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Changes in the lower Chesapeake Bay food chain in presence of the sea nettle *Chrysaora quinquecirrha* (Scyphomedusa)

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ABSTRACT: The abundance of 4 levels of the lower Chesapeake Bay food chain (Chlorophyll *a*, herbivores, ctenophore *Mnemiopsis leidyi*, and Scyphomedusa *Chrysaora quinquecirrha*) were monitored twice weekly at 4 stations from May 10 through Sep 30, 1982 in the Lafayette and Elizabeth Rivers (Virginia). The herbivore standing stock, largely copepods, declined sharply in late May when *M. leidyi* appeared, but rebounded a month later when *C. quinquecirrha* medusae reduced the ctenophore population. Despite the additional presence of *Aurelia aurita* (Scyphomedusa) from Jul onward, herbivore abundance remained at moderate levels until the end of the study period. Phytoplankton abundance fluctuated and may have been responsible for brief periods of food shortage; however, the major periods of low herbivore abundance do not seem to have been kept low by food limitation. *M. leidyi* made a modest resurgence in late Aug when the *C. quinquecirrha* population underwent its seasonal decline. Our data suggest that *C. quinquecirrha* contributes to the secondary productivity of the lower Chesapeake Bay by controlling *M. leidyi* during summer.

INTRODUCTION

Coelenterate medusae are gelatinous organisms with fast growth rates and high metabolic requirements (Krüger, 1968; Kerstan, 1977; Möller, 1980a). They are predaceous and, although their feeding behavior and diets have been observed for some time, the food-chain ramifications of their feeding activity have been investigated only recently for a few species. Huntley and Hobson (1978) found that feeding of the leptomedusa *Phialidium gregarium* reduced herbivore populations and allowed a second spring phytoplankton bloom in a British Columbian (Canada) fjord. Möller (1979) reported that the *Aurelia aurita* (Scyphomedusa) population of Kiel Bight, F. R. Germany, sharply reduced the copepod population with resultant increases in the phytoplankton and protozoan populations of the area. By investigating feeding rate and population dynamics of this species he concluded that the scyphomedusa significantly affected larval fish populations by consuming the larvae directly and competing with them for food (Möller, 1980a, b). According to Lindahl and Hernroth (1983) the *A. aurita* and *Cyanea capillata* of the Gullmar fjord, Sweden, 'regulate' the pelagic ecosystem during summer. A conse-

quence of the sharp reduction in zooplankton standing stock is oxygen depletion in the depths of the fjord due to decaying phytoplankton and dying medusae which accumulate there. In freshwater, the limnomedusa *Craspedacusta sowerbyi* affects the zooplankton composition of Wisconsin (USA) lakes by reducing the density of other invertebrate plankton predators. As in the other ecosystems, the medusa has virtually no predators in the water column (Dodson and Cooper, 1983).

Chrysaora quinquecirrha (Desor, 1848), the sea nettle, is found from the southern coast of New England to the tropics along the East coast of North America (Mayer, 1910). Its population is greatest in the Chesapeake Bay where the medusa stage is extremely abundant in late spring and summer. Most previous studies of the species have been of the polyp stage (e.g. Cones, 1969; Loeb and Blanquet, 1973; Cargo and Rabenold, 1980). The ecology of the medusa has generally been neglected. Medusa abundance estimates have been made by visual counts from a pier (Cargo and Shultz, 1967; Cones and Haven, 1969) or in combination with ctenophore observations (Herman et al., 1968).

The medusa of *Chrysaora quinquecirrha* feeds on the

ctenophore *Mnemiopsis leidyi* in the Chesapeake Bay (McNamara, 1955), as well as on crustacean zooplankters (Cargo and Shultz, 1966; Feigenbaum et al., 1982). After a season of preliminary work (Feigenbaum et al., 1982) we began the present study with the aim of determining the food chain ramifications of sea nettle abundance in our region.

MATERIALS AND METHODS

Abundance estimates were made at 4 stations in the Lafayette and Elizabeth Rivers (Fig. 1). The stations were sampled approximately twice a week from May 6 to Oct 1, 1982 from a 4.9 m boat. Zooplankton were sampled with a specially designed net-within-a-net which separated the crustaceans from the gelatinous animals. This net was towed obliquely by first letting out a predetermined length of line (the length varied with station and tide level), allowing the net to sink close to the bottom and then hauling it in using a power windlass with the boat underway. The catch of the inner net (505 μm) – gelatinous organisms – was sorted to species and the abundance of each measured

Fig. 1. Location of stations occupied during the study. In parentheses: depths in m

volumetrically (ml of organisms m^{-3} of water filtered). The catch of the outer net (153 μm), the 'herbivore fraction', was filtered out, placed in a Whirl Pak plastic bag, transported in a cooler on Blue Ice, and frozen back in the laboratory. Later, these organisms were defrosted and examined under a stereo microscope. Detritus and sediment were removed by pipetting, the remainder of the contents dried at 60 °C and weighed on a microbalance (Unimatic CL41). Two to 4 replicate tows were made at each station. A flow meter (General Oceanics, A2030-GC) was used to monitor the amount of water filtered during each tow.

