

# A physical–biological interaction underlying variable phenological responses to climate change by coastal zooplankton

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*Species-specific differential responses to climate warming that alter phenologies can dramatically affect community function. Using time series data from a Northwest Atlantic estuary, we show that the phenology of a top zooplankton predator, the ctenophore *Mnemiopsis leidyi*, has shifted more in response to climate warming over the past ~50 years than that of its major prey species, the copepod *Acartia tonsa*. Before climatic warming, *A. tonsa* was the dominant secondary producer in the estuary and its main period of production occurred before the seasonal appearance of *M. leidyi*. However, since 2000, the seasonal peak abundances of the two species have overlapped, intensifying the predator–prey relationship and resulting in the near extirpation of the once-abundant copepod from the estuary. We propose that the physical mechanism driving the different phenological responses of the two species is differential spring warming of the winter refugia of these two species. Substantial amplification of warming patterns in shallow embayments affects overwintering *M. leidyi* but has little influence over seasonal excystment of overwintering *A. tonsa* eggs located in the broader, deeper regions of the Bay. In this way, large-scale climatic changes are expressed as local-scale temperature variations that differentially affect alternate planktonic life histories to produce novel spring population growth dynamics of the two species and, ultimately, a new summer planktonic community dynamic in Narragansett Bay.*

## INTRODUCTION

Climate warming has been linked to alterations in seasonal patterns, or phenologies, of terrestrial (Menzel and Fabian, 1999; Post and Stenseth, 1999), freshwater (Winder and Schindler, 2004) and marine species (Edwards and Richardson, 2004). Phenological shifts in response to temperature change can have dramatic impacts on community functioning if the synchrony of biologically associated relationships, such as predator–prey cycles, is disrupted and the individual populations' cycles shift out of phase with one another (Cushing, 1990; Stenseth and Myrseth, 2002). Marine planktonic

communities are particularly vulnerable to disruption of relationships among species because species response patterns to warming vary (Greve *et al.*, 2001; Edwards and Richardson, 2004; Hays *et al.*, 2005), and average annual increases of little more than 1°C appear to result in substantial changes in coastal marine community dynamics (Oviatt, 2004). The underlying mechanisms whereby relatively small alterations in regional temperature regimes give rise to substantial interspecific differences in responses have not often been resolved (Stenseth *et al.*, 2002).

Phenological alterations involving two dominant zooplankton, the copepod *Acartia tonsa* and the ctenophore

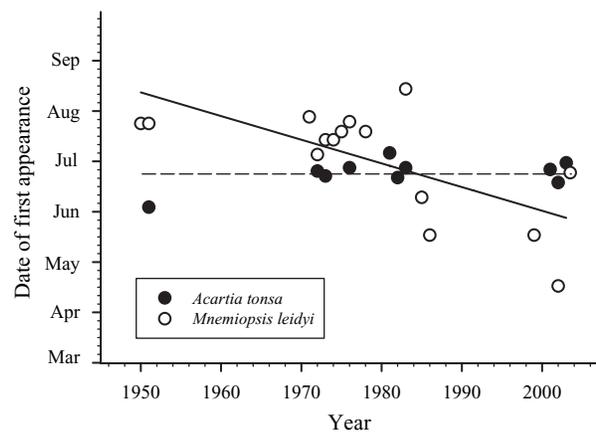
*Mnemiopsis leidyi*, in Narragansett Bay, RI, USA, have provided an opportunity to examine the mechanisms that underlie species-specific responses to climate warming in coastal ecosystems. Both species are important members of the plankton communities along much of North and South America's Atlantic coastlines. Although present all year in warmer latitudes, both species are strongly seasonal in temperate regions such as Narragansett Bay which experience winter temperatures near 0°C. There, they are frequently dominant summer species and historically have followed a regular seasonal cycle characterized by spring–summer peaks in *A. tonsa* coupled with late summer–early fall peaks in *M. leidyi* (Hulsizer, 1976; Durbin and Durbin, 1981). The regularity of seasonal cycles of the two species is based on their trophic roles. *Acartia tonsa* has been the dominant secondary producer in the estuary (Durbin and Durbin, 1981), and its seasonal decline has been related to the predatory impact of *M. leidyi* (Kremer, 1979; Deason and Smayda, 1982). *Acartia tonsa* is one of *M. leidyi*'s major prey items (Kremer, 1994), and predation by *M. leidyi* is capable of influencing planktonic community structure in its both endemic (Purcell and Decker, 2005) and introduced (Shiganova, 1998) ranges. Populations decline during cold months, and both species are either absent or present in negligibly low concentrations at central Bay stations that have been sampled during winter months (Sullivan *et al.*, 2001).

