Interannual Variation in Gelatinous Zooplankton and Their Prey in the Rhode River, Maryland

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ABSTRACT. The lobate ctenophore *Mnemiopsis leidyi* is an important predator of zooplankton and ichthyoplankton both within and outside its native range, and it is a dominant consumer within the Chesapeake Bay food web. We sampled the Rhode River, a subestuary of Chesapeake Bay, during 2004 and 2005 to quantify the abundances of *M. leidyi*, its scyphomedusan predators, and its mesozooplankton prey, and conducted ctenophore egg production experiments in 2004. Despite low mesozooplankton densities, ctenophores produced up to 9,380 eggs individual^{-1} day^{-1}. Temporal patterns, as well as peak abundances, of copepods, ctenophores, and sea nettles (*Chrysaora quinquecirrha*; the major predator of *M. leidyi*) varied considerably between years. This interannual variation may have been caused by direct and indirect effects of physical factors, especially low salinities during 2004, on all components of the food web. In 2004, zooplankton abundances peaked in June, *M. leidyi* abundances steadily increased throughout the summer, and *C. quinquecirrha* was rare. In contrast, during 2005, *C. quinquecirrha* density increased during midsummer. As this medusa increased in abundance, *M. leidyi* numbers declined and copepod abundances increased. Shallow systems with salinities near the minimum threshold for *C. quinquecirrha* ephyra production may exhibit more extreme interannual variability than deeper, higher-salinity systems and may serve as models to provide insight into factors controlling gelatinous zooplankton dynamics.

INTRODUCTION

The lobate ctenophore *Mnemiopsis leidyi* is native to Atlantic and Caribbean estuaries and coastal waters from Massachusetts to southern Argentina and has been introduced to several Eurasian systems including the Black, Caspian, Baltic, and North Seas (Purcell et al., 2001; Kube et al., 2007). *Mnemiopsis leidyi* can tolerate a wide range of temperatures, salinities, and dissolved oxygen (DO) concentrations. It occurs in waters with salinities ranging from less than 5 to more than 36 (Purcell et al., 2001; Purcell and Decker, 2005) and can survive exposure to DO concentrations of 0.5 mg L^{-1} for at least 4 d (Decker et al., 2004). Optimal temperatures for *M. leidyi* reproduction are approximately 18°–20°C (Costello et al., 2006).

In late spring and early summer, *M. leidyi* can be abundant in Chesapeake Bay and its tributaries, where it is a dominant consumer, potentially capable of clearing much of the daily standing stock of zooplankton and ichthyoplankton

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(Cowan et al., 1992; Cowan and Houde, 1993; Purcell et al., 1994; Purcell and Decker, 2005). In mesohaline portions of the Chesapeake Bay system, the major predator of *M. leidyi*, the scyphomedusa *Chrysaora quinquecirrha*, usually becomes abundant in early July and persists through the end of summer (Cargo and King, 1990). As *C. quinquecirrha* population densities increase, *M. leidyi* abundances typically decline and zooplankton populations rebound (Purcell and Cowan, 1995). However, in years when *C. quinquecirrha* populations are low, *M. leidyi* may exert much greater and prolonged control within the food web. *Chrysaora quinquecirrha* polyps are generally found in salinities of 7 to 20 and strobilate when temperatures exceed 17°C (Cargo and Schultz, 1967; Cargo and King, 1990). Medusae are most abundant at salinities of 10–16 (using the Practical Salinity Scale) and temperatures of 26°–30°C (Decker et al., 2007). Thus, interannual variation in salinity and temperature can strongly affect the timing and spatial distribution of *C. quinquecirrha* and its control of *M. leidyi*.

The Rhode River is a small, shallow subestuary on the western shore of Chesapeake Bay (Figure 1) characterized by summer salinities that vary interannually in both absolute maxima and timing of these maxima. Similar to other tributaries in the Chesapeake Bay system, this estuary supports a gelatinous zooplankton food web throughout late spring and summer months. The most abundant gelatinous species are the zooplanktivorous *M. leidyi* and its scyphomedusan predator and competitor *C. quinquecirrha*. Average spring–summer salinity in the Rhode River is near the lower limit required for strobilation by *C. quinquecirrha*. In addition, interannual variation in water temperature has the potential to cause variation in the timing of initial and peak occurrences of these gelatinous species and their prey. As a result, the Rhode River can have two distinct gelatinous food webs: one in which the top predator (*C. quinquecirrha*) exerts control over the intermediate consumer (*M. leidyi*) and one in which the intermediate consumer is not controlled by predation.

