

# Oyster-Sea Nettle Interdependence and Altered Control Within the Chesapeake Bay Ecosystem

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**ABSTRACT:** Research on the effects of declining abundances of the Eastern oyster (*Crassostrea virginica*) in Chesapeake Bay and other estuaries has primarily focused on the role of oysters in filtration and nutrient dynamics, and as habitat for fish or fish prey. Oysters also play a key role in providing substrate for the overwintering polyp stage of the scyphomedusa sea nettle, *Chrysaora quinquecirrha*, which is an important consumer of zooplankton, ctenophores, and ichthyoplankton. Temporal trends in sea nettle abundances in visual counts from the dock at Chesapeake Biological Laboratory, trawls conducted in the mesohaline portion of the Patuxent River, and published data from the mainstem Chesapeake Bay indicate that sea nettles declined in the mid 1980s when overfishing and increased disease mortality led to sharp decreases in oyster landings and abundance. Climate trends, previously associated with interannual variation in sea nettle abundances, do not explain the sharp decline. A potentially important consequence of declining sea nettle abundances may be an increase in their ctenophore prey (*Mnemiopsis leidyi*), and a resultant increase in predation on ichthyoplankton and oyster larvae. Increased predation on oyster larvae by ctenophores may inhibit recovery of oyster populations and reinforce the current low abundance of oysters in Chesapeake Bay.

## Introduction

The effects of overfishing of higher trophic levels on marine food webs and fisheries yields have received considerable, well-deserved attention in recent years (Jackson et al. 2001; Myers and Worm 2003). Marine food webs subjected to heavy fishing removals often have reduced piscivore populations, increased abundances of planktivores relative to piscivores, and fisheries characterized by progressively decreasing mean trophic levels (Pauly et al. 1998). Instead, commercial fisheries in many estuarine systems now target mid trophic level species. In Chesapeake Bay during 1990–2000, 63% of the commercial landings by weight were comprised of planktivores, another 31% by species whose diets are dominated by benthic invertebrates, and only 6% by fish species that are wholly or partially piscivorous (NMFS unpublished data). These percentages reflect the predominance of the Atlantic menhaden (*Brevoortia tyrannus*) and blue crab (*Callinectes sapidus*) fisheries. Eastern oyster (*Crassostrea virginica*), which now makes up about 1% of the landings, once yielded landings approximately 100-fold higher. Shellfish and Gulf menhaden (*Brevoortia patronus*) comprised 92% of the commercial landings in state and federal waters of Louisiana during the same time period (NMFS

unpublished data). In the North Carolina Pamlico-Albemarle sound and mesohaline tributaries, 82% of 1990–2000 commercial landings were shellfish and Atlantic menhaden (Hesselman unpublished data). Planktivorous fishes and shellfish support important fisheries in a number of European and Asian estuaries as well (DeJong and Van Raaphorst 1995; Pinnegar et al. 2003; Sugiyama et al. 2004).

Reduced abundances of mid trophic level species can be particularly important because the structure of the food web at that point can strongly influence the transmission of both nutrient enrichment and fishing effects through the food web (Hart 2002). Anthropogenic influence on the abundance of mid trophic level species can also strongly affect estuarine food webs where these species create habitat and influence the physical environment as well as playing an important direct role in food web interactions. Ecosystem engineers, such as oysters and corals, have a disproportionate effect on the ecosystems they inhabit, and their decline can dramatically alter system structure and function (Coen et al. 1999; Coleman and Williams 2002; Newell 2004).

In this paper we examine temporal patterns of abundances of several key species in the Chesapeake ecosystem and suggest that one of the most important effects of the decline in oysters on the estuarine food web is mediated through the effect of oysters on the scyphomedusa *Chrysaora quinquecirrha* (sea nettle; Fig. 1). Sea nettles are dominant consumers in Chesapeake Bay (Cowan and Houde 1993; Purcell and Cowan 1995), are seasonally

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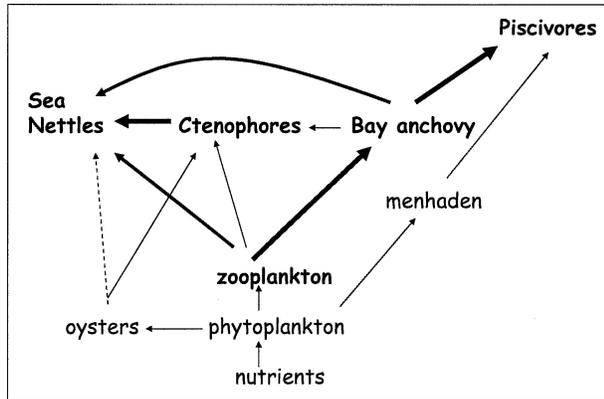


