

Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977

Ellen E. Deason and Theodore J. Smayda

Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02881, USA

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Abstract. Plankton dynamics at a station in lower Narragansett Bay, RI are compared for six summer and fall seasons, 1972–1977. In four of these years, initiation of the summer pulse of the ctenophore *Mnemiopsis leidyi* was accompanied by a rapid decline in zooplankton abundance and a summer phytoplankton bloom. Termination of the phytoplankton bloom coincided with depleted ctenophore abundance and increased zooplankton biomass in two of the years. Yearly variations in the summer abundance of the diatom *Skeletonema costatum* were positively related to the magnitude of the ctenophore pulse. The magnitude of ctenophore population was related to the zooplankton biomass present at the start of the pulse. These relationships, the timing and magnitude of the plankton events suggest that *M. leidyi* regulated summer zooplankton and phytoplankton dynamics. Ctenophores may control phytoplankton blooms indirectly through their predation on herbivorous zooplankton and directly by the nutrient excretion accompanying such grazing. This evidence that a planktonic carnivore two trophic steps removed from the phytoplankton regulates the latter's dynamics in Narragansett Bay is analogous to reported regulation of benthic algal (kelp) dynamics by the sea otter, lobster and various crabs through their predation on herbivorous sea urchins. The factors responsible for the seasonal decrease in ctenophores remain unresolved; ctenophore predators on *Mnemiopsis* are absent in Narragansett Bay. Infection by the vermiform larval anemone, *Edwardsia lineata*, grazing by the butterfish, *Peprilus triacanthus*, and changes in food availability, temperature and salinity likewise do not explain this disappearance.

Introduction

The lobate ctenophore *Mnemiopsis leidyi* is ecologically important in estuaries along the Atlantic coast of the US, including: Narragansett Bay (Kremer and Nixon, 1976; Deason, in press); Barnegat Bay (Mountford, 1980); Chesapeake Bay (Bishop, 1967; Burrell, 1968; Herman *et al.*, 1968; Miller and Williams, 1972; Heinle, 1974; Burrell and Van Engel, 1976); and in North Carolina estuaries (Miller, 1970; 1974; Williams and Baptist, 1966). A decline in the standing stock of non-gelatinous zooplankton has often been associated with pulses of this, and other species of ctenophores (Bigelow, 1915; Nelson, 1925; Bigelow and Leslie, 1930; Russell, 1931; 1935; Barlow, 1955; Conover, 1961; Fraser, 1962; 1970; Cronin *et al.*, 1962; Hopkins, 1966; Herman *et al.*, 1968; Sage and Herman, 1972). The potential for *in situ* regulation of zooplankton population dynamics through ctenophore predation was demonstrated in experimental microcosms by Reeve and Walter (1976), who also reviewed the literature on quantitative aspects of the predatory effects of ctenophores (Reeve and Walter, 1978).

In Narragansett Bay, the copepod *Acartia tonsa* dominates non-gelatinous summer zooplankton populations, which characteristically decline in abundance during August or September (Martin, 1965; Hulsizer, 1976; Deason, unpublished). Kremer (1979) estimated that >1 cm sized *M. leidyi* cropped max-

imally from 5 to 10% of *A. tonsa*'s standing stock daily (bay-wide average), with localized maxima of 30%. Mean zooplankton removal rates by both adult and larval ctenophores were subsequently estimated (Deason, in press) to be 20% per day, with localized maxima ranging to 90% per day.

Summer phytoplankton dynamics in Narragansett Bay are characterized by considerable annual variation in maximum abundance and cycles (Smayda, 1976; unpublished); ~55% of the annual carbon production of 310 g C m^{-2} occurs during June through August (Furnas *et al.*, 1976). Field observations and experimental data suggested to us that summer phytoplankton dynamics in Narragansett Bay are influenced by grazing processes, and that ctenophores were implicated. The present study presents the relationships between ctenophore, zooplankton and phytoplankton dynamics found at a station in unpolluted, lower Narragansett Bay. Trends in the timing and magnitude of summer fluctuations over a six year period are compared. Microcosm experiments designed to quantify these interrelationships are presented in Deason and Smayda (1982).

Materials and Methods

As part of a long-term, ongoing study of plankton dynamics, ctenophores, zooplankton and phytoplankton were sampled weekly at 0900 hours regardless of tidal cycle at a station (2) located at $41^{\circ}34'07''\text{N}$, $71^{\circ}23'31''\text{W}$. The depth at this station is 8 m. Phytoplankton were collected in quantitative surface samples and counted live in a Sedgwick-Rafter chamber. Oblique zooplankton tows were made with a 0.3 m diameter, $153 \mu\text{m}$ mesh net fitted with a flowmeter. The unpreserved samples were subdivided in the laboratory into two aliquots with a CM^2 splitter. One aliquot, dried at 60°C , was used for dry weight determination; the other aliquot was preserved and used to estimate zooplankton numerical abundance and species composition. Zooplankton data for 1972–1973 are taken from Hulsizer (1976).