Water samples were taken from 2 depths: approximately 1 m above the bottom (NIO Bottle); and from just below the surface (dipped). Once aboard, these samples were mixed into 3 replicate bottles. Fifty ml samples were removed from each and filtered with a Gelman glass fiber filter (Type A/E) using a Stylex syringe with filter attachment. The filters were then folded over, placed in covered Petri dishes in the cooler and returned to the laboratory where they were frozen. The samples were subsequently analyzed for chlorophyll *a* and phaeopigments using the fluorometric determination technique of Strickland and Parsons, (1972). Surface temperatures and salinities were measured with a thermometer and refractometer (AO 10419).

Each station was visited either of 2 fixed times in the tidal cycle, depending on whether the tide was high or low during the morning hours. Station A was always occupied at either high or low tide; Station B, 45 min later and Stations C and D 1 and 2 h respectively after B.

The relative proportions of copepods to meroplankters were obtained by examining well-mixed subsamples (an average of 754 organisms each) of plankton tows made by another study during the same period near Stations C and D. An average of 3 sub-samples was counted for each of 14 dates. These samples were obtained with a 153 μm net.

RESULTS

The results obtained for Station A are presented in Fig. 2. Station A was farthest upstream in the Lafayette River and had the most consistent presence of sea nettles during the study. It was also the shallowest (Fig. 1) station and had the highest temperatures and lowest salinities during summer (Table 1).

Sea nettles appeared at Station A during the first week of June and were generally abundant until mid-August. Their abundance declined thereafter, but *Chrysaora quinquecirrha* remained at this station through the end of our sampling program.
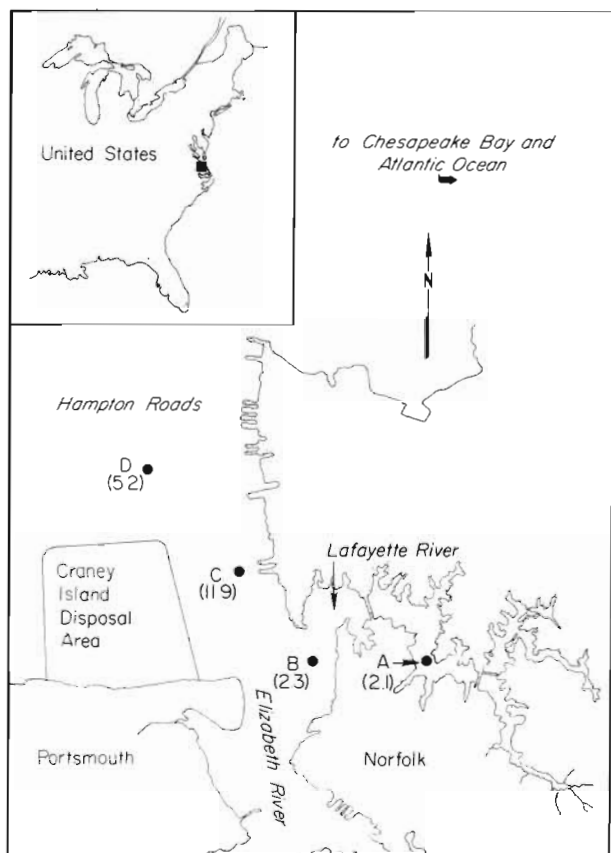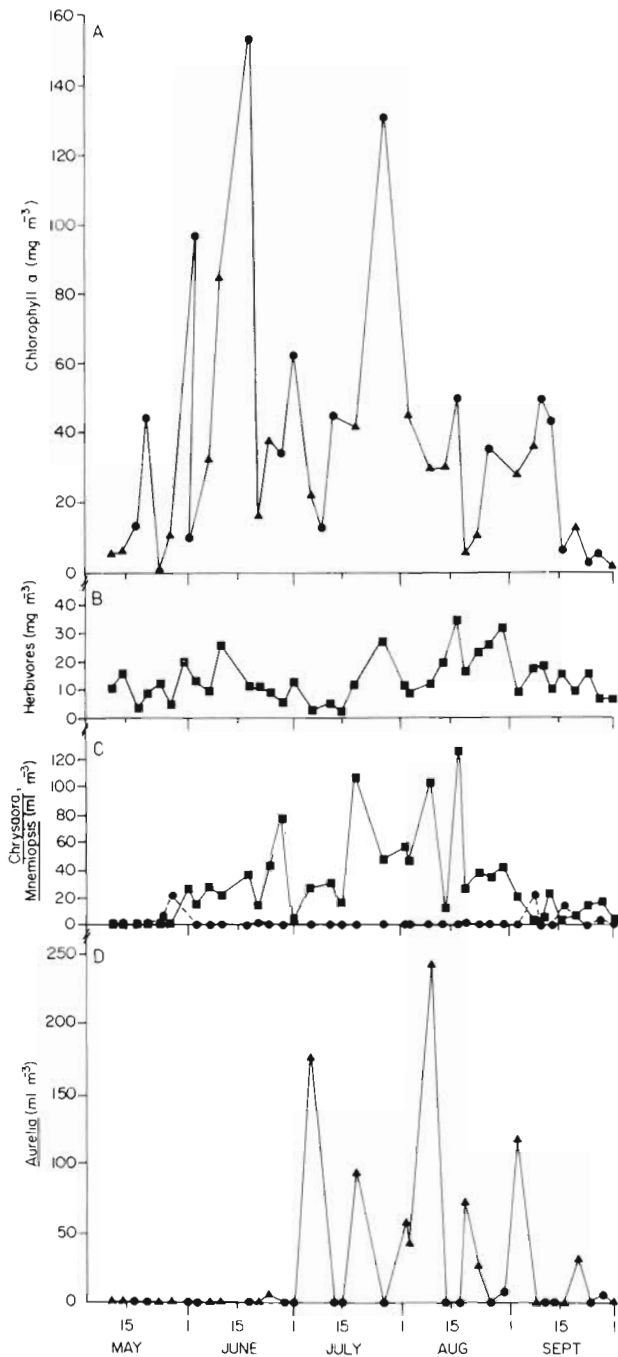
Fig. 2. Abundance of chlorophyll *a* and of organisms monitored at Station A. In (a) and (d) circles indicate low tide and triangles indicate high tide collections. In (c) *Mnemiopsis leidyi* values appear as circles, *Chrysaora quinquecirrha* values as squares

Table 1. Monthly averages of surface temperature (°C) and salinity (‰) at each station in 1982

Month	Station			
	A T/S	B T/S	C T/S	D T/S
May	23.5/15.8	23.2/17.2	21.2/17.3	21.0/16.6
Jun	25.9/15.3	25.4/15.7	24.9/14.3	24.8/13.3
Jul	26.9/14.2	26.8/15.7	26.6/16.4	26.4/16.3
Aug	26.2/14.8	25.9/16.6	25.6/17.9	25.6/17.5
Sep	23.6/18.2	23.4/19.6	23.8/19.5	23.7/19.3

The ctenophore *Mnemiopsis leidyi* appeared at Station A before *C. quinquecirrha* (mid May), but its abundance declined to a very low level 1 wk after the appearance of the medusa. *M. leidyi* reappeared in modest abundance in early September when the *C. quinquecirrha* population was small. This inverse rela-

tion between *C. quinquecirrha* and *M. leidyi* was also observed in 1981 (Feigenbaum et al., 1982).

The abundance of the herbivore fraction was highly variable at Station A during the early part of the study. In June, herbivore abundance declined and remained low through mid-July at which time the population rebounded, reaching its peak abundance during August. It remained at a mid-level during Sepember.

Chlorophyll *a* concentrations were variable, but 4 to 5 times higher at this station than at any of the others.

The abundance of the moon jelly *Aurelia aurita* was extremely patchy. *A. aurita* was rarely caught at Station A during a low tide (mean low tide abundance: 1.02 ml m^{-3}), but was continually abundant during high tides from the date of its first appearance through mid-September (mean high tide abundance: 72.2 ml m^{-3}) (Fig. 2d).

The small hydromedusa *Nemopsis bachei* was also found at Station A. It was most abundant at the start of the study (mean abundance: 5.7 ml m^{-3} for the first 2 dates) and remained in low numbers through June 18, after which it was not found.

Stations B, C and D lie approximately along a straight line in the Elizabeth River and the results of these Stations are reported together (Fig. 3 to 5).

At the start of our sampling in early May, herbivore abundance was relatively high at each station. At that time *Chrysaora quinquecirrha* was absent from the water column and the *Mnemiopsis leidyi* population was at a low level. The herbivore population declined sharply at all 3 stations in mid to late May. This was a few days before *M. leidyi* became abundant. The number of herbivores remained low until late June, about a week after the *M. leidyi* population declined. The *M. leidyi* decrease began just after the appearance of *C. quinquecirrha* in the water column. In late June, the herbivore population at all 3 stations displayed a large, rapid increase. Herbivore abundance subsequently fell, but not to the low levels of the late May to June period. Throughout the study the abundance of *C. quinquecirrha* at each of these stations was more variable than at Station A.
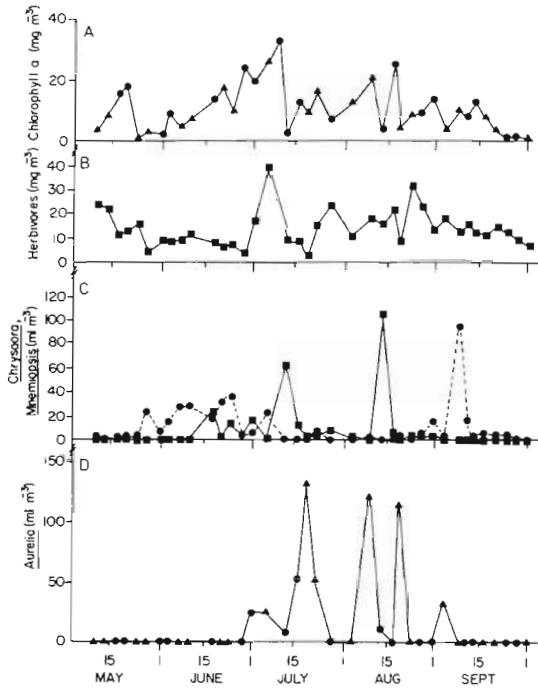
Fig. 3. Abundance of chlorophyll a and of organisms monitored at Station B. Symbols same as in Fig. 2
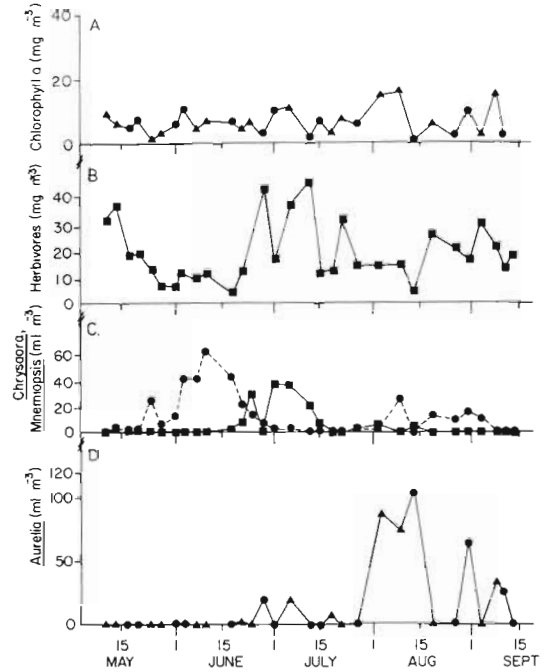

Fig. 5. Abundance of chlorophyll a and of organisms monitored at Station D. Symbols same as in Fig. 2
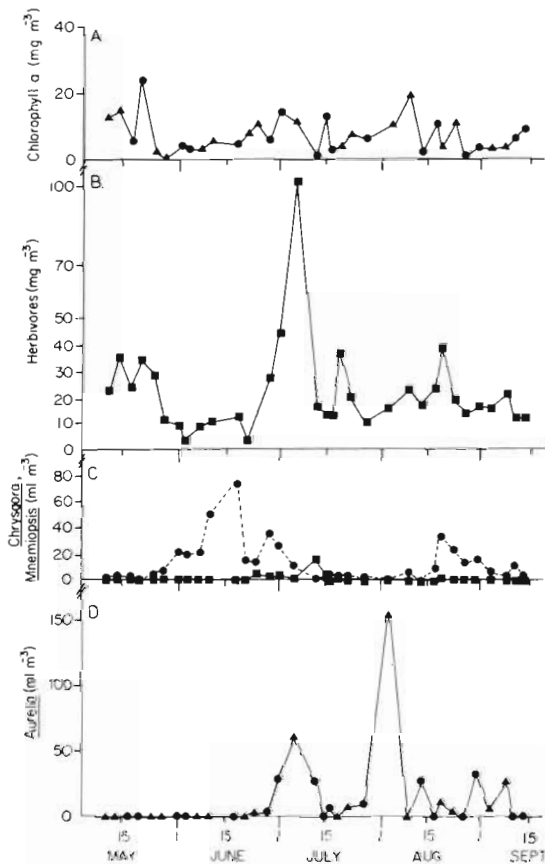
During the study period the herbivore fraction in the vicinity of Stations C and D was dominated by copepods. These made up 75.4 % (by number) of the total herbivores from late May through June and 93.7 % of the total during the rest of the study (Table 2). The abundance of meroplankters was not high enough to have significantly affected the shape of the herbivore plots at these stations.

