Limnol. Oceanogr., 50(1), 2005, 376–387

Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000

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Abstract

The mesohaline region of Chesapeake Bay had high densities of the scyphomedusan *Chrysaora quinquecirrha* and low densities of the ctenophore *Mnemiopsis leidyi* in 1987–1990 and 1995. By contrast, 1996–2000 had much lower medusa and higher ctenophore densities. Predation on copepods (*Acartia tonsa*) was intense in 1996–2000, and copepod densities were low when ctenophores were abundant. At equivalent sizes, the feeding potentials of ctenophores were greater than those of medusae, with clearance rates about 1.2 times greater by volume and about 3 times greater by carbon biomass. *M. leidyi* ctenophores more negatively influence copepod populations than *C. quinquecirrha* medusae because they are more effective predators of copepods and have broader spatial and temporal occurrence, wider salinity and temperature ranges, greater densities, and a more flexible life history. Because they consume ctenophores, *C. quinquecirrha* medusae positively affect copepod abundance. *C. quinquecirrha* and *M. leidyi* could be considered keystone predators because of their far-reaching effects on the plankton food web. The balance between medusae and ctenophores in Chesapeake Bay was greatly affected by climatic factors. Medusa abundances were high when dry years prevailed prior to and during 1987–1990 and 1995. By contrast, medusa abundances were low when dry and wet years alternated before and during 1996–2000. Significant variables that favored medusae in 1987–1990 and 1995 were high salinity, warm temperature, and high solar irradiance. The North Atlantic Oscillation Index was significantly inversely correlated with medusa numbers from 1960–1995. Climate clearly affects gelatinous predator abundances, with consequences that cascade throughout the plankton food web.

When jellyfish and ctenophores occur in large populations, their predation can have substantial effects on the plankton food web. For example, because the predominant species in Chesapeake Bay, the scyphomedusan *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*, are voracious consumers of zooplankton and ichthyoplankton, they could be detrimental to fish populations (e.g., Cowan and Houde 1993; Purcell et al. 1994*a*,*b*; Purcell and Arai 2001). Food web analyses suggest that because of their high trophic positions and great abundances, these gelatinous species are extremely important to plankton dynamics and to planktivorous fish populations during summer in Chesapeake Bay (Baird and Ulanowicz 1989).

The mesohaline Chesapeake Bay has large populations of *C. quinquecirrha* medusae and *M. leidyi* ctenophores. New *C. quinquecirrha* medusae (ephyrae) are budded from benthic polyps when water temperature reaches 17°C in spring. Large medusae first are seen in May or June in the tributaries of the mesohaline region, and a month later in the mainstem bay (Purcell 1992; Purcell et al. 1994*b*). The greatest population densities (up to 16 m^{-3}) occur in the tributaries in July and August (Purcell 1992). Usually, few medusae remain by October. During the 1960s, medusae were so abundant that a congressional act was passed to provide funding in 1968–1972 for research on them. Ctenophores, which are holoplanktonic, proliferate in spring, and greatest biovolumes are found in July and August (Purcell et al. 1994*b*). So that the vast quantities of this species would not interfere with plankton sampling, methods were developed to exclude them from plankton nets and to dissolve them if collected (Heinle 1965; Burrell and Van Engel 1970).

Hydrographic conditions affect the timing, distributions and sizes of *C. quinquecirrha* and *M. leidyi* populations and, consequently, determine which species predominates during summer in Chesapeake Bay. Numbers of *C. quinquecirrha* medusae in summer were most strongly correlated with discharge from the Susquehanna River in January through June (negative), and secondarily to May temperatures (positive) and salinity (positive) over 27 yr (Cargo and King 1990). In years of low precipitation, river discharge is reduced, salinities rise, and large populations of medusae develop in the mesohaline portion of the bay because budding of ephyrae from polyps is greatest at salinities between 9 and 25 (Purcell et al. 1999). Warm temperatures and high salinities in spring cause adult medusae to appear as early as May, rather than in July as is typical; conversely, low salinities can delay medusa appearance until August. Summer abundances of ctenophores were positively correlated with winter temper-

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Acknowledgments

For data from 1995 to 2000, we thank E. D. Houde, his students and technicians, C. A. Pacey, M. Kiladis, and L. Brink, for help with field sampling and some data management. Funding was provided by NSF grant DEB-9412113 to the TIES group and by NSF grants OCE-9633607 and ADVANCE Fellows award 0137419 to J.E.P. For data from 1987 to 1990, we thank M. R. Roman for use of some zooplankton data, as well as F. P. Cresswell, D. A. Nemazie, and D. C. Kennedy for assistance in the field and laboratory. That research was funded by NOAA grants NA86AA-D-SG006 and NA890AA-D-SG063 to the University of Maryland Sea Grant Program.

atures (Purcell et al. 2001), and *M. leidyi* appears earlier in spring when conditions are warm (Sullivan et al. 2001). *M. leidyi* is euryhaline, occurring at salinities from 0.1 to 25.6 in the Chesapeake Bay.

C. quinquecirrha medusae consume *M. leidyi* ctenophores and can eliminate them from the tributaries in the summer (Purcell and Cowan 1995); however, large ctenophores are able to escape from the medusae (Kreps et al. 1997). Therefore, a wet spring would allow ctenophores to reproduce and grow before medusae appear; conversely, a dry spring would favor an early medusa population that could control ctenophore abundance. Thus, hydrographic conditions are central to ctenophore and medusa population dynamics and their predation effects on zooplankton in Chesapeake Bay.

The highly productive Chesapeake Bay has abundant mesozooplankton populations, which provide food for the medusae and ctenophores. In the mesohaline regions, the calanoid copepod, *Acartia tonsa*, predominates in summer (May to November), with the peocilostomatoid copepod *Oithona colcarva* and meroplankton (polychaete, barnacle, and bivalve larvae) sometimes being extremely abundant (Brownlee and Jacobs 1987). Copepods are the main prey items in *M. leidyi* and *C. quinquecirrha* in Chesapeake Bay, with varying proportions of other zooplankton taxa and ichthyoplankton depending on their availability (Purcell 1992; Purcell et al. 1994*a*,*b*).

Vertical distributions of zooplankton, medusae, and ctenophores are affected by hypoxic bottom waters in Chesapeake Bay. Seasonal intensification of stratification in Chesapeake Bay begins in March–April, and in the mesohaline portion of the main Bay, waters below the pycnocline become severely hypoxic (<1.0 mg O_2 L^{-1}) by summer (Boicourt 1999). This has important consequences for copepods in Chesapeake Bay; *A. tonsa* is rare below the pycnocline when dissolved oxygen is <2.0 mg O_2 L^{-1} (Roman et al. 1993; Keister et al. 2000) and avoids severely hypoxic bottom waters <0.5 mg O_2 L^{-1} in laboratory experiments (Decker et al. 2003). No *C. quinquecirrha* medusae or *M. leidyi* ctenophores were observed in extensive underwater video profiles or by SCUBA divers, and few *A. tonsa* were collected in discrete-depth samples, in waters with <0.1 mg O^2 L^{-1} below the abrupt (1-m-thick) oxycline in July 2000, August 2000, or July 2001 (Purcell, Decker, and Breitburg unpubl.). Therefore, in this paper, we limit our analysis to surface waters above the oxycline.

In this paper, we compare predation effects of *C. quinquecirrha* medusae and *M. leidyi* ctenophores on copepod populations in the mesohaline Chesapeake Bay in summer (July–August) 1987–1990 and 1995 (hereafter written as 1987–1995), when medusa densities were high, with effects in summer 1996–2000, when ctenophore densities were high. We also compare the predation potential of *C. quinquecirrha* and *M. leidyi* by size (length or diameter, volume, and carbon biomass). We then explore differences between the two periods in environmental factors (river discharge, surface water salinity and temperature, oxycline depth, solar irradiance, North Atlantic Oscillation Index) that could affect the balance between medusae and ctenophores.

Materials and methods

Field sampling 1987–1990—Sampling was conducted along a five-station transect in the mesohaline Chesapeake Bay during spring, summer, and fall 1987–1990 (Purcell et al. 1994*b*; unpubl.). We limit our analysis here to three deep, central stations (38°27–34.2′N, 76°22.8′–76°28.2′W) and to the summer for biological sampling (28 June to 31 August), which correspond with the later sampling stations and dates (Fig. 1; Table 1). Vertical profiles of salinity, temperature, and dissolved oxygen made with a conductivity–temperature–depth (CTD) before biological sampling revealed pycnocline and oxycline depths, which coincide.

Medusa and ctenophore densities were determined with a 1-m-diameter, 1.6-mm mesh plankton net with a flowmeter towed above the oxycline (to about 11 m depth) in the deep channel station (bottom depth 20 m) and to near bottom (<11 m) at the other stations. Water volumes filtered by the oblique net tows were from 60 to 160 m^3, except in 1990 when net tows were vertical and filtered about 26 m^3. Samples were poured through a plastic colander (pores 4×5 mm) that retained medusae and ctenophores. The species were separated gently by hand, and the volume of each species was measured in 250- or 1,000-ml graduated cylinders. These samples were preserved in 5% Formalin, and specimens were counted and measured in the laboratory. Numbers and sizes of living ctenophores were estimated by counting and measuring preserved tentacle bulbs (method of Purcell 1988). Densities of medusae and ctenophores were standardized (No. m^{-3}).

Zooplankton samples were collected concurrently with a submersible diaphragm pump and 2.5-cm-diameter hose by pumping water (20–40 L min^{-1}) at 1-m intervals; results are reported here for above the pycnocline. The water was filtered through a 64-μm mesh net on deck, and the samples preserved in 5% buffered Formalin. Zooplankton densities were determined by counting three 5-ml subsamples. Only the numbers of *A. tonsa* (adults and copepodite stages standardized to No. L^{-1}) are presented here. Data from 1990 are unavailable.

Field sampling 1995–2000—Sampling was conducted as part of the NSF-sponsored LMER (Land Margin Ecosystem Research) project in Chesapeake Bay called TIES (Trophic Interactions in Estuarine Systems). Bay-wide sampling occurred during April–May, July–August, and October–November in 1995–2000 at 34–50 stations; however, only data from the region corresponding to the 1987–1990 stations are presented here (Fig. 1; Table 1). Salinity, temperature, and dissolved oxygen profiles were made with a CTD, and pycnocline and oxycline depths were determined as before.

Medusae and ctenophores were sampled with an opening–closing 1-m^2 Tucker trawl fitted with 280-μm mesh nets and a General Oceanics flowmeter in two nets; only summer data are reported here. Two-minute oblique hauls were made from the pycnocline to the surface. When no well-defined pycnocline was present at the shallow stations, samples were taken in the surface and bottom halves of the water column; only surface samples are reported here. Water volumes filtered by each net ranged from 70 to 162 m^3. Samples were

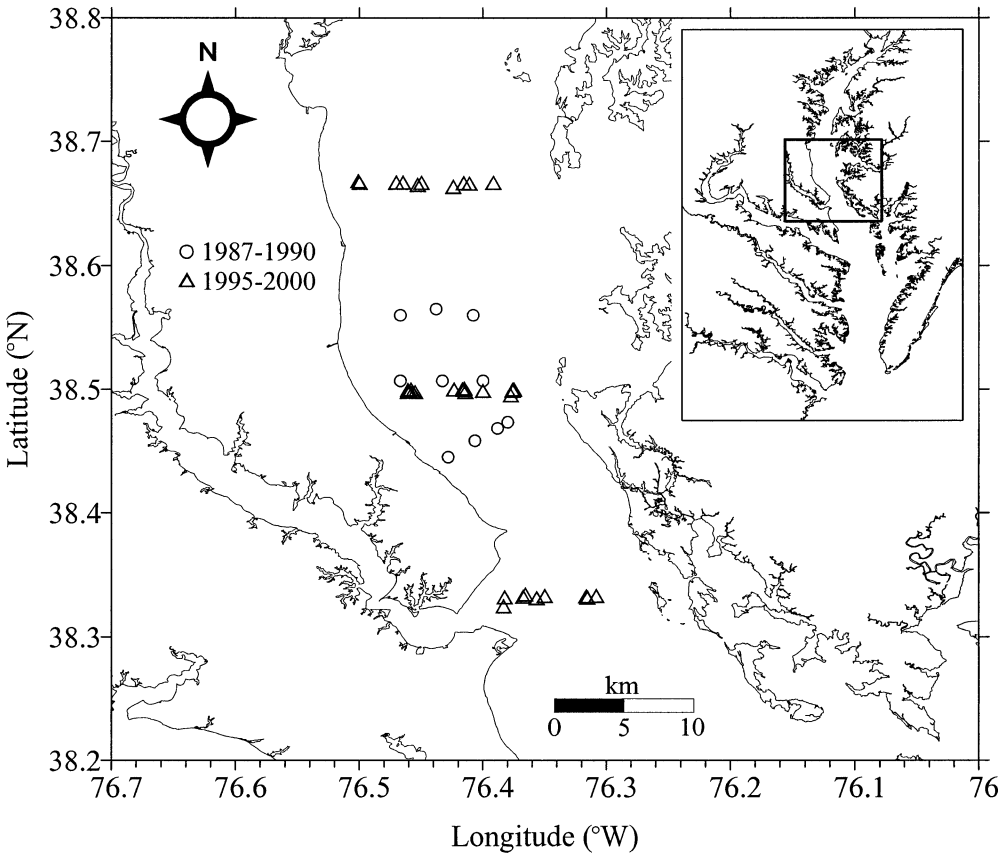

Fig. 1. Sampling stations in the mesohaline Chesapeake Bay during summer 1987–1990 and 1995–2000. Inset map shows whole bay with sampling region marked as a rectangle.

Table 1. Dates of sampling and number of samples collected in the mesohaline Chesapeake Bay (38°19.8′–38°40.2′N) during 1987–2000. NA, not available; —, data not reported here.

Year and season	Sampling dates	CTD stations	Jellyfish stations	Copepod stations
1987 spring	1 May	3	—	—
1988 spring	29 Apr	3	—	—
1989 spring	11 May	3	—	—
1990 spring	15 May	3	—	—
1995 spring	1 May	7	—	—
1996 spring	1 May	6	—	—
1997 spring	20 Apr	6	—	—
1998 spring	14 Apr	6	—	—
1999 spring	22 Apr	7	—	—
2000 spring	1 May	5	—	—
1987 summer	7 Jul, 6–20 Aug	10	11	10
1988 summer	28 Jul, 12–31 Aug	9	9	9
1989 summer	28 Jun, 3 Aug	6	9	9
1990 summer	15 Aug	5	8	NA
1995 summer	27 Jul	10	10	8
1996 summer	20 Jul	3	3	1
1997 summer	11–13 Jul	5	5	2
1998 summer	11 Aug	6	6	4
1999 summer	29 Jun	7	7	3
2000 summer	28 Jul	7	7	3

poured through a colander that retained medusae and ctenophores, which were rinsed, counted, and measured (medusa diameter, ctenophore total length). Densities of medusae and ctenophores were standardized to No. m^{-3}.

Zooplankton from 1995 were counted from the Tucker trawl samples, which were split by a Folsom plankton splitter; all specimens were counted from 0–6 splits. In 1996–2000, zooplankton were not analyzed from Tucker trawl samples because ethanol used as a preservative reacted with ctenophore matter to form a gel. Therefore, zooplankton were counted from samples taken in the surface layer with a 10-liter Niskin bottle, filtered through a 35-μm sieve, and preserved in 5% Formalin. Samples were brought to 200 ml volume, and at least 200 organisms were counted from a minimum of one quarter of the whole sample. All zooplankton in the subsamples were identified and counted. Densities of copepods (adults and copepodite stages) were standardized (No. L^{-1}).

Predation by medusae and ctenophores on copepods—Individual ingestion rates of *C. quinquecirrha* medusae on *A. tonsa* copepods were calculated from the regression (Eq. 1) linking copepod density (X_1, No. L^{-1}), bell diameter (X_2, mm), and temperature (X_3, °C) to copepods eaten (Y, No. $medusa^{-1}$ d^{-1}) from Purcell (1992).

$$\log Y = 0.85 \log X_1 + 1.43 \log X_2 + 3.96 \log X_3 - 6.43 \quad (1)$$

Ingestion rates were converted to individual clearance rates (C_{Chry}, liters cleared $medusa^{-1}$ d^{-1}) by dividing by copepods (No. L^{-1}) and to population clearance rates (liters cleared m^{-3} d^{-1}) by then multiplying by medusae (No. m^{-3}).

The clearance rates of *M. leidyi* ctenophores were measured at 25°C in 1-m^3 mesocosms at the Horn Point Laboratory in Cambridge, Maryland. Clearance rates were calculated from the regression (Eq. 2) linking ctenophore wet weight (X, g) to the volume of *A. tonsa* copepods cleared (C_{Mnem}, liters cleared $ctenophore^{-1}$ d^{-1}) in Purcell et al. (2001).

$$C_{Mnem} = 11.22X^{0.5413} \quad (2)$$

Individual clearance rates were converted to population clearance rates (liters cleared m^{-3} d^{-1}) by multiplying by ctenophore densities (No. m^{-3}).

For feeding comparisons between medusae and ctenophores, measured live medusa diameter (D, mm) and ctenophore volume (V, ml) were converted to carbon biomass (CB, mg) according to the following equations.

$$CB_{Chry} = 0.000215\ D^{2.903} \quad \text{(from Purcell 1992)} \quad (3)$$

$$CB_{Mnem} = 0.561V \quad \text{(calculated from Nemazie et al. 1993)} \quad (4)$$

Environmental effects on medusa abundance—Discharge from the Susquehanna River, which delivers about half of the freshwater annually to northern Chesapeake Bay (Smodlaka et al. 1999), was strongly correlated with *C. quinquecirrha* medusa numbers in 1960–1989 (Cargo and King 1990). We compared the mean monthly discharge from the Susquehanna River, obtained from U.S. Geological Survey Water Resources station at Conowingo, Maryland, and averaged for January through June of each year between our sampling periods (1987–1995 and 1996–2000).

Salinity, temperature, and dissolved oxygen concentrations are known to affect the production, abundance, and depth distribution of medusae (Cargo and King 1990; Purcell et al. 1999; Keister et al. 2000; Condon et al. 2001). We used CTD data from spring and summer cruises to compare surface water salinity and temperature, and depth of the oxygenated layer at each station between sampling periods (1987–1995 and 1996–2000). Salinity and temperature data from spring represent conditions when medusa and ctenophore populations are initiated. The depth of the bottom of the oxycline, designated as where dissolved oxygen concentration was 1.0 mg L^{-1}, was used to represent the depth of the habitable water column in summer when stratification is well established.

Solar irradiance might affect the timing or abundance of medusae. The rates at which *C. quinquecirrha* polyps began to strobilate and at which 100% strobilation was achieved were positively related to the amount of light (0, 10, or 24 h d^{-1}) during the requisite prestrobilation chilling and rewarming of winter–spring (Loeb 1973). We obtained data on the daily high solar irradiance from 1 March to 30 June at Gloucester Point, Virginia, from the Virginia Institute of Marine Science Scientific Data Archive (http://www.vims.edu/data_archive) and compared those data between our sampling years in 1988–1995 and 1996–2000.

The North Atlantic Oscillation Index (NAOI) has been correlated with abundances of other medusa species (Lynam et al. 2004). To determine whether *C. quinquecirrha* medusa abundance was related to the NAOI, we obtained data from the National Center for Atmospheric Research (Climate and Global Dynamics Division [United States], http://www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html). The total numbers of medusae counted biweekly by D. G. Cargo from the pier at the Chesapeake Biological Laboratory, Solomons, Maryland, in 1960–1995, as well as surface water salinity and temperature measured concurrently, are available from the Chesapeake Bay Program Web site (http://www.chesapeakebay.net/data/index.htm). We correlated the December–March NAOI with total medusae (counts yr^{-1}), 1 May salinity, and 1 May temperature.

Statistical analyses—Comparisons between the two periods (1987–1995 and 1996–2000) were made for medusa, ctenophore, and copepod densities; clearance rates; and environmental factors (river discharge, salinity, temperature, oxycline depth, solar irradiance, and NAOI) by *t*-test after data were checked for normality and equal variances. Mann–Whitney rank sum tests were used when those assumptions failed. Correlations were run with Pearson product–moment correlation. We used SigmaStat 3.0 software for all analyses. Statistical significance was accepted at $\alpha = 0.05$.

Results

Medusa and ctenophore densities—Medusa populations differed greatly in the two periods (Fig. 2A). In 1987–1995,

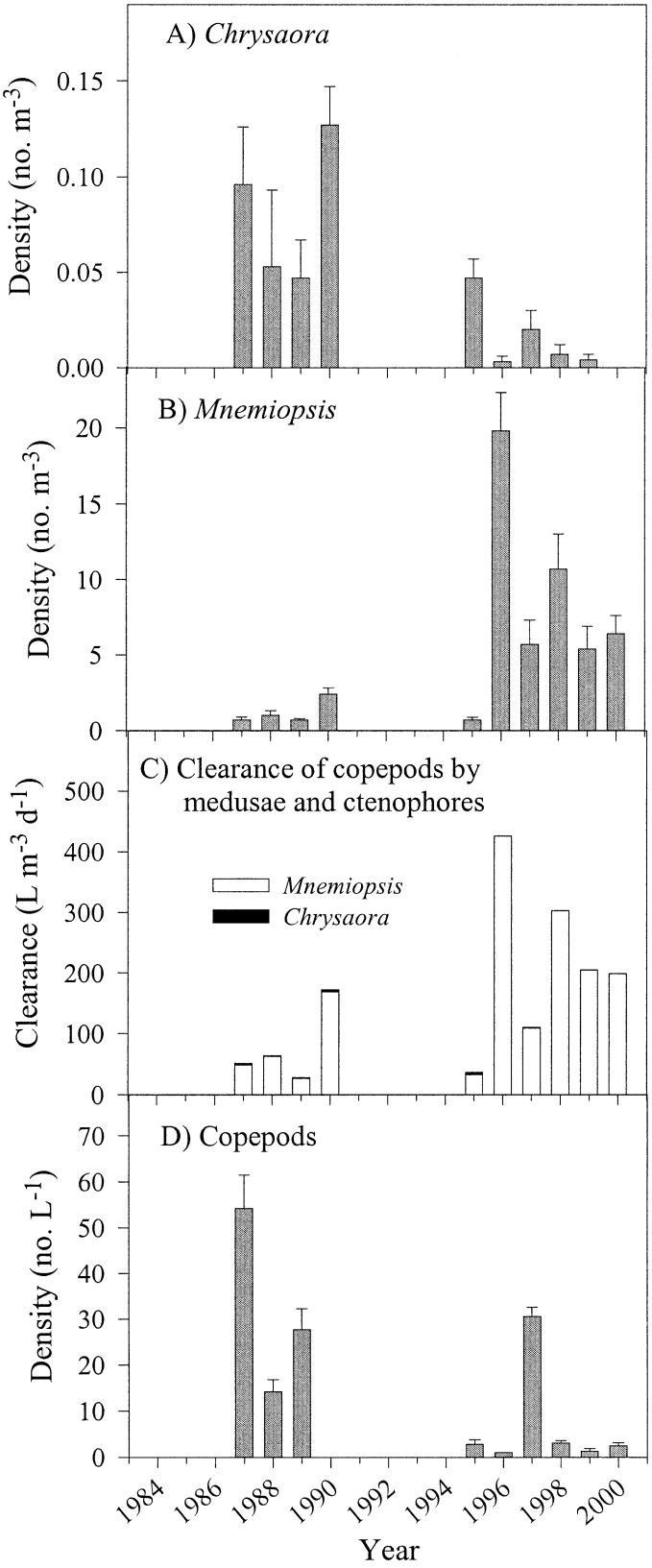

Fig. 2. Densities of (A) *Chrysaora quinquecirrha* medusae, (B) *Mnemiopsis leidyi* ctenophores, (C) their population clearance rates of *Acartia tonsa* copepods, and (D) densities of *A. tonsa* copepods at stations in the mesohaline Chesapeake Bay during sampling in July or August 1987–1995 (*Chrysaora* years) and 1996–2000 (*Mnemiopsis* years). Bars represent means ± SE.

when river discharge was low and spring salinities and summer temperatures were high (Fig. 3A–D), medusae were consistently abundant (>0.047 medusae m^{-3}) in the mesohaline region of Chesapeake Bay (*Chrysaora* years). In 1996–2000, when river discharge was variable, salinities and temperatures were lower, medusa densities were approximately 10–50% of those in 1987–1995, and the difference was significant ($t_8 = 4.03$, $p = 0.004$). Medusa densities were 15 times greater in 1995, which had low discharge, high salinity, and warm temperature, than in 1996, which had high discharge, low salinity, and cool temperature. Among 1996–2000, 1997 showed relatively greater medusa densities and a cascading pattern with reduced ctenophore densities and clearance and high copepod densities. In 1999, which had relatively low discharge and high salinity, medusae were not abundant, possibly because sampling was earlier (29 June) than in other years (July–August) and because of cool temperatures.

Ctenophore densities were low in the mesohaline region during the summers of 1987–1995 when medusa densities were greatest (Fig. 2B). In 1996–2000 (*Mnemiopsis* years), ctenophore densities were generally 5–20 times greater than when medusae were abundant (1987–1995), and the difference between sampling periods was significant ($t_8 = -3.10$, $p = 0.015$). Densities of ctenophores were lowest in 1995 and highest in 1996 of any year sampled.

Densities were always much greater for ctenophores than for medusae at sampling stations in all years (Fig. 2A,B). Ctenophore densities generally were >1 m^{-3} and up to tens per cubic meter. By contrast, medusa densities usually were 0.05–0.1 m^{-3} in 1987–1995 and <0.02 m^{-3} in 1996–2000.

Predation by medusae and ctenophores on copepods—Combined clearance rates of medusa and ctenophore populations feeding on copepods mirrored the pattern of ctenophore densities in the mesohaline region (Fig. 2C,D). The combined percentages of the copepod standing stock calculated to be removed by medusae and ctenophores were only 0.3–0.6% d^{-1} during 1987–1995 (*Chrysaora* years). Calculated predation rates during 1996–2000 (*Mnemiopsis* years) were generally much greater than in the earlier period and ranged from 1.1% to 58.7% of the copepods consumed daily. The difference between sampling periods was significant ($t_8 = -2.97$, $p = 0.018$). Predation on copepods by medusae contributed only slightly to the total clearance (Fig. 2D).

Copepod densities in the mesohaline region generally were greater in 1987–1995, when ctenophore densities and clearance rates were low, than in 1996–2000, when ctenophore densities and clearance rates were high (Fig. 2D); however, the difference between sampling periods was not significant ($t_7 = 1.46$, $p = 0.19$).

At equivalent sizes, either in linear, volumetric, or carbon units, *M. leidyi* ctenophores had greater clearance rates of *A. tonsa* copepods than *C. quinquecirrha* medusae (Fig. 4). For length or diameter (Fig. 4A), small individual ctenophores had greater clearance rates than small medusae. At about 80 mm, medusae and ctenophores had similar clearance rates. For live volume (ml) of similarly sized individuals, clearance rates of ctenophores were about 1.2 times those of medusae (Fig. 4B). At equal carbon biomass, clearance rates of cteno-

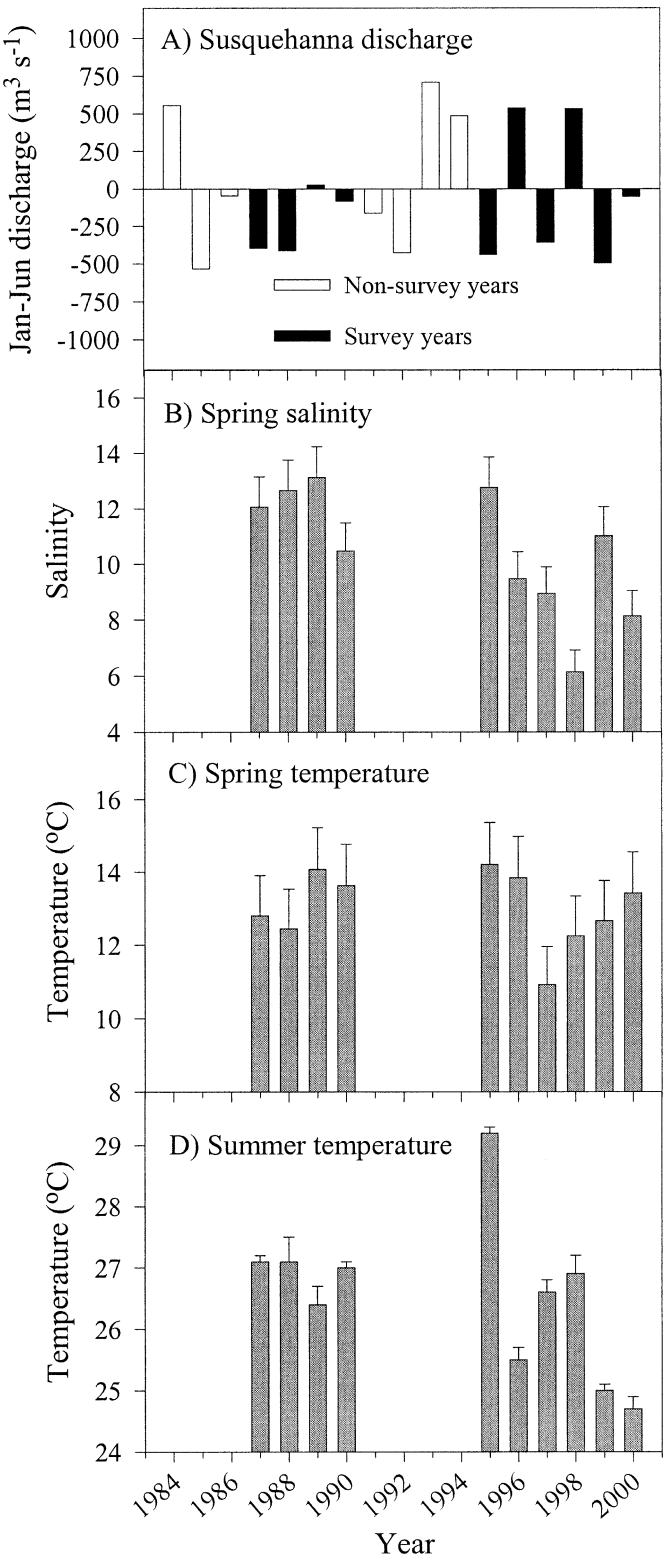

Fig. 3. (A) Deviations from the long-term (1968–2000) Susquehanna River discharge averaged from January through June. Years in which sampling occurred have black bars (1987–1995, *Chrysaora* years, and 1996–2000, *Mnemiopsis* years). (B) Spring salinity, (C) spring temperature, and (D) summer temperature at stations during sampling in the mesohaline Chesapeake Bay. Bars represent means ± SE.

phores were about 2.8 times those of medusae. Equivalent clearance rates were achieved by ctenophores with about one fifth of the carbon biomass of medusae.

Medusae reach larger sizes than ctenophores, and at larger sizes, medusae have higher clearance rates than ctenophores. *C. quinquecirrha* medusae reach 180 mm diameter, but maximum *M. leidyi* ctenophore length is about 80 mm. The maximum clearance rate of *A. tonsa* copepods by individual (ind) medusae in our samples was 180 L ind^{-1} d^{-1}, and the maximum clearance rate by individual ctenophores was about 70 L ind^{-1} d^{-1}.

Medusa and ctenophore sizes and individual clearance rates differed between sampling periods (Fig. 4). In 1987–1995, medusae were smaller than ctenophores in linear and volumetric measures, with similar carbon biomasses, and had lower individual clearance rates, except in 1995. By contrast, in 1996–2000, medusae were larger than ctenophores by all size measures, except for 2000, when only two small medusae were collected (data not included). Individual medusa clearance rates did not differ significantly between periods ($t_6 = -1.93$, $p = 0.10$), although 1995 was the only year that did not fit the pattern. Individual ctenophore clearance rates differed significantly between sampling periods ($t_8 = 6.15$, $p = 0.0003$).

Environmental effects on medusa abundance—Mean monthly discharge from the Susquehanna River was averaged for January through June each year for 1984–2000 and presented as the differences from the long-term mean (1968–2001; Fig. 3A). Sampling in 1987–1990 was during a prolonged period of low precipitation in the Chesapeake Bay watershed, which was reflected by reduced river discharge from the Susquehanna River and high salinities in the bay. By contrast, river discharge in 1994–2000 showed great interannual variations, alternating between record lows and highs. Because of the great variation in 1996–2000, differences between monthly mean river discharge (January–June) in 1987–1995 and 1996–2000 were not significant for untransformed data ($t_8 = -1.3$, $p = 0.23$) or for log-transformed or ranked data, even though discharge in 1996–2000 was markedly above the long-term mean in 2 of the 5 yr.

Salinities were higher and temperatures were warmer in *Chrysaora* years (1987–1995) than in *Mnemiopsis* years (1996–2000). Salinities in spring, when medusa and ctenophore populations are initiated (Fig. 3B), were higher in *Chrysaora* years than in *Mnemiopsis* years ($t_8 = 3.74$, $p = 0.006$). Summer salinities (data not shown) were not significantly different between the two periods ($t_8 = 1.03$, $p = 0.86$). Surface water temperatures were generally warmer in 1987–1995 than in 1996–2000 (Fig. 3C), and differences were significant in summer ($t_8 = 2.51$, $p = 0.036$), but not in spring ($t_8 = 1.32$, $p = 0.22$).

The depths of the bottom of the oxycline, measured at 1.0 mg O_2 L^{-1}, did not differ significantly between *Chrysaora* years (10.8 ± 0.41 m) and *Mnemiopsis* years (11.9 ± 1.08 m) ($t_8 = -0.96$, $p = 0.37$). Therefore, the habitable depths of the water column and vertical distributions of the medusae and ctenophores should have been similar in the two periods.

The daily high irradiance from 1 March to 30 June was greater in *Chrysaora* years (1,472.7 ± 20.7 μ-mol m^{-2} s^{-1})

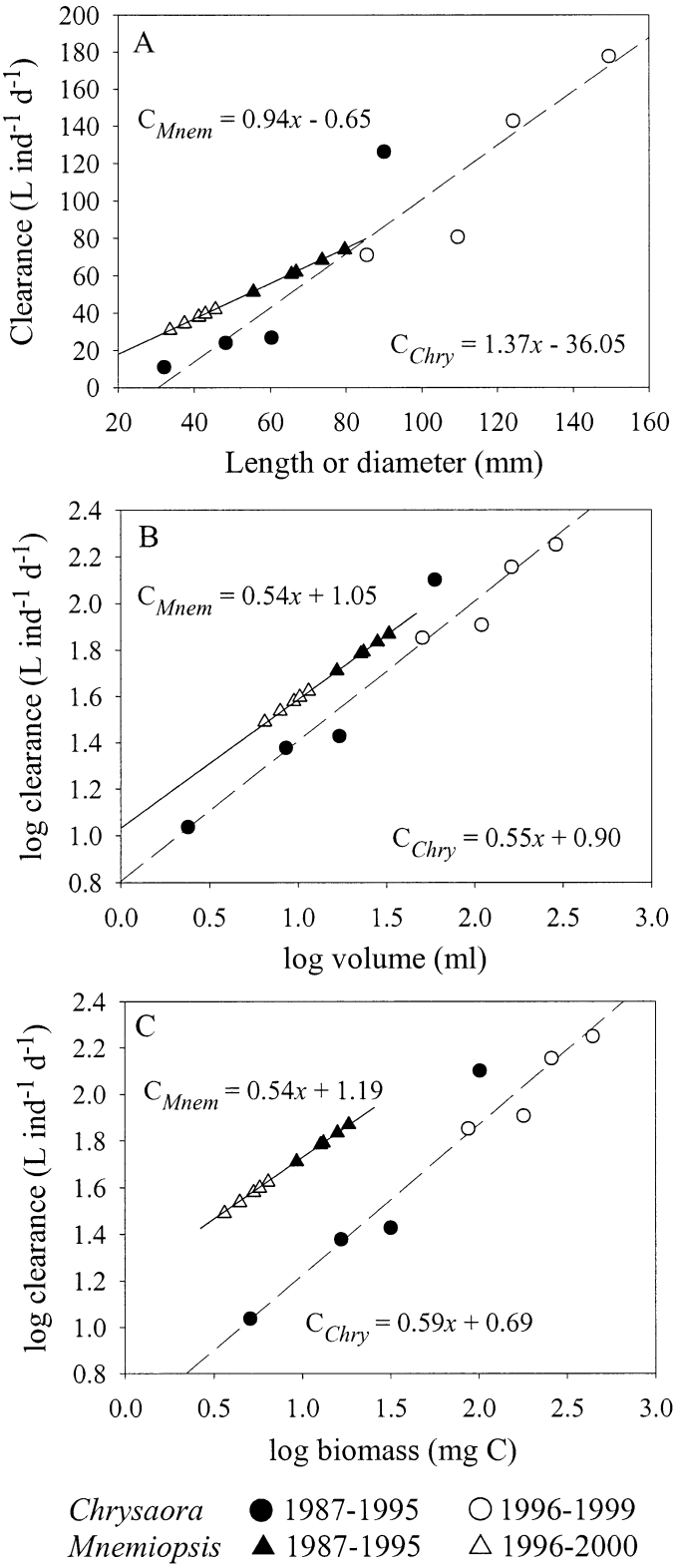

Fig. 4. Comparisons of individual clearance rates of copepods by *Chrysaora quinquecirrha* medusae and *Mnemiopsis leidyi* ctenophores according to size; (A) medusa diameter or ctenophore total length, (B) volume, (C) carbon biomass. Sizes are means from sampling in the mesohaline Chesapeake Bay in July or August 1987–1995 (*Chrysaora* years) and 1996–2000 (*Mnemiopsis* years).

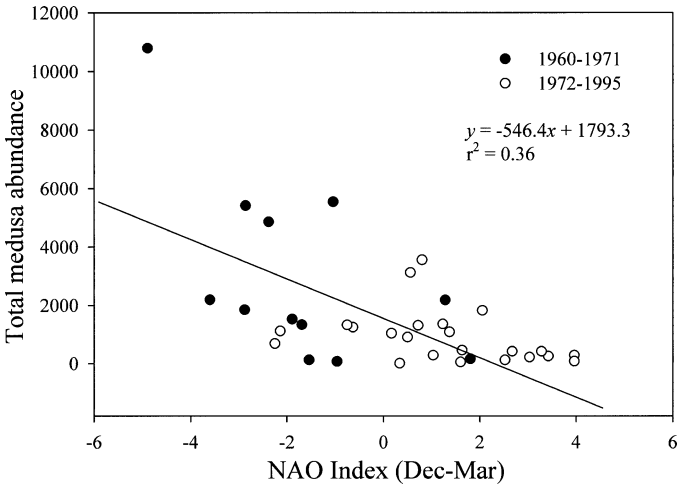

Fig. 5. Total numbers of *Chrysaora quinquecirrha* medusae counted at Solomons, Maryland on Chesapeake Bay versus the North Atlantic Oscillation Index (December–March) in 1960–1995. 1960–1971 was cooler and drier than average, while 1972–1995 was generally warmer and wetter (Austin 2002).

than in *Mnemiopsis* years (1,231.1 ± 18.65 μ-mol m^{-2} s^{-1}) (Mann–Whitney rank sum test; T = 181,500.0, $p < 0.001$).

The greatest numbers of medusae in 1960–1995 occurred when the NAOI was strongly negative (Fig. 5). The numbers of medusae were inversely correlated with the NAOI during 1960–1995 (Pearson correlation coefficient (PCC) = −0.60, p = 0.00015). The correlation of medusa abundance with the NAOI was much stronger during this period than with January–June Susquehanna River discharge (PCC = 0.18, p = 0.37), 1 May salinity (PCC = −0.05, p = 0.79), or 1 May temperature (PCC = 0.25, p = 0.15) (data not shown). Results from the NAOI were not consistent on a yearly basis, however. Differences in the NAOI between our sampling periods 1987–1995 and 1996–2000 were not significant (t_8 = 1.49, p = 0.18), and in fact, most years contrasted with the long-term (1960–1995) pattern; during three of the five *Chrysaora* years, the NAOI was strongly positive, and the only strongly negative NAOI was in 1996 (an anomalous event, Greene and Pershing [2003]), when medusa densities were very low.

Discussion

Relative abundance of medusae and ctenophores in Chesapeake Bay—Ctenophores (1–20 m^{-3}) always were more abundant than medusae (<0.01–0.13 m^{-3}) in the mainstem Chesapeake Bay during our sampling in summer. Ctenophore densities were even greater than estimated, because nets severely undersample small ctenophores; densities of *M. leidyi* <1 cm were 10 times greater by camera-net than when measured with a 333-μm mesh net, in which densities were 2.25 times greater than with a 1.6-mm mesh net (Purcell, Heidelberg, and Olney unpubl.).

Because ctenophore collection and processing differed between 1987–1990 and 1995–2000, we sought to compare our results against independent sampling. We obtained data from the Chesapeake Bay Monitoring Program (CBMP), which

used a 20-cm-diameter, 202-μm mesh net at station CB4.3C (38°33.4′N, 76°26.1′W) in the center of our sampling region (CBP 2000). The CBMP data corroborated our results, with greater ctenophore densities in 1996–2000 than in 1987–1995 ($t_8 = -2.826$, $p = 0.022$ for log-transformed data).

Our different methods in 1987–1990 and 1995–2000 might have contributed to differences in measured ctenophore size. Although the larger mesh size used in 1987–1990 (1.6 mm) could lead to larger mean ctenophore sizes than in 1995–2000 (253 μm), both nets should have collected post-larval ($\geq$1 cm) ctenophores equally well; larval ctenophores were lost in both studies when samples were drained through a colander (4 $\times$ 5 mm pores). Also, ctenophore samples were rinsed in 1995–2000, which might have abraded them and reduced measured lengths. The smaller net used in 1987–1990 (0.78-m^2 mouth area) would be expected to collect fewer medusae than in 1995–2000 (1-m^2 mouth area), but the opposite occurred, suggesting that differences in sampling gear did not bias the results for medusae.

Differences in the life cycles of scyphomedusae and ctenophores allow much greater populations of ctenophores to develop. *C. quinquecirrha* is constrained to one main production event annually; dioecious medusae are produced asexually from benthic polyps in spring after water temperature reaches 17°C following prolonged cooling (Loeb 1972). The polyps are restricted to waters above the seasonal oxycline of about 11 m depth (Cargo and Schultz 1967); therefore, polyps are distributed mainly in the tributaries, and consequently, medusa densities are greatest there. By contrast, the hermaphroditic ctenophores have no asexual stage and develop directly in the plankton from fertilized eggs. Ctenophores produce eggs in both spring and summer (Purcell et al. 2001) and probably through much of the year in Chesapeake Bay.

C. quinquecirrha medusae are more restricted temporally and spatially than *M. leidyi* ctenophores in Chesapeake Bay. The medusae are limited by low ($\leq$5) and high ($\geq$25) salinity and cool temperature ($<$17°C) and occur mainly in the mesohaline regions of the tributaries and mainstem bay in late spring to early autumn (Cargo and Schultz 1967; Purcell 1992; Purcell et al. 1999; Brown et al. 2002). Unusually low salinities and cool temperatures in 1996 shifted their population center southward compared with 1995, and medusa densities were lower throughout the bay in 1996 (maximum 0.0004 m^{-3}) than in 1995 (maximum 0.09 m^{-3}; Purcell et al. 1999). By contrast, ctenophores were collected over wide ranges of temperature (10–29°C) and salinity (0.1–25.6) from early spring through autumn throughout the length of Chesapeake Bay, and also in winter (Purcell et al. 1994*b*, 2001, unpubl.). The ctenophores appear not to be constrained by temperature and salinity, but to be limited mainly by food and predators (Reeve et al. 1989; Kremer 1994).

Relative importance of medusae and ctenophores as predators in Chesapeake Bay—In a previous analysis of the 1987 and 1988 data (*Chrysaora* years), Purcell et al. (1994*b*) estimated predation by *C. quinquecirrha* medusae and *M. leidyi* ctenophores in mid–Chesapeake Bay and concluded that the combined predation could not limit the copepod populations in spring or autumn, when medusae and ctenophores were few, or in summer, when copepod production was high. In that paper, ctenophore clearance rates in summer 1987–1988 were calculated according to experiments in 20-liter containers at 20–25°C from Kremer (1979), and combined medusa and ctenophore predation was estimated to remove $\leq$7.5% d^{-1} of the copepod biomass (carbon) or $\leq$13% of the copepod daily production (carbon). In our present analyses, for all years, we calculated ctenophore clearance rates with an equation from experiments in 1-m^{-3} mesocosms at 25°C, which approximately tripled the earlier estimates. Nevertheless, the previous conclusion is unchanged; predation by medusae and ctenophores probably was insufficient in summer 1987–1988 (*Chrysaora* years) to reduce copepod populations in the mainstem mesohaline bay.

By contrast, in *Mnemiopsis* years, ctenophore predation appeared to reduce copepod densities in the mainstem bay. Our results showed that *M. leidyi* cleared up to an average of 45% d^{-1} of the copepod standing stock in the mesohaline sampling region. Potential clearance estimates at individual stations sometimes exceeded 100% d^{-1}. Abundance patterns certainly suggest reduced copepod populations when ctenophores were numerous (Fig. 2). Biovolumes of *M. leidyi* often are inversely correlated with zooplankton abundances, for example, in Chesapeake Bay (reviewed in Purcell 1988) and in the Black Sea, where it was accidentally introduced in the early 1980s (e.g., Shiganova 1998; Purcell et al. 2001), suggesting that ctenophore predation might control zooplankton populations at times. We believe *M. leidyi* controls copepod populations in Chesapeake Bay when and where ctenophore populations are not reduced by medusa predation.

At equivalent sizes, *M. leidyi* ctenophores had higher clearance rates on copepods than did *C. quinquecirrha* medusae (Fig. 4). The voracious predation of *M. leidyi* has been known for many years (Reeve et al. 1978). Retention of *A. tonsa* copepods and nauplii were high—46% and 62%, respectively—after contact with the lobes of *M. leidyi* (Waggett and Costello 1999). By contrast, $>$99% of copepods escaped from near encounters (not contacts) with *C. quinquecirrha* medusae (Suchman and Sullivan 1998). The feeding mechanisms of the two predators differ greatly, as detailed in those two papers.

Differences in zooplankton collection methods in 1987–1990 and 1995 and in 1996–2000 could have affected our estimates of *A. tonsa* copepod densities. All methods should have retained the copepodites and adults that were used in this analysis. Avoidance of the Niskin bottle might have reduced copepod density estimates in 1996–2000; however, independent data from CBMP station CB4.3C (CBP 2000) with a 202-μm mesh net of 20 cm showed the same pattern in *A. tonsa* abundance, with higher copepod densities in 1987–1990 than in 1995–2000 ($t_8 = 2.472$, $p = 0.039$). Therefore, we conclude that predation by *M. leidyi*, and not sampling differences, caused low copepod densities in 1996–2000.

Consequences of predation on M. leidyi *ctenophores*—The hierarchy of ctenophores over medusae as predators of copepods in the mainstem Chesapeake Bay is reversed in the tributaries when medusae are abundant. *C. quinquecirrha*

medusae can be much more abundant in the tributaries, where densities can exceed 13 m^{-3}, than in the mainstem bay (Purcell 1992). Medusa predation on ctenophores can eliminate ctenophores in the tributaries (Purcell and Cowan 1995). Decreasing copepod densities during the summer and calculated medusa predation rates on copepods suggested that medusae might reduce copepod populations in the tributaries (Purcell 1992). Similarly, at two shallow stations in the mainstem bay stations in July and August 1987–1988, medusa densities, biovolumes, and predation effects were much greater than at the three stations in deeper water used in our present analysis (Purcell et al. 1994*b*). This paper excludes both shallow stations (5 m) in 1987–1989, because all stations in 1995–2000 were >5 m deep. In the mainstem bay, where medusa abundance is lower, they only hold the ctenophore population in check. Large ctenophores escape from contact with the medusae (Kreps et al. 1997), which results in the average size of ctenophores being larger in years with greater medusa abundances (1987–1995; Fig. 4).

Other predators of *M. leidyi* undoubtedly affect their population sizes sampled during summer in Chesapeake Bay. The scyphomedusan *Cyanea capillata* might be an important predator of ctenophores (Båmstedt et al. 1997). This species can be abundant in the mid-bay in February–May; however, its population abundance and dynamics in Chesapeake Bay and the effects on *M. leidyi* are poorly known. During TIES sampling in April–May 1995–2000, *C. capillata* medusae were collected in the same mesohaline region as the summer samples (Fig. 1). Average medusa densities varied greatly between years, from 0 to 0.042 m^{-3}, but no ctenophores were collected in May 2000 when *C. capillata* medusae were most numerous (Purcell et al. unpubl.). Therefore, *C. capillata* medusae might reduce the ctenophore population before *C. quinquecirrha* medusae appear in the mainstem bay in some years. The ctenophore, *Beroe ovata,* also is a voracious predator of *M. leidyi.* It appears first in the higher salinity waters of the southern bay, and spreads northward with increasing salinities as the summer progresses (Purcell et al. 2001). No *B. ovata* were collected at the summer mesohaline stations in 1987–2000 (Fig. 1; Purcell et al. unpubl.); therefore, they did not affect *M. leidyi* abundances presented here but are probably important in other areas and months. Butterfish (*Peprilus triacanthus*) also are known predators of *M. leidyi* (in Oviatt and Kremer 1977), but the fish reside mainly in high-salinity waters in the southern bay beyond our sampling region.

Scyphomedusae, such as *C. quinquecirrha,* generally are considered detrimental to fisheries because they consume eggs and larvae of fish, as well as zooplankton that are the foods of zooplanktivorous fish larvae and fish, which in turn, are foods of prized food fish and marine mammals (reviewed in Purcell and Arai 2001). Nevertheless, evidence suggests that *C. quinquecirrha* medusae may be beneficial predators overall. They might benefit shellfish fisheries in Chesapeake Bay because they consume few bivalve veligers and instead consume *M. leidyi* ctenophores, which do eat veligers (Purcell et al. 1991). Similarly, *C. quinquecirrha* might benefit finfish fisheries in Chesapeake Bay by reducing ctenophore predation on copepods by eating the ctenophores. Average total clearance of copepods in *Chrysaora* years was 70.3 L m^{-3} d^{-1} (range 28–172) and in *Mnemiopsis* years was 248.4 L m^{-3} d^{-1} (range 110–426) at our stations (Fig. 2C). Thus, in *Chrysaora* years, more copepods would be available to zooplanktivorous fish, such as bay anchovy (*Anchoa mitchilli*), which is eaten by game fish, striped bass (*Morone saxitalis*), and blue fish (*Pomatomus saltatrix*) (Vasquez 1989).

The implications of the variation in control of *M. leidyi* ctenophores by *C. quinquecirrha* medusae for the food web are complex and difficult to predict. The medusae eat ctenophores, crustacean zooplankton, mero- and ichthyoplankton, but few veligers, nauplii, or microplankton; however, the early ephyra stage eats microplankton (ciliates and rotifers) and larval ctenophores, but not dinoflagellates (Purcell 1992; Olesen et al. 1996). In addition to copepods, postlarval ctenophores eat many copepod nauplii and microzooplankton (Stoecker et al. 1987), meroplankton such as mollusk veligers (Purcell et al. 1991), and ichthyoplankton (Purcell et al. 1994*a*). In Chesapeake Bay in June 1993, larval ctenophores (2–9 mm) had a diverse diet that included diatoms (27.7%), dinoflagellates (21.7%), ciliates (14.0%), invertebrate eggs (12.2%), copepod nauplii (2.7%), copepods (1.3%), rotifers (0.8%), and meroplankton (0.5%) (3,340 prey items in 131 ctenophore larvae; Heidelberg and Purcell unpubl. data). Therefore, medusa and ctenophore feeding have somewhat different effects on members of the mesozooplankton and microplankton that could lead to different community compositions as medusa control of ctenophores varies. Other zooplanktivores in the system, such as bay anchovy, add to the complexity of community interactions. Piraino et al. (2002) hypothesized that gelatinous predators could be considered keystone predators or a keystone guild, defined by especially important roles in increasing diversity and stability in the ecosystem. *C. quinquecirrha* and *M. leidyi* in Chesapeake may illustrate the keystone predator concept because their predation has important effects throughout the food web.

Climatic limitations on populations of medusae, ctenophores, and copepods—Salinity and temperature are known to affect the timing and sizes of medusa populations in the mesohaline Chesapeake Bay. Asexual production of *C. quinquecirrha* ephryrae from benthic polyps occurs when both water temperature reaches 17°C and salinity exceeds 7 (Purcell et al. 1999), which can occur in early spring or as late as summer. During 1987–1990 and 1995–2000, the various combinations of temperature and salinity affected medusa abundance and, consequently, ctenophore populations and predation effects on copepods. The most favorable conditions for *C. quinquecirrha* medusae are salinity between 10 and 16 and warm spring (≥17°C) and summer temperatures (26–30°C; Brown et al. 2002), in which early development of medusae can limit ctenophore numbers. Conversely, a combination of low salinities and cool spring temperatures reduces and delays medusa populations (Purcell et al. 1999), allowing ctenophores to become numerous and large enough to escape from medusae (Kreps et al. 1997) before medusae appear.

We think that during several years of favorable conditions (e.g., the 1960s and 1987–1990), medusae become more abundant than during several years of variable conditions

(e.g., 1995–2000). This is probably because of an increase in the benthic polyp populations in extended favorable conditions; polyp production increased significantly from salinities of 5 to 20 (Purcell et al. 1999). Egg production rates of medusae were greater in warmer temperatures (20, 25, 30°C) and higher salinities (13, 18, 25, 30) than at 15°C and 7 salinity (Asplen and Purcell unpubl.), which also could lead to an increase in polyps in periods of favorable conditions.

Strobilation in scyphomedusae appears to depend on light as well as water conditions. Strobilation of *Aurelia aurita* in England and *A. labiata* in Washington state occurs in winter when temperatures and light levels are low and strobilation is inhibited by light (Custance 1964; Purcell unpubl.). Strobilation of *C. quinquecirrha,* which occurs after seasonal chilling and rewarming, was accelerated in longer light periods (0, 10, 24 h light d^{-1}; Loeb 1973). We show here that years of high solar irradiance in spring, when ephyrae develop from polyps in Chesapeake Bay, had abundant medusae in the summer.

Although *M. leidyi* ctenophores were collected over wide ranges of temperature (10–29°C) and salinity (0.1–25.6) in Chesapeake Bay (Purcell et al. 1994*b,* unpubl.), effects of temperature and salinity on them have been described. Cool spring temperatures (<12°C) are correlated with small ctenophore size in spring in the Chesapeake Bay and the Black Sea, and cold winter temperatures (<4°C) prevent ctenophore overwintering in the Sea of Azov (reviewed in Purcell et al. 2001). Size-specific ctenophore egg production was lower in spring, when temperature, salinity, and prey densities were lower than in summer in Chesapeake Bay (Purcell et al. 2001). Both ctenophore size and size-specific egg production were less at cool temperature (9°C) and low salinity (7) than at the warmer temperatures (15, 19, 25–27°C) and higher salinities (14, 21, 28) tested in the laboratory (one-way ANOVAs, $p < 0.05$; Purcell et al. unpubl.). Warmer conditions in Narragansett Bay, Rhode Island, during the 1980s were correlated with earlier appearances of *M. leidyi* than in the 1970s and before (Sullivan et al. 2001).

In addition to direct effects of environmental factors on medusa and ctenophore physiology and behavior, there also would be effects on the food web that would determine the timing and amounts of zooplankton prey available to them. The volume of freshwater discharge into Chesapeake Bay determines the amounts of nutrients and governs the magnitude and location of the spring phytoplankton bloom; furthermore, nutrients are retained and recycled within the bay, maintaining high production throughout the summer (reviewed in Harding et al. 1999). Thus, high river discharge results in high-nutrient inputs and high primary and secondary production in the mesohaline bay. If not limited by predation, we would expect copepods to be more abundant in years of greater river discharge when nutrients and production are greater; however, the opposite pattern was observed (Figs. 2, 3). Direct effects of temperature and salinity on *A. tonsa* copepods also might exist, even though the copepods are found over broad ranges of temperature and salinity (Cervetto et al. 1999). Temperature alone explained 72% of the variation in egg production by *A. tonsa,* with reduced production at temperatures below 20°C and above 27°C (White and Roman 1992). Kimmel and Roman (2004) found no significant relationships of any physical or biological parameters with *A. tonsa* abundance at CBMP station CB4.3C in our sampling region.

Jellyfish abundances have been linked to climate conditions previously. Goy et al. (1989) showed that blooms of *Pelagia noctiluca* medusae occurred at intervals of about 12 yr over the past 200 yr in the Mediterranean Sea. A combination of low rainfall, high temperature and high atmospheric pressure from May to August was the best predictor of a *P. noctiluca* bloom. Anderson and Piatt (1999) and Brodeur et al. (1999) use fishery trawl surveys in the Gulf of Alaska from 1953–1997 and in the Bering Sea from 1979–1997, respectively, to document dramatic increases of jellyfish, primarily *Chrysaora melanaster,* during the 1980s and 1990s. This increase followed a regime shift in 1972 from mostly negative North Pacific Pressure Indices (NPPI) in the 1950s and 1960s to mostly positive indices; positive NPPIs and jellyfish increases were accompanied by sea surface warming. In Narragansett Bay, Rhode Island, *M. leidyi* ctenophores have appeared earlier and reached greater peak abundances in the 1980s and 1990s compared with the 1950s and 1970s (Sullivan et al. 2001). This was associated with an increase of 2°C in spring water temperatures and a positive phase of the NAO. In the North Sea during 1971–1986, abundances of scyphomedusae, *A. aurita,* and *Cyanea lamarckii,* but not *C. capillata,* were inversely correlated with the December–March NAOI (Lynam et al. 2004); negative NAOI are associated with cooler than average water temperatures in the North Sea (Beaugrand 2003). Our results showed that in years when *C. quinquecirrha* medusa numbers were great, temperatures were warmer than when numbers were small. Except for the results of Lynam et al. (2004), increased abundances of gelatinous zooplanktivores have been related to ocean warming.

The NAO has been connected to variations in marine and terrestrial ecosystems, primarily in Europe (e.g., Ottersen et al. 2001; Austin 2002; Beaugrand 2003; Lynam et al. 2004). The 1960s were characterized by predominantly negative NAOIs and had very large populations of medusae in Chesapeake Bay. By contrast, NAOIs were generally positive in the 1980s and 1990s (Greene and Pershing 2003), and medusa numbers were lower than in the 1960s (Fig. 5). The dramatic 1-yr drop from positive to a negative NAOI in 1996 (Greene and Pershing 2003) did not result in abundant medusae; high precipitation and river discharge caused low salinity conditions in Chesapeake Bay in 1996, which are unfavorable to medusae. The cooler and drier than average 1960s were followed by a regime shift after Hurricane Agnes in 1972. The extremely low salinity conditions caused by the hurricane could have reduced polyp populations in the bay. The post-1972 regime, which prevails to the present, is characterized by warmer and wetter than average conditions; the late 1980s diverged from this pattern, being cooler and drier than average (Austin 2002). Therefore, data suggest that medusa populations in Chesapeake Bay would continue to be low while the NAOIs continue to be generally positive.

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Received: 20 February 2004
Accepted: 16 August 2004
Amended: 3 September 2004