Fig. 1. Simplified Chesapeake Bay food web. Solid arrows indicate trophic connections; dashed arrows indicate habitat provision. A reduction in oyster abundance reduces habitat for sea nettle polyps, which may result in reduced predation mortality of ctenophores and a greater shunting of energy to ctenophores relative to planktivorous and piscivorous fishes. Bolder arrows represent trophic pathways that are predicted to increase in importance as sea nettle abundances increase.

abundant in other Atlantic and Gulf of Mexico estuaries, and have congeners in the Eastern and Western Pacific and the Eastern Atlantic oceans. Oysters historically created the most extensive hard substrate habitat in Chesapeake Bay. Oyster shell serves as the primary substrate for the sessile, overwintering polyp stage of the sea nettle. Polyp abundance on substrates, such as twigs, sticks, piers and human debris, is low (Cones 1968; Cones and Haven 1969), and polyps on submerged vegetation are unlikely to survive the winter senescence of these plants in Chesapeake Bay (Cones and Haven 1969). The indirect effects of declining sea nettle abundances may include decreased probability of oyster population recovery and increased shunting of energy within the food web to gelatinous predators rather than fish.

#### DATA SOURCES AND ANALYSES

Data on temporal patterns of sea nettle abundance come from three sources. Visual counts of sea nettle medusae were made along the length of the pier at Chesapeake Biological Laboratory (CBL) in Solomons, Maryland, up to 5 d wk<sup>-1</sup> during the months medusa were present from 1960–1988, 1989–1998, 2001–2002, and August–September 2005. Data through 1986 were published in Cargo and King (1990). Counts were continued past that date but were not published. Counts were conducted by Cargo with help from M. Wiley and H. Millsaps through 1991, by M. Wiley during 1992–1993, by H. Millsaps during 1994–1998, by E. Setzler-Hamilton (trained by H. Millsaps) during 2001–2002, and by R. Burrell from our laboratory

(also trained by H. Millsaps) beginning in August 2005. In three comparison counts, Burrell's counts averaged 20% higher than simultaneous counts by Millsaps.

Except as noted below, analyses of interannual variation here use the mean counts for the 4-wk period each year with the highest sea nettle abundances. The timing of peak sea nettle abundances can vary, and sometimes occurs in September. Limiting analyses to July and August as in Cargo and King (1990) can confound the timing and magnitude of peak sea nettle abundance. We excluded 1972 (the year of Hurricane Agnes) from analyses because no samples were taken in July and there are no independent data indicating the timing of peak sea nettle abundances that year. We included 2005 counts even though they did not begin until August because peak densities in 2005 Patuxent River trawls (described below) occurred on August 10. We also compared analyses with and without 1969 included. Mean peak and mean July–August sea nettle counts in 1969 were more than twice that in any other year in the data record. Our analyses of the Cargo and Millsaps data set also differ from that of Purcell and Decker (2005), who used total annual counts. We chose to use the 4-wk peak because the number and timing of samples varied somewhat among years. Purcell and Decker's analyses also only included data through 1995.

The second data set consists of sea nettle and ctenophore samples taken during 1992–1993, 1998–2001, and 2003–2005 with 226–244  $\mu\text{m}$  mesh 1-m<sup>2</sup> Tucker trawls at two sites in the mesohaline Patuxent River (Keister et al. 2000; Breitburg et al. 2003, unpublished data). All unqualified references to ctenophores in this paper refer to the lobate ctenophore, *Mnemiopsis leidyi*. Samples were drained on 2-mm mesh sieves or in colanders, and total volume and numbers of each species were determined on board. Each density estimate used in analyses here consists of an average of duplicate surface, pycnocline, and bottom-layer trawls during 1992–2001 or more than 2 upper and lower water column trawls during 2003–2005. Multiple samples taken at the same site, date, and diel period (day or night) were averaged. Sea nettle densities (number m<sup>-3</sup>) and ctenophore biovolume (ml m<sup>-3</sup>) are reported. We also reanalyze data reported in Purcell and Decker (2005) for the mainstem Chesapeake Bay. As with the Patuxent samples, gelatinous zooplankton for that study were collected with a 1-m<sup>2</sup> Tucker trawl.

Data on oyster landings in Maryland waters were used to estimate changes over time in the abundance of oyster shell substrate available to sea nettle polyps. We used landings data provided by C. Judy, the Shellfish Program Director of Maryland De-

partment of Natural Resources (unpublished data) because several different sets of annual estimates were found online and in reports. Summer sea nettle abundances were compared to the previous winter's oyster landings. We used Maryland-wide data instead of Patuxent River oyster landings in analyses because the low number of watermen fishing oysters in the Patuxent results in high interannual variation in river landings that is likely independent of stock levels.

