

# Seasonality of the copepods *Acartia hudsonica* and *Acartia tonsa* in Narragansett Bay, RI, USA during a period of climate change

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## Abstract

Seasonality of species living at the boundaries of biogeographic zones may be more sensitive to climate change than in other regions. This is apparently the case for the ctenophore, *Mnemiopsis leidyi*, in Narragansett Bay, RI, which is the historical northern boundary of its distribution in the Northwest Atlantic. Seasonal advancement of population pulses of this ctenophore correlates with an increase in average annual temperatures of 1.2 °C over the last ~50 years. Do other zooplankton in Narragansett Bay show evidence of altered phenologies? Here we examine patterns of seasonal succession of the copepod congeners, *Acartia tonsa* and *Acartia hudsonica*, for evidence of alteration over the period 1950–2004. A warming trend might be expected to limit springtime abundance of *A. hudsonica*, a temperate–boreal species that produces resting eggs in response to warm weather. Conversely, increasing temperatures could favor the summer dominant, *A. tonsa*, over its congener, allowing a shift to earlier appearance in spring, thus preserving the predator-free window that has previously allowed it a period of high production prior to ctenophore population pulses in late summer. Contrary to these predictions we found that *A. hudsonica* has become the dominant copepod of the congener pair. There has been no seasonal advancement of populations of *A. tonsa*, whose numbers have plummeted due to intensification of the predator–prey interaction with *M. leidyi*. In contrast, advancement of seasonal appearance of *A. hudsonica* is evident in sustained population increases earlier in spring (March rather than in May), although, as predicted, there is curtailment of its distribution in late spring. This latter shift is likely exacerbated by ctenophore predation. This study demonstrates the complexity of predicting individual species responses to climatic warming, even for species with well-known patterns of seasonal and geographic distribution.

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**Regional index terms:** USA; Rhode Island; Narragansett Bay

## 1. Introduction

Coastal marine systems that lie at the boundaries between warm and cold waters can provide information rich in data to help understand and predict the response of plankton communities to climate variation. It is in these regions that detectable changes of global warming may become first evident as the ranges of species expand or contract due to the strong

response of shallow waters to atmospheric forcing (Parsons and Lear, 2001; Oviatt et al., 2002). In addition, trophic interactions in aquatic ecosystems with strongly seasonal environments can be dramatically perturbed by climate change if species react differentially (Greve et al., 2001; Edwards and Richardson, 2004; Winder and Schindler, 2004; Purcell and Decker, 2005). Recent studies provide evidence of strong and varied responses by both jellyfish and copepods to climate change (Lynam et al., 2004; Molinero et al., 2005; Purcell and Decker, 2005) but the diverse responses by different species have made it difficult to forecast community-level responses to climate change.

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We examined records of plankton abundance and distribution from Narragansett Bay, RI, USA, an estuary that lies at the northern border of the Virginian Biogeographic Province. For the period 1955–2004 we documented responses to climate change by three species, the ctenophore *Mnemiopsis leidyi* and the copepods, *Acartia tonsa* and *Acartia hudsonica*. These species constitute a predator–prey complex that is important throughout estuaries on the Atlantic seaboard of North and South America. During this time, estuaries of the northwest Atlantic seaboard, including Narragansett Bay, have exhibited a warming trend in winter and spring (Hawk, 1998; Nixon et al., 2004) with an average annual temperature increase of 1.2 °C. Sullivan et al. (2001) documented earlier seasonal appearance and increased abundance of the comb-jelly *M. leidyi* since the 1980s in a pattern that correlated with increasing temperatures. Because Narragansett Bay and Cape Cod constitute the historical northern boundary of distribution of *M. leidyi* (Mayer, 1912), increases in temperature might be expected to favor increased presence of this predator in an estuary as a direct effect of increased survival in warm winters, earlier reproduction in spring, or both. But what about the responses of other planktonic species, especially prey of the ctenophore? Are seasonal distributions of other species changing predictably in response to climate according to their temperature tolerance, and are patterns of seasonal succession being preserved?

The copepods *Acartia tonsa* and *Acartia hudsonica* are dominant species in the zooplankton along the northwestern Atlantic seaboard where their seasonal and geographic distributions are clearly related to temperature (Lee and McAlice, 1979). *Acartia hudsonica* is a temperate–boreal species although it is found as far south as Chesapeake Bay. However, its presence is restricted to cool temperatures. *Acartia tonsa* ranges from tropical to boreal waters and is found year round in the warmer parts of its geographic range but only in summer in northern, cooler climates. The seasonal succession of *A. hudsonica* and *A. tonsa* is well documented where the two species co-occur (Jeffries, 1962; Lee and McAlice, 1979). These copepods are the primary prey of ctenophores in Narragansett Bay (Kremer, 1976; Deason, 1982) and their patterns of abundance and distribution have been well documented by previous investigators (Frolander, 1955; Jeffries, 1962; Martin, 1965; Hulsizer, 1976). Durbin and Durbin (1981) showed that both copepod species are dominant secondary producers in the plankton of Narragansett Bay, with summer production by *A. tonsa* exceeding that of winter production of *A. hudsonica*.

In Narragansett Bay seasonality of both *Acartia hudsonica* and *Acartia tonsa* is clearly related to production and hatching of resting eggs which is controlled by temperature (Zillioux and Gonzalez, 1972; Sullivan and MacManus, 1986; Avery, 2005). *Acartia hudsonica* produces resting eggs in response to temperatures above 15 °C, resulting in its disappearance from the plankton in June or July, and reappears in low numbers in December and January (Sullivan and MacManus, 1986). In contrast, *A. tonsa*, hatches from resting eggs in the sediments when temperatures exceed 15 °C and produces resting eggs in the winter. Given the different temperature sensitivity of these two species, one might predict increasing abundance or an

increased period of dominance of *A. tonsa* in response to warmer winters or earlier springs that mimic conditions in estuaries further to the south. *Acartia hudsonica* might experience a reduced abundance in spring if warming occurs earlier and resting egg production begins sooner. The question addressed here is whether copepod responses to climate change follow patterns predicted from these considerations. Additionally, we consider interactions with their primary predator, *Mnemiopsis leidyi*.