The objectives of this study were to examine temporal and spatial patterns in abundances of *M. leidyi* and *C. quinquecirrha* within and near the Rhode River and to examine how those patterns varied in relationship to water temperature, salinity, and the abundance of mesozooplankton prey. We also examined temporal and spatial variation in egg production by *M. leidyi*. This study was conducted during the summers of 2004 and 2005, years with very different temporal patterns of *M. leidyi* and *C. quinquecirrha* densities.

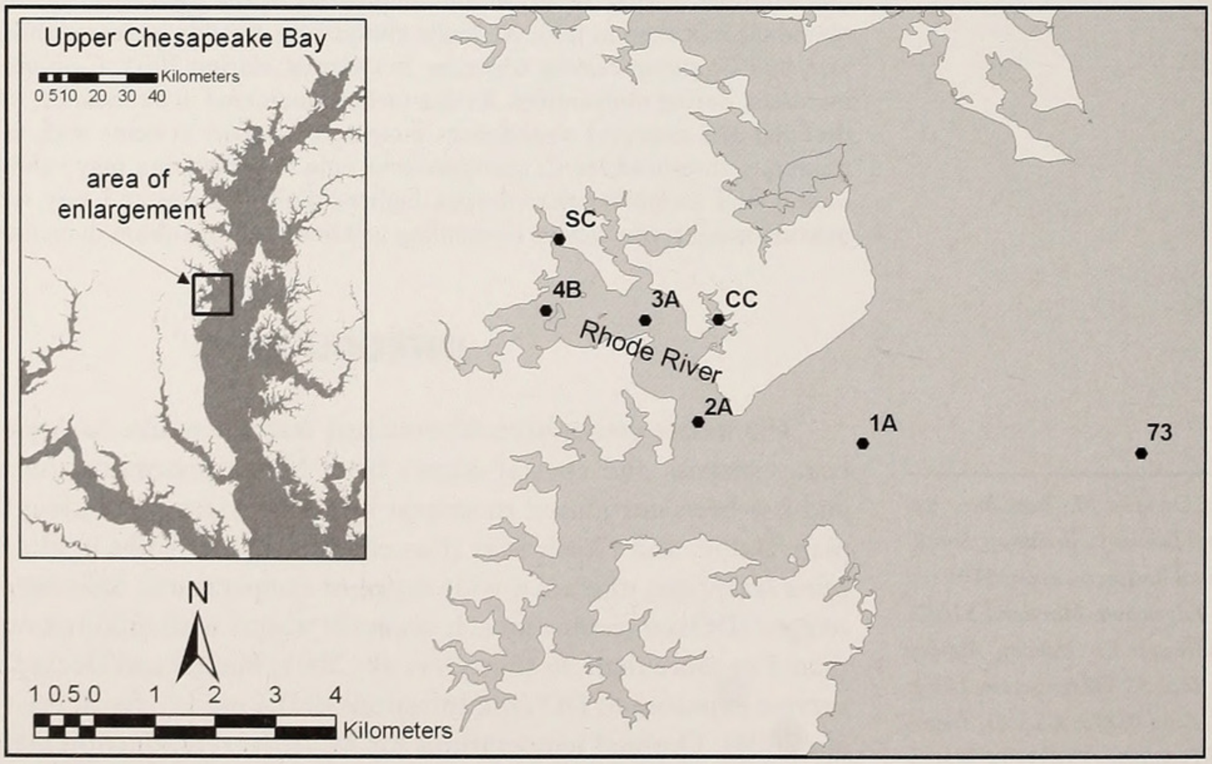


FIGURE 1. The Rhode River and its location in the Chesapeake Bay. Dots indicate location of sampling sites; the SERC dock is located directly inshore (northwest) of site 4B.