Cargo and King (1990) suggested that the January-June Chesapeake streamflow strongly influenced interannual variation in sea nettle abundances reflected in their CBL pier count data because of the negative effect of low salinity on ephyra production. Their analysis included July-August data for 1960–1986. We reexamined this relationship to determine whether trends in river discharge might explain the decline in sea nettle counts at the CBL pier and densities in Patuxent River trawls. Stream discharge data for the portion of Chesapeake Bay above the mouth of the Potomac River were provided by J. Manning (unpublished data) of the U.S. Geological Survey (USGS) who updated provisional data found on the USGS website (<http://md.water.usgs.gov/monthly/bay1.html>).

A more recent analysis of the Cargo and King (with added years by Wiley and Millsaps) 1960–1995 data set suggested a significant relationship between the North Atlantic Oscillation (NAO), which influences a suite of environmental variables and sea nettle abundance (Purcell and Decker 2005). We repeated this analysis with the complete 1960–2005 pier count data set. We used the site-based December-March NAO index to examine climate effects on sea nettle abundances so that our analyses would be directly comparable to those of Purcell and Decker (2005; <http://www.cgd.ucar.edu/cas/jhurrell/Data/naodjfmindex.1864-2005.xls>).

To explore whether declining sea nettle abundances might result in an increase in their ctenophore prey, we examined temporal patterns in ctenophore abundance in mesohaline stations in the Maryland portion of Chesapeake Bay (stations CB2.2, CB3.3C, CB4.3C, and CB5.2) and its tributaries (the Patuxent, Choptank, and Potomac Rivers) sampled by the Chesapeake Bay Zooplankton Monitoring Program from 1985 to 2002 (<http://www.chesapeakebay.net/data/index.htm>). These samples were taken with a 20-cm diameter, 202- $\mu$ m mesh net and drained on a 2-mm mesh sieve prior to onboard determination of total volume and numerical abundance of each species. Data used in correlations are the mean June or July-August ml ctenophores  $m^{-3}$  through the entire water column for all tributary or mainstem bay sites listed above.

In the first 3 yr of the monitoring program, *Beroe ovata* (a ctenophore predator of *M. leidyi*) and *M. leidyi* were lumped into a single ctenophore category. In order to include 1985–1987 in our data set, we lumped both species for our analysis. In years the two species were counted separately, *Beroe* was either not present or averaged only a small percent of the June–August biovolume of *M. leidyi*. It is not known whether sea nettles consume *Beroe* spp.

Curve-fitting was done with SigmaPlot (Version 8.0, Jandel Scientific, San Rafael, California). Both linear and nonlinear fits were tested, and the best fit is reported. Where  $R^2$  values were similar for several linear and nonlinear relationships, and where no significant fits were found, only linear regression results are reported. Statistical analyses used SAS (Version 9.1, SAS Institute Inc., Cary, North Carolina).

## Results

### TEMPORAL PATTERNS IN SEA NETTLE AND OYSTER ABUNDANCES

Three data sets that overlap in time provide evidence that sea nettle abundances have declined since the mid 1980s and have remained far below historical levels since about 1990. The first data set consists of visual counts of sea nettles made from the CBL pier from 1960 to 2005 (Fig. 2). Although there is considerable interannual variation in mean 4-wk peak sea nettle abundances in this data set, there is a strong pattern of high interannual variation and peak counts exceeding 100 in 19 of 26 years during 1960–1986 as compared to consistently low counts during 1990–2005. The second data set from the mesohaline mainstem Chesapeake Bay published by Purcell and Decker (2005) indicates that sea nettle densities were approximately 4-fold higher in 1987–1990 than in 1995–2000. The third data set, of trawl data from the mesohaline Patuxent River, indicates that mean July–August densities during 1992–2005 were low, averaging 0.07  $ind\ m^{-3}$ . Mean sea nettle densities were 0.15  $ind\ m^{-3}$  in 1992–1993 (based on annual means;  $n = 12$  sets of duplicate trawls per year), as compared to a mean of 0.03  $ind\ m^{-3}$  during 1999–2005 ( $n = 6, 12, 1,$  and 12 sets of duplicate trawls for 1998, 2001, 2003, and 2004, respectively, and 12 sets of unreplicated trawls in 2005; Fig. 3).

Oyster landings in Maryland peaked in the late 19th century, declined until the 1960s primarily as a result of overfishing and associated habitat destruction, and then declined again beginning in the mid 1980s as a consequence of the combined stresses of overfishing, disease, and habitat degradation (NRC 2004; Fig. 2). Major die-offs of market-sized oysters related to both *Perkinsus marinus* and