Climatic warming has been accompanied by alterations in the timing of the *Acartia*–*Mnemiopsis* population cycles within Narragansett Bay. During the period extending from 1951 to 2003, the recorded dates of first appearance by *M. leidyi* at central Narragansett Bay stations have advanced as much as 2 months (59 days) relative to the mean historic appearance date (Sullivan *et al.*, 2001). However, the phenology of *A. tonsa* has varied little during this same time interval (Fig. 1). The differential phenological response of *A. tonsa* and *M. leidyi*, similar to instances of seasonal shifts that have been described for other plankton (Edwards and Richardson, 2004), is enigmatic because the spatial and thermal ranges of the two species are known to overlap (Hulsizer, 1976; Durbin and Durbin, 1981), and hence, they would be expected to experience similar cues governing their seasonality. Further complicating this scenario is the relatively small change in temperature during this period. Historical time series demonstrate annual warming during the last 45 years of ~1.2°C in Narragansett Bay (Hawk, 1998; Oviatt, 2004) as well as nearby coastal waters of Woods Hole, MA, USA (Nixon *et al.*, 2004). Here, we present evidence supporting a mechanism to describe how a relatively small average annual temperature increase can cause variable

phenological alterations among co-occurring species (*M. leidyi* and *A. tonsa*) that result in substantially altered planktonic community structure.

## METHOD

Historical data on the date of first appearance and maximum concentrations of *A. tonsa* and *M. leidyi* were compiled from several sources (Frolander, 1955; Hulsizer, 1976; Durbin and Durbin, 1981; Sullivan and MacManus, 1986; B. K. Sullivan, U. Rhode Island, unpublished data) which shared sampling locations near either the central or the outer estuary sites. We have used a long-term temperature data set (Nixon *et al.*, 2004) from nearby Woods Hole, MA, USA, in order to examine temperature patterns from 1950 to 2003. Annual and seasonal temperature anomalies relative to historical averages for Narragansett Bay (Oviatt, 2004) and Woods Hole (Nixon *et al.*, 2004) provided background data for our annual comparisons. Nixon *et al.* (Nixon *et al.*, 2004) have demonstrated that the Woods Hole data set closely resembles a shorter data set (1956–97) from the outer Narragansett Bay near Newport, RI, USA (Hawk, 1998). However, the Woods Hole data set possesses daily temperature resolution over a >100-year period, whereas the Newport data set is of monthly resolution, covers a shorter period and possesses important gaps. Consequently, the Woods Hole temperature data set was used to determine the dates at which 10 and



**Fig. 1.** Historical patterns in the phenology of *Acartia tonsa* and *Mnemiopsis leidyi* at central estuary stations in Narragansett Bay, RI, USA. Linear regression indicates that *A. tonsa* phenology has not significantly altered ( $P = 0.195$ ) during the period from 1950 to 2003. By contrast, the first appearance of *M. leidyi* has shifted significantly ( $P = 0.006$ ) earlier in the year during the same period. Data have been assembled from historical references (Frolander, 1955; Hulsizer, 1976; Durbin and Durbin, 1981; Sullivan and MacManus, 1986; Sullivan, unpublished data) and the present study.