## 2. Materials and methods

### 2.1. Field work

Copepods and ctenophores were collected weekly at two open water stations (GSO offshore and Fox Island) and one near shore station (GSO dock) in Narragansett Bay during 2000–2004 chosen to match locations sampled in earlier published studies of plankton to allow comparisons with data from historical records (Fig. 1). All stations are located in the east passage of Narragansett Bay. Fox Island (41.50° N, 71.33° W) is the site of a long-term, ongoing plankton time series (Li and Smayda, 1998; Smayda, 1998) and is close to the site sampled by Deason and Smayda (1982) and Durbin and Durbin (1981). GSO dock is shallow (3 m) compared to the other stations located in the east passage of the Bay, Fox Island and GSO offshore (6 and 14 m), and is inshore of GSO offshore but at the same position (41.50° N, 71.04° W) sampled by Frolander (1955), and Jeffries (1962). Martin (1965) sampled slightly to the south at 41.43° N, 71.42° W.

The copepods *Acartia tonsa* and *Acartia hudsonica* were enumerated from 64 µm mesh net tows collected with a ¼ m diameter mouth opening and equipped with a flow meter. One tow per station sampled the entire water column with the volume filtered varying between 0.4 and 1 m<sup>3</sup> depending on station depth. The samples were preserved in 5% formalin buffered with Na<sub>2</sub>B<sub>4</sub>O<sub>7</sub>. Subsamples containing at least 200 individuals were processed under a dissecting microscope at 50× magnification. Data reported here are for copepodite stages CI–adult of *A. tonsa* and *A. hudsonica*.

*Mnemiopsis leidyi* were collected with two replicate tows per station using a ½ m diameter, 1 mm mesh net with flow-meter and were counted live, within 3 h of collection. Volume sampled per tow varied from 0.9 to 79 m<sup>3</sup> depending on station depth and abundance of ctenophores. When ctenophores were very numerous vertical tows from top to bottom of the water column were used to keep volume sampled low and to prevent net clogging. Otherwise longer oblique tows were used. Both total and oral–aboral lengths were recorded. Data reported here are for ctenophores >1 cm total length which are comparable to lengths reported for earlier studies taken with nets with larger mesh sizes (up to 6 mm, see discussion in Deason and Smayda, 1982). Vertical profiles of temperature were collected with a YSI sonde model 600XLM-M.

### 2.2. Comparisons with historical data

Abundances (numbers m<sup>-3</sup>) of *Acartia hudsonica* and *Acartia tonsa* during spring and summer 2000–2003 were