METHODS

We sampled seven sites: six within the Rhode River and one just beyond the mouth of the river in the mainstem Chesapeake Bay. Sites were chosen based on prior research conducted in the Rhode River and designed to cover its entire length. At each site, weather conditions were noted and temperature, DO, and salinity were recorded at the surface and subsequent 1 m depth intervals with a YSI 600QS meter. Additional temperature, DO, and salinity data were available from the monitoring station located at the dock of the Smithsonian Environmental Research Center (SERC) in the Rhode River, which was equipped with a YSI 6600 meter (C. Gallegos, SERC, unpublished data).

Gelatinous zooplankton samples were collected in duplicate 3 min stepped oblique tows using a 0.5 m diameter, 202 μm mesh hoop plankton net towed at approximately 2 knots and equipped with a General Oceanics flowmeter (model 2030). Excess water was strained from the sample, total volume of gelatinous zooplankton was measured, and all individuals were identified to species and enumerated. Bell diameters of *C. quinquecirrha* and the oral to aboral lengths of up to 15 *M. leidyi* were recorded. Remaining specimens of *M. leidyi* were classified as either larger than or equal to or less than 3.0 cm.

Mesozooplankton samples were collected using 0.3 m diameter, 202 μm mesh paired hoop nets. Samples were rinsed through a 2 mm sieve to remove gelatinous zooplankton and preserved with 10% buffered formalin; mesozooplankton species were subsequently identified and enumerated.

Whole water column chlorophyll data were collected by another research group (C. Gallegos, SERC) at the four central Rhode River sites (1A, 2A, 3A, 4B; see Figure 1) on different days during each sampling week. Chlorophyll *a* (chl *a*) was measured with a Spectronics Genesis 5 spectrophotometer and converted into micrograms per liter ($\mu g\ L^{-1}$).

Mnemiopsis leidyi egg production assays were conducted in 2004 using established methodology (Kremer, 1976; Grove and Breitburg, 2005). Undamaged individuals covering the size range from each site (3–8 cm) were randomly assigned to jars containing 3 L filtered Rhode River water and left overnight at ambient water temperatures. At approximately 0900 the following morning, adult ctenophores were removed and lengths and volumes recorded. Water from each jar was strained through a 35 μm sieve, preserved with 10% acid Lugol's solution (Sullivan and Gifford, unpublished data; Grove and Breitburg, 2005), and eggs were enumerated. Egg production was normalized by ctenophore volume to facilitate comparisons among individuals.

Data were analyzed using analysis of variance (Proc GLM: SAS v. 9.1) on rank-transformed data. Student–Newman–Keuls tests were used for a posteriori comparisons. Regression models were used to examine the effects of ctenophore volume, site, date, and interactions between these factors on egg production. Nonsignificant interaction terms with $P \geq 0.25$ were dropped from statistical models.

RESULTS

PHYSICAL PARAMETERS

Temperature, salinity, and DO all varied among sites and between years (Table 1; Figure 2; two-way analysis of variance [ANOVA]). Surface water temperature varied among sites ($F = 38.21$, $P < 0.01$), and was cooler adjacent to, and near the mouth of, the Rhode River and at the deeper sites. Surface salinity also varied significantly among sites ($F = 3.55$, $P < 0.01$), and was generally highest at the Bay site (Site 73) and at sites near the mouth of the Rhode River. Minimum DO concentration varied among sites ($F = 7.33$, $P < 0.01$) and was significantly lower at the Bay site than elsewhere.

Measurements at the SERC dock indicated that surface water temperatures reached 25°C more than 3 weeks earlier in 2004 than in 2005 but exceeded 30°C only during 2005. Salinity remained below 8 except for a brief period in 2004 but exceeded 8 for most of the summer in 2005. Daytime low DO concentrations ($<2\ mg\ L^{-1}$) were occasionally recorded in the bottom waters during cruises; all low daytime DO measurements in 2004 and all but one in 2005 were recorded at the Bay site. The continuous YSI 6600 monitor at the SERC dock indicated that low DO concentrations occurred near the surface within the Rhode River in the early morning hours of both years (C. Gallegos, SERC, personal communication, 2004). Analysis of our weekly sampling data indicated that temperature ($F = 5.38$, $P = 0.02$), salinity ($F = 135.18$, $P < 0.01$), and DO concentrations ($F = 6.39$, $P = 0.01$) were all significantly higher in 2005 than in 2004.

2004 BIOTA

Chlorophyll *a* concentrations peaked in early June, declined, and then rose continually during the period sampled from mid-June through early September 2004 (see

TABLE 1. Mean environmental conditions measured at each site sampled for 2004 and 2005. See Figure 1 for site locations. Chlorophyll *a* concentrations are whole-water integrated values (C. Gallegos, SERC); minimum dissolved oxygen (DO) values are based on near-bottom measurements; temperature and salinity are from surface waters (<1 m depth); NA = site not sampled.

	2004				2005			
Site	Chlorophyll *a* (µg L^{-1})	Minimum DO (mg L^{-1})	Temperature (°C)	Salinity	Chlorophyll *a* (µg L^{-1})	Minimum DO (mg L^{-1})	Temperature (°C)	Salinity
73[a]	NA	2.31	25.40	7.76	NA	3.46	26.26	9.79
1A	24.55	5.20	25.95	8.20	21.37	6.61	26.64	9.26
2A	24.76	5.77	26.66	8.04	37.02	6.88	27.58	9.44
CC	NA	4.70	29.14	7.35	NA	5.14	28.91	9.10
3A	32.43	4.73	27.54	7.94	28.20	5.21	28.00	8.87
SC	NA	4.23	28.09	7.78	NA	5.31	27.97	9.38
4B	44.34	5.22	28.41	7.29	32.29	5.19	28.62	9.08

[a] Because of sea conditions, site 73 was not sampled during mid- to late summer 2004 as frequently as other sites; thus, averages are not necessarily representative of physical conditions at site 73 relative to other sites measured on the same dates.

Figure 2). Mesozooplankton samples in both years were dominated (>95% of individuals) by the calanoid copepod *Acartia tonsa*. During 2004, mesozooplankton densities varied significantly among dates ($F = 6.28$, $P < 0.01$). Peak densities of 4–7 individuals L^{-1} occurred on 21 June and 7 July and then declined to approximately 1.0 individuals L^{-1} for the rest of the season (see Figure 2).

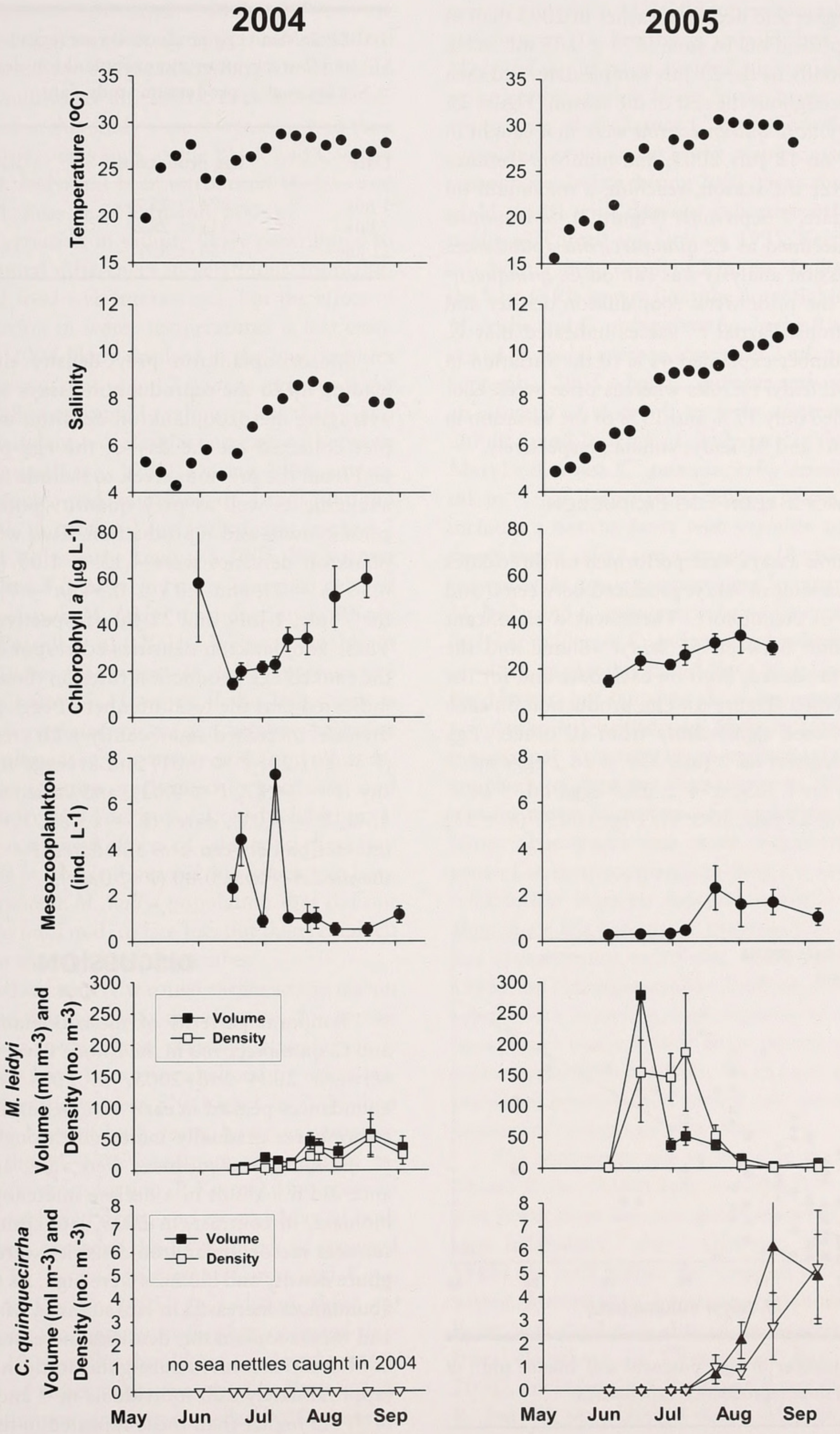
Mnemiopsis leidyi volumes also varied significantly among dates (one-way ANOVA on ranks; $F = 6.08$, $P < 0.01$). Numerical densities and volumes were lowest in mid-June ($\leq 0.62 \pm 0.25$ individuals m^{-3} and $\leq 2.3 \pm 0.77$ mL m^{-3}, respectively), and then gradually increased to a maximum of 51 ± 30.2 individuals m^{-3} and 58 ± 33.5 mL m^{-3} on 19 August (see Figure 2), the date that coincided with highest densities of "recruits" (individuals ≤ 1 cm in length). Regression analyses indicated a significant relationship between the zooplankton density of the prior week and both *M. leidyi* volume ($r^2 = 0.13$, $P < 0.01$) and the density of recruits ($r^2 = 0.21$, $P < 0.01$). However, the previous week's chl *a* concentration explained a greater percentage of the variation in both these measures of *M. leidyi* abundance for the sites at which chl *a* data were available (1A, 2A, 3A, 4B) (volume: $r^2 = 0.33$, $P < 0.01$; density of new recruits: $r^2 = 0.25$, $P < 0.01$). *Chrysaora quinquecirrha* abundances were low during 2004. A few medusae were seen in the field during August and early September but were never caught with either the 0.5 m diameter hoop net or the larger 1 m^2 neuston net, which was deployed in an attempt to more accurately sample the low-density *C. quinquecirrha* population.

2005 BIOTA

Temporal patterns and peak abundances of most biota in 2005 differed from those in 2004 (see Figure 2). Mid-June chl *a* concentrations in 2005 were similar to those in the corresponding time period in 2004, and as in 2004 generally increased during the remainder of the season. However, sampling did not detect an early June chl *a* peak in 2005, and maximum chl *a* concentrations in late summer 2005 reached only about two-thirds the concentrations reached in 2004 (Figure 2). Mesozooplankton densities varied among dates (one-way ANOVA on ranks, $F = 4.87$, $P < 0.01$). The 21 July peak density of 2.3 individuals L^{-1} was both later and lower than peak densities in 2004. Early June through early July mesozooplankton densities remained below 1 individual L^{-1} and were similar to mid-July–early September densities in 2004.

The timing of the increase in mesozooplankton densities in 2005 corresponded to a decrease in *M. leidyi* densities and the appearance of *C. quinquecirrha*. *M. leidyi* densities varied significantly among dates (one-way ANOVA on ranks: $F = 13.98$, $P < 0.01$). Peak *M. leidyi*

FIGURE 2. (*facing page*) Weekly mean temperature (°C) and salinity at the SERC dock (C. Gallegos, unpublished data), and river-wide mean (±SE) chlorophyll *a* concentration (µg L^{-1}), mesozooplankton abundance (number L^{-1}), and *Mnemiopsis (M.) leidyi* and *Chrysaora (C.) quinquecirrha* abundance (volume, mL m^{-3}; density, number m^{-3}) for 2004 (left) and 2005 (right).


2004
2005
Temperature (°C)
35
30
25
20
15
Salinity
12
10
8
6
4
Chlorophyll *a* (μg L-1)
80
60
40
20
0
Mesozooplankton (ind. L-1)
8
6
4
2
0
M. leidyi Volume (ml m-3) and Density (no. m-3)
300
250
200
150
100
50
0
Volume
Density
C. quinquecirrha Volume (ml m-3) and Density (no. m-3)
8
7
6
5
4
3
2
1
0
Volume
Density
no sea nettles caught in 2004
May
Jun
Jul
Aug
Sep

densities were higher and occurred earlier in 2005 than in 2004. Volumes peaked on 16 June (279 ± 205 mL m^{-3}), declined substantially by the 21 July sample date, and then remained low throughout the rest of the season (Figure 2). Medusae of *Chrysaora quinquecirrha* were first caught in our sample nets on 18 July 2005, and numbers continually increased over the season, reaching a maximum on the last sample date, 7 September (Figure 2). *Mnemiopsis leidyi* densities declined as *C. quinquecirrha* abundances increased. Regression analysis was run on *C. quinquecirrha* density and the prior week zooplankton density and chl *a* concentrations. Partial r^2 values indicated that *C. quinquecirrha* number explained 41% of the variation in the number of *M. leidyi* recruits whereas prior week zooplankton explained only 17% and 13% of the variation in number of recruits and *M. leidyi* volume, respectively.

MNEMIOPSIS LEIDYI EGG PRODUCTION

Egg production assays were performed on three dates in July 2004. *Mnemiopsis leidyi* produced between 0 and 668 eggs mL^{-1} of ctenophore. There was a significant positive correlation between *M. leidyi* volume and the number of eggs produced, both on each date and for the three dates combined (Figure 3). Egg production on each date in 2004 differed significantly from all others. Egg production was highest on 7 July, 355 ± 28.2 eggs mL^{-1} ($n = 36$); lower on 1 July, 274 ± 25.7 eggs mL^{-1} ($n = 33$); and lowest on 22 July, 50 ± 8.71 eggs mL^{-1} ($n = 35$) (see Table 2).

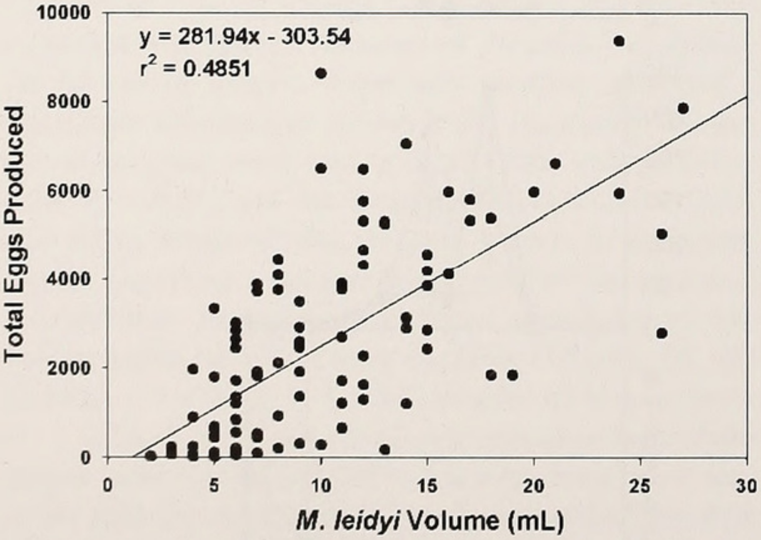


FIGURE 3. Total number of eggs produced and volume (mL) of each *M. leidyi* in all three reproduction experiments.

TABLE 2. Mean egg production rate (eggs mL^{-1} ctenophore ± SE) and 2-week mean mesozooplankton density (number L^{-1} ± SE) for each reproduction study date.