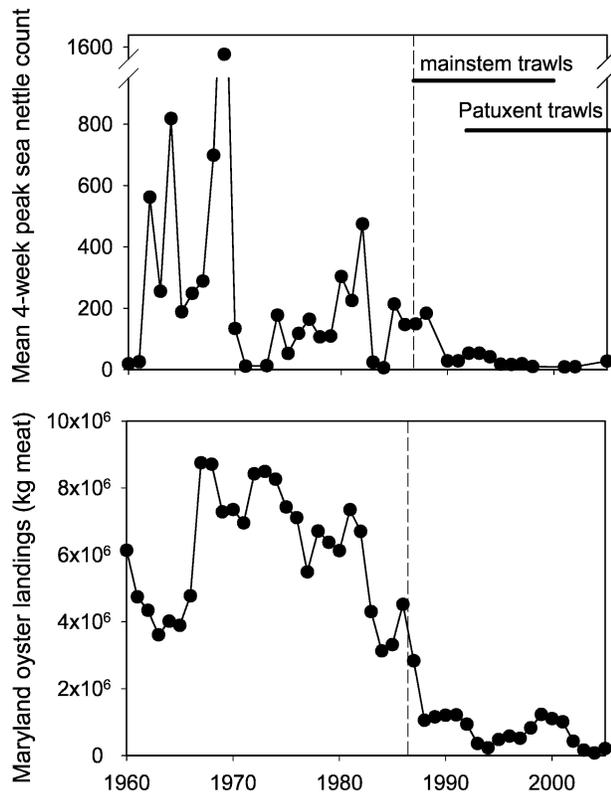


Fig. 2. Temporal pattern of sea nettle counts and Maryland oyster landings during 1965–2005. The dashed vertical line indicates 1987, when high levels of disease-related mortality began reducing oyster abundances below 1960–1986 levels. The timing of other data sets discussed in manuscript are indicated as mainstem trawls (Purcell and Decker 2005) and Patuxent trawls (Keister et al. 2000; Breitburg et al. 2003; Breitburg et al. unpublished data).

*Haplosporidium nelsoni* infections were reported in Maryland during summer 1987. Current oyster landings are only 2% of historical 1870–1900 landings. The decline in landings may underestimate the decline in hard substrate available to sea nettle polyps because of heavy siltation in oyster bars with few living oysters (Smith et al. 2005).

A comparison of temporal patterns of oyster landings and sea nettle pier counts since 1960 indicates that abundances of both species declined during the same period and have remained low since that time. Current oyster landings are only 11% of that prior to the mid 1980s decline. Annual landings during 1959–1960 through the 1985–1986 oyster seasons averaged  $2,096,383 \pm 22,834$  (standard error) bushels  $\text{yr}^{-1}$ , as compared to  $227,553 \pm 8,842$  bushels  $\text{yr}^{-1}$  during the 1989–1990 through 2004–2005 seasons. Recent sea nettle pier counts are only 10% of that prior to the mid 1980s oyster decline. Peak annual counts during 1960–1986 averaged  $257 \pm 12$ , as compared to  $26 \pm 1$  during 1990–2005.

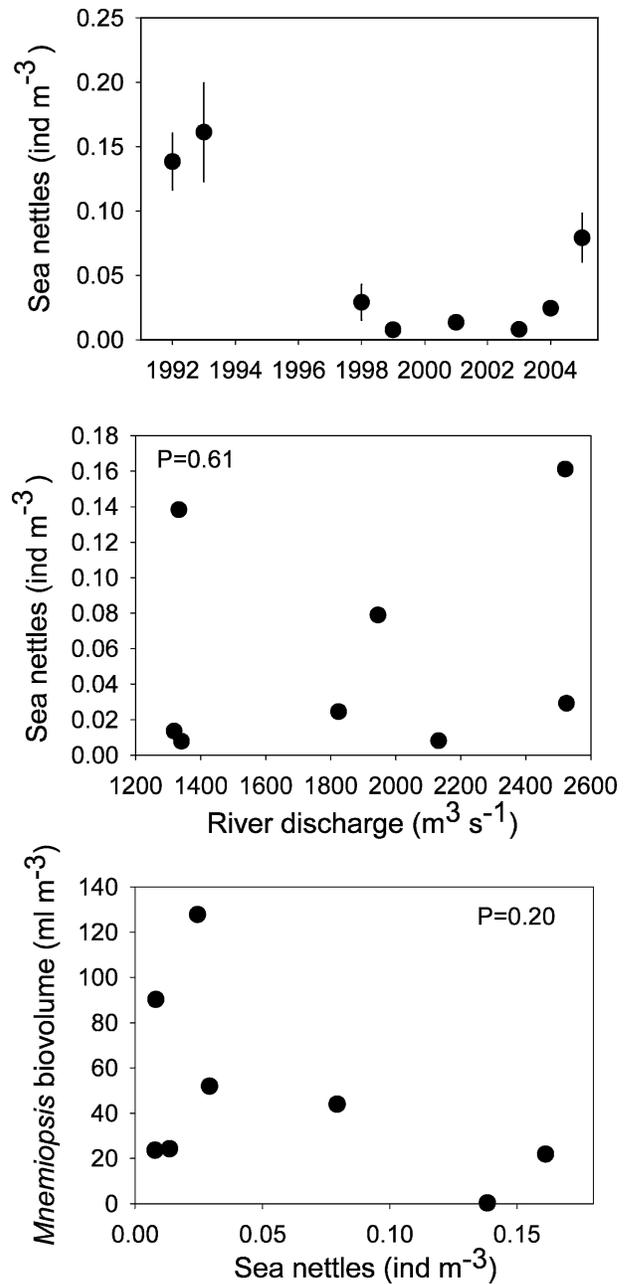


Fig. 3. Density ( $\pm$  SE) of gelatinous zooplankton in mesohaline Patuxent River trawl collections during 1992–2005, plotted against river discharge for the portion of the Chesapeake Bay north of the mouth of the Potomac River, and compared to *M. leidy* biovolume. The relationship between sea nettle and ctenophore abundances is better described using sea nettle number than volume.