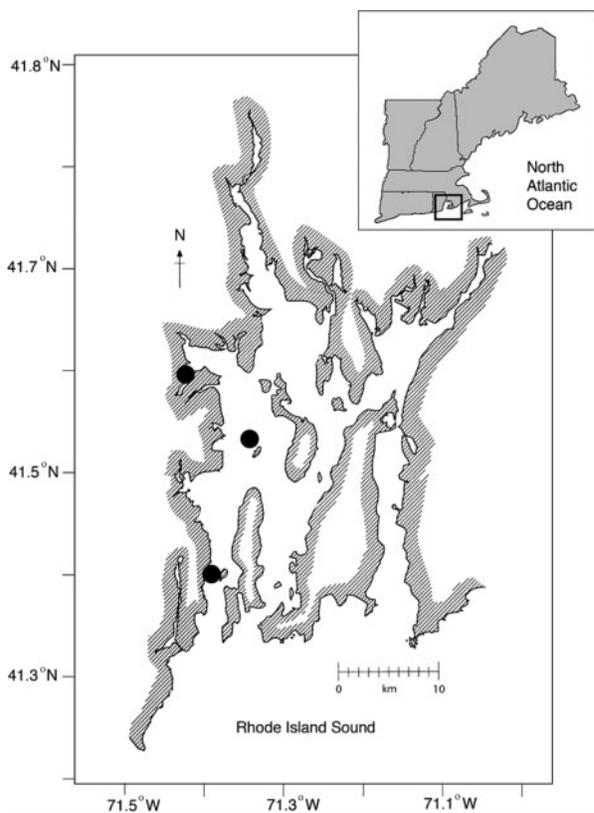
15°C thresholds were reached during spring months between the years 1950 and 2003.

In order to discern the mechanism relating these previously documented patterns of temperature change with phenological patterns of *A. tonsa* and *M. leidy*, we needed a more spatially and temporally detailed database and used a recent data set collected in Narragansett Bay during 2001–03 (Costello *et al.*, 2006). Field sampling locations for this data set (Fig. 2) reflected conditions near the mouth of the Narragansett Bay estuary (41°30.6'N, 71°24.0'W), the central estuary (41°30'N, 71°20'W) and a shallow embayment (41°40'N, 71°24'W) with restricted exchange with the main body of the estuary. We sampled the three sites on a weekly basis for two complete annual cycles (November 2001–October 2003) and collected biological (ctenophore and mesozooplankton) and hydrographic data (temperature and salinity) with a YSI Model 600XLM sonde at each station. Inclement weather caused incomplete sampling once during 2001–02 and four times during 2002–03. The onshore–offshore salinity variations were typically low (Costello *et al.*, 2006). Large *M. leidy* (>1.0 cm) were

collected by two oblique tows with a 0.5-m diameter net (1-mm mesh) equipped with a flowmeter and counted while still alive. Small ctenophores (<1.0 cm) and *A. tonsa* were collected with a 64- $\mu$ m mesh net, preserved immediately with 4% buffered formaldehyde or a 5% acid Lugol's solution and enumerated in the laboratory using a stereomicroscope.