Fig. 4. Abundance of chlorophyll a and of organisms monitored at Station C. Symbols same as in Fig. 2

Table 2. Relative proportions, by number, of copepods and meroplankters near Stations C and D during the study (1982)

Date		% Copepods		% Meroplankters	No. of samples examined
May	23	72.6		27.4	2
May	29	61.6		38.4	4
Jun	11	85.7		14.3	2
Jun	15	80.9		19.1	2
Jun	22	76.1	75.4 *	23.9	4
Jul.	12	97.6		2.4	2
Jul	13	85.6		14.4	2
Jul	31	94.8		5.2	4
Aug	6	92.9		7.1	4
Aug	19	95.5		4.5	4
Aug	31	97.3		2.7	4
Sep	17	87.9		12.1	2
Sep	20	96.9		3.1	2
Sep	23	94.8	93.7 **	5.2	4

* Mean of May 23 to Jun 22 period
** Mean of Jul 12 to Sep 23 period

Chlorophyll *a* levels were relatively high at the beginning of the study, dropped sharply in late May and steadily rose through June. They dropped again briefly in mid-July, were high in early August, and then declined during the remainder of the study period.

Aurelia aurita appeared at Stations B to D in late June and remained through early September. Its abundance appeared highly variable, as at Station A. *Mnemiopsis leidyi* returned to these 3 stations in abundance in mid-to-late August, but not at its May-June levels (with the exception of Sept 8 at Station B).

The estuarine area sampled during this study is complex. However, the patterns of interactions at Stations B, C and D are quite similar. To reduce the 'noise' caused by patchiness and other small-scale complexities the results obtained at the 3 stations are combined and smoothed by plotting 3-date moving averages in Fig. 6. This procedure facilitates discussion. However, all calculations are based on the actual individual station data.

DISCUSSION AND CONCLUSIONS

Sampling

The similar patterns of interactions found at Stations B, C and D (Fig. 3 to 5) indicate that we have been successful in monitoring the major trends of the herbivores, ctenophores and sea nettles. The chlorophyll patterns are also similar although estimates of chlorophyll *a* abundance and of *Aurelia aurita* are affected by the tidal cycle. At Station A, which was sampled exactly at either high or low tide, all the high estimates of chlorophyll and low estimates of *A. aurita* were obtained at low tide (Fig. 2a, d). Similar tidal effects are also evident at Station B (Fig. 3a, d), sampled 45 min after Station A. Stations C and D show no evidence of tidal influence, as expected, since they were sampled between slack periods.

Estimates of *Aurelia aurita* abundance are quite variable even at Stations C and D (Fig. 4d and 5d). *A. aurita* is a large medusa and individuals often had volumes of several hundred ml. It is likely that this species was not adequately sampled during the study.