From 1975 to 1977 ctenophores were collected with a large square net, 1 m on a side. Mesh size was 1.8 mm in 1975 and 1.0 mm in 1976–1977. *M. leidyi* was divided into size classes based on total length; the animals being measured and enumerated in the field immediately after collection. Animals were sized in a Petri plate containing a measurement grid. In 1973 (Hulsizer, 1976) and 1974, ctenophore abundance was determined from animals caught in the zooplankton tows ($153 \mu\text{m}$ mesh). The 1972 and 1974 data sets were obtained from Kremer's (1975a) ctenophore census for stations 1 and 19 (located near station 2) based on 6.4 mm mesh net collections. The smallest ctenophores collected by Kremer were ~9 mm. In order to utilize these different estimates, the ctenophore abundances used for 1973–1977 were restricted to animals $> 1 \text{ cm}$ (Table I). (The diagonal of the mesh opening was taken as the smallest size ctenophore effectively sampled by each net.) Thus, for the 1975–1977 data set the procedure consisted simply of subtracting out the number of ctenophores found by us in the $< 1 \text{ cm}$ size class. Complete data for these years is presented elsewhere (Deason, in press). For 1973 and 1974, reported ctenophore abundance was reduced by 90%. This factor was derived from a comparison of samples collected on the same days with the $153 \mu\text{m}$ net and Kremer's net. This adjustment was not unreasonable based on sampling

Table 1. Collection of ctenophore data.

Year	Stations	Mesh size (mm)	Smallest sampled (mm)	Conversion	Source
1972	1, 19	6.4	9.1	none	Kremer, 1975a
1973	2	0.153	0.2	- 90%	Hulsizer, 1976
1974	2	0.153	0.2	- 90%	
	1, 19	6.4	9.1	none	Kremer, 1975a
1975	2	1.8	2.5	- <1 cm size class	present
1976	2	1.0	1.4	- <1 cm size class	present
1977	2	1.0	1.4	- <1 cm size class	present

during 1976 and 1977 which indicated that 90% of the ctenophore numbers were often in the <1 cm size class (Deason, in press).

The data were integrated monthly, using a Keuffel and Esser compensating polar planimeter 620022.

Results

Plankton cycles for 1972–1977 from June through November are shown in Figures 1–3. The diatom *Skeletonema costatum* usually dominates the summer phytoplankton bloom in Narragansett Bay (Smayda, 1957; 1973). In 1972 (Figure 1), it began its increase in early July, after a June pulse, reached a maximum of 11 000 cells/ml in mid-August and persisted through autumn. Zooplankton biomass, low during 1972, started its summer decline in early July, one month before *M. leidy* occurred in large numbers, and continued to decline until mid-August, i.e., the period of the summer phytoplankton increase. The ctenophore population reached its maximum (16 animals m^{-3}) in late September (ctenophores were not sampled thereafter).

In 1973 (Figure 1), the plankton populations exhibited more rapid fluctuations. *S. costatum* increased ~250-fold during the first week in August, one week after the precipitous zooplankton decline, and attained a maximum (39 000 cells/ml) in mid-August; secondary peaks occurred in October and November. *Mnemiopsis* numbers increased rapidly to 70 m^{-3} the last week in July, fluctuated in abundance during August, and declined in early September. Secondary peaks were observed in late September and late October. Zooplankton biomass dropped sharply to non-detectable levels coincident with the major ctenophore pulse during late July at station 2. Thereafter, following an increase in September, zooplankton biomass decreased to <10 $mg m^{-3}$ when the ctenophores increased during late September and late October.

In 1974 (Figure 2), the *S. costatum* maximum occurred in July and August (maximum 30 000 cells/ml). The summer bloom terminated sharply in mid-September; a secondary peak occurred in November. Zooplankton biomass began to decline in mid-July after the start of the phytoplankton bloom, reached its nadir in mid-August, and then increased rapidly, averaging 81 $mg m^{-3}$ dry weight in September and October. *Mnemiopsis* numbers increased gradually through July and early August to a maximum number of 31 m^{-3} , then decreased

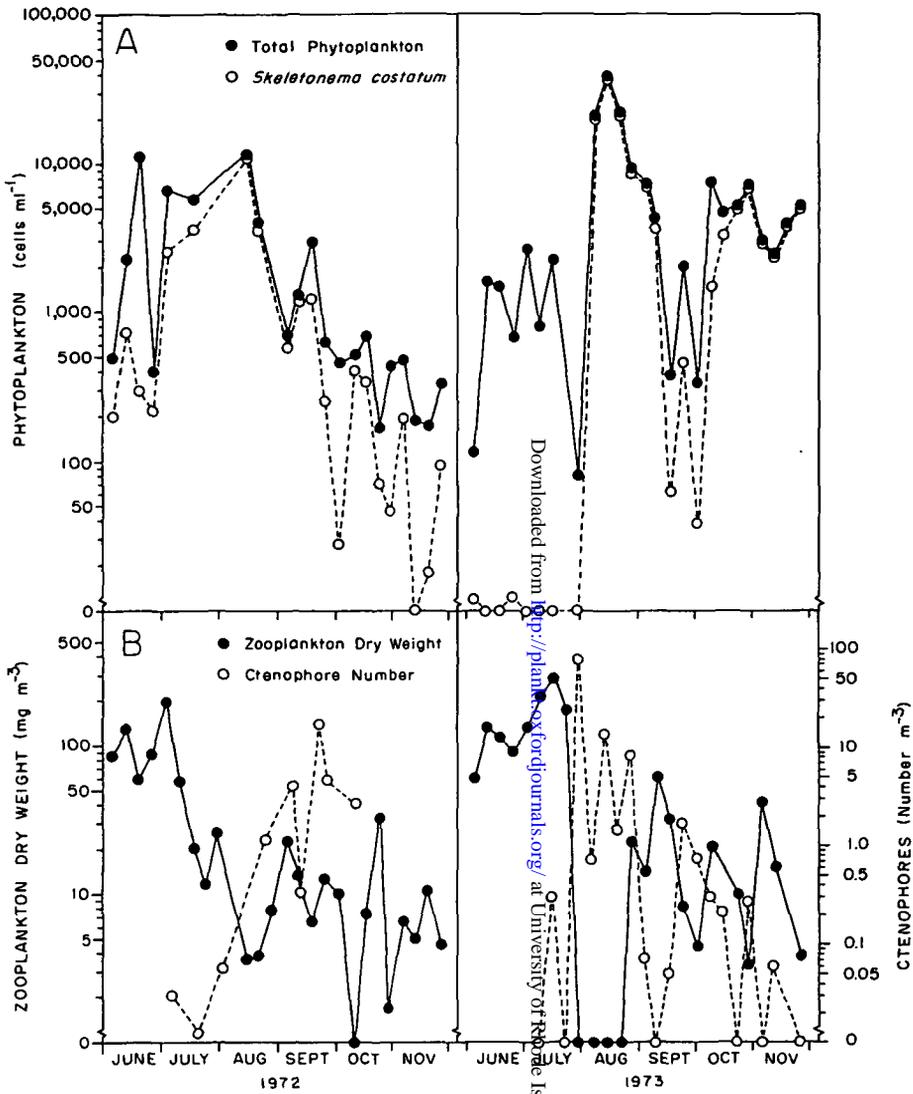


Fig. 1. (A) The abundance of total phytoplankton and the diatom *S. costatum*, summer-fall of 1972 and 1973. (B) Zooplankton biomass and abundance of the ctenophore *M. leidyi* (>1 cm in length), summer-fall of 1972 (including data from Kremer, 1975a) and 1973.

rapidly coincident with an influx of *Boreo ovata*, which is predatory on *Mnemiopsis*, at the end of August (Kremer and Nixon, 1976). A sharp increase in zooplankton and the termination of the summer phytoplankton bloom accompanied this decrease in *Mnemiopsis*.

The 1975 *S. costatum* population (Figure 2) increased in June, declined in July, bloomed again in August (maximum 59 000 cells/ml), followed by a gradual decline through October. The start of the August *Skeletonema* bloom was con-

Ctenophore-zooplankton-phytoplankton field studies

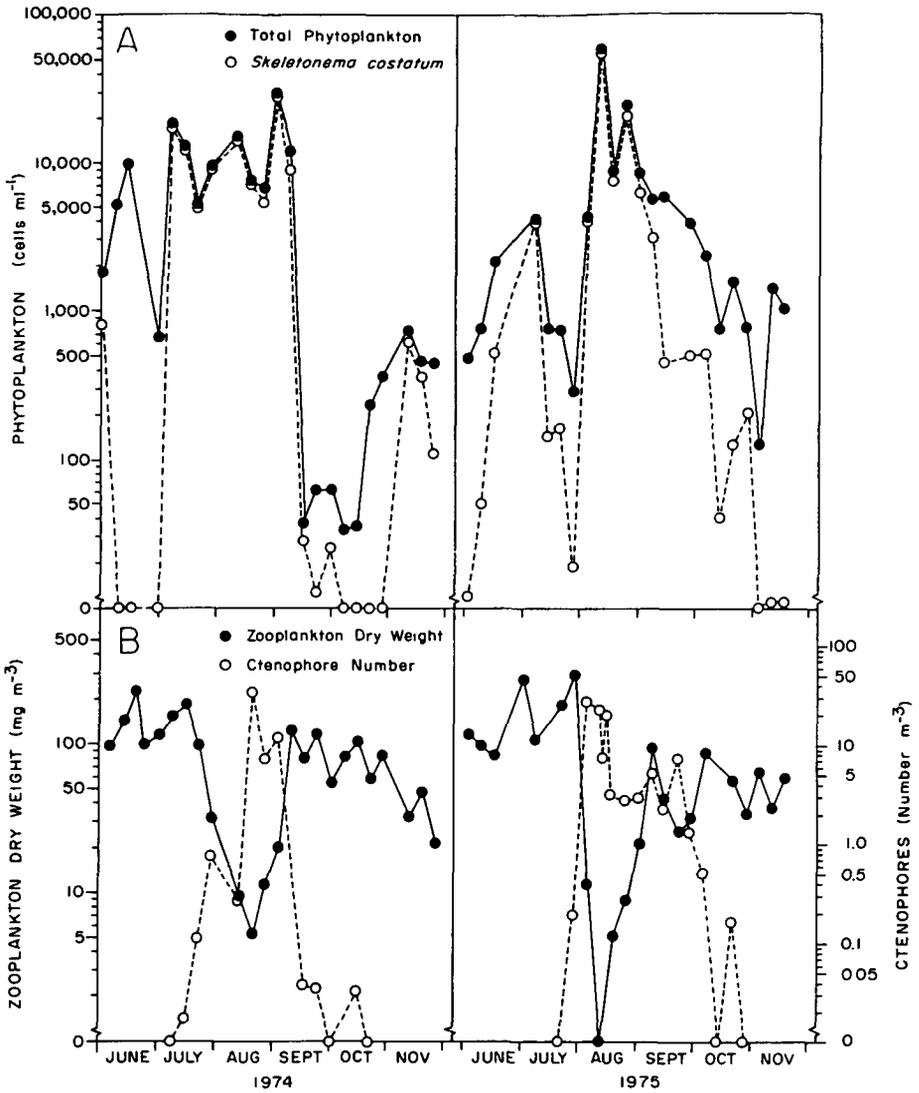


Fig. 2. (A) The abundance of total phytoplankton and the diatom *S. costatum*, summer-fall of 1974 and 1975. (B) Zooplankton biomass and abundance of the ctenophore *M. leidyi* (>1 cm in length), summer-fall of 1974 (including data from Kremer, 1975a) and 1975.

comitant with a rapid increase in *M. leidyi* (maximum 27 m⁻³) and a drop in zooplankton biomass. Thereafter, zooplankton biomass increased until early September, during which the abundance of large ctenophores was more or less constant and phytoplankton abundance decreased. Zooplankton declined during the secondary increase in ctenophore abundance which persisted in October.

In 1976 (Figure 3), *S. costatum* increased to 13 000 cells/ml during August and dropped sharply in early September. Zooplankton biomass declined less during

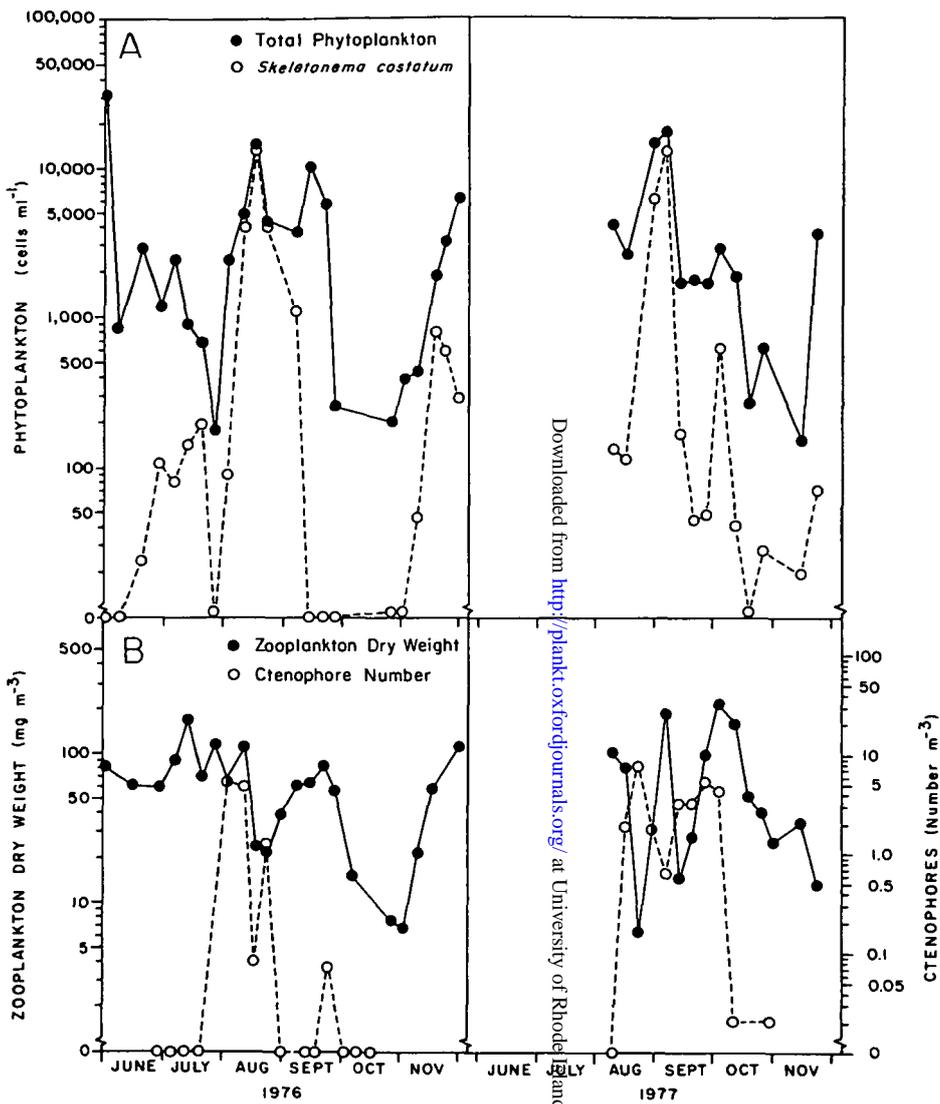


Fig. 3. (A) The abundance of total phytoplankton and the diatom *S. costatum*, summer-fall of 1976 and 1977. (B) Zooplankton biomass and abundance of the ctenophore *M. leidyi* (> 1 cm in length), summer-fall of 1976 and 1977.

the 1976 summer than in previous years, and did not decrease at station 2 until ctenophores had been present for several weeks. (This may be an artifact; exceptionally long diatom chains were retained by the 153 μm net and caused an overestimate of the zooplankton dry weight.) Biomass increased with the decline of the *M. leidyi* population in late August and early September. The maximum ctenophore population of only 5 m^{-3} was present in early August.

Data collection during the 1977 summer started in August (Figure 3). Growth

of the *S. costatum* population began later than in previous years, with a September maximum of 13 000 cells/ml, followed by a decline throughout the fall. The bloom followed a pulse of *M. leidy* in late August (maximum 7 m^{-3}) and associated zooplankton biomass declined to 6 mg m^{-3} . A secondary ctenophore pulse in September also accompanied a decrease in zooplankton biomass.

The data have been integrated by month to facilitate comparison between the different years. The size of the initial *M. leidy* population was directly related to food abundance (i.e., zooplankton). This is clearly illustrated in Figure 4 which relates integrated zooplankton biomass for the first month (July, except August in 1977) of the *M. leidy* pulse to the mean integrated ctenophore abundance for July and August. When integrated monthly abundances are compared, a general inverse trend becomes evident, with high zooplankton biomass occurring only during months with low ctenophore populations (Figure 5). (The anomalous point for 1973 occurred when ctenophores increased dramatically on the last sample date in July. The zooplankton response a week later was reflected in the August samples.) The monthly abundances for *Skeletonema* and zooplankton during summer and fall are also inversely related (Figure 6). High *S. costatum* populations occurred in months characterized by low zooplankton biomass.

The overall result of these linked interactions clearly emerges in the plot of integrated *Skeletonema* abundance averaged over the season of ctenophore influence versus the mean of integrated *M. leidy* abundance (Figure 7). The relationship is direct: years with large ctenophore pulses were also the years with large summer-fall *S. costatum* blooms.

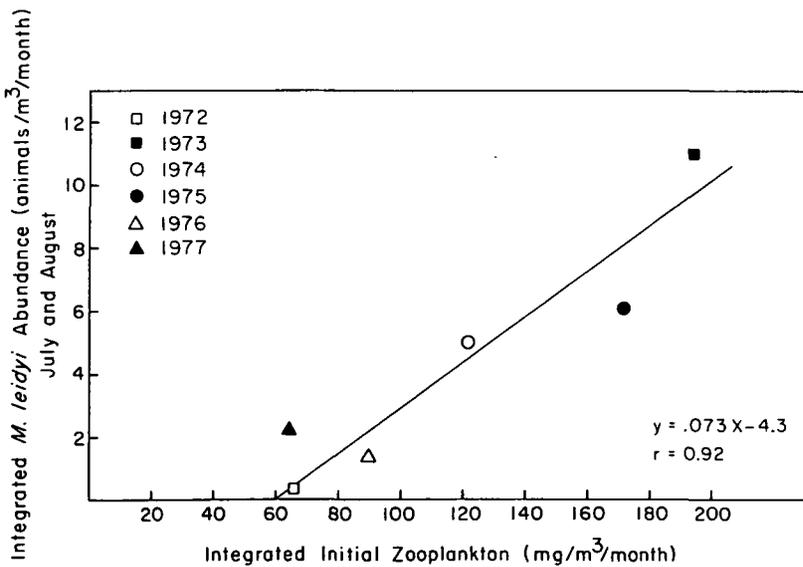


Fig. 4. Relationship between the size of the initial *M. leidy* population (mean integrated abundance in July and August) and the abundance of the initial food supply (integrated zooplankton biomass in July, except August in 1977).

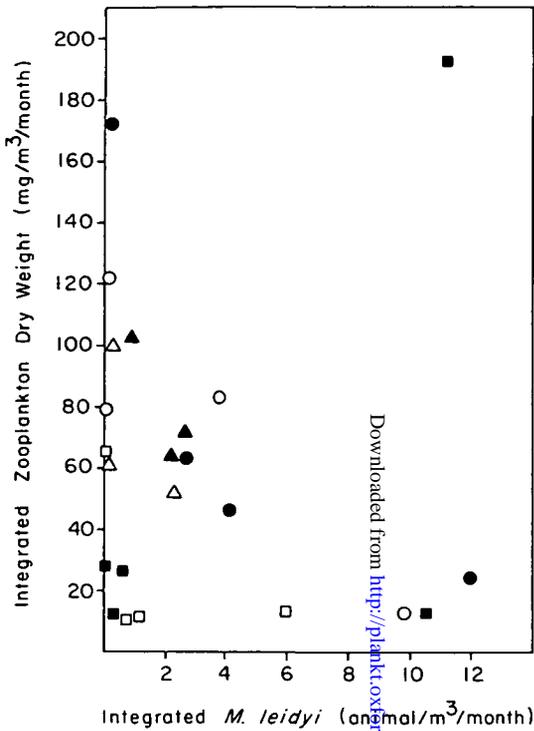


Fig. 5. Monthly relationship between the abundance of ctenophore *M. leidy* and zooplankton biomass during summer-fall. Symbols as in Figure 4.

Discussion

The characteristics of the summer population dynamics of the phytoplankton, zooplankton and ctenophores in 1973, 1975, 1976, and 1977 suggest that rapid increases in ctenophore abundance caused the observed decreases in zooplankton and, thereby, indirectly triggered the observed *S. costatum* blooms. Although the zooplankton linkage is less evident in 1976, the phytoplankton bloom and the onset of the ctenophore increase coincided. In 1972 and 1974, sustained phytoplankton blooms coincided with the seasonal decrease in zooplankton biomass. These blooms started before the decline in zooplankton biomass began, which commenced before the ctenophore maximum. Ctenophores did not increase at station 2 as rapidly in 1972 and 1974 as in the other four years when fluctuations in the ctenophore-zooplankton-phytoplankton population coincided.

Termination of the *S. costatum* bloom may likewise be related to the zooplankton and ctenophore cycles in some years. In 1974, when predation by a rare occurrence of *B. ovata* rapidly depleted the *M. leidy* population (Kremer and Nixon, 1976), zooplankton biomass increased sharply followed immediately by a rapid phytoplankton decline. Similarly, in September, 1976, a decline in the *Mnemiopsis* population was associated with a zooplankton increase and phytoplankton decrease. In 1973, a secondary peak of *S. costatum* during the autumn

Ctenophore-zooplankton-phytoplankton field studies

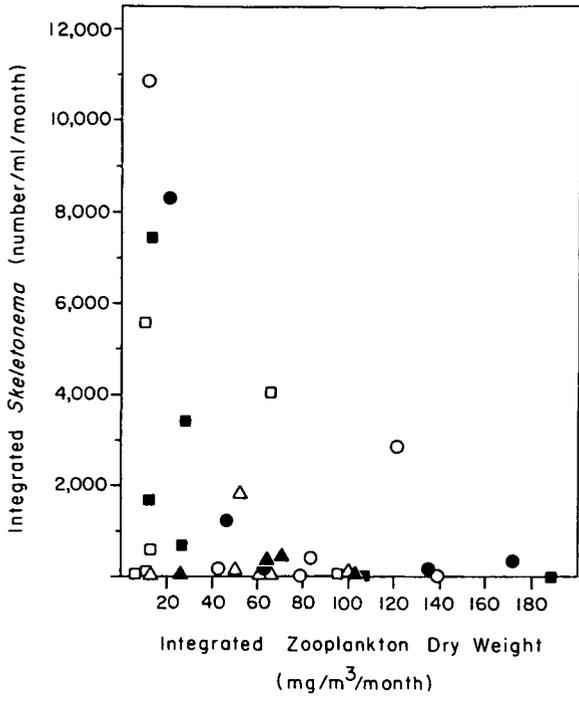


Fig. 6. Monthly relationship between zooplankton biomass and the abundance of the diatom *S. costatum* during summer-fall. Symbols as in Figure 4.

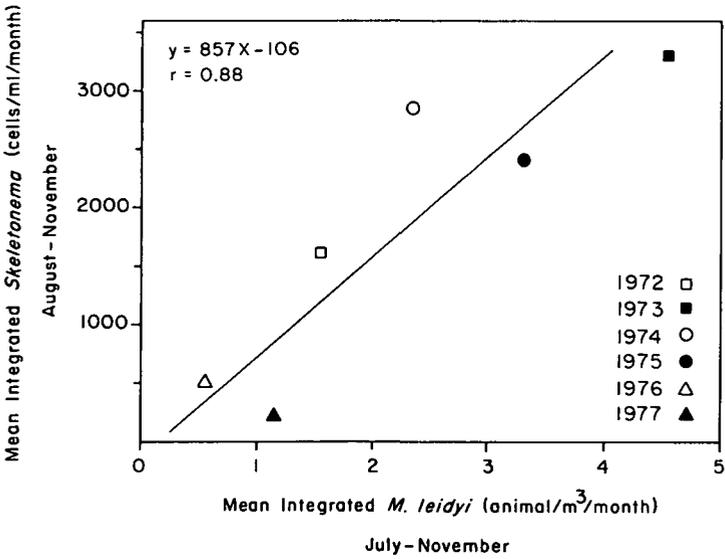


Fig. 7. Seasonal relationship between the abundance of the ctenophore *M. leidyi* and the diatom *S. costatum*.

correlated well with the very low zooplankton biomass present then.

There is, thus, apparently a synchronous timing in the fluctuations in phytoplankton, zooplankton and >1 cm ctenophore pulses in Narragansett Bay. In addition, the magnitude of the maximum populations produced also seems to be inter-related (Figures 4–7). This is suggested by the direct relationship characterizing zooplankton biomass levels during the first month of *M. leidy*'s seasonal occurrence, and the magnitude of the latter's mean integrated abundance in July-August (Figure 4). A three-fold increase in mean July zooplankton biomass was associated with a five-fold increase in ctenophore abundance. This relationship provides field evidence that food supply contributes to annual variations in the initiation and magnitude of the ctenophore pulses. The explosive ctenophore increases observed in Narragansett Bay, accordingly, reflect both the high fecundity and growth rate potential of these carnivores, realized when food supply is adequate. Food availability has been hypothesized (Kremer, 1975a) to be a major factor regulating the spatial and temporal variations in *M. leidy* fecundity during the summer in Narragansett Bay, a view partially supported by a simulation model (Kremer, 1976a). The relationship of ctenophore abundance to initial food levels may not hold for all years, however. During 1978 and 1979, for example, the ctenophore populations consisted almost entirely of animals <1 cm in length. Despite high zooplankton biomass levels in July of those years, the ctenophore pulses and biomass were reduced relative to earlier years (Deason, in press). Coupling of ctenophore populations with food supply has also been reported for Biscayne Bay, Florida (Baker, 1973). The congeneric species *M. mc-cradyi*, which occurs there most of the year rather than in a single seasonal pulse, was encountered most frequently at stations with high zooplankton biomass, and least frequently at stations characterized by low zooplankton biomass.

The inverse relationships between *M. leidy* abundance and zooplankton biomass (Figure 5), and zooplankton and *Skeletonema* abundance (Figure 6) are not necessarily indicative of causal relationships. However, together they suggest one explanation for the direct relationship between *Skeletonema* and ctenophore abundance observed in Narragansett Bay. That is, predation by *Mnemiopsis* on zooplankton reduced the latter's standing stock and, hence, its grazing pressure on phytoplankton as well. In addition, *Mnemiopsis* may have directly stimulated phytoplankton (Kremer, 1975b; 1976b; Deason, in press). Phytoplankton growth locally is often nutrient-limited, specifically by nitrogen (Smayda, 1974; Furnas *et al.*, 1976). These aspects of the ctenophore-phytoplankton trophic coupling can be quantified.

Calculated predation rates of natural populations of *M. leidy* in Narragansett Bay are large enough to affect zooplankton abundance significantly. On the average, this ctenophore cropped 5–10% of the zooplankton standing stock daily throughout this bay, and up to 30% daily in localized areas (Kremer, 1979). This is probably a minimal estimate, however, since Kremer's calculations refer only to ctenophores caught in a 6.4 mm net. Smaller (<1 cm) individuals of *M. leidy*, which may account for 90% of total ctenophore abundance (Deason, in press), are capable of significant predation (Reeve *et al.*, 1978; Deason, in press). Based on predation estimates for the entire ctenophore population (i.e., all sizes),

almost 20% of the zooplankton standing stock was cropped daily bay-wide in August, 1976, with localized predation ranging up to 90% (Deason, in press).

The growth rates of natural summer phytoplankton populations in Narragansett Bay incubated in dialysis sacs from which zooplankton were excluded have been examined by Vargo (1976). He found growth rates of *S. costatum* exceeded two divisions per day during periods when its *in situ* standing stocks were low. At such growth rates, a release in herbivorous grazing pressure, such as would occur during ctenophore predation on zooplankton, would be sufficient to stimulate a bloom. (Summer *S. costatum* dynamics are too complex to be attributed solely to predation control, however.)

Nutrient dynamics also have a major influence on summer phytoplankton growth in Narragansett Bay. The summer period is often characterized by nutrient limitation (Smayda, 1974), with high turnover rates of nitrogen and phosphorus required to allow the observed production rates (Durbin *et al.*, 1975; Furnas *et al.*, 1976; Vargo, 1979). An important source of this nutrient is excretion by the benthic community which, based on Hale's (1975) measurements, contributes from 20 to 50% of the daily summer nitrogen demand. Zooplankton excretion may also be an important nutrient source then. With regard to *M. leidy*, Kremer (1975b) estimated that it excreted 10–60 μg at $\text{NH}_3\text{-N m}^{-3} \text{ day}^{-1}$ during its biomass peak. This represented 0.25–25% of the ambient ammonia concentrations (Kremer, 1976b). Seasonal mean excretion rates during 1975–1979, including the contribution of *M. leidy* larvae, ranged from 0.55 to 14.7 μg at $\text{NH}_3\text{-N m}^{-3} \text{ day}^{-1}$. These represented a range from <1% to ~5% of the daily phytoplankton nitrogen requirements (Deason, in press). Non-gelatinous zooplankton in Narragansett Bay excreted (minimally) ~5% of the daily nitrogen requirement in 1972 (Vargo, 1979) and ranged from 0.6 to 20% in 1974 (Furnas *et al.*, 1976). Thus, *M. leidy* may excrete nitrogen at levels which equal or exceed that from the non-gelatinous zooplankton.

These relationships in the timing and magnitude of plankton events suggest that *M. leidy* may regulate summer zooplankton and phytoplankton dynamics in Narragansett Bay. Experimental studies are consistent with this observation (Deason and Smayda, 1982). Phytoplankton blooms may be controlled, even stimulated, indirectly by this ctenophore through its predation on the herbivorous zooplankton populations, and directly by its excretion of nutrients during grazing on zooplankton. This is not to claim that summer phytoplankton dynamics in Narragansett Bay are solely regulated as a consequence of ctenophore grazing activities on zooplankton. There is an inter-annual variability in summer zooplankton dynamics which cannot be attributed to exclusive regulation by ctenophore predation. For example, during 1972 and 1974 the *M. leidy* pulse followed the start of the zooplankton decrease; this timing precluded a major initiating role by *M. leidy*. In an ecological simulation model of Narragansett Bay (Kremer and Nixon, 1978), summer zooplankton abundance also decreased both with, and without an arbitrary predation component. However, unlike Kremer's (1979) conclusion, we believe that in many cases *M. leidy* can be a major force in initiating the initial summer decline in zooplankton in Narragansett Bay.

We cannot explain the seasonal disappearance of *M. leidy* after October

(Figures 1–3) in Narragansett Bay. The 20-year range in temperatures (8° to 11°C) found in mid-November is well within its tolerance, as is the salinity (Nelson, 1925). Food limitation likewise is not clearly responsible. It actively grazes in the temperature range accompanying its disappearance (Kremer, 1976a), a time when zooplankton biomass levels are also usually high (Figures 1–3). While animals were found to be infected with the vermiform larval sea anemone, *Edwardsia lineata*, parasitic in *M. leidy* (Crowell, 1976), its demise could not be related to such infection. Nor can grazing be established as the cause of its disappearance, based on available data. Although *M. leidy* disappeared during a rare appearance of the well known ctenophore predator *B. ovata* in lower Narragansett Bay (Kremer and Nixon, 1976), this predator is normally absent. *Chrysaora quinquecirrha*, the well known medusan predator of *M. leidy* in Chesapeake Bay (Herman *et al.*, 1968; Miller, 1974) is absent in Narragansett Bay. Oviatt and Kremer (1977) have suggested that predation by the butterfish, *Peprilus triacanthus* probably accounts for the late summer-early fall decline in ctenophore abundance, based on 1971 butterfish biomass estimates. We have not been able to correlate monthly and annual variations in ctenophore abundance with similar abundance estimates of the butterfish caught in 30 min bottom trawls collected at station 2, (Jeffries, unpublished).

The influence of ctenophore pulses on phytoplankton blooms that we have described for Narragansett Bay has not been reported in other locations, to our knowledge. Differences in phytoplankton species composition in enclosure experiments have been observed to accompany variations in the abundance of the ctenophore *Bolinopsis infundibulum* (Gamble *et al.*, 1977). Nonetheless, there is some field evidence that other gelatinous predators may control phytoplankton abundance. In Saanich Inlet, British Columbia, Huntley and Hobson (1978) observed a second spring phytoplankton bloom and a decline in herbivore populations concomitant with an increase in the leptomedusan *Phialidium gregarium*. Möller (1979) proposed that the mass occurrence of the carnivorous medusan *Aurelia aurita* in the Kiel Bight was responsible for a reduction of copepod stocks which allowed a summer buildup of phytoplankton. Annual mass occurrences of the tentaculate ctenophore *Pleurobrachia pileus* were shown (Greve, 1971) to be coupled to the pulses in copepod and larval meroplankton abundance, following the vernal phytoplankton bloom in the German Bight. We would predict increased phytoplankton abundance accompanied these latter zooplankton dynamics.

The significant feature of our observations is that a planktonic carnivore two trophic steps removed from that of the phytoplankton can, under certain circumstances, apparently regulate the latter's dynamics, indirectly via herbivore predation and directly through essential nutrient excretion. Such regulation, well-known for the primary producer-herbivore link in marine food webs, will obviously vary seasonally, annually and, probably, regionally. This precludes generalities on the importance of this trophic linkage, although investigators should be cognizant that such trophic coupling can occur.

In retrospect, such coupling is not surprising, given several reports that benthic macroalgal abundance and species composition are also regulated by carnivorous

trophic levels. A most elegant example has been reported for Nova Scotia benthic communities (Breen and Mann, 1976; Mann, 1977). A 50% decrease in the lobster population (*Homarus americanus*) was accompanied by an increase in its prey, the sea urchin *Strongylocentrotus droebachiensis*, a voracious herbivore on macroalgae, whose increased grazing pressure destroyed 70% of the kelp beds (*Laminaria* spp.). That is, a direct relationship occurs between lobster abundance and kelp biomass, and inversely between each of these trophic levels and herbivorous sea urchin abundance. Similar relationships characterize populations of sea urchins, kelp and the sea otter, *Enhydra lutris*, which feeds on sea urchins, in western Aleutian waters (Estes and Palmisano, 1974). Elsewhere, inter-related population dynamics characterized sea urchins, kelp and the sea star, *Pycnopodia* sp. (Paine and Vadas, 1969); and sea urchins, kelp and various crabs (Muntz *et al.*, 1965). Future studies must establish just how important ctenophores and leptomedusae are as regulators of lower trophic level dynamics, i.e., phytoplankton, in planktonic food webs.

Acknowledgements

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Ctenophore-zooplankton-phytoplankton field studies

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