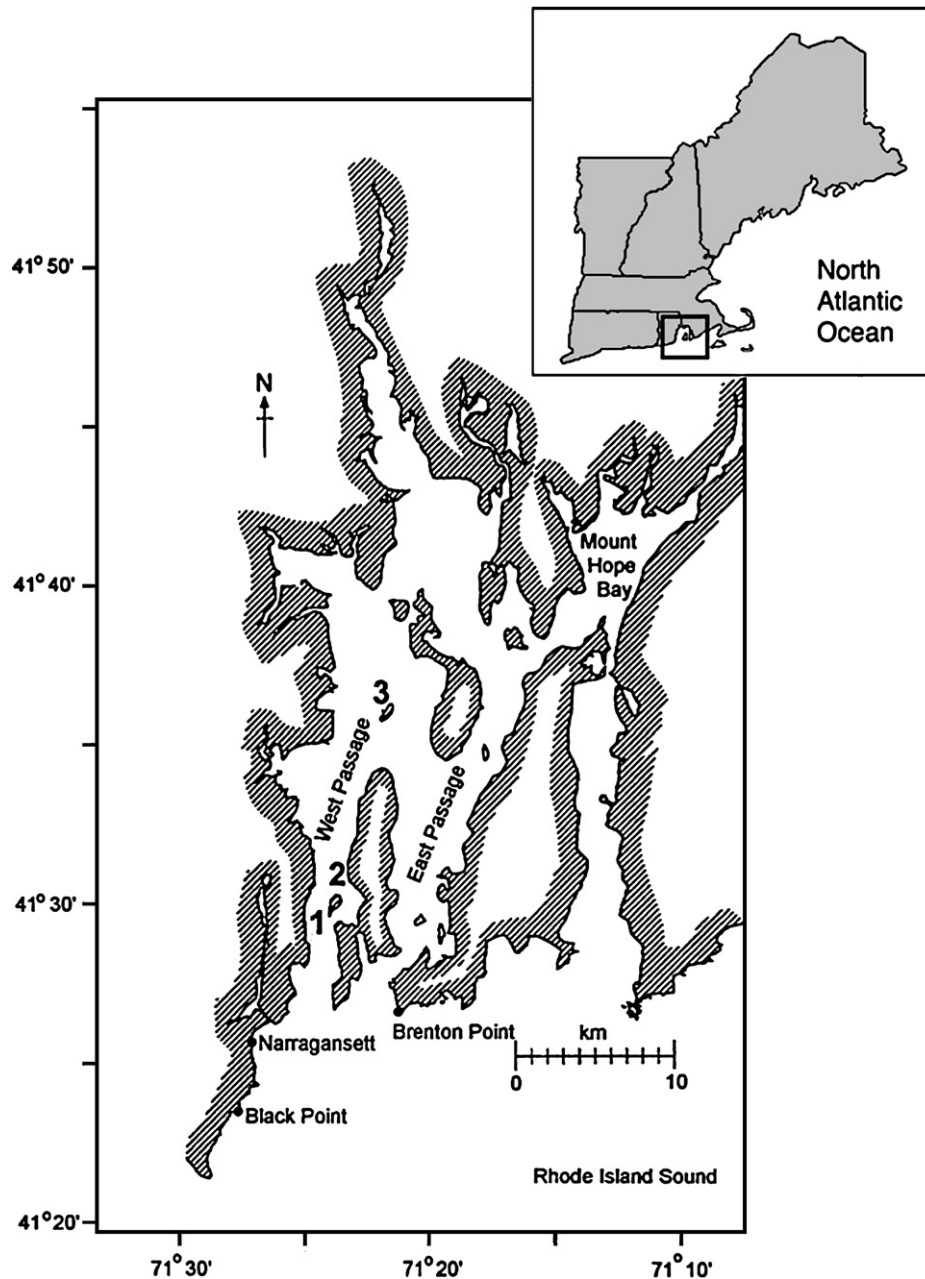


Fig. 1. Station locations in Narragansett Bay, Rhode Island, USA. Station 1, GSO dock, is indicated in the text as “GSO inshore”; Station 2 is “GSO offshore”, and Station 3 is “Fox Island”.

compared to earlier periods when quantitative data were available from published records. Ratios of maximum and mean abundances during May–June (*A. hudsonica*) and July–August (*A. tonsa*) were calculated. Use of a ratio avoided the problem of comparing absolute values that arise from the different mesh sizes of plankton nets used in the various studies across years. For 1981–1983 previously published data from 13 m<sup>3</sup> MERL mesocosms (Sullivan and MacManus, 1986) are used to examine copepod abundance patterns in the absence of *Mnemiopsis leidyi*. The mesocosms were filled with unfiltered Narragansett Bay water (GSO dock) containing a natural plankton assemblage from which ctenophores were excluded. In addition enclosures contained sediments from

the Bay from which copepod resting eggs hatched to populate the enclosures. The enclosures were scaled to match the Bay in terms of sunlight, temperature, tidal mixing and flushing rate (3.7% volume of unfiltered bay water per day).

### 3. Results

Four historical accounts of the period 1950–1981 indicate that both maximum and average abundances of *Acartia tonsa* during July and August nearly equaled or exceeded maximum and average numbers of the winter–spring copepod *Acartia hudsonica* (Table 1), with ratios of maximum abundance of *A. tonsa* to *A. hudsonica* ranging from 0.99 to 1.15, and ratios

Table 1

Relative abundance of the copepods *Acartia tonsa* and *Acartia hudsonica* expressed as ratios of abundance (*A. tonsa*:*A. hudsonica*). The values are based on maximum or mean abundances of copepodites and adults combined (number  $\text{m}^{-3}$ ) for May–June (*A. hudsonica*) and July–August (*A. tonsa*). Dates are in month-year format. Note that ctenophores were absent from MERL controls; control data are not used in regressions

Year	Reference	Station	Ratio of maximum abundance	Ratio of average abundance	Date increase/disappearance <i>A. hudsonica</i>	Date 15 °C surface temp.	NAOI winter
1951	Frolander (1955)	GSO offshore	1.13	0.86	5-1/8-13	6-4	−1.26
1958	Jeffries (1962)	GSO offshore	ND	ND	4-30/7-20	6-18	−1.02
1973	Hulsizer (1976)	Fox Island	1.15	0.40	4-19/7-30	6-13	+2.52
1976	Durbin and Durbin (1981)	Station 1	0.99	0.80	3-22/7-12	6-7	+1.37
1982	Sullivan and MacManus (1986)	GSO inshore	0.03	0.03	5-18/7-20	6-15	+0.85
		MERL control	0.76	0.68	4-20/8-24		
1983	Sullivan and MacManus (1986)	GSO inshore	0.27	0.39	4-5/7-12	6-15	+3.42
		MERL control	2.27	2.29	No increase/8-23		
2000	This paper	GSO inshore	0.08	0.05	3-17/7-5	6-5	+2.80
2001	This paper	GSO inshore	0.33	0.50	3-9/7-5	6-1	−1.87
2002	This paper	Fox Island	0.03	0.01	2-6/6-19	5-29	+0.76
		GSO offshore	0.05	0.03	2-20/6-19	6-5	
2003	This paper	Fox Island	0.18	0.07	3-5/7-9	6-7	+0.20
		GSO offshore	0.08	0.05	3-12/7-16	6-11	
2004	This paper	GSO offshore	0.11	0.09	3-22/6-27	5-17	−0.07

of average abundance from 0.4 to 0.86. While abundance data were not available from Jeffries (1962) who reported values as percent of total copepods, it is clear from this account that *A. tonsa* reached numbers comparable to those of *A. hudsonica*. Durbin and Durbin (1981) reported that production rates of *A. tonsa* exceeded those of *A. hudsonica*. Deason and Smayda (1982) reported zooplankton dry weight for which maximum values in July exceeded those in June for every year they were recorded (1972–1976). Also evident from the historical accounts is that populations of *A. tonsa* declined rapidly very shortly after the appearance of *Mnemiopsis leidyi* in the water column (Fig. 2).

In contrast to the period prior to the 1980s, abundance of *Acartia tonsa* was very much reduced relative to that of *Acartia hudsonica* (Table 1, Figs. 3 and 4). From 1982 to 2004, ratios of maximum abundance of *A. tonsa* to *A. hudsonica* ranged from 0.03 to 0.33 and ratios of average abundance ranged from 0.01 to 0.50. Numbers of *A. tonsa* relative to *A. hudsonica* remained high in MERL enclosure experiments without ctenophores (1982–1983) and provide evidence of the impact of ctenophore predation. *Acartia tonsa* in the ctenophore free enclosures also greatly exceeded those observed in the Bay during 1982 and 1983. During 2000–2004 *Mnemiopsis leidyi* became abundant in mid to late June and the *A. tonsa* population was barely detectable except in 2001, the only year in which abundance of *M. leidyi* remained below  $40 \text{ m}^{-3}$  in June and July (Figs. 3 and 4).