Interactions

The amounts of chlorophyll *a* at each station occasionally dropped to very low levels. While these may have caused some brief periods of food shortage for the herbivore stocks, the 2 major periods of low herbivore abundance (late May and July) do not seem to have
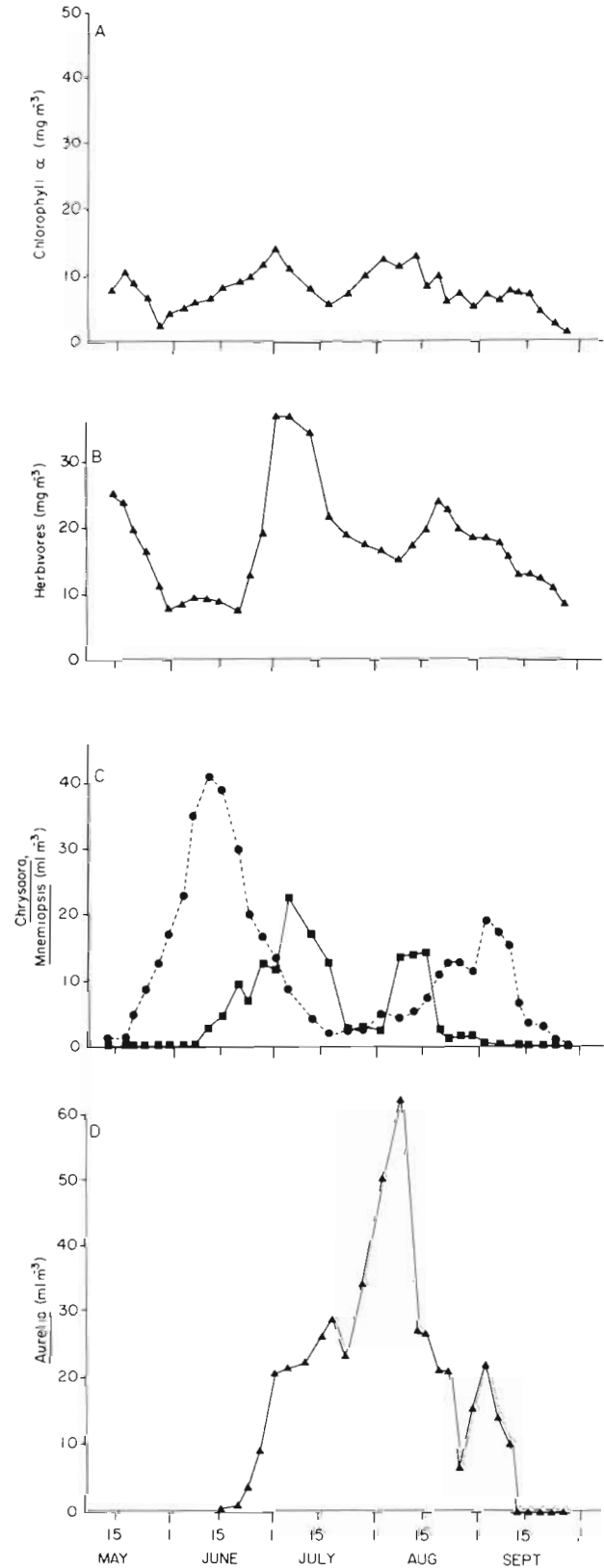

Fig. 6. Three-date moving averages of the combined abundance data for Stations B, C and D. In (c) *Mnemiopsis leidyi* values appear as circles, *Chrysaora quinquecirrha* values as squares

Table 3. Timing of zooplankton population build-ups and declines from May through July 1982

		Station B	Station C	D	Mean
Herbivore decline	Start	May 10	May 20	May 13	May 14
	End	May 27	Jun 3	May 27	May 29
	Duration	17 d	14 d	14 d	15 d
Mnemiopsis build-up	Start	May 20	May 20	May 20	May 20
	End	Jun 24	Jun 18	Jun 10	Jun 17
	Duration	35 d	29 d	21 d	28 d
Chrysaora build-up	Start	Jun 10	Jun 21	Jun 18	Jun 16
	End	Jul 12	Jul 12	Jul 1	Jul 8
	Duration	32 d	21 d	13 d	22 d
Mnemiopsis decline	Start	Jun 24	Jun 18	Jun 10	Jun 17
	End	Jul 8	Jul 12	Jul 1	Jul 10
	Duration	18 d	24 d	21 d	22 d
Herbivore build-up	Start	Jun 28	Jun 21	Jun 18	Jun 22
	End	Jul 6	Jul 6	Jun 28	Jul 3
	Duration	8 d	15 d	10 d	11 d
Aurelia build-up	Start	Jun 28	Jun 24	Jun 21	Jun 24

been maintained by food limitation. As Fig. 6b shows, the low levels of late May and July each persisted for 2 to 3 wk even though chlorophyll levels were on the rise at these times. The herbivore declines may have been influenced by food supply, but the low herbivore standing stocks in mid-June and early August cannot be explained by food limitation. On the contrary, studies by Heinle (1966) and Durbin et al. (1983) indicate that *Acartia tonsa,* probably the major species of our herbivore fraction, would show a rapid biomass increase with increasing food availability, given the opportunity at this time of year.

An analysis of the build-ups and declines of the significant animal populations is given in Table 3 for the dynamic May to July period. Based on the average starting date of the herbivore decline (May 14) and of the *Mnemiopsis* build-up (May 20) it is apparent that the decline began before the ctenophore's appearance at these stations.

