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Experimental evaluation of herbivory in the ctenophore *Mnemiopsis leidyi* relevant to ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA

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Abstract. Herbivory of *Mnemiopsis leidyi* and its interactions with phytoplankton and non-gelatinous zooplankton were examined in small-scale microcosm experiments. Clearance rates for *M. leidyi* incubated with phytoplankton were generally negative, but ranged up to 4.5 l ctenophore^{-1} day^{-1} when the large (80 μm ϕ) diatom *Ditylum brightwelli* was offered as a food source. These highest ingestion rates would provide *Mnemiopsis* with only 21% of its daily carbon requirements for respiration. Mean shrinkage of *M. leidyi* was 8.2–51% when incubated with phytoplankton. Although *M. leidyi* neither fed actively on phytoplankton, nor satisfied its nutritional needs on such a diet, the chain-forming diatom *Skeletonema costatum* became entangled in mucus strands and balls produced by *M. leidyi* in the absence of zooplankton. Attachment onto mucus occurred at phytoplankton concentrations commonly observed in Narragansett Bay and may be important in the formation of "marine snow" during summer *M. leidyi* pulses; phytoplankton sinking rate and the "package size" available to herbivores would also be affected. The experiments support our previous hypothesis based on field observations in Narragansett Bay that *M. leidyi* indirectly regulates phytoplankton abundance there during the summer bloom as a consequence of predation on zooplankton. The extent to which *M. leidyi* influenced phytoplankton dynamics in the microcosms was dependent on the relative abundance and physiological state of the three trophic levels. A food web diagram for *M. leidyi* is presented.

Introduction

Field studies suggested to us that the ctenophore *Mnemiopsis leidyi* may regulate summer phytoplankton dynamics in Narragansett Bay through the dual mechanism of predation on herbivorous zooplankton and the accompanying excretion of nutrients (Deason and Smayda, 1982). We based our conclusion on indirect evidence, namely the synchronous timing that characterized fluctuations in phytoplankton, zooplankton and >1 cm ctenophore pulses and, particularly, correlations in abundance between these three different trophic groups consistent with ctenophore regulation of phytoplankton dynamics.

Direct experimental evidence that *M. leidyi*, or other ctenophores, can assimilate phytoplankton is lacking. Nelson (1925), employing microscopy, observed nanophytoplankton and detritus within *M. leidyi* and concluded that it is capable of herbivory. However, *Coscinodiscus* and other diatoms noted in the gut contents of *Beröe cucumis* (Lebour, 1923) may have been ingested adventitiously with ctenophore prey (Swanberg, 1974), and phytoplankton found within *Pleurobrachia bachei* may have originated in the guts of ingested copepods (Hirota, 1974). Moreover, *M. mccradyi* lost weight at the same rate as starved individuals when fed only algae and detritus (Baker and Reeve, 1974). Thus, ctenophores are usually considered to be exclusively carnivorous. None-

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theless, an ability of *M. leidyi* to utilize phytoplankton, or detritus, to meet their energy requirements has been suggested (Miller, 1970; Miller and Williams, 1972). Based on energetic calculations and available biomass of phytoplankton and zooplankton, Heinle (1974) concluded that *M. leidyi* cannot be strictly carnivorous and, hence, required herbivorous and/or detritivorous food supplementation to satisfy its energy balance. He suggested a non-selective filter feeding strategy as the most efficient one for ctenophores and jellyfish.

The present study utilized experimental, small-scale microcosms to examine whether *M. leidyi* actively grazes on phytoplankton. Observations on its grazing on zooplankton and on the interrelationships between ctenophore, zooplankton and phytoplankton populations, linked through predation, grazing and nutrient excretion, were also made. Particular emphasis was placed on testing our conclusion that ctenophore dynamics regulates summer phytoplankton dynamics in lower Narragansett Bay (Deason and Smayda, 1982).

Materials and Methods

Five microcosm experiments were conducted in 115 l plastic containers filled with 40–50 l of filtered Narragansett Bay seawater and inoculated with various combinations of phytoplankton, zooplankton and ctenophores. Two preliminary experiments (I, II) were carried out in a controlled temperature room at 22°C under dim light; phytoplankton were kept in suspension by gentle bubbling with air. Experimental microcosms III, IV and V were incubated outdoors, placed in a large tank with running sea water used as a coolant. Microcosm temperatures ranged from 20 to 23°C. A screen placed over the containers on bright days reduced light to ~60% of incident radiation which ranged from 137 to 662 langleys/day. The containers were stirred twice daily with a small paddle.

Each microcosm experiment, which lasted from 3 to 5 days, consisted of a phytoplankton control (P) and various plankton combinations: zooplankton + ctenophores (Z + C); phytoplankton + ctenophores (P + C); phytoplankton + zooplankton (P + Z); phytoplankton + zooplankton + ctenophores (P + Z + C). Each treatment in Experiment IV was replicated twice; the other experiments were not replicated. The initial biological conditions of the experiments are given in Table I. Phytoplankton was added to filtered Narragansett Bay seawater either from a 64 μm mesh net tow or pumped directly from Narragansett Bay into the microcosms, to provide a natural phytoplankton assemblage. The fragility of *M. leidyi* larvae permitted use of only post-larval specimens, which were hand-dipped from Narragansett Bay and maintained in small aquaria until experimental use. Zooplankton were collected with a 153 μm mesh net tow, kept resuspended in 50 l of unfiltered seawater, and reconcentrated for addition to the microcosms.

Microcosms were sampled at least once daily, after thorough mixing, for phytoplankton enumeration in a Sedgwick-Rafter chamber. Zooplankton abundance was determined at the beginning of the experiment in an aliquot of the inoculum, and at its termination following filtration of the microcosm contents through a 153 μm mesh net. Ctenophores were measured daily with a ruler, without removal from the microcosms. Lengths were converted to weight and

Table I. Experimental conditions in microcosm experiments.

Experiment	Date	Phytoplankton source	Initial concentration		*M. leidyi* (number per 50 l microcosm)	Mean abundance P : Z : C $ml^{-1} : l^{-1} : l^{-1}$
			Phytoplankton (cells ml^{-1})	Zooplankton (number l^{-1})		
I	August 21, 1975	64 μm net tow	2040–3860	30–74	6–7	21 065 : 314 : 1
II	August 27, 1975	64 μm net tow	2250–2270	–	4	28 250 : – : –
III	July 13, 1976	*Ditylum* culture	11–26	123–273	5	250 : 2730 : 1
IV	July 19, 1976	pumped bay water	251–371	16–27	5	3050 : 206 : 1
V	August 3, 1976	pumped bay water	73–132	71	1	6200 : 3550 : 1
					2	3300 : 1775 : 1
					3	1617 : 1173 : 1

carbon using the equations of Kremer and Nixon (1976) and Kremer (1976).