The availability of data from two stations in 2002 and 2003 allows an estimate of sampling variance. Patterns of abundance of both copepods and ctenophores are relatively similar across both stations (Fig. 4), indicating low sampling variability and similarity of patterns across all of lower Narragansett Bay.

From being the most abundant member of the summer zooplankton, typically reaching maximum abundances of  $10,000\text{--}30,000$  copepodites and adults  $\text{m}^{-3}$ , *Acartia tonsa* was reduced to very low numbers in summer averaging no

more than  $1400 \text{ m}^{-3}$  and were typically  $170\text{--}1000 \text{ m}^{-3}$  (Figs. 3 and 4). In contrast, abundance of the winter–spring copepod dominant *Acartia hudsonica* has remained high in spring with maximum and average abundances ranging from  $30,900\text{--}62,100$  and  $9500\text{--}28,400 \text{ m}^{-3}$ , respectively, during 2002–2004. The result is a shift from co-dominance of the two *Acartia* species to dominance by *A. hudsonica* based on within year ratios (Table 1).

*Acartia hudsonica* populations are increasing earlier in spring than in the past, with high numbers being sustained as early as March in recent years compared to April in the historical studies (Fig. 5). In addition, the historical accounts showed that populations of *A. hudsonica* generally began to decline well before *Mnemiopsis leidyi* were present (Fig. 2); however, the copepods' complete disappearance from the water column may have been hastened by predation, as their absence rarely preceded appearance of the ctenophores (Fig. 5). In recent years, *A. hudsonica* has disappeared from the water column sooner (June or early July) than in the past (mid-July or August), corresponding to the earlier appearance of *M. leidyi* in spring (Fig. 5). The date on which *A. hudsonica* disappeared from the water column was not correlated with the date of spring warming to  $15^\circ\text{C}$  (Spearman Rank Order Correlation  $p > 0.05$ ). Regression analysis indicated significant trends in date of spring population increase with years of observation from 1951 to 2004 ( $p = 0.002$ ;  $F = 17.13$ ), as well as for date of summer disappearance ( $p = 0.001$ ;  $F = 21.2$ ). On a year-to-year basis, however, this change did not correlate with the NAO winter index, an indicator of winter temperatures from December to March (Spearman Rank Order Correlation).

#### 4. Discussion

Recent observations in both estuarine and more open seas indicate that changing abundance of copepods and jellyfish