Date	Egg production	Zooplankton density
1 July	274 (± 25.7)	2.72 (± 0.56)
7 July	355 (± 28.2)	4.13 (± 1.03)
22 July	50 (± 8.7)	1.03 (± 0.34)

Mesozooplankton prey density during the week leading up to the reproduction assays was estimated by averaging mesozooplankton densities measured in samples collected on the day of the egg production assay and from the previous week to include food immediately available as well as prey quantity potentially affecting prior growth and reproduction. Two week average zooplankton densities were 4.13 ± 1.03 ($n = 6$), 2.72 ± 0.56 ($n = 7$), and 1.03 ± 0.34 ($n = 7$) individuals L^{-1} for 7 July, 1 July, and 22 July, respectively (see Table 2). These zooplankton densities corresponded directly with the ranked egg production rates on these dates. ANOVA indicated that the total number of eggs produced per individual increased significantly with ctenophore volume ($F = 201.24$, $P < 0.01$) and average zooplankton density ($F = 34.87$, $P < 0.01$), and varied among sites ($F = 5.70$, $P < 0.01$), dates ($F = 13.82$, $P < 0.01$), and the interaction between sites and dates ($F = 3.39$, $P < 0.01$); the model r^2 was 0.80 ($P < 0.01$).

DISCUSSION

Temporal patterns of mesozooplankton, *M. leidyi*, and *C. quinquecirrha* in the Rhode River differed strongly between 2004 and 2005. In 2004 mesozooplankton abundances peaked in early summer and then declined as ctenophores gradually increased throughout the season. *C. quinquecirrha* medusae were rare, and their appearance did not result in a decline in ctenophore density or biomass. In contrast, in 2005, late spring through early summer mesozooplankton densities were low and ctenophore density and biomass were high. As *C. quinquecirrha* abundances increased in late summer, *M. leidyi* decreased and mesozooplankton densities increased. Peak densities of *M. leidyi* measured during this study in the Rhode River (approximately 200 individuals m^{-3} and nearly 300 mL m^{-3}) are higher than those reported in the Pamlico River, North Carolina (just over 60 mL m^{-3}; Miller, 1974) or the mid-Chesapeake Bay (Purcell et al. 2001), but similar to abundances reported for Narragansett Bay, Rhode Island (Deason, 1982; Sullivan et al., 2001). Peak Rhode River densities measured in this study were lower, however, than those reported for systems such as the Black and Caspian Seas to which *M. leidyi* has been introduced (Kideys and Romanova, 2001; Bilio and Niermann, 2004).

Interannual variation in salinity likely contributed to observed interannual differences in gelatinous zooplankton densities and food web interactions, but the effect of interannual variation in water temperatures is less clear. Low salinities in 2004 likely resulted in the low densities of *C. quinquecirrha* in that year. *Chrysaora quinquecirrha* polyps are generally not found in salinities less than 7 and become more abundant as salinities increase to between 7 and 10 (Cargo and King, 1990). During 2004, surface salinity did not reach 5 until mid-June, or 7 until July, and never reached 10. In contrast, surface salinity reached 7 by mid-June and 10 by early August in 2005. We suggest that salinities below 5 in May and early June also delayed or reduced early-season *M. leidyi* reproduction in Rhode River in 2004 (Purcell et al., 2001). We were unable to find published studies that report *M. leidyi* reproductive rates at salinities below 5. However, if this hypothesis is correct, there is a very narrow margin between salinities that prevent recruitment of *C. quinquecirrha* and allow *M. leidyi* populations to grow unchecked by predation and salinities that hinder *M. leidyi* populations by limiting reproduction. The combined effects of salinity on these two gelatinous species in Rhode River in 2004 appears to have resulted in a persistent *M. leidyi* population that did not become abundant until mid- to late July but then remained abundant at least through early September.

Although surface waters warmed earlier in the season during 2004 than during 2005, the effect of this warming on gelatinous zooplankton seasonal abundances is not clear and may have been overwhelmed by other factors. Spring temperatures were 5°C higher in 2004 than in 2005. By early May of both years, however, temperatures exceeded the 9°–13°C minimum temperature required for *M. leidyi* reproduction (P. Kremer, University of Connecticut, unpublished data), and by mid-May of both years, temperatures exceeded the 17°C threshold required for strobilation by *C. quinquecirrha* (Cargo and King, 1990; Purcell and Decker, 2005). In addition, there are no data to suggest that temperatures that occurred during the warmer 2004 spring should have reduced growth or reproduction of either gelatinous species. By late July 2005, surface water temperatures exceeded 30°C, the temperature at which *M. leidyi* suffers mortality in laboratory experiments (D. Breitburg, unpublished data). However, *M. leidyi* could have avoided high midday surface temperatures by moving lower in the water column, and the appearance of predatory *C. quinquecirrha* is a more parsimonious explanation as the major cause of the seasonal ctenophore decline during 2005, given the high percentage of *M. leidyi* with damage indicative of encounters with medusae (Purcell and Cowan, 1995; Kreps et al., 1997).

With a mean depth of 2 m, the shallow bathymetry of the Rhode River may limit the potential for coexistence of *M. leidyi* and *C. quinquecirrha*. In the Rhode River, densities of *M. leidyi* averaged less than 2 mL m^{-3} in August and September 2005 when *C. quinquecirrha* densities reached an average of 2–6 mL m^{-3}. In contrast, Keister et al. (2000) found 26.6 mL *M. leidyi* m^{-3} in the Patuxent River, Maryland, when *C. quinquecirrha* density averaged 11.8 mL m^{-3}. The deeper water column of the Patuxent, which includes a bottom layer with variable and sometimes severely hypoxic DO concentrations (Breitburg et al., 2003), may provide greater opportunity for spatial separation of *M. leidyi* and *C. quinquecirrha* and increase survival of *M. leidyi* at moderate *C. quinquecirrha* densities.

Prey availability could limit *M. leidyi* abundance and production, but our data do not suggest that low mesozooplankton densities were likely to have caused the large interannual variation in ctenophore abundances. Mesozooplankton densities were higher in 2004 than in 2005, and the temporal pattern of mesozooplankton and ctenophore abundances was more suggestive of ctenophore control of mesozooplankton than the reverse. An inverse relationship between copepod densities and ctenophore abundance has been noted previously in both Chesapeake Bay (Feigenbaum and Kelly, 1984; Purcell and Cowan, 1995) and Narragansett Bay (Sullivan et al., 2001). In both years of our sampling, high densities of *M. leidyi* recruits were found in the Rhode River during periods of lowest mesozooplankton densities. We did not sample microzooplankton, however, and cannot rule out their potential influence on ctenophore abundance.

The maximum egg production we measured in the Rhode River (9,000 eggs individual^{-1} *M. leidyi* day^{-1}) was lower than the maximum reported value of 14,000 eggs individual^{-1} day^{-1} (Kremer, 1976; Reeve et al., 1989) but well within the range of values reported elsewhere. *Mnemiopsis leidyi* egg production in the Rhode River was similar to that of field-collected ctenophores from elsewhere in Chesapeake Bay (Purcell et al., 2001), including the Patuxent River (D. Breitburg and R. Burrell, unpublished data). *Mnemiopsis leidyi* from the Patuxent produced a maximum of 610 eggs mL^{-1} of ctenophores at mesozooplankton abundance of 1 individual L^{-1}, which is very close to the rate found in this study of 668 eggs mL^{-1} at 2.2 mesozooplankton individuals L^{-1}. Variation among dates in the relationship between zooplankton density and egg production suggests an interesting pattern of trade-offs in energy allocation to somatic growth versus reproduction, or nutritional constraints.

Predicted changes in sea-surface temperatures and rainfall throughout the world may lead to changes in the geographic ranges of many aquatic organisms. The Rhode River provides an interesting model that may aid predictions of climate change-related shifts in ranges and predator–prey dynamics because it is often near the threshold of salinity tolerances and the dynamics of the system can fluctuate markedly from year to year. These characteristics of the Rhode River allowed us to examine the gelatinous zooplankton food web within the river during two distinct years: one with, and one without, strong influence by a top predator. Differences in species abundances and food web interactions observed here may help to predict dynamics in other systems as environmental conditions, and the range of *C. quinquecirrha*, change. Although generally considered a nuisance species by swimmers and fishermen, *C. quinquecirrha* may benefit fisheries and habitat by controlling densities of *M. leidyi*, which is an important predator of oyster larvae—a prey not utilized by *C. quinquecirrha* (Purcell et al., 1991; Breitburg and Fulford, 2006).

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