Nutrients were added to the final microcosm experiment (V) treatments after collection of the daily sample. Concentrations added yielded: 0.34 $\mu M\ l^{-1}$ ammonia, 0.048 $\mu M\ l^{-1}$ phosphate, and 0.52 $\mu M\ l^{-1}$ silicate. These concentrations approximated the rate of nutrient release from the benthic *Nephthys-Nucula* community (Hale, 1974) found in Narragansett Bay, assuming a mean water column depth of 10 m and continuous 24 h nutrient excretion. Chlorophyll *a* and phaeopigment concentrations were determined by fluorometric analysis (Lorenzen, 1966) of duplicate 10–25 ml samples.

The rate of zooplankton grazing on phytoplankton was calculated for the P + Z microcosm from the equation:

$$F = \ln E_1 - \ln E_2 + kt\ (V/Nt) \quad (1)$$

where *F* is the filtering rate, or volume swept clear, *E* the experimental phytoplankton concentration at times 1 and 2, *V* the volume of the microcosm, N the number of animals, *t* the elapsed time, and *k* the growth rate of phytoplankton in the control.

Although lobate ctenophores do not "filter" their food, prey removal can be calculated in terms of volume swept clear. Zooplankton predation by ctenophores was calculated for the Z + C and P + Z + C microcosms using the P + Z treatment as a control. Weight-specific clearance rates were calculated by substituting *W* (ctenophore dry weight) for *N* in Equation (1). The reduction in phytoplankton abundance in the presence of ctenophores in the P + C microcosm was also calculated using Equation (1).

The feeding behavior of *M. leidyi* when offered phytoplankton alone and phytoplankton + zooplankton as food sources was also observed in other experiments. From 100 to 10 000 cells ml^{-1} of *S. costatum* were inoculated, in duplicate, into filtered seawater held in 2 l beakers, and copepodite and naupliar stages of *A. tonsa* added to one set to yield 30–50 animals l^{-1}. Single individuals of *M. leidyi* ~4 cm in length were added to the beakers, and their behavior observed for several hours. They were then placed in large Petri dishes, together with media, for closer observation under a dissecting microscope. Following this treatment, the viability of *S. costatum* and *A. tonsa* was determined by staining with neutral-red (Crippen and Perrier, 1973).

Results

Experiment I

Experiment I, conducted for five days at 22°C, was inoculated with 2040–3860 phytoplankton cells ml^{-1} from a net tow collection made during post-boom nutrient conditions, and consisting almost entirely of *S. costatum*. Zooplankton populations added to the P + Z, Z + C and P + Z + C microcosms consisted largely of the copepods *A. tonsa* and *Centropages typicus*; initial concentrations ranged from 30 to 74 l^{-1}. Six or seven *M. leidyi* ranging in length from 5 to 50 mm were added to the P + C, Z + C and P + Z + C microcosms.

Control phytoplankton populations (P) grew (k = 0.28) the first day, then declined steadily over the next 4 days (Figure 1). The phytoplankton population

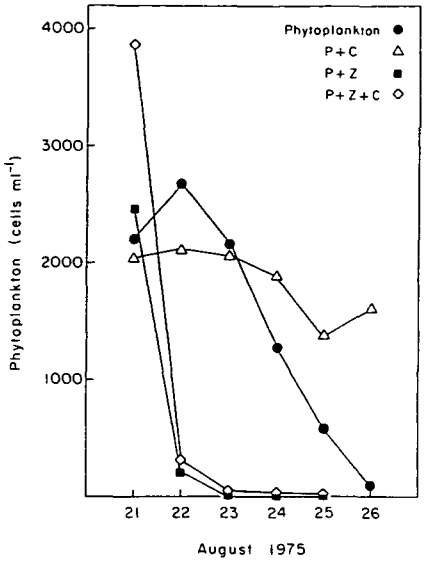

Fig. 1. Experiment I. Phytoplankton concentrations when reared alone P (●); with zooplankton P + Z (■); with *M. leidyi* P + C (△); and together with zooplankton and *M. leidyi* P + Z + C (◇).

declined rapidly the first day and remained at low levels in the presence of zooplankton with (P+Z+C) and without (P+Z) ctenophore addition. Zooplankton filtration rate over the entire experiment was 49 ml animal^{-1} day^{-1} (Table II). In the microcosm with *M. leidyi* (P+C), phytoplankton abundance remained more or less constant the first three days and the terminal population exceeded the control by 17-fold. Thus, the abundance of *S. costatum* was seemingly prolonged in the presence of ctenophores relative to the phytoplankton control (Figure 1).

Zooplankton populations declined the last two days of the experiment in all treatments. Prior to this period, *M. leidyi* filtered at rates averaging 1.7 and 2.0 l ctenophore^{-1} day $^{-1}$. Sixteen of the 20 experimental ctenophores shrank during the experiment (Table III). Most of the larger animals were heavily parasitized with *Edwardsia* larvae (see Crowell, 1976), which may have reduced the body size independently of nutritional effects.

Experiment II

This experiment compared phytoplankton growth in the presence (P+C) and absence (P) of *M. leidyi* over a four day period at 22°C under conditions similar to those in Experiment I. The phytoplankton, again collected by net from a post-bloom population, consisted almost entirely of *S. costatum*. Four *M. leidyi* (25–55 mm in body length) were added to the P+C microcosm.

Phytoplankton grew rapidly in both treatments during the first day of incubation (k = 1.15 divisions/day), declined after the second day, and reached virtually identical terminal populations. The observed differences in responses and yield were not statistically significant. Ctenophores did not reduce phytoplankton abundance based on filtration rates calculated over the experimental period. If

Table II. Zooplankton and *Mnemiopsis leidyi* clearance rates.