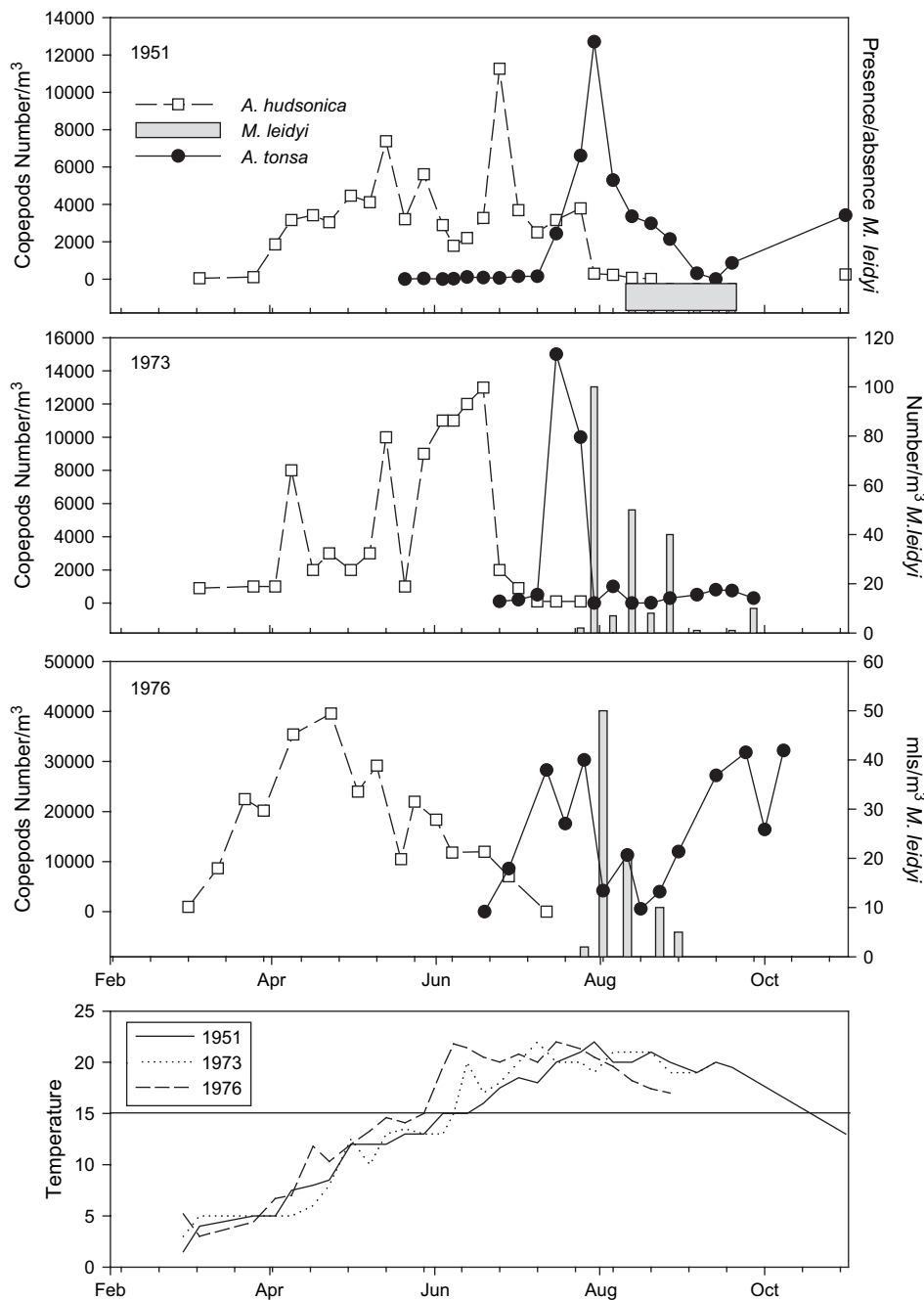


Fig. 2. Abundance and seasonal distribution of *Acartia hudsonica*, *Acartia tonsa* copepodites and adults, and *Mnemiopsis leidyi* in 1951, 1973 and 1976. Data are regraphed from representative historical studies: [Frolander \(1955\)](#) (GSO offshore), [Hulsizer \(1976\)](#) (Fox Island); [Durbin and Durbin \(1981\)](#) (Station “1”, north of Fox Island). For 1951 presence of *M. leidyi* in the samples is denoted by a continuous gray bar because only presence/absence data were reported. For 1976 the abundance of *M. leidyi* was measured as volume of ctenophores collected per m<sup>3</sup> of water sampled (mls/m<sup>3</sup>). Surface water temperatures for all years are plotted. The solid horizontal line indicates the date on which 15 °C was reached.

can be related to climate variability (e.g. [Brodeur et al., 1999](#); [Mills, 2001](#); [Lynam et al., 2004](#); [Molinero et al., 2005](#); [Purcell and Decker, 2005](#)). For the ctenophore, *Mnemiopsis leidyi*, in Narragansett Bay, which is the northern limit of its distribution, predators are few. Temperature and flushing rate of the estuary appear to be the main factors controlling the ctenophore's seasonality and abundance ([Costello et al., 2006a](#)). Indirect effects of climate change will be evident in copepod prey of ctenophores ([Purcell and Decker, 2005](#)), unless the

copepods escape predation by similar alteration in their phenology. In fact, our study shows that seasonality of the former summer dominant, *Acartia tonsa*, has not been as responsive to climate change as that of *M. leidyi*, while that of *Acartia hudsonica* has shifted significantly.

Advancement of the seasonal appearance of the comb-jelly *Mnemiopsis leidyi* in Narragansett Bay has been documented and associated with climatic warming during the period 1950–2003 ([Sullivan et al., 2001](#); [Costello et al., 2006a](#)). In



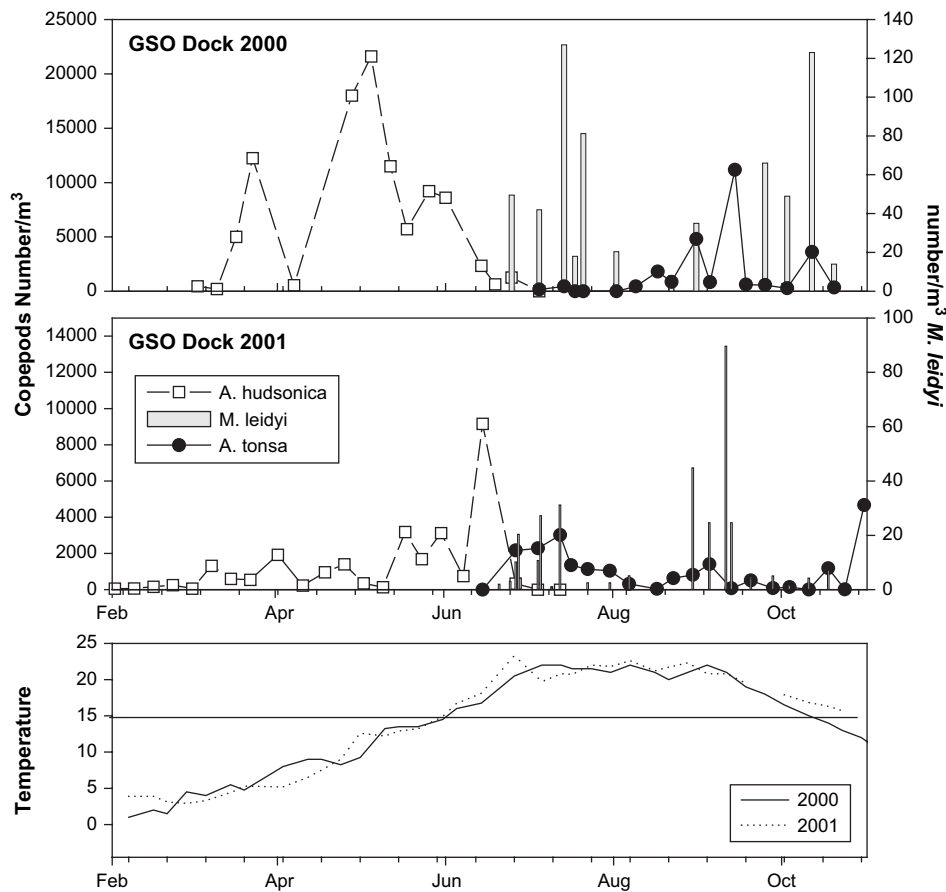


Fig. 3. Abundance and seasonal distribution of *Acartia hudsonica*, *Acartia tonsa* copepodites and adults, and *Mnemiopsis leidyi* >1 cm long at the GSO dock station during 2000–2001. Ctenophore data are averages of two replicate tows. Surface water temperatures for both years are plotted. The solid, horizontal line indicates the date on which 15 °C was reached.

this paper we extend the observations to 2004 for ctenophores and dominant copepod species in the system. Our question was whether changes in phenology of the copepods would be altered in synchrony with changes in the top predator, *M. leidyi*, or would exhibit different patterns. Climate warming might have been expected to advance seasonal appearance of *Acartia tonsa*, a temperate copepod that occurs year round in the southern part of its range, as it has for *M. leidyi*. In fact, there was no change in its seasonality (Costello et al., 2006b) and thus, its abundance was strongly diminished by predation. In contrast, seasonality of the copepod congener, *Acartia hudsonica*, has changed, including advancement of date of its population pulses in spring and a curtailment of its abundance in early summer, both changes that are predicted responses to a warming climate. Earlier resting egg production by *A. hudsonica* in response to earlier spring warming could produce this pattern; however, the shift did not correspond to the date on which the water reached 15 °C, when resting eggs are formed (Avery, 2005). Moreover, while the date of the 15 °C threshold varies, it has not changed consistently over time (Table 1). Unfortunately there is no recent information available on resting egg production or hatching of nauplii of *Acartia* spp. in Narragansett Bay. Variables explaining population decline in spring are also confounded by the

appearance of *M. leidyi* and its predatory impact. Regardless of the mechanisms responsible, the outcome is that the contribution of *A. hudsonica* to the ecosystem productivity has remained high and may even have increased, so that it is now the dominant species of the congener pair.

The explanation for the differential responses of *Acartia hudsonica* and *Acartia tonsa* to climate warming may lie in the fact that temperatures in winter have warmed more than temperatures in spring. Thus, although climatic warming is a demonstrated phenomenon in Narragansett Bay (Hawk, 1998; Oviatt, 2004) and other nearby estuaries (Nixon et al., 2004) there has been no change in the biologically important temperature threshold (15 °C) for spring populations (Table 1). A complete analysis of spring temperatures from 1950 to 2003 based on a daily temperature record is published by Costello et al. (2006b). Rather, the most substantial average warming in this region has occurred during the winter months (December–February). This fact may be responsible for lack of change in phenology of *A. tonsa* in contrast to the change observed for *A. hudsonica* with respect to its earlier population pulses in spring by approximately 1.5–2.0 months. Resting eggs of *A. hudsonica* hatch in winter resulting in a small number of over-wintering adults of *A. hudsonica* by December–February, a pattern that is consistent across both

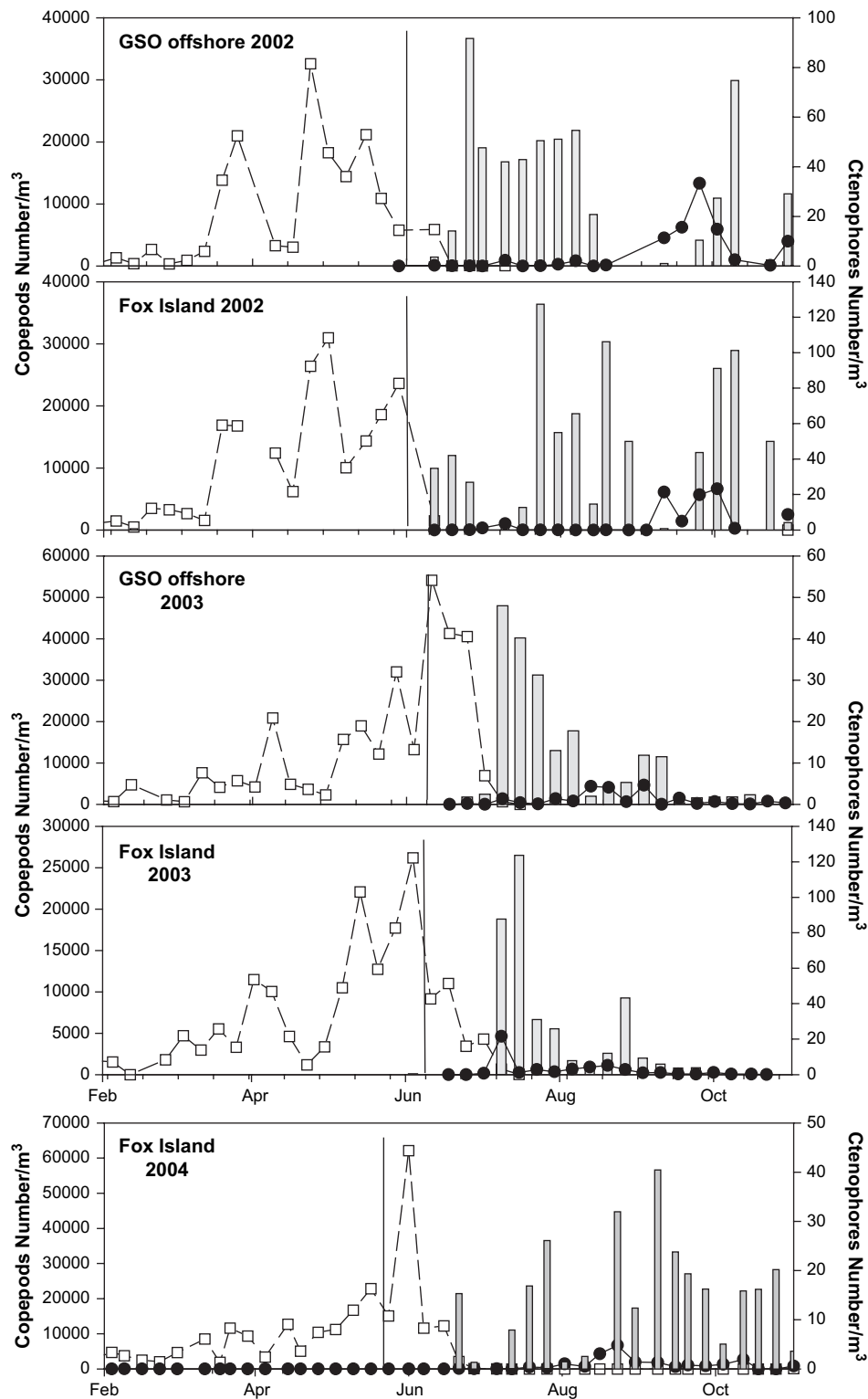


Fig. 4. Abundance and seasonal distribution of *Acartia hudsonica*, *Acartia tonsa*, and *Mnemiopsis leidyi* at two stations sampled on the same day (GSO offshore and Fox Island) during 2002–2004. Symbols as in Fig. 3. The vertical horizontal lines indicate the date on which 15 °C was reached.

recent and historical studies (Frolander, 1955; Martin, 1965; Hulsizer, 1976; Sullivan and MacManus, 1986; this paper, Fig. 4). Thus, we suggest, these adults are poised to take advantage of warming temperatures whenever they occur in late winter, resulting in temperature dependent population increases via production of immediately hatching eggs.

Costello et al. (2006b) address the question of why phenology of the ctenophore predator, *Mnemiopsis leidyi*, a warm water species, has responded to climate warming that occurs mainly in winter. They hypothesize that the entirely pelagic life history of *M. leidyi* and its habit of over-wintering in shallow, rapidly warmed regions of the estuary, results in phenological

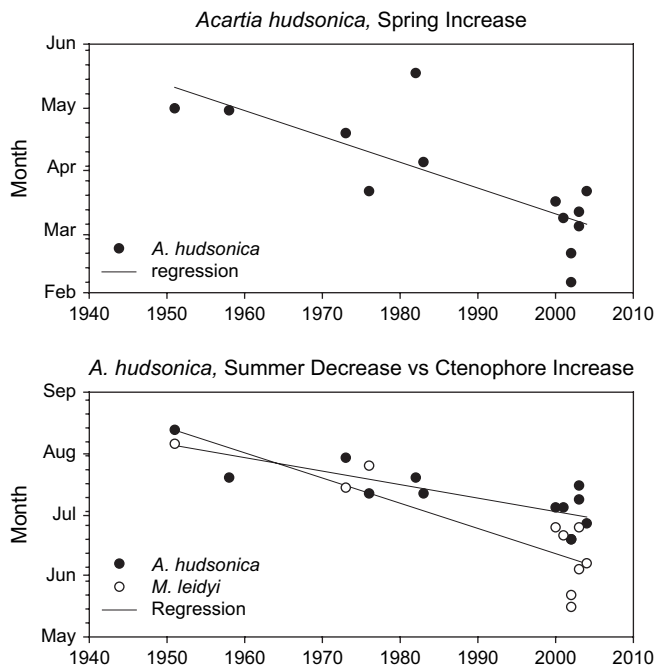


Fig. 5. Events in Narragansett Bay relating to *Acartia hudsonica* population dynamics. For original literature references refer to Table 1. For 2002 and 2003 dates are plotted for both stations (GSO offshore and Fox Island) to indicate variance across stations. Since *A. hudsonica* are present throughout winter in low numbers, a “spring increase” was defined as numbers of copepodites and adults that are a factor of 10 higher than average winter abundance, sustained for a period of  $\geq 3$  successive weeks. Dates for 1958 are approximate based on percent composition for *A. hudsonica* vs. *A. tonsa* reported by Jeffries (1962), Fig. 8. Data for *M. leidy* refer to date of first appearance of individuals  $> 1$  cm in oral–aboral length. All regressions were significant ( $p \leq 0.002$ ).

responsiveness to changes in winter temperatures. In contrast, *Acartia tonsa* over-winters as a resting egg primarily in the deeper regions of Narragansett Bay which warm later in the season. In this paper we add the hypothesis that phenology of *Acartia hudsonica* is responsive to changes in winter temperatures, as is *M. leidy*, due to wintertime hatch of its resting eggs that allows a pelagic stage over-wintering strategy. This has resulted in altered phenology in the predicted direction, and in a manner consistent with larger temperature changes in winter than spring. The net effect is a change in dominance of the copepod congeners in the community.

These results are important because they show how difficult it is to predict the patterns of species response to climate change even when the life histories and geographic distributions are well known. They speak for the need for continued monitoring of species responses to climate change in regions which lie at the border of biogeographical provinces.

## 5. Conclusions

The phenology of *Acartia tonsa*, once the dominant summer copepod species in Narragansett Bay, RI, USA, has remained stable over a 50+ year period despite warming of waters in this region. In contrast, there is evidence of seasonal advancement of its congener *Acartia hudsonica*, a winter–spring

species and also of the ctenophore, *Mnemiopsis leidy*. What is surprising is that two species, *A. tonsa* and *M. leidy*, both with distributions that lie primarily to the south of Narragansett Bay, in warmer waters, have responded so differently to climate change. As a result, the predator–prey interaction between these two species is greatly intensified compared to the past resulting in severely depleted numbers of *A. tonsa*. The fact that copepod production in summer is so reduced is likely to affect other species dependent upon larval or adult copepods for food, such as larval fish. Grazing impacts of copepods on summer phytoplankton or microzooplankton are also likely to be very different than in the past. Increased productivity of *A. hudsonica* in spring, resulting from earlier seasonal pulses of this species in response to warming, may also be expected to alter winter–spring phytoplankton bloom dynamics. It is clear that phenologies of both copepod species and gelatinous zooplankton are sensitive to climate change and that continued monitoring of these populations is necessary to determine the stability and consequences of emerging phenological shifts.

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## References

- Avery, D.E., 2005. Induction of embryonic dormancy in the calanoid copepod *Acartia hudsonica*: proximal cues and variation among individuals. *Journal of Experimental Marine Biology and Ecology* 314, 203–214.
- Brodeur, R.D., Mills, C.E., Overland, J.E., Walters, G.E., Schumacher, J.D., 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fisheries Oceanography* 8, 296–306.
- Costello, J.H., Sullivan, B.K., Gifford, D.J., Van Keuren, D., Sullivan, L.J., 2006a. Seasonal refugia, shoreward thermal amplification and metapopulation dynamics of the ctenophore *Mnemiopsis leidy* in Narragansett Bay, RI, USA. *Limnology and Oceanography* 51, 1819–1831.
- Costello, J.H., Sullivan, B.K., Gifford, D.J., 2006b. A physical–biological interaction underlying variable phenological responses to climate change by coastal zooplankton. *Journal of Plankton Research* 28, 1099–1105.
- Deason, E.E., 1982. *Mnemiopsis leidy* (Ctenophora) in Narragansett Bay, 1975–1979: abundance, size composition and estimation of grazing. *Estuarine, Coastal and Shelf Science* 15, 121–134.
- Deason, E.E., Smayda, T.J., 1982. Experimental evaluation of herbivory in the ctenophore *Mnemiopsis leidy* relevant to ctenophore–zooplankton–phytoplankton interactions in Narragansett Bay, Rhode Island, USA. *Journal of Plankton Research* 4, 219–236.
- Durbin, A.G., Durbin, E.G., 1981. Standing stock and estimated production rates of phytoplankton and zooplankton in Narragansett Bay, Rhode Island. *Estuaries* 4, 24–41.
- Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430, 881–883.
- Frolander, H., 1955. The Biology of the Zooplankton of the Narragansett Bay Area. Ph.D. thesis, Brown University, Providence, RI, USA (unpublished).



- Greve, W., Lange, U., Reiners, F., Nast, J., 2001. Predicting the seasonality of North Sea zooplankton. *Senckenbergiana Maritima* 31, 263–268.
- Hawk, J.D., 1998. The Role of the North Atlantic Oscillation in Winter Climate Variability as it Relates to the Winter–Spring Bloom in Narragansett Bay. M.S. thesis, University of Rhode Island, Narragansett, RI, USA (unpublished).
- Hulsizer, E.E., 1976. Zooplankton of lower Narragansett Bay, 1972–1973. *Chesapeake Science* 17, 260–270.
- Jeffries, H.P., 1962. Succession of two *Acartia* species in estuaries. *Limnology and Oceanography* 7, 354–364.
- Kremer, P., 1976. Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. In: Wiley, M.L. (Ed.), *Estuarine Processes*, vol. I. Academic Press, pp. 197–215.
- Lee, W.Y., McAlice, B.J., 1979. Seasonal succession and breeding cycles of three species of *Acartia* (Copepoda: Calanoida) in a Maine estuary. *Estuaries* 2, 228–235.
- Li, Y., Smayda, T.J., 1998. Temporal variability of chlorophyll in Narragansett Bay during and eighteen year time series. *ICES Journal of Marine Science* 55, 661–667.
- Lynam, C.P., Hay, S.J., Brierley, A.S., 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography* 49, 637–643.
- Martin, J.H., 1965. Phytoplankton–zooplankton relationships in Narragansett Bay. *Limnology and Oceanography* 10, 185–190.
- Mayer, A.G., 1912. Ctenophores of the Atlantic Coast of North America. Pub. 162. Carnegie Institute of Washington.
- Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions. *Hydrobiologia* 451, 55–68.
- Molinero, J.C., Ibanez, F., Nival, P., 2005. North Atlantic Climate and north-western Mediterranean plankton variability. *Limnology and Oceanography* 50, 1213–1220.
- Nixon, S.W., Granger, S., Buckley, B.A., Lamont, M., Rowell, B., 2004. A one hundred and seventeen year coastal water temperature record from Woods Hole, Massachusetts. *Estuaries* 27, 397–404.
- Oviatt, C., Keller, A., Reed, L., 2002. Annual primary production in Narragansett Bay, RI with no bay-wide winter–spring phytoplankton bloom. *Estuarine, Coastal and Shelf Science* 56, 1013–1026.
- Oviatt, C., 2004. The changing ecology of temperate coastal waters during a warming trend. *Estuaries* 27, 895–904.
- Purcell, J.E., Decker, M.B., 2005. Effects of climate on relative predation by scyphomedusae and ctenophores on copepod in Chesapeake Bay during 1987–2000. *Limnology and Oceanography* 50, 376–387.
- Parsons, L.S., Lear, W.H., 2001. Climate variability and marine ecosystems impacts: a North Atlantic perspective. *Progress in Oceanography* 49, 167–188.
- Smayda, T.J., 1998. Patterns of variability characterizing marine phytoplankton with examples from Narragansett Bay. *ICES Journal of Marine Science* 55, 562–573.
- Sullivan, B.K., Van Keuren, D., Clancy, M., 2001. Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. *Hydrobiologia* 451, 113–120.
- Sullivan, B.K., MacManus, L.T., 1986. Factors controlling seasonal succession of the copepods *Acartia hudsonica* and *A. tonsa* in Narragansett Bay, RI: temperature and resting egg production. *Marine Ecology Progress Series* 28, 121–128.
- Winder, M., Schindler, D.E., 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85, 2100–2106.
- Zillioux, E.J., Gonzalez, J.G., 1972. Egg dormancy in a neritic calanoid copepod and its implications to overwintering in boreal waters. In: Battaglia, B. (Ed.), *Fifth European Marine Biology Symposium*, Padova, Italy. Piccin Editore, pp. 217–230.