A time series analysis, based on correlation coefficients, was also performed on the herbivore-ctenophore interaction for this period. In this procedure, also used by Matthews and Bakke (1977), correlation coefficients were computed for each station (B, C, D) using time delays of 0 to 10 d. Since the relations did not appear linear, an exponential decay fit $(y = ae^{-bx})$ was used to calculate the r values. Table 4 shows that *Mnemiopsis leidyi* abundance was best correlated with a 3 d herbivore advance (r = −0.516; .05 > P > .02) (the herbivore decline is 3 d ahead of the ctenophore build-up). This is a better indication of the true advance than the starting dates alone since all data points are considered.

Ctenophores, especially lobates, are often responsible for sizable declines in copepod abundance (e.g. Reeve et al., 1978; Kremer, 1979) and it is possible that the ctenophore-herbivore interaction began in waters away from our stations. The advance is least at Station D (2 d) and greatest at Station B (4 d), so it may have been initiated in Hampton Roads, the James River or the Chesapeake Bay itself (Fig. 1). On the other hand, other factors such as food limitation,

Table 4. Time delays giving the highest correlation coefficients for the period May 10 to July 15 using an exponential decay $(y = ae^{-bx})$ fit

Interaction	Station B	Station C	D	Mean	df	P
Mnemiopsis (x)-Herbivore (y)						
(days added to herbivore)	+ 4	+ 3	+ 2	+ 3	15	.02 < P < .05
r values	− 0.505	− 0.417	− 0.626	− 0.516		
Chrysaora (x)-Mnemiopsis (y)						
(days subtracted from *Mnemiopsis*)	− 5	− 2	− 5	− 4	15	.05 < P < .10
r values	− 0.379	− 0.320	− 0.566	− 0.422		

species replacement or poor reproductive success may have influenced the herbivore decline. Deason and Smayda (1982) reported that *Mnemiopsis leidyi* pulses in Narragansett Bay followed the start of the zooplankton decreases in 2 of the 6 yr of their study, and a simulation model study of that bay (Kremer and Nixon, 1978) established that summer zooplankton abundance decreased both with and without a predation component. The initiation of the herbivore decline prior to collection of larger ctenophores may have also been due to predation by larval ctenophores which either passed through the net or went unnoticed during the sorting process on board. Stanlaw et al. (1981) showed that the larvae of the congener, *M. mccradyi* are capable of consuming large numbers of copepod nauplii.

The lowest herbivore levels were reached after 15 d of decline, a drop of 8.84 % d^{-1}. Though *Mnemiopsis leidyi* may not have initiated the decline, it undoubtedly contributed to it. Miller (1974) estimated that *M. leidyi* in Pamlico Sound, North Carolina (USA), consumed 25 % of the copepod standing stock per day while Deason and Smayda (1982) found that this ctenophore daily cropped almost 20 % of the zooplankton biomass in Narragansett Bay, Rhode Island, in August 1976 with localized predation of up to 90 %.

In the late spring, our *Mnemiopsis leidyi* population had a reciprocal pattern of abundance with the herbivore stock, reaching its peak in mid-June when the herbivores were at their lowest levels (Fig. 6). This suggests that the ctenophore played a role in keeping the herbivore population low. In turn, the reduced herbivore abundance may have been a factor in the ctenophore decline which began on June 17 (Table 3).

Chrysaora quinquecirrha appeared at Stations B to D on June 16, a day before the decline of the *Mnemiopsis leidyi* population (Table 3). Table 4 shows that *C. quinquecirrha* abundance is best correlated with a 4 d ctenophore lag (the ctenophore decline is 4 d behind the medusa build-up), although the correlation is not significant (.05 < P < .10). The *M. leidyi* decline which took 22 d was 11.3 % d^{-1}. *C. quinquecirrha* feeds readily on *M. leidyi* in the laboratory (McNamara, 1955; Burrell, 1968; Miller, 1974; Feigenbaum et al., 1982) and as the following analysis shows, reported laboratory clearance rates for *C. quinquecirrha* would seem to be high enough to account for this decline.

The only feeding rate available for *Chrysaora quinquecirrha* preying on ctenophores has been reported by Miller (1974). He found the medusae cleared 0.85 m^3 d^{-1} cm^{-1} in 9 feeding trials in plastic swimming pools. The average abundance of *C. quinquecirrha* at Stations B to D from June 17 to July 10, the period of the ctenophore decline, was 10.6 ml m^{-3}. Assuming an average medusa size of 7 ml (and 4 cm in

diameter), the mean at Station A in August (Kelly, 1983), there were 1.5 medusae and 6 cm of medusa diameter m^{-3} at this time. According to Miller's (1974) rate, these medusae would have cleared 5.1 m^3 d^{-1} m^{-3} (= 510 % of the ctenophore population daily) and eliminated the ctenophores from the water column in a matter of hours.

The feeding-rate estimate of Feigenbaum et al. (1982), though based on crustacean prey, seems more realistic. They found that *Chrysaora quinquecirrha* medusae of 4 cm diameter feeding on *Artemia* sp. in the laboratory had a volume swept clear of 10 l h^{-1} (= 0.24 m^3 d^{-1} = 0.06 m^3 d^{-1} cm^{-1}). At this rate the 1.5 medusae m^{-3} present during the ctenophore decline would have cleared 36 % (1.5 × 0.24) of the ctenophores daily.

The lack of a significant negative correlation between *Mnemiopsis leidyi* and *Chrysaora quinquecirrha* suggests that other factors were also involved in the ctenophore decline. These could include predation by butterfish and harvestfish of the genus *Peprilus* (Oviatt and Kremer, 1977). (The intraphyletic predator *Beröe* was not found in the study.) The possibility that the ctenophores were food-limited at their peak abundance has already been mentioned. In addition, the correlation may have been affected by relative movement of the ctenophores and *C. quinquecirrha* to and from the stations.

Five d after the decline of the *Mnemiopsis leidyi* population, herbivore abundance began to rise, peaking at its highest level of the study period on July 3. *Acartia tonsa* can double its weight in 2 d at the temperatures found in our study (Heinle, 1966) and this sharp rise was likely the result of reduced predation pressure and increased food availability (Durbin et al., 1983). For a similar situation, Kremer and Nixon (1976) reported that zooplankton biomass increased sharply when predation by *Beröe ovata* reduced the *M. leidyi* population of Narragansett Bay.

Fig. 6 shows that the herbivore population did not remain high, but declined through early August. Several factors may have been at work during this long summer decline. Among these is the possibility that the phytoplankton levels of early July could not support the peak herbivore abundance, predation by *Chrysaora quinquecirrha* itself and also predation by *Aurelia aurita*. Sea nettles do consume crustaceans. Heinle (1966) suggested that *Acartia tonsa* was a significant food source for *C. quinquecirrha* in the Chesapeake Bay, and Kelly (1983) found that crustacean zooplankton comprised 95.8 % of the sea nettle diet at Station A in August, when ctenophores were absent from the water column.

Aurelia aurita began to appear in the water column in late June. This large medusa can sharply reduce

copepod biomass (Möller, 1980b) and undoubtedly consumed a large number of herbivores. Its abundance at Stations B to D peaked on August 8, about the same time that herbivore abundance reached its lowest point of the summer (Fig. 6).

During the last part of the study the ctenophores made a modest come back (Fig. 6). This was probably allowed by the declining *Chrysaora quinquecirrha* (the second *C. quinquecirrha* peak is somewhat misrepresented in the 3-date moving averages because it was actually due to a single tow, packed with medusae) and may have contributed to the final decline of the herbivores in the study period.

We have no explanation for the declining *Mnemiopsis leidyi* population at the end of the study. Similar unexplained fall declines were also observed in Narragansett Bay (Deason and Smayda, 1982). The decline of the 2 scyphozoans was expected, since these medusae die after spawning and reproduction is seasonal in the Chesapeake area.

Had the ctenophore not been an abundant resident of the study area we would have expected the results to be similar to those reported for other medusa-dominated ecosystems – a decline in the crustacean zooplankton with an increase in phytoplankton stocks (Huntley and Hobson, 1978; Möller, 1979; Lindahl and Hernroth, 1983). Similar food-chain effects have also been reported for ecosystems controlled by other predators, from ctenophores to lobsters (see Deason and Smayda, 1982 for a brief review). However, because the sea nettle feeds on both ctenophores and crustaceans it was not possible to predict the summer plankton dynamics of the lower Chesapeake Bay area.

In Fig. 6 of particular interest is that herbivore stocks were lowest during the period of peak ctenophore abundance and at moderately high levels during most of the period when the 2 large medusa species were present. The lower Chesapeake Bay area is extremely complex. Nevertheless, our data suggest that by controlling *Mnemiopsis leidyi* during the summer, *Chrysaora quinquecirrha* contributes to the secondary productivity of the water column. Future work is needed to sort out the effects of the many different factors at work in this region.

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