Experiment	Day	On Phytoplanton			On Zooplankton			
		ml zooplankton^{-1} day^{-1} (P + Z)	liter ctenophore^{-1} day^{-1} (P + C)	liter gm dry wt^{-1} day^{-1}	liter ctenophore^{-1} day^{-1} (Z + C)	liter gm dry wt^{-1} day^{-1}	liter ctenophore^{-1} day^{-1} (P + Z + C)	liter gm dry wt^{-1} day^{-1}
I	1–2	41.4	0.94	4.5	−1.3		1.9	12.5
	2–3	73.6	−1.1		4.6	25.8	2.1	14.1
	3–4	0.0	−2.6					
	4–5	74.6	−2.7					
	1–3				1.7	9.4	2.0	14.1
	1–5	49.1	−3.3					
II	1–2		0.17	0.8				
	2–3		0.66	3.3				
	3–4		0.04	0.2				
	4–5		−15.6					
	1–5		−3.6					
III	1–2	62.1	4.5	22.7			6.9	29.1
	2–3		2.1	10.7			3.8	14.5
	3–4		1.0	7.1			5.7	26.5
	1–4		2.5	16.5			5.5	28.3
IV	1–2		0.2	0.9				
	2–3		1.3	6.7				
	3–4		−0.2					
	4–5		−0.5					
	1–5	23.5	0.2	1.1			5.3	28.5
V	1–4	13.7					(P + Z + C) −1.3	
							(P + Z + 2C) 4.1	30.5
							(P + Z + 3C) 1.3	19.1

Table III. Average changes in total length of *M. leidyi*.

Experiment	Ctenophores microcosm^{-1}	Initial size range (mm)	Duration (days)	Mean *M. leidyi* length change, % (±S.D.), in microcosms		
				Z+C	P+Z+C	P+C
I[a]	6–7	5–50	5	−39.2(±9.8)	−23.6(±37.3)	−24.7(±22.7)
II[a]	4	25–55	4			−50.8(±10.5)
III	5	15–40	3		+7.5(±17.1)	−23.3(± 8.6)
IV[b]	5	15–50	4		+3.8(±13.0)	−8.2(±10.7)
V	1	25	4		+10	
	2	20–22	4		+11.1	
	3	20–25	4		+ 0	

[a]Several animals parasitized.
[b]Mean of 2 replicates.

phytoplankton were indeed grazed or damaged by ctenophores, it was during the the initial days of the experiment, and at the low rate of 0.04–0.66 l ctenophore^{-1} day^{-1} (Table II). All experimental ctenophores shrank (Table III) and were heavily parasitized.

Experiment III

Experiments I and II suggested that if *M. leidyi* did consume *S. costatum*, this occurred at insignificant rates. The possibility that the small size of the chain-forming *S. costatum* precluded its utilization by *Mnemiopsis*, and that this ctenophore is herbivorous on larger sized phytoplankters was tested in Experiment III using a culture of the large (~80 μm) diatom *Ditylum brightwelli*. Zooplankton populations added to the P+Z and P+Z+C microcosms (123–273 l^{-1}) were characterized by the copepods *A. tonsa* and *Centropages hamatus*. The P+C and P+Z+C microcosms were inoculated with three *M. leidyi* ranging in length from 15 to 40 mm. Temperatures ranged from 20 to 23°C over the three day experiment.

The *D. brightwelli* population in the control increased throughout the experiment ($\bar{k}$ = 1.03 divisions/day); the maximum growth rate (k_{max} = 1.50) occurred between days 2 and 3 (Figure 2A). *D. brightwelli* also increased more slowly ($\bar{k}$ = 0.61; k_{max} = 1.15) in the presence of ctenophores (P+C). These responses contrast sharply with the rapid decreases of *Ditylum* to non-detectable levels within a day in the presence of zooplankton, either alone or with added *M. leidyi*. Zooplankton filtration rates were 62.1 ml animal^{-1} day. Calculated ctenophore filtration rates on *Ditylum* (1.0–4.5 l ctenophore^{-1} day^{-1}) exceeded those calculated on *S. costatum*; the overall rate was 2.5 l ctenophore^{-1} day^{-1} (Table II). Zooplankton populations declined rapidly in the P+Z+C microcosm relative to the P+Z control (Figure 2B). Filtration of *M. leidyi* on zooplankton ranged from 3.8 to 6.9 l ctenophore^{-1} day^{-1} (Table II).

The length of the ctenophores in the P+C microcosm decreased by an average of 23.3%, whereas four of the five *M. leidyi* incubated with zooplankton and *D. brightwelli* (P+Z) increased in length during the experiment (Table III). The

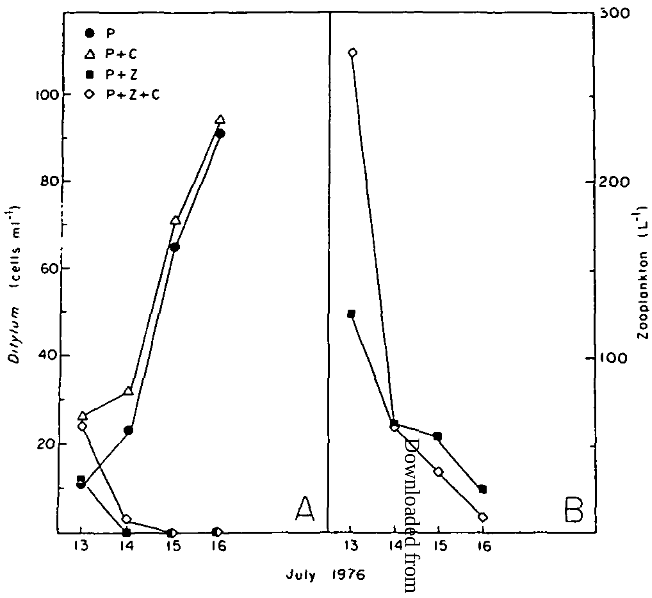

Fig. 2. Experiment III. A. *D. brightwelli* concentrations when reared alone or in various plankton combinations. Symbols as in Figure 1. B. Zooplankton concentrations.

smallest ctenophore exhibited the maximum length increase: +30%. In the P+Z+C microcosm, *M. leidyi* produced eggs, were observed to swim, and contained zooplankton in their gut. In the P+C treatments, however, *M. leidyi* usually sounded and remained at the bottom of the microcosms.

Experiment IV

In Experiment IV, conducted for four days, the P, P+Z and P+Z+C microcosms were replicated twice. Water temperature averaged 20°C at 0900, increasing to 23°C at 1500 hours. The natural phytoplankton assemblage (250–370 cells ml^{-1}) pumped from Narragansett Bay into the microcosms was dominated by the diatoms *Rhizosolenia fragilissima* and *Thalassionema nitzschioides*. Initial zooplankton concentrations were 16–27 l^{-1}; *A. tonsa* and benthic larvae dominated this community. Five *M. leidyi*, 15–50 mm in length, were added to each P+C and P+Z+C microcosm.

Phytoplankton grew in all microcosms throughout the experiment (Figure 3). Growth rates in the controls (P), which averaged 1.51 divisions per day, with k_{max} 2.79 between days 2 and 3, were similar to those in the P+C microcosms: $\bar{k}$ = 1.50, k_{max} = 2.49. Phytoplankton abundance increased ~50-fold in the P and P+C microcosms during the experiment, by 27-fold in the P+Z+C microcosm and by only 7-fold in the P+Z treatment ($\bar{k}$ = 1.17 for P+Z+C, and 0.77 for P+Z).

Zooplankton filtration rate was 23.5 ml $animal^{-1}$ day^{-1} (Table II). Apparent removal of phytoplankton by *M. leidyi* was observed during the first 2 days of the experiment at rates ranging from 0.19 to 1.3 l $ctenophore^{-1}$ day^{-1}. Removal

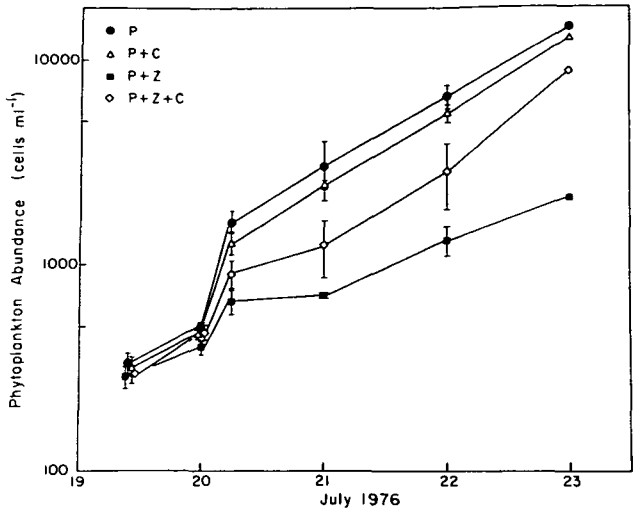

Fig. 3. Experiment IV. Phytoplankton concentrations when reared in various microcosm treatments as identified by the symbols in Figure 1. Mean of two replicates and ranges are shown.

averaged over the four day experiment was very low: 0.21 l ctenophore^{-1} day^{-1}. Zooplankton increased in the P + Z microcosm during the course of the experiment, but declined in the presence of *M. leidyi* (P + Z + C). Ctenophore predation rate on zooplankton was 5.3 l ctenophore^{-1} day^{-1} (Table II).

In the P + C microcosms, four ctenophores decreased in length and six showed no change; the average change was −8.2% total length (Table III). In contrast, *M. leidyi* present in the P + Z + C microcosms increased their length by an average of 3.8%; only two animals shrank. Eggs were produced in both replicates of P + Z + C.

Experiment V

This four day experiment, conducted with three levels of ctenophore abundance and simulated benthic nutrient excretion, was designed to assess the effect of variable ctenophore abundance on microcosm dynamics under natural enrichment (PN) associated with benthic excretion. Treatments were PN, PN + Z, PN + Z + 1C, PN + Z + 2C, PN + Z + 3C and a control without nutrient addition (P). (1C, 2C and 3C indicate that one, two and three ctenophores, respectively, were added to the microcosm.) Temperature ranged from 20 to 23°C. The phytoplankton inoculum (70 − 130 cells ml^{-1}) was pumped from Narragansett Bay. Flagellates, *Cerataulina pelagica* and *S. costatum* were the dominant phytoplankters. *A. tonsa* was the most abundant zooplankter, followed by *Centropages hamatus*. The cladoceran *Evadne nordmanni* accounted for 10% of the initial zooplankton abundance, but was not present in any of the microcosms at the termination of the experiment. The length of *M. leidyi* ranged from 20 to 25 mm.

Phytoplankton growth varied greatly among microcosms (Figure 4). Phytoplankton abundance in the control (P) and enriched microcosm (PN) was

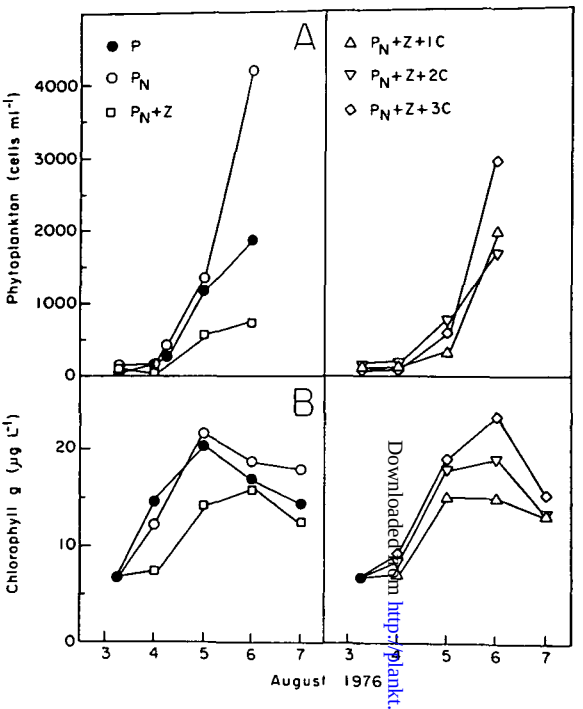

Fig. 4. Experiment V. A. Phytoplankton and B. Chlorophyll *a* concentrations in various microcosms. The symbols are as identified in Figure 1, except that PN indicates nutrient enrichment and phytoplankton and 1C, 2C, 3C designate presence of 1, 2 and 3 ctenophores, respectively.

similar until day 3. On day 4, abundance in PN exceeded by >2-fold that in P, although maximum and mean growth rates were similar: 3.03 (P) and 3.07 (PN), and 1.70 (P) and 1.91 divisions/day (PN), respectively. The presence of zooplankton reduced maximum phytoplankton abundance relative to PN by 5.7-fold. Zooplankton filtration rate over the duration of the experiment was 13.7 ml animal^{-1} day.

In the combined presence of *M. leidyi* and zooplankton, phytoplankton populations were reduced relative to PN by only 1.5- to 2.5-fold in contrast to the 5.7-fold decrease in the presence of zooplankton alone (PN + Z). The mean daily division rate (k) was 1.44, 1.33 and 1.97 day^{-1} in the presence of one, two and three ctenophores, respectively; k_{max} was 2.60, 1.82 and 2.28 day^{-1}. Thus, phytoplankton abundance in those microcosms containing both ctenophores and zooplankton was about 2- to 4-fold greater than in the microcosm containing only zooplankton (PN + Z). This demonstrates the positive effect that ctenophore presence can have on phytoplankton abundance, presumably a result of their predation on zooplankton.

Ctenophores grew in the PN + Z + 1C and PN + Z + 2C microcosms; their body lengths increased by 10% (Table III). However, in the PN + Z + 3C microcosm body lengths of the three *M. leidyi* did not change. *M. leidyi* grazing was not measurable in PN + Z + 1C, but clearance rates were 4.1 and 1.3 l ctenophore^{-1}

day^{-1} in the P + Z + 2C and P + Z + 3C microcosms, respectively (Table II).

Chlorophyll *a* concentrations varied less than phytoplankton cell numbers in the different treatments (Figure 4B). Maxima were reached after two days in the P and PN microcosms (20.3 and 21.6 μg l^{-1}), and after three days in the other microcosms. Maximal concentrations were similar in the PN + Z (15.0) and PN + Z + 1C (15.7) microcosms, and increased to 23.5 μg l^{-1} with increasing ctenophore concentration. The maximum daily growth rate of chlorophyll *a* was similar in all treatments (range 0.87 – 1.10).

Phaeophytin *a* concentrations increased in all microcosms, but were 2-fold higher in the microcosms containing zooplankton. Maxima in the latter ranged from 6.2 to 7.6 μg l^{-1} as compared to 3.1 – 3.8 μg l^{-1} in P and PN. Phaeopigment:chlorophyll *a* ratios were also twice as high in the zooplankton treatments (maxima: 0.32 – 0.44) as in the microcosms with only phytoplankton (maxima: 0.18 – 0.21).

Observations of M. leidyi mucus formation

M. leidyi was physically more active in 2 l beakers during short term incubations in the presence of *A. tonsa* than with *S. costatum* alone. With *S. costatum* alone, the ctenophores descended to the bottom of beaker and remained motionless following this initial activity. When prey was added, *M. leidyi*, lobes extended, swam forward slowly in the manner described by Reeve and Walter (1978). In the presence of zooplankton, the ctenophores alternated active swimming movements with passive suspension, during which they hung vertically in the water column. *Mnemiopsis* produced strands of mucus in the presence of *S. costatum* at concentrations between 1000 and 10 000 cells ml^{-1}, both in the presence and absence of *A. tonsa*, but not at cell concentrations of 100 ml^{-1}. The matrix of this mucus contained *S. costatum* chains (Figure 5). *A. tonsa* copepodites and naupli, digested remnants and fecal pellets also stuck to this mucus in incubations with zooplankton. Microscopic examination revealed that copepodites and nauplii were digested. While diatom chains occasionally entered the pharynx, they were expelled along with zooplankton remains in a mucus ball. Most of the *Skeletonema* chains, however, were incorporated into mucus outside the mouth. Staining with neutral-red indicated that many of the chains contained viable cells, and that even some *A. tonsa* were also alive.

Discussion

The experimental concentrations of phytoplankton and zooplankton used in the microcosms were comparable to summer levels recorded in lower Narragansett Bay, whereas the ctenophore concentrations (20 – 140 m^{-3}) were higher to compensate for lower weight-specific ingestion rates of post-larval animals (Kremer, 1979; Deason, in press).

The addition of zooplankton to the microcosms (P + Z) led to marked decreases in phytoplankton abundance and chlorophyll *a* concentrations, and increased phaeopigment concentrations and phaeophytin:chlorophyll ratios. Ambient ammonia and nitrate + nitrite were generally depleted more slowly in the P + Z microcosms than in the control. These expected results indicate that the

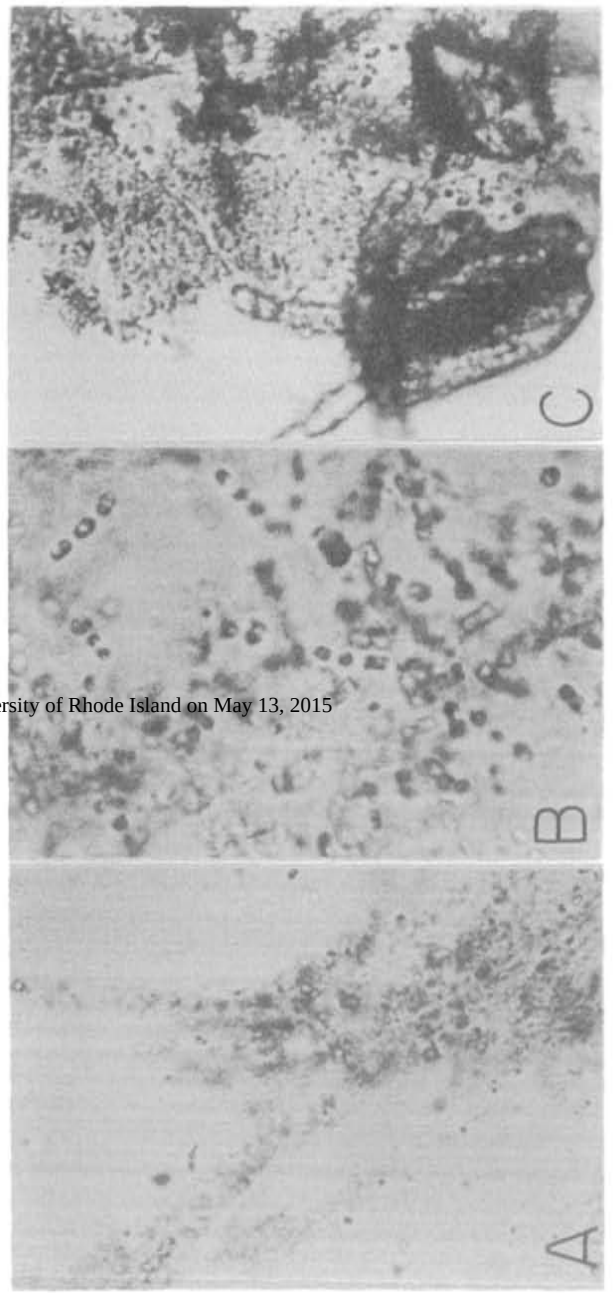

Fig. 5. A. Overview of mucus strands produced by *M. leidyi* at 1000 cells ml^{-1} *S. costatum* (90x). B. Chains of *S. costatum* entangled in mucus at 1000 cells ml^{-1} (225x). Darkened cells are stained with neutral-red, indicating viability. *C. A. tonsa* nauplius entangled in mucus formed at 10 000 cells ml^{-1} and 30 copepods l^{-1} (165x).

microcosms functioned naturally with respect to *in situ* processes, at least at this step of the food web.

A central question addressed in our investigation was whether *M. leidyi* is herbivorous on phytoplankton. Our results, which allowed 15 daily measurements in four different experiments of *Mnemiopsis* clearance rates on phytoplankton, suggest that *M. leidyi* is incapable of effective herbivory to meet its energetic requirements. Several lines of evidence support this conclusion. Phytoplankton abundance in the P + C and P microcosms was similar (Figures 2,3), unlike the inverse associations obtained between phytoplankton and zooplankton abundance. Although positive daily phytoplankton clearance rates by *Mnemiopsis* were calculated early in each experiment (excluding Experiment III) these rates were very low (Table II) and became negative after a few days.

The highest phytoplankton clearance rate occurred when *D. brightwelli* was offered as a sole food source. Since this diatom may therefore be large enough (80 μm ϕ) for effective removal by *M. leidyi*, a simple carbon budget was constructed to examine the contribution of its apparent ingestion to ctenophore metabolic demand (Table IV). *M. leidyi* respires 12.3% of its body carbon daily at 21.8°C (Kremer, 1977). The average cell volume of the *Ditylum* clone used was 25 000 μm^3, or 800 pg carbon $cell^{-1}$ based on the Strathmann (1967) equation. Assuming a constant weight-specific ingestion rate over the experimental size range used (15 – 40 mm), the mean daily ingestion rate of *M. leidyi* was 0.026 mg carbon. [mg *M. leidyi* $carbon^{-1}$].day^{-1}, or 2.6% of its body carbon. The terminal carbon content of *M. leidyi* predicted for the three day experiments with *Ditylum*, based on carbon loss due to respiration with, and without a carbon gain from ingestion, is remarkably close to that calculated from observed body length (Table IV). Ingestion provided only a small proportion (21%) of the carbon required daily for respiration. Since clearance rates for phytoplankton were even lower in the other microcosm experiments, it is unlikely that *M. leidyi* would be able to satisfy its nutritional needs by feeding on phytoplankton. Moreover, the observed shrinkage of *M. leidyi* in all P + C microcosms (Table III) suggests that *M. leidyi* requires more nutrition than it can obtain from phytoplankton.

Table IV. Carbon budget for *M. leidyi* in Experiment III P + C microcosm.

Ctenophore	Initial Length (mm)	Initial Carbon[a] (mg)	Daily carbon change Respiration loss[b] (mg C)	Daily carbon change Ingestion gain[c] (mg C)	Carbon content after 3 days Predicted – Respiration Alone (mg C)	Carbon content after 3 days Predicted – Respiration + Ingestion (mg C)	Carbon content after 3 days Observed[a] (mg C)
1	40	5.19	−0.64	+0.13	3.27	3.66	3.03
2	40	5.19	−0.64	+0.13	3.27	3.66	2.16
3	30	3.03	−0.37	+0.08	1.92	2.16	2.16
4	25	2.16	−0.27	+0.06	1.35	1.53	1.41
5	15	0.83	−0.10	+0.02	0.53	0.59	0.59

[a]From equations of Kremer and Nixon (1976) and Kremer (1976).
[b]From Kremer (1977); daily respiration loss = (0.123) (body carbon).
[c]Weight-specific daily ingestion rate equalled (0.026) (body carbon).

Mnemiopsis is characterized by a complex system of mucus and ciliary feeding (Main, 1928) and is sensitive to its degree of starvation and food concentration (Reeve and Walter, 1978). Thus, although *M. leidyi* did not appear to feed actively on phytoplankton, it conspicuously entangled phytoplankton cells in mucus strands and ejected mucus balls, even in the absence of zooplankton (Figure 5). A similar phenomenon has been observed at high zooplankton concentrations (Burrell, 1968; Reeve and Walter, 1978; Kremer, 1979). Even though the *S. costatum* cells took up neutral-red dye shortly after entanglement in mucus, i.e., they were still viable, the extent to which such entanglement causes mortality, and the long term effects of mucus capture on viability are unknown. The positive phytoplankton clearance rates found in the microcosm experiments may therefore actually represent removal by mucus entanglement rather than active ingestion *per se*. Such a mechanism might also explain Nelson's (1925) observations of an apparent feeding on nanophytoplankton and detritus by *M. leidyi*.

The formation of mucus at 1000, but not 100 cells ml^{-1} of *S. costatum* suggests a threshold value somewhere between these concentrations. Summer concentrations of 1000 cells ml^{-1} of *S. costatum* are not unusual in Narragansett Bay. If mucus formation at experimental phytoplankton concentrations is representative of *in situ* formation, then *M. leidyi* may be an important *in situ* source of macroscopic mucus aggregates reported by local scuba divers (Tomas, personal communication). Incorporation of phytoplankton into these aggregates in the microcosm experiments was accompanied by increased phaeopigment levels similar to that reported to accompany "marine snow" accumulations in Monterey Bay (Trent *et al.*, 1978). Mucus aggregation also increases the "package size" of the phytoplankton, which would influence phytoplankton sinking rates (Smayda, 1970) and phytoplankton availability to herbivores unable to feed on unaggregated small particles. In Narragansett Bay, for example, summer populations of menhaden, *Brevoortia tyrannus*, feed actively on phytoplankton only it it exceeds 13 – 16 μm (Durbin and Durbin, 1975). *M. leidyi* is to be included amongst those zooplankton groups which produce macroscopic mucus aggregates of potential importance as food sources (Parsons and Strickland, 1962; Alldredge, 1972), including appendicularians (Alldredge, 1972), pteropods (Gilmer, 1972), salps and doliolids (Pomeroy and Deibel, 1980), and gastropod and annelid larvae (Hamner *et al.*, 1975).

Our experiments support our hypothesis based on field observations (Deason and Smayda, 1982) that the summer dynamics of the *M. leidyi* populations in Narragansett Bay indirectly regulate phytoplankton dynamics through grazing pressure on zooplankton. That is, in the presence of ctenophores, microcosm phytoplankton populations generally increased and zooplankton populations decreased. When ctenophores were excluded from the microcosms, these plankton responses were reversed. However, the extent to which *M. leidyi* indirectly influenced phytoplankton abundance as a consequence of predation on zooplankton was dependent on the relative proportions and physiological states of the three populations. For example, adding *Mnemiopsis* had little effect in Experiment III (Figure 2) which was characterized by a high zooplankton:phytoplankton ratio. Low growth rates of nutrient-limited, post summer bloom

phytoplankton in Experiment I and II likewise precluded an increase in phytoplankton, even when zooplankton grazing was reduced by the ctenophore addition. Variability in these factors could contribute to the variations in timing and magnitude of changes in summer plankton populations observed in lower Narragansett Bay (Deason and Smayda, 1982). The influence of *M. leidyi* on phytoplankton species composition is presented elsewhere (Smayda and Deason, in review).

The hypothesized (Deason and Smayda, 1982) direct influence of ctenophores on phytoplankton dynamics through their nutrient excretion accompanying grazing was not examined during the microcosm experiments.

A tentative food-web model for *M. leidyi* based on our experimental and previously published results is presented in Figure 6. Caloric intake by *M. leidyi* results primarily from grazing on zooplankton and meroplanktonic larvae. Copepods, cladocerans and larval annelids, mollusks and barnacles are frequently found in the stomodaeum. The size of ingested prey ranges from ~0.6 to 6 mm (Burrell and Van Engel, 1976) although spiny crab zoea (0.7 mm) were not grazed, and polychaete larvae are less desirable prey (Nelson, 1925). *M. leidyi* sounds during turbulent mixing (Miller, 1974), a behaviorism also observed in the microcosms from which zooplankton were excluded (P + C). During such proximity to the sediments it possibly feeds on benthic organisms, including the adventitious uptake of benthic microalgae, particularly should this proposed behavior employ mucus-web prey capture. This species is known to graze on harpacticoid copepods (Mountford, 1980).

The *Mnemiopsis* food web is relevant to aquaculture and marine engineering. Nelson (1925) observed *M. leidyi* to graze voraciously on bivalve larvae in Barnegat Bay, and found a close correlation between *Mnemiopsis* abundance and the intensity of oyster sets and wood borer infestation. In 1921, the episodic *M. leidyi* was absent and ca. 1000 spat set (?typographical error in original paper) per cultch shell as against only 7 per shell during 1923, when it reappeared.

Ctenophores have been implicated in delayed fattening of summer herring (Manteufel, 1941) and retarded sexual maturity in mackerel (Scott, 1913),

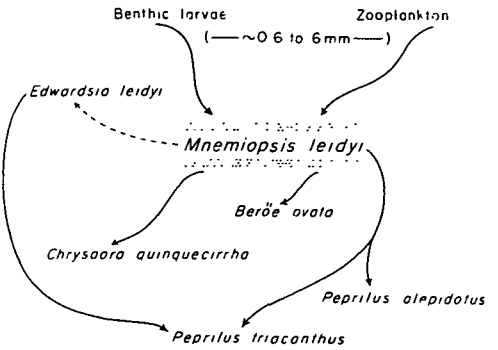

Fig. 6. Tentative food web model for *M. leidyi* based on experimental results herein and from accounts in the literature. Dashed vector leading to *E. leidyi* indicates uncertainty as to whether this species is parasitic on, detrimental to, or a benign endobiont in *M. leidyi*. See text for further details.

possibly because of their lower nutritional value to these species (see Reeve and Walter, 1978). However, the extent to which *M. leidyi*, as for *Pleurobrachia* (Fraser, 1962), feeds on fish eggs and larval fish, is uncertain. Based on gut content analyses, ctenophore predation of fish eggs in Scottish waters appeared to be insignificant (Fraser, 1970). Burrell and Van Engel (1976) concluded that larval fish were incidental items on the diet of *M. leidyi* in the York River.

The fate of energy consumed by ctenophores remains a mystery (Herman *et al.*, 1968). Few animals are known to feed on *M. leidyi*, foremost of which are the scyphomedusan *Chysaora quinquecirrha* (Miller, 1974; Heinle, 1974) and the ctenophore *Beröe ovata* (see Bishop, 1972; Heinle, 1974). Both the harvest fish, *Peprilus alepidotus* (Herman *et al.*, 1968), and butterfish, *Peprilus triacanthus* (Oviatt and Kremer, 1977), are predators on *M. leidyi*, the latter appearing to be nutritionally adequate for juvenile butterfish, insofar as the carbon requirement is concerned. The vermiform larval sea anemone, *Edwardsia leidyi*, frequently infects *M. leidyi* (Crowell, 1976). It is unknown to what extent this endobiont is parasitic. Infected ctenophores often are as vigorous as uninfected ones. Interestingly, Oviatt and Kremer (1977) reported that the butterfish appeared to select *E. leidyi* from its ctenophore host. Although tissue damage results, *M. leidyi* can regenerate tissue. This capability, and a possible preference of the butterfish for the conspicuous, pink *Edwardsia* over infected and uninfected ctenophores, may influence the degree to which such predation pressure on *M. leidyi* occurs.

Thus, the food web involving *M. leidyi* seems to be relatively simple based on available information. The relatively few predators identified to date are a very significant feature. Moreover, the distributional and/or seasonal ranges of occurrence for *M. leidyi* and its predators frequently do not overlap. In Narragansett Bay, for example, neither *C. quinquecirrha*, nor *B. ovata* are indigenous, and are therefore not usually predatory on *Mnemiopsis* in this ecosystem. The butterfish does occur, however, and may be the primary predator on *Mnemiopsis*. Indeed, grazing experiments led Oviatt and Kremer (1977) to conclude that this predator accounts for the local late summer-early fall decline of *M. leidyi*. However, the field evidence is less convincing (Deason and Smayda, 1982). In Barnegat Bay (Mountford, 1980) potential predators (medusae, ctenophores and fish) on *M. leidyi* are seasonally asynchronous in occurrence. The available evidence suggests, therefore, that *M. leidyi* may be relatively free from predation, is capable of explosive growth, and does not always appear to be food-limited (Kremer, 1979). A general explanation for its marked episodic appearances and characteristic inter-annual variations in abundance is presently not possible, either generally or for a specific region.

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References

Alldredge,A.L.: 1972, 'Abandoned larvacean houses: A unique food source in the pelagic environment.' *Science, N.Y.* **177**, 885-887.

Baker,L.D. and Reeve,M.R.: 1974, 'Laboratory culture of the lobate ctenophore *Mnemiopsis mccradyi* with notes on feeding and fecundity.' *Mar. Biol.* **26**, 57-62.

Bishop,J.W.: 1972, 'Ctenophores of the Chesapeake Bay.' *Chesapeake Science* **13**(Suppl.), 98-100.

Burrell,V.G.: 1968, 'The ecological significance of a ctenophore *Mnemiopsis leidyi* (A. Agassiz), in a fish nursery ground,' M.A. Thesis, The College of William and Mary, Virginia.

Burrell,V.G. and Van Engel,W.A.: 1976, 'Predation by and distribution of a ctenophore *Mnemiopsis leidyi* A. Agassiz, in the York River.' *Estuarine and Coastal Mar. Sci.* **4**, 235-242.

Crippen,R.W., and Perrier,J.L.: 1973, 'The use of neutral red and Evans blue for live-dead determination of marine plankton.' *Stain Technol.* **49**, 97-104.

Crowell,S.: 1976, 'An Edwardsiid larva parasitic in *Mnemiopsis*,' pp. 247-250. In: *Colenterate ecology and behavior.* Mackie,G.O. (ed.), Plenum Press, NY.

Deason,E.E.: in press, '*Mnemiopsis leidyi* in Narragansett Bay, 1975-1979: abundance, size composition and estimation of grazing'. *Estuarine, Coastal and Shelf Science.*

Deason,E.E. and Smayda,T.J.: 1982, 'Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972-1977.' *J. Plankton Res.* **4**,

Durbin,A.G. and Durbin,E.G.: 1975, 'Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration.' *Mar. Biol.* **33**, 265-277.

Fraser,J.H.: 1962, 'The role of ctenophores and salps in zooplankton production and standing crop.' *Rapp. P.-V. Reun., Cons. Int. Explor. Mer* **153**, 121-123.

Fraser,J.H.: 1970, 'The ecology of the ctenophore *Pleurobrachia pileus* in Scottish waters.' *J. Cons. Explor. Mer* **33**, 149-168.

Gilmer,R.W.: 1972, 'Free-floating mucus webs: A novel feeding adaptation in the open ocean.' *Science, N.Y.* **176**, 1237-1240.

Hale,S.S.: 1974, 'The role of benthic communities in the nutrient cycles of Narragansett Bay', M.S. thesis, University of Rhode Island, Kingston, R.I., 123 p.

Hamner,W.M., Madin,L.P., Alldredge,A.L., Gilmer,R.W. and Hamner,P.P.: 1975, 'Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior.' *Limnol. Oceanogr.* **20**, 907-917.

Heinle,D.R.: 1974, 'An alternate grazing hypothesis for the Patuxent estuary.' *Chesapeake Science* **15**, 146-150.

Herman,S.S., Mihursky,J.A. and McErlean,A.J.: 1968, 'Zooplankton and environmental characteristics of the Patuxent River estuary 1963-1965.' *Chesapeake Science* **9**, 67-82.

Hirota,J.: 1974, 'Quantitative natural history of *Pleurobrachia bachei* in La Jolla bight.' *Fish. Bull.* **72**, 295-335.

Kremer,P.M.: 1976, 'Excretion and body composition of the ctenophore *Mnemiopsis leidyi* (A. Agassiz): comparisons and consequences.' pp. 351-362. In: *10th European Symposium on Marine Biology*, vol. 2, Persone,G. and Jaspers,E. (eds.) Universa Press, Wetteren, Belgium.

Kremer,P.M.: 1977, 'Respiration and excretion by the ctenophore *Mnemiopsis leidyi.' Mar. Biol.* **44**, 43-50.

Kremer,P.M.: 1979, 'Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island.' *Estuaries* **2**, 97-105.

Kremer,P.M. and Nixon,S.W.: 1976, 'Distribution and abundance of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay.' *Estuarine and Coastal Mar. Sci.* **4**, 627-639.

Lebour,M.V.: 1923, 'The food of planktonic organisms. II.' *J. Mar. Biol. Assoc. U.K.* **13**, 70-92.

Lorenzen,C.J.: 1966, 'A method for the continuous measurement of *in vivo* chlorophyll concentration.' *Deep-Sea Res.* **13**, 223-227.

Main,R.J.: 1928, 'Observations on the feeding mechanism of a ctenophore, *Mnemiopsis leidyi.' Biol. Bull.* **55**, 69-78.

Manteufel,B.P.: 1941, 'Plankton and herring in the Barents Sea.' *Trudy Polyarnyi Nauchno-Issledovatel'skii I. Proektnyi Institut Morskogo Rybnogo Khozyaistva I. Okeanografii of Union of Soviet Socialist Republics* **7**, 125-218.

Miller,R.J.: 1970, 'Distribution and energetics of an estuarine population of the ctenophore, *Mnemiopsis leidyi*,' Ph.D. dissertation, North Carolina State University, Raleigh.

Miller,R.J.: 1974, 'Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz).' *Chesapeake Science* **15**, 1-8.
Miller,R.J. and Williams,R.B.: 1972, 'Energy requirements and food supplies of ctenophores and jellyfish in the Patuxent River Estuary.' *Chesapeake Science* **13**, 328-331.
Mountford,K.: 1980, 'Occurrence and predation by *Mnemiopsis leidyi* in Barnegat Bay, New Jersey.' *Estuarine and Coastal Mar. Sci.* **10**, 393-402.
Nelson,T.C.: 1925, 'On the occurrence and food habits of ctenophores in New Jersey inland coastal waters.' *Biol. Bull.* **48**, 92-111.
Oviatt,C.M. and Kremer,P.M.: 1977, 'Predation on the ctenophore *Mnemiopsis leidyi* by butterfish, *Peprilus tricanthus*, in Narragansett Bay, Rhode Island.' *Chesapeake Science,* **18**, 236-240.
Parsons,T.R. and Strickland,J.D.H.: 1962, 'Oceanic detritus.' *Science, N.Y.* **136**, 313-314.
Pomeroy,L.R. and Deibel,D.: 1980. 'Aggregation of organic matter by pelagic tunicates.' *Limnol. Oceanogr.* **25**, 643-652.
Reeve,M.R. and Walter,M.A.: 1978, 'Nutritional ecology of ctenophores - a review of recent research.' *Adv. Mar. Biol.* **15**, 249-289.
Scott,A.: 1913, 'The mackerel fishery off Walney in 1913.' *Report of the Lancashire Sea-Fisheries Laboratories* **22**, 19-25.
Smayda,T.J.: 1970, 'The suspension and sinking of phytoplankton in the sea.' *Oceanogr. Mar. Biol. Ann. Rev.* **8**, 353-414.
Smayda,T.J. and Deason,E.E.: in review, 'Experimental observations on the influence of *Mnemiopsis leidyi* (Ctenophora) on phytoplankton species composition.'
Strathmann,R.R.: 1967, 'Estimating the organic carbon content of phytoplankton from cell volume or plasma volume.' *Limnol. Oceanogr.* **12**, 411-418.
Swanberg,N.: 1974, 'The feeding behavior of *Beröe ovata*.' *Mar. Biol.* **24**, 69-76.
Trent,J.D., Shanks,A.L. and Silver,M.W.: 1978, 'In situ and laboratory measurements on macroscopic aggregates in Monterey Bay, California.' *Limnol. Oceanogr.* **23**, 626-635.