River discharge patterns did not explain the mid 1980s decline in sea nettle abundances, and once the unusually high 1969 value was removed, explained little of the interannual variation in the data set originally analyzed by Cargo and King

TABLE 1. Relationship between January–June discharge above the mouth of the Potomac River and visual counts of sea nettles at the Chesapeake Biological Laboratory Pier. The original analysis by Cargo and King (1990) included July–August counts for 1960–1986. Results of the best-fit model (exponential decline or linear) are shown. na = not applicable. Data were analyzed with and without 1969 included because sea nettle counts in that year were more than twice as high as in any other year in the data record.

Years	Sea Nettle Data	Model	1969 Data	R <sup>2</sup>	p
1960–1986	July–August mean	exponential	included	0.35	0.001
1960–1986	4-wk peak mean	exponential	included	0.29	0.005
1960–1986	July–August mean	linear	removed	0.15	0.06
1960–1986	4-wk peak mean	linear	removed	0.18	0.03
1990–2005	4-wk peak mean	linear	na	0.05	0.47
1960–2005	4-wk peak mean	linear	removed	0.07	0.10

(1990; Table 1). There was no long-term trend in January–June river discharge above the Potomac River during the 1960–2005 period (correlation between year and streamflow:  $R = 0.02$ ,  $p = 0.90$ ) and no significant difference in streamflow between the 1960–1986 period prior to the oyster and sea nettle decline and the 1990–2005 period following the decline of both species ( $F = 0.00$ ,  $p = 0.999$ ). There were also multi-year droughts, conditions thought conducive to high sea nettle abundances, in both the 1960s, when sea nettle abundances were at their maxima, and during 1999–2002, when sea nettle abundances were at extremely low levels.

A re-examination of the 1960–1986 Solomons pier count data indicates a strong negative relationship between January–June river discharge (from Table 1 in Cargo and King 1990) and both July–August mean counts (from Table 1 in Cargo and King 1990) and 4-wk peak mean sea nettle counts. Statistical results are summarized in Table 1 of this manuscript. Somewhat less of the interannual variation is explained by river discharge for the peak mean than July–August mean because peak densities sometimes occur in September in low salinity years. A second analysis with 1969 removed to examine the pattern in the absence of the single year of unusually high sea nettle counts suggests that river discharge typically explained little of the interannual variation in sea nettle counts even in the original data set (Table 1). No relationship was found between peak sea nettle counts and river discharge during 1990–2005.

Trawl data also do not support a strong role of river discharge influencing interannual variation in sea nettle densities following the decline of oysters (Fig. 3). Both the early 1990s and the 1998–2005 periods include one or more years with above

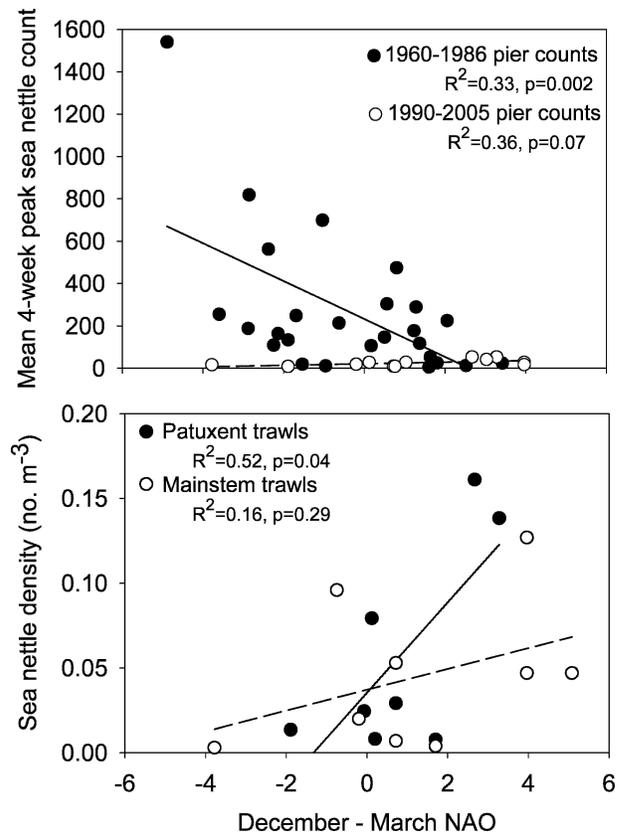


Fig. 4. Relationship between sea nettle abundance and NAO index. Inclusion of 1969 data had little effect on the analysis.

average rainfall and one or more years with below average rainfall. River discharge in the Maryland portion of Chesapeake Bay did not explain a significant portion of the interannual variation in sea nettle densities in trawls (linear regression:  $R^2 = 0.04$ ,  $p = 0.61$ ).

Our analysis suggests that the relationship between the NAO and sea nettle abundances may have changed as sea nettle densities declined (Fig. 4). An analysis of 1960–1986 mean 4-wk peak sea nettle counts regressed against mean December–March NAO (<http://www.cgd.ucar.edu/cas/jhurrell/Data/naodjfmindex.1864-2005.xls>) yielded a negative relationship between CBL pier counts and NAO, similar to findings of Purcell and Decker (2005;  $R^2 = 0.33$ ,  $p = 0.002$  for this analysis versus  $R^2 = 0.36$  reported in Purcell and Decker). In contrast, there was a trend towards a positive relationship between sea nettle pier counts and NAO for the 1990–2005 portion of the data set ( $R^2 = 0.32$ ,  $p < 0.07$ ), a positive relationship between the NAO and sea nettle densities in our Patuxent River trawl data set encompassing 1992–2005 ( $R^2 = 0.52$ ,  $p = 0.04$ ), and no significant relationship between the NAO index and data reported in Purcell and Decker (2005) for

the mainstem Chesapeake Bay 1987–1999 ( $R^2 = 0.16$ ,  $p = 0.29$ ). Sea nettle densities in recent years have been low regardless of NAO index values.

#### FOOD WEB RESPONSES TO DECLINING SEA NETTLE ABUNDANCE

Sea nettles are the dominant predators of the ctenophore, *M. leidyi*, in Chesapeake Bay (Feigenbaum and Kelly 1984; Purcell and Cowan 1995; Purcell and Decker 2005; Fig. 1). When abundant, sea nettles can eliminate or reduce ctenophore biomass and abundance. During the period of 1985–2002, when sea nettles densities declined, the biovolume ( $\text{ml m}^{-3}$ ) of ctenophores (mostly *M. leidyi*) collected in the Chesapeake Bay Zooplankton Monitoring Program increased in both the tributaries and mainstem of the mesohaline Maryland portion of the Chesapeake Bay (Fig. 5). Peak densities occurred in the late 1990s. A similar increase was found by Purcell and Decker (2005) for the mainstem Chesapeake Bay. High ctenophore biovolume also tended to be associated with low sea nettle density in the Patuxent River (Fig. 3) but the relationship was not statistically significant ( $p = 0.20$ ).

A number of climatic factors can influence the abundance of *M. leidyi* (Sullivan et al. 2001; Oviatt 2004; Purcell and Decker 2005) and have been suggested to have led to increasing ctenophore abundances in Chesapeake and Narragansett Bays. If declining sea nettle abundances have contributed to the increasing ctenophore abundances in Chesapeake Bay, the increase should be greatest when and where sea nettles historically were most abundant and potentially exerted the greatest control on their ctenophore prey. We predicted that the rate of increase in ctenophore abundance should be greater in the mesohaline reaches of tributaries, where sea nettles reach their greatest abundances (Purcell et al. 2001), than in the mesohaline mainstem Chesapeake Bay, and that the increase should be greater in July and August, when sea nettle biomass typically peaks, than in June.

The ratio of tributary to mainstem bay mean July–August ctenophore biovolumes increased during the 1985–2002 sampling period (Fig. 5;  $R^2 = 0.39$ ,  $p = 0.006$ ). Mean biovolume tended to be lower in the tributaries than in the mainstem in the early part of the time series and higher than in the mainstem in later years. Log-transformed ctenophore biovolume significantly increased in July and August in both the tributaries and mainstem ( $R^2 = 0.41$ ,  $p = 0.004$  for both comparisons) and also showed a trend towards increasing in June (tributary sites:  $R^2 = 0.20$ ,  $p = 0.06$ ; mainstem sites:  $R^2 = 0.19$ ,  $p = 0.07$ ). Analysis of variance (ANOVA) on log-transformed data indicated that the rate of

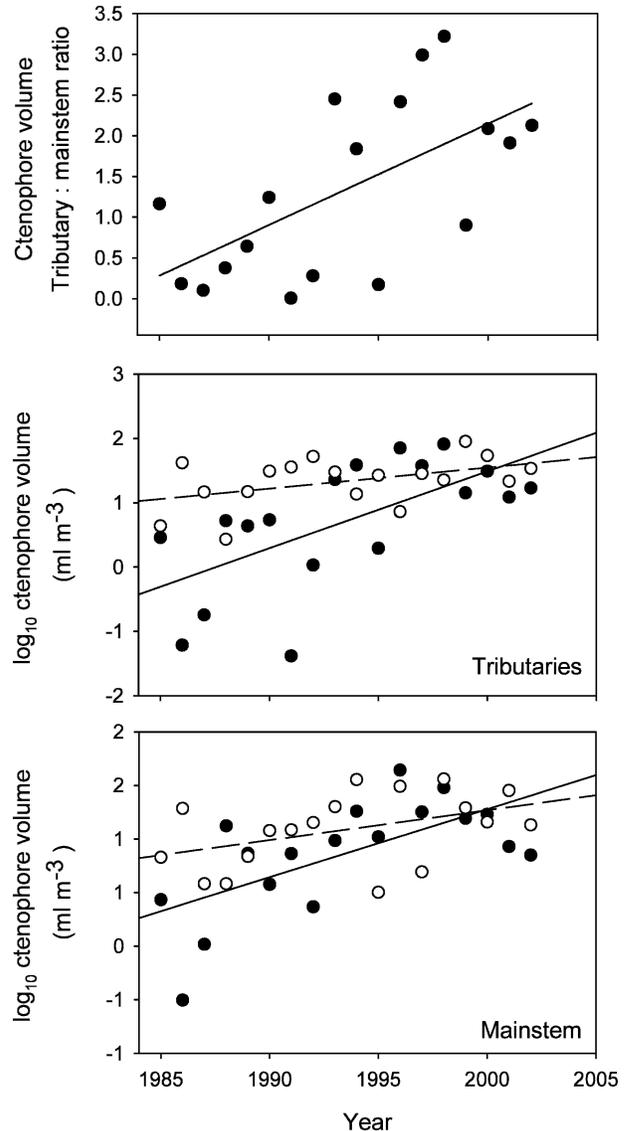


Fig. 5. Ratio of ctenophore biovolumes in tributaries versus mainstem samples during June–August and intramural changes in seasonal patterns of ctenophores abundance in mesohaline tributaries and mainstem Chesapeake Bay stations. In the bottom two panels, open circles are June biovolumes; closed circles are July–August biovolumes.

increase was greater in July–August than in June (two-way ANOVA with year as continuous variable; year:  $F = 27.38$ ,  $p < 0.0001$ ; June versus July–August:  $F = 6.95$ ,  $p = 0.01$ ; year  $\times$  month interaction:  $F = 6.90$ ,  $p = 0.01$ ; Fig. 5).

#### Discussion

Our analysis indicates that the decline in oyster abundances, caused by overfishing, disease, and habitat degradation, has important effects on estua-

rine food webs beyond those previously highlighted. The importance of oysters to water filtration, nutrient cycling, and habitat provision for fish and benthic invertebrates is well established (Newell 1988, 2004; Coen et al. 1999). Our results indicate oysters also exert a strong influence on food web structure, as well as the potential success of oyster restoration, because of their pivotal role in providing habitat for the sessile overwintering stage of a dominant pelagic consumer, the scyphomedusan sea nettle.

Prior to the mid 1980s oyster decline, sea nettle abundances in the Maryland portion of Chesapeake Bay were higher and exhibited considerable interannual variation, which was influenced by climate variability (Cargo and King 1990; Purcell and Decker 2005). We suggest that by the late 1980s the abundance of shell substrate available to settling sea nettle planula and growing polyps declined below a critical threshold. Once that threshold was reached, interannual variation in sea nettle abundance no longer responded to interannual variability in climate, but instead remained low.

The coincidence of temporal patterns of sea nettle and oyster abundance in Narragansett Bay may be even more striking than that in the Chesapeake system. Sea nettles occurred in Narragansett Bay during the 19th and early 20th centuries (Fewkes 1881; Fish 1925) and presumably earlier, while oysters were virtually eliminated from Narragansett Bay following the 1938 hurricane. Today, both sea nettles and oysters are restricted to a few coastal Rhode Island salt ponds (Fofonoff personal communication; Oviatt personal communication; Sullivan-Watts personal communication; Gifford personal communication). Along the Gulf of Mexico coast of the U.S., which retains large oyster populations, sea nettle densities have remained stable or increased (Graham 2001).

This threshold in hard substrate available to sea nettle polyps in Chesapeake Bay appears to have triggered a more systemic threshold response that is reinforced by the relaxation of sea nettle control over ctenophores, which are predators of oyster larvae (see also Purcell and Decker 2005). This low sea nettle, high ctenophore regime is characterized by increased predation on zooplankton and ichthyoplankton, increased predation on oyster larvae (Purcell and Decker 2005), and a likely increased shunting of energy to gelatinous zooplankton relative to fish (Fig. 1). Oysters ultimately mediate the flow of energy to planktivorous and piscivorous fishes by influencing the balance between sea nettles and ctenophores.