## RESULTS AND DISCUSSION

In order to evaluate how climate changes affect these species, it is essential to understand the roles of temperature in their life histories. Although both *A. tonsa* and *M. leidy* co-occur, their life histories and distribution patterns involve important differences that impact historic and present phenologies. *Acartia tonsa* is primarily a summer species in Narragansett Bay and overwinters as resting eggs in the sediments (Sullivan and MacManus, 1986). Spring population growth of *A. tonsa* is initiated predominantly by hatching of these resting eggs when spring water temperatures exceed 15°C (Zillioux and Gonzalez, 1972). Once hatched in the spring, continued population growth by *A. tonsa* occurs by direct hatching of planktonic eggs to feeding nauplii. *Acartia tonsa* resting eggs occur throughout the estuary, and viable larvae have been hatched from eggs collected in various locations in Narragansett Bay (Sullivan and MacManus, 1986). In contrast to *A. tonsa*, *M. leidy* possesses a completely planktonic life cycle and produces no known cysts or resting eggs. Consequently, spring growth of *M. leidy* populations depends upon egg production by overwintering adults. Ctenophore egg production is temperature-dependent and is negligible below 10°C (Kremer, 1975; Costello *et al.*, 2006). Winter seawater temperatures fall below this threshold for long periods (>90 days) of the winter in Narragansett Bay, and during these cold periods, *M. leidy* populations cannot replace individuals lost through mortality or advection. Average estimates of estuary-wide flushing rates, 28–43 days (Pilson, 1985; Abdelrhman, 2005), are much shorter than the seasonal non-reproductive period of *M. leidy* with the result that advective losses of *M. leidy* are high during winter months. Consequently, *M. leidy* populations decline during cold periods and the severity and length of the cold period influence *M. leidy* winter population decreases (Costello *et al.*, 2006). However, the rates of population decline are not uniform throughout the estuary, and losses due to advection of the weakly swimming *M. leidy* reflect differential flushing rates characterizing various regions of the Bay. Intensive weekly field sampling during 2001–03 along the inshore–offshore gradient demonstrated that *M. leidy* was eliminated from mid-estuary

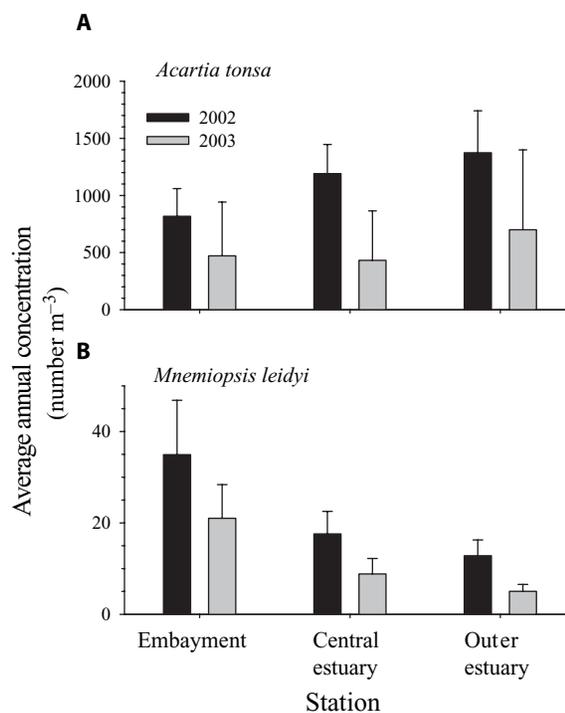


**Fig. 2.** Sampling locations in the Narragansett Bay estuary. Sampling stations represent an inshore–offshore depth gradient moving from an inshore station of 3–4 m to the central Bay station of 6–7 m to the outer Bay of 10–12 m.

stations but remained within a number of shallow embayments during the winter (Costello *et al.*, 2006). These embayments were characterized by restricted exchange with the open Bay and, hence, long fluid residence times (Abdelrhman, 2005). Overwintering *M. leidy* at the inshore embayment reappeared and began reproducing much earlier (>30 days) than at central estuary sites. Transport from such inshore regions provides inocula for population growth throughout the estuary (Costello *et al.*, 2006).

The divergent copepod and ctenophore life histories result in a critical spatial disparity that affects spring growth patterns of both species. Whereas spring growth of *A. tonsa* populations is initiated by excystment of benthic resting eggs distributed throughout the estuary, spring population growth of *M. leidy* is initiated within small, shallow embayments along the periphery of the estuary that have retained overwintering *M. leidy* populations. Spatial distributions of both species intersect throughout the estuary during summer months, but the spatial distinction between their population centers is reflected by their average concentration levels along the inshore–offshore depth gