aliquots of a pre-counted concentrated stock were used, with at least one control tank to check for accuracy of the aliquoting method.

Gut contents were determined for freshly caught ctenophores within 5 min of collection. Since the body tissues of *Bolinopsis* are transparent, it is possible to count the number of ingested prey using a dissecting microscope without damaging the ctenophores. The gut residence time of food was measured experimentally by serial microscopic observation of ctenophores that had been allowed to feed briefly.

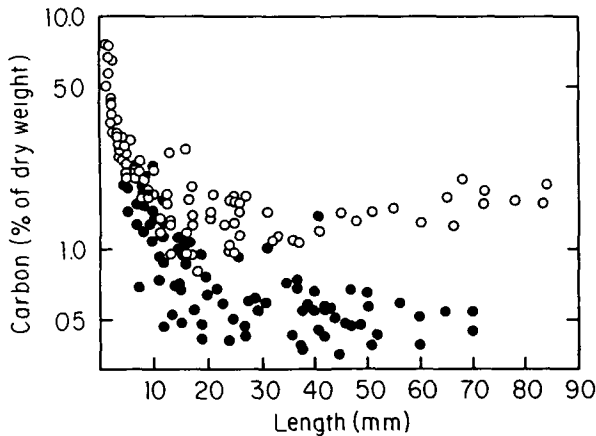
Prey zooplankton abundance was estimated from 5-min surface tows, using 0.5 m mouth diameter, 64  $\mu\text{m}$  mesh nylon nets with flow meters. Collections were subsequently size-fractionated to quantify the >200- $\mu\text{m}$  fraction, the size actually ingested by *Bolinopsis*.

The carbon and nitrogen composition was determined using a Carlo Erba Elemental Analyzer (Model 1106). Ctenophores were dried at 60°C for several days, then ground with a mortar and pestle and redried prior to analysis. The dry weight of copepod prey was determined for counted subsamples of the 200–330- $\mu\text{m}$  screened fraction dried on preweighed teflon filters. Carbon conversions were made based on elemental results for dried aliquots of the same size fraction.

**Table I.** Dry weights and carbon content for representative sizes of *B. vitrea* and *M. mccradyi* and ratio of the carbon content of the two species

<i>Bolinopsis</i>				<i>Mnemiopsis</i>			Carbon ratio
Length (mm)	Dry wt (mg)	%C of dry wt <sup>a</sup>	C (mg)	Dry wt (mg)	%C of dry wt	C (mg)	
5	4.2	1.76	0.073	1.9	4.42	0.083	1.14
10	18.8	1.15	0.22	10.0	3.02	0.30	1.36
20	84.5	0.75	0.63	53.5	1.34	0.72	1.14
30	203.8	0.58	1.19	142.7	1.24	1.77	1.49
40	380.4	0.49	1.86	286.3	1.13	3.24	1.74
50	617.4	0.50	3.09	491.2	1.29	6.34	2.06
60	917	0.50	4.59	763.7	1.39	10.6	2.31
70	1281	0.50	6.41	1109	1.69	18.7	2.91

<sup>a</sup>Values for lengths 5–40 mm based on non-linear least squares regression on data in Figure 1 assuming exponential decay. Values for lengths >50 mm based on mean of carbon measurements for *Bolinopsis* >50 mm



**Fig. 1.** The carbon composition as a percentage of the dry weight for a range of sizes of *B. vitrea* (solid circles) and *M. mccradyi* (open circles).

## Results

### *Morphometrics and elemental composition*

*Bolinopsis* and *Mnemiopsis* have a similar size range and general body shape. For *B. vitrea* the relationship between total length including lobes (mm) and dry weight (mg) has been measured to be  $DW = 0.127L^{2.17}$  (Kremer *et al.*, 1986). The comparable equation for *M. mccradyi* is  $DW = 0.038L^{2.42}$  (Baker, 1973). Table I gives a comparison of the dry weights and carbon content for the two species for a range of sizes. As with other soft-bodied 'gelatinous' zooplankton, the carbon to dry weight ratio was low due to high salt content of the dried material. For equivalent lengths, *Bolinopsis*

**Table II.** The carbon content of lobate *B. vitrea* held at controlled food concentrations for 3 days. Sample sizes are given in parentheses

Treatment	%C of dry wt ( $\bar{x} \pm SD$ )			
	Initial	Day 1	Day 2	Day 3
Initial	0.51 $\pm$ 0.07			
Starved		0.51 $\pm$ 0.09 (5)	0.42 $\pm$ 0.08 (4)	0.47 $\pm$ 0.15 (5)
10 prey l <sup>-1</sup>		0.52 $\pm$ 0.11 (5)	0.58 $\pm$ 0.13 (5)	0.60 $\pm$ 0.05 (3)
50 prey l <sup>-1</sup>		0.62 $\pm$ 0.17 (4)	0.79 $\pm$ 0.17 (5)	0.72 $\pm$ 0.10 (4)

had a slightly heavier weight than *Mnemiopsis*. It was much more delicate and watery, however, and was lower by about a factor of 2–3 in the ratio of carbon to dry weight (Table I, Figure 1). A similar pattern has been measured in salps. For animals of equivalent length, offshore species of *Pegea* have less carbon than more coastal and shelf forms (Madin and Harbison, 1978; Madin *et al.*, 1981).

In both species of ctenophores, smaller specimens had higher carbon to dry weight ratios, which correlated with the larval tentaculate stage, tentacles being relatively carbon-rich. *Bolinopsis vitrea* becomes fully lobate without tentacles when the overall length is about 18 mm, while *M. mccradyi* loses its tentacles at about 10 mm. This difference was reflected in the length at which the two species reach their average baseline carbon content (Figure 1). *Mnemiopsis mccradyi* was cultured from egg, but, relying on field collections, we were unable to determine the elemental composition of very small specimens of *B. vitrea*. An increase in the ratio of carbon to dry weight for very large specimens of *Mnemiopsis*, was also measured for ctenophores from the field or grown in the laboratory (Table I, Figure 1). It is probable that only ctenophores in abundant food conditions would be likely to reach lengths exceeding 50 mm, and therefore would be expected to be relatively rich in carbon.

The atomic ratio of carbon to nitrogen was similar over the entire range of sizes and the ratio for *B. vitrea* ( $4.04 \pm 0.78$ ,  $n = 95$ ) was similar to the ratio for *M. mccradyi* ( $4.57 \pm 0.44$ ,  $n = 31$ ). These results are typical of animals whose organic matter is relatively high in protein and consistent with biochemical measurements on two species of non-beroid ctenophores from the North Sea (Hoeger, 1983).

The ratio of carbon to dry weight for *B. vitrea* was found to be affected by food availability (Table II). Over a period of 3 days, the carbon content of the ctenophores at the highest food concentration increased about 50% relative to the values for the freshly collected ctenophores. Plasticity in composition with food availability also occurs in *M. mccradyi* (Kremer, 1982; Reeve and Syms, 1984).

### Feeding experiments

The effect of food concentration on the ingestion rate was measured at five food concentrations (50 $\times$  range) for both tentaculate and lobate *B. vitrea* (Figure 2A). Experimental prey consisted of the 200–330- $\mu$ m screened size fraction of ambient plankton

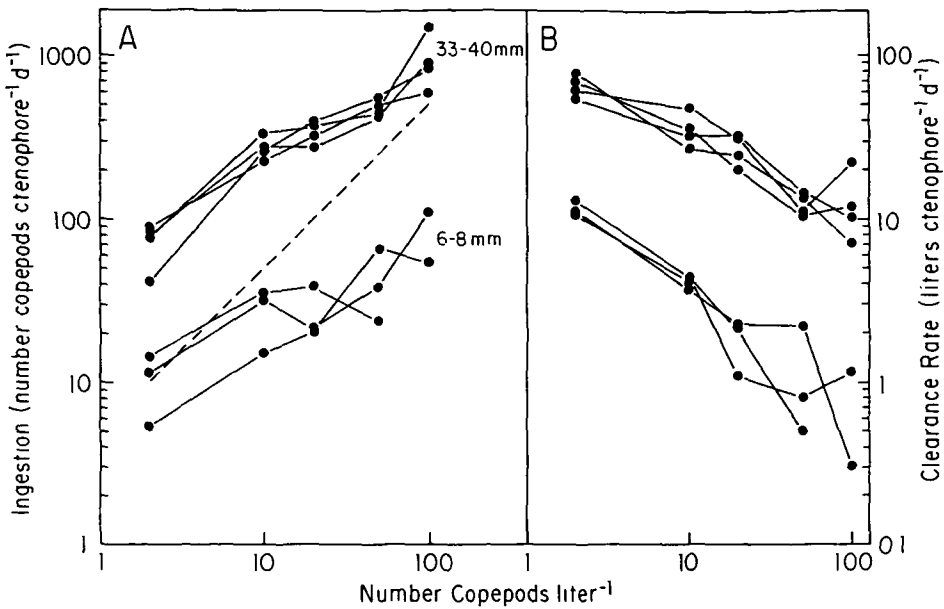


Fig. 2. Feeding experiments with *B. vitrea* measured the ingestion rate over a wide range of food concentrations for two size groups of ctenophores (A). The copepods used as prey were all from the 200–330- $\mu$ m screened fraction and had an average weight of 2.5  $\mu$ g C copepod<sup>-1</sup>. Clearance rates calculated from the ingestion results decreased with increasing food availability (B)

(primarily calanoid copepods). Observations of lobate *Bolinopsis* (30 mm) indicated that this species does not consume small copepod stages (<100- $\mu$ m screened fraction). In the feeding experiments the ingestion rate continued to increase in food concentrations up to 100 prey l<sup>-1</sup>, but it was not linear (45° dashed line in Figure 2A). Although the ctenophores did not satiate and reach a maximum ingestion rate, feeding effort as measured by clearance rate (Gauld, 1951) declined with increasing food concentration (Figure 2B). This indicated that the ctenophores were not 'automatic' feeders but changed their feeding rate in response to a change in food availability. Previous studies (Reeve *et al.*, 1978; Kremer, 1979) have suggested that lobate ctenophores were automatic feeders, except at extremely high food concentrations. We are convinced now that the results of all such experiments are highly dependent on the animals' previous nutritional state and experimental duration. Some recent experiments with *Mnemiopsis* <20 mm in length (M.R. Reeve and M.A. Syms, unpublished data) have produced results similar to those for *Bolinopsis*.

At extremely high food concentrations of 200 prey l<sup>-1</sup> *B. vitrea* deteriorated rapidly and disintegrated after only 8–12 h, while *M. mccradyi* was able to thrive in this food environment (Reeve *et al.*, 1978; personal observation). Although average ambient concentrations do not approach these levels, we have measured concentrations of small-scale patches as high as 100 prey l<sup>-1</sup> in the Bahamas, indicating that short-term exposures to high food concentrations are possible. Organisms that are characteristic of relatively oligotrophic environments, may be generally maladapted to high

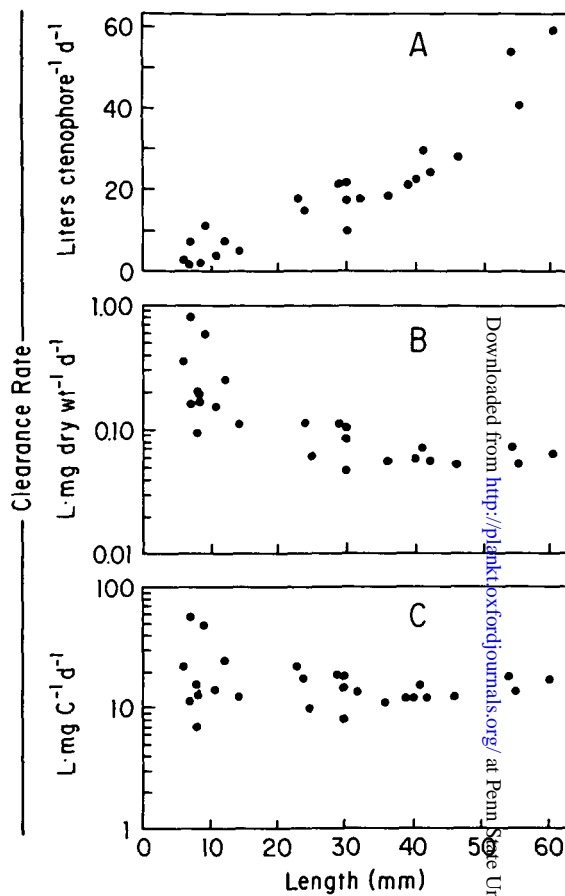


Fig. 3. Results of feeding experiments for a range of sizes of *B. vitrea* at 20 copepods l<sup>-1</sup>: (A) clearing rate per ctenophore; (B) the clearing rates per unit dry weight; and (C) clearing rate per unit carbon weight.

food concentrations compared with coastal species. Harbison *et al.* (1986) observed that an oceanic salp, *Pegea confoederata*, responded poorly to food concentrations characteristic of neritic waters.

Feeding rates in Figure 2 were based on 8–12-h experiments. Since measurements of this kind can obscure short-term dynamics, feeding rates were also measured over 10 short time intervals for a total time of 20 h at prey concentrations between 5 and 50 prey l<sup>-1</sup>. Animals were gently transferred to fresh containers at the start of each new period. Results were erratic, with no overall changes in clearance rate over time. By comparison, in experiments of a similar design with *Mnemiopsis*, the feeding effort (as measured by clearance rate) fell rapidly within the first 2 h then gradually stabilized.

Measurements of feeding rates for a variety of sizes of *Bolinopsis* were carried out at a single food concentration (20 copepods l<sup>-1</sup>) to determine the effect of size on the ingestion rate. The absolute ingestion and clearance rates increased with size (Figure 3A), but the clearance rate per unit dry weight decreased with size (Figure 3B), imply-

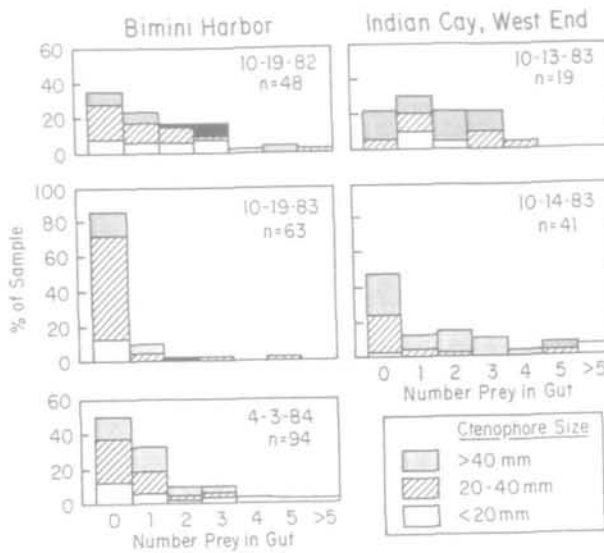


Fig. 4. The gut contents of freshly collected *B. vitrea* were measured on five different dates at two locations. These histograms present the relative percentages of numbers of prey items for three size classes of ctenophores.

ing that the ctenophores are less effective at capturing food as they grow. The feeding behaviour of ctenophores depends on the prey coming into contact with the colloblasts. As the ctenophores grow, these areas on the tentacles, auricles, and lobes do not increase in proportion to the volume as expressed by the dry weight.

These weight-based results (Figure 3B) were combined with the composition data of Figure 1 to calculate the clearing rate per unit carbon. For this calculation, the data of *Bolinopsis* in Figure 1 were fitted using a nonlinear least squares regression (Marquardt, 1963) assuming an exponential decline with length. Apparently, as these animals grow, their organic content is reduced so that on an organic basis, the ability to collect food remains essentially unchanged (Figure 3C). The mean clearance rate per unit carbon of *Bolinopsis* was  $14.5 \pm 4.3$  (SD)  $l\ mg\ C^{-1}\ day^{-1}$  over the entire size range (excluding two outliers). Clearance rates for *Mnemiopsis* fed for 4 h at  $100\ prey\ l^{-1}$  were about half this rate at  $6.5 \pm 2.6\ l\ mg\ C^{-1}\ day^{-1}$ . *Bolinopsis* is considerably more dilute than *Mnemiopsis* in its organic composition, therefore for equivalent carbon biomass *Bolinopsis* is larger, with a greater food collection area.

#### Estimates of environmental ingestion rates for ctenophores

As noted above, laboratory measurements of ingestion rates are specific to the conditions of the experiment. In addition, delicate species may not feed at natural rates under laboratory conditions. Therefore we used two independent methods to estimate environmental ingestion rates for *B. vitrea*. The first combined observations of gut contents with experimental measurements of digestion times, while the second combined results of the feeding experiments with measurements of ambient prey concentrations. Although both these approaches are commonly used by zooplankton ecologists in-

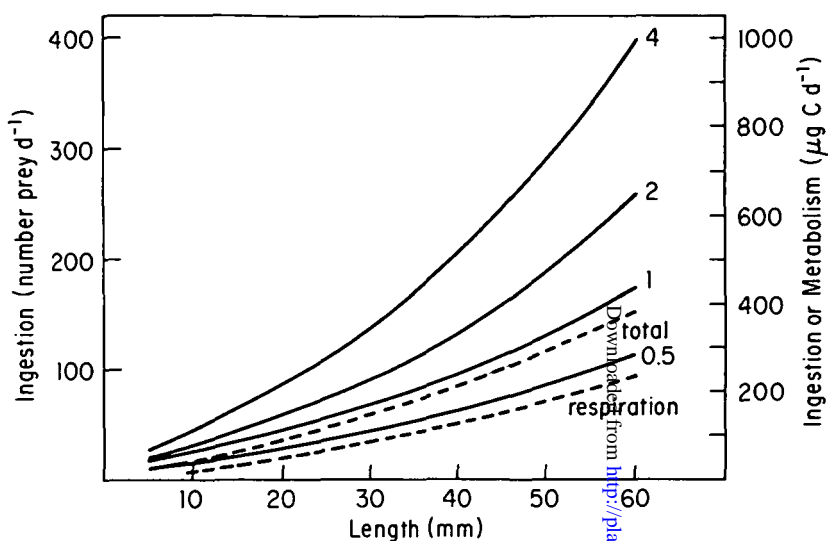


Fig. 5. Calculations of ingestion and metabolic rates for *B. virrea*. Numbers next to lines are number of prey  $l^{-1}$ . The solid lines for ingestion are based on results in Figures 2 and 3A, using an average prey weight of  $2.5 \mu\text{g C}$ . Dashed lines represent the respiratory and total metabolic demand for carbon based on Kremer *et al.* (1986).

investigating carnivores (Miller, 1970; Nagasawa and Marumo, 1972; Anderson, 1974; Szyper, 1978; Reeve *et al.*, 1978; Feigenbaum, 1979; Kremer, 1979; Reeve, 1980a; Purcell, 1981a,b; Purcell and Kremer, 1983), they are rarely combined and compared within a single study (Sullivan and Reeve, 1982).

Quantitative observations of gut contents for freshly caught *Bolinopsis* were made on five different dates in two locations (Figure 4). Field-collected ctenophores rarely had more than three prey items in their guts, and more than half of the samples contained no visible food. Similarly low frequencies were found by M.R.Reeve (unpublished data) for *Mnemiopsis*, and Harris *et al.* (1982) for *Pleurobrachia*. Experimental measurements of digestion times were made in order to calculate ingestion rates. Lobate *Bolinopsis* (total length  $>20$  mm) generally required 1–2 h to digest the prey (copepods  $200-330\text{-}\mu\text{m}$  screened fraction) irrespective of the number of prey ingested ( $x = 1.9 \pm 1.1$  SD,  $n = 29$ ). These results are about double the digestion times reported for *Mnemiopsis*  $\geq 5$  mm at comparable temperatures (Reeve, 1980b). The digestion time for tentaculate *Bolinopsis* ( $<20$  mm) was affected by the number of ingested prey. Tentaculate *B. virrea* with three or more prey items in their guts required about 3 h to complete digestion ( $2.9 \pm 1.0$ ,  $n = 8$ ).

Combining these measurements of digestion time with observations of gut contents (Figure 4), it was possible to calculate an estimate of ambient ingestion rates. We assumed the average carbon content of each prey item was  $2.5 \mu\text{g C}$ , the measured weight in the  $200-330\text{-}\mu\text{m}$  fraction and representative of typical prey. If the digestion time were 2 h, even a ctenophore with an average of three prey items in its gut, would be expected to ingest only about  $100 \mu\text{g C day}^{-1}$ . On the basis of the metabolic measurements made concurrently (Kremer *et al.*, 1986), this ingestion rate would be



sufficient to meet the metabolic requirements of only the smaller ctenophores (Figure 5, dashed line). It is likely, however, that our observations underestimated the actual average gut contents of the ctenophores, because our measurements were based only on daytime samples. Several studies have reported a substantial increase in the gut contents of planktonic predators at night (Nagasawa and Marumo, 1976; Szyper, 1978; Purcell, 1981c, 1982; Sullivan and Reeve, 1982; Madin *et al.*, 1983).

The second estimate of ingestion by *Bolinopsis* combined results of feeding experiments with estimates of field prey availability. Our zooplankton samples in the Bahamas indicated that potential prey concentrations rarely averaged more than 5 prey  $l^{-1}$ . This implied that for *B. vitrea* the results from feeding experiments at the lowest food concentrations were the most ecologically relevant. Clearance rates for a range of sizes of *B. vitrea* at low food concentrations were estimated from the pattern for clearance rate over a wide range of food concentrations (Figure 2B) and combined with the trend with size from experiments at 20 prey  $l^{-1}$  (Figure 3A). These rates were used to calculate a range of estimates for *in situ* ingestion rates at four food concentrations (0.5–4 prey  $l^{-1}$ ) (Figure 5). Numbers of prey ingested were converted to carbon equivalents again assuming 2.5  $\mu\text{g C prey}^{-1}$ , the average measured carbon for copepods from the 200–330- $\mu\text{m}$  screened fraction used in the feeding experiments. This size represents an intermediate value based on zooplankton samples and gut content analyses.

These estimates of ingestion were compared to the measured metabolic requirements of freshly collected *Bolinopsis* (Figure 5, dashed lines, derived from Kremer *et al.*, 1986) to evaluate the rate of ingestion that was necessary to permit growth of the ctenophores. Growth would be expected to occur when assimilated carbon (ingestion  $\times$  digestive efficiency) exceeded total metabolic demands (respiration plus organic leakage). If we assume a digestive efficiency of 75% (Reeve *et al.*, 1978), then according to results of the feeding experiments, growth of populations of *Bolinopsis* could occur in prey concentrations exceeding about 1  $l^{-1}$  (1000  $\text{m}^{-3}$ ). Similar calculations made for *Mnemiopsis*, using published metabolic results (Kremer, 1982) and ingestion results from feeding experiments at 100 prey  $l^{-1}$ , indicated that prey concentrations an order of magnitude higher were necessary to sustain a population of *Mnemiopsis* (Figure 6).

Despite several attempts we were never successful at getting direct measurements of growth rates for *Bolinopsis*. Although we could usually hold the ctenophores in apparently good conditions for 2–3 days, they soon began to deteriorate. This prevented direct comparisons of growth with *Mnemiopsis* under identical conditions.

#### *Ctenophore distribution and food supply*

Experimental and field observations lead us to conclude that the distribution of both *Bolinopsis* and *Mnemiopsis* is regulated to some degree by prey availability, and the abundance of ctenophores is correlated with the relative biological productivity of different habitats. We have most consistently encountered populations of *Bolinopsis* in the vicinity of Bimini in the western and Highborne Cay in the eastern Bahamas. Over 16 stations through the length of the Abaco chain of islands, the average 200- $\mu\text{m}$  zooplankton density was 170  $\text{m}^{-3}$  while at six stations in the vicinity of Highborne Cay, the average was an order of magnitude greater at 1700, with a maximum of 5400  $\text{m}^{-3}$ . Densities approaching 1000  $\text{m}^{-3}$  were often characteristic of Bimini Harbor. Based

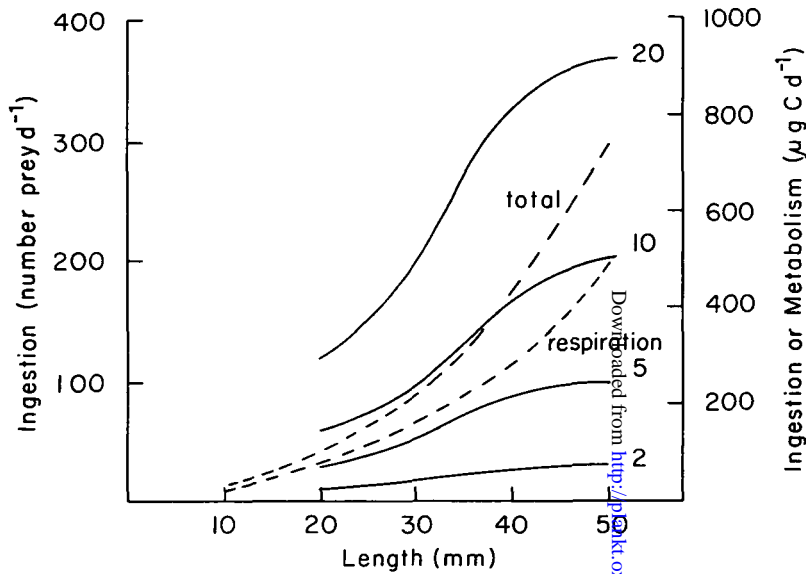


Fig. 6. Calculation of ingestion and metabolic rates for *M. mccradyi*. Numbers next to lines are number of prey  $l^{-1}$ . Average prey size was assumed to be  $2.5 \mu\text{g C}$ . Solid lines for ingestion were extrapolated from results of feeding experiments at  $100 \text{ prey } l^{-1}$  (P.Kremer and M.R.Reeve, unpublished data). Ingestion values for ctenophores  $< 20 \text{ mm}$  are not given because for small *Mnemiopsis*, clearance rate is not independent of food concentration (M.R.Reeve and M.A.Syms, unpublished data). Dashed lines represent the respiratory and total metabolic demand for carbon based on Kremer (1982).

on our limited sampling, *Bolinopsis* populations are encountered only in locations where there is a relatively high concentration of prey zooplankton (i.e.  $> 1000 \text{ copepods } m^{-3}$ ).

A similar pattern is demonstrated for *Mnemiopsis* where in the 60-km-long Biscayne Bay, there is a gradient of decreasing zooplankton biomass from the north to the south (Baker, 1973; Reeve, 1975), corresponding to a gradient of decreasing urbanization. In central Biscayne Bay in the early seventies, Baker (1973) showed that over a 15-month sampling period, the occurrence of *Mnemiopsis* decreased from a maximum of 87% to a minimum of 33% over a 15-km north-south transect. This correlated well to the average annualized zooplankton biomass which decreased by a factor of 3.5 over this transect. The overall average 200- $\mu\text{m}$  net zooplankton was about  $3000 \text{ m}^{-3}$ .

To the south, we never saw ctenophore blooms in south Biscayne Bay and the adjacent Card Sound during extensive sampling programs (Reeve and Cosper, 1973), where 200- $\mu\text{m}$  net zooplankton averaged about  $1000 \text{ m}^{-3}$ . At the north end of Biscayne Bay, *Mnemiopsis* is almost always present, often in bloom conditions sporadically throughout the year. This location is shallow, poorly flushed and surrounded on all sides by urban development. Here, 200- $\mu\text{m}$  net plankton averaged  $14\,500 \text{ m}^{-3}$ , with a peak of  $38\,000 \text{ m}^{-3}$  (unpublished data).

The two species seem to have different minimum prey densities for population growth. The populations of *Bolinopsis* thrive in Bahamian environments at the lowest end of

food concentrations for Biscayne Bay, from which *Mnemiopsis* is absent. Biscayne Bay waters are contiguous with the reef areas outside the bay where *Bolinopsis* can sometimes reach bloom conditions. *Bolinopsis* must be continuously transported into the bay, but the populations do not develop. Presumably characteristics of the estuarine habitat, other than food availability, prevent *Bolinopsis* from establishing itself. Our experimental results indicate that *Bolinopsis* has both a greater ingestion rate and a lower metabolic rate than *Mnemiopsis* of comparable length (Figures 5 and 6). Therefore, our results support the contention that *Mnemiopsis* is excluded from many habitats in the region because it requires much higher ambient food levels than *Bolinopsis*.

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