*M. leidyi* has both a higher feeding rate per unit biomass and volume than do sea nettles (Purcell and Decker 2005) and a greater capacity for a rapid numerical increase than either sea nettles or the

dominant trophically similar zooplanktivorous fish, the bay anchovy, *Anchoa mitchilli*. *M. leidyi* has a generation time of about 2 wk, approximately the same as the calanoid copepod *Acartia tonsa*, which comprises over 90% of mesozooplankton biomass during summer in the mesohaline Chesapeake Bay. Both sea nettles and bay anchovy typically have annual generation times. All three species have high reproduction rates, but daily egg production of medium sized (e.g., 5 cm) individual hermaphroditic ctenophores can exceed the number of eggs spawned per bay anchovy female during spawning events (Zastrow et al. 1991; Purcell et al. 2001). The potential rate of population increase resulting from strobilization by sea nettle polyps and egg production by bay anchovy is considerably lower than that of ctenophores, which combine high egg production (up to 14,000 eggs ind<sup>-1</sup> d<sup>-1</sup>; Kremer 1976) with short generation time. Because of the combination of higher feeding rates and greater potential for numerical response, as well as greater utilization of copepod nauplii and microzooplankton, ctenophores are more likely than sea nettles to deplete the zooplankton prey they share with planktivorous fishes, and inflict heavier predation mortality on fish eggs and larvae. Thus, a decline in oyster abundance that favors increased abundance of ctenophores should ultimately reduce energy flow to top piscivores through summer breeding planktivorous fishes such as bay anchovy (Fig. 1).

Although many aspects of sea nettle and ctenophore diets are similar, one key difference is that ctenophores readily prey on oyster larvae while sea nettles do not (Purcell et al. 1991). A decline in oyster abundance that ultimately results in an increase in ctenophores, results in an increase in ctenophore predation on oyster larvae, reinforcing the regime shift from a moderate-to-high oyster state to a low oyster state. This is a potentially important example of hysteresis in which the trajectory describing the decline of oysters may be unavailable as a restoration trajectory without active intervention.

Pilot experiments indicate that clearance rates of ctenophores feeding on oyster veliger larvae are similar to those of ctenophores feeding on the calanoid copepod *A. tonsa* (Fulford and Breitburg unpublished data). We applied the average *Acartia* clearance rate estimates listed in Purcell et al. (2001) to Chesapeake Bay Zooplankton Monitoring Program tributary data shown in Fig. 5 and results of individual trawls from the Patuxent River, and assumed an average ctenophore length of 5 cm. These calculations indicate that ctenophores currently consume 10–25% of oyster larvae on average throughout the summer, and locally can consume 40% to nearly 100% of oyster larvae at peak

densities. Predicted clearance rates are about 35% higher if Chesapeake-specific clearance rates measured in 1-m<sup>3</sup> mesocosms are used (Purcell et al. 2001; Purcell and Decker 2005) or if ctenophore biomass is dominated by smaller individuals. Oyster spawning in Chesapeake Bay occurs from late May or June through September or early October, with peak spawning in July (Thompson et al. 1996). Highest abundance of oyster larvae potentially coincides with the time period at which ctenophore densities and predation potential are low if sea nettles are abundant, but high if sea nettle densities are low. Under the current low sea nettle regime, locally high densities of ctenophores can likely limit oyster recruitment, reinforcing the low oyster, low sea nettle, high ctenophore state. This trophic consequence of the habitat role of oyster likely contributes to the list of factors, including disease, habitat destruction, overfishing, and siltation, that impede recovery of oysters in Chesapeake Bay.

Our analysis does not address the presumed low abundance of sea nettles at high oyster densities prior to increased fishing pressure following European colonization and eutrophication in the mid 20th century. The scant discussion of sea nettles in historic writings has been interpreted to suggest that sea nettles, which have a quite painful sting, were generally low in abundance (Kennedy and Mountford 2001). The longer term historical trajectory may have been one of increasing sea nettles with increasing eutrophication until a low-oyster threshold was crossed, at which point abundances declined. Under current nutrient loading and fishing pressure, the magnitude of increase in oyster biomass targeted in restoration strategies (i.e., a 10-fold increase, CBP 2000) would likely return Chesapeake Bay to a mid 20th century high sea nettle regime, not to an earlier low sea nettle, high oyster regime.

Oyster population recovery has been cited as an important ecological tool for improving water clarity and secondary production in Chesapeake Bay and elsewhere. If ecosystem structure has crossed a threshold into a new state, as we suggest here, ecosystem responses to such recovery efforts become more difficult to predict. The food web consequences of low oyster abundance represent a change in ecosystem structure that may be difficult to reverse by small scale, incremental improvements in oyster habitat or adult mortality. Complex feedback between the benthic and pelagic components of estuarine systems, and within food webs, may be extremely important to our understanding of how estuarine ecosystems respond to overfishing and other stressors, and how to manage and restore these ecosystems once they have been fundamentally changed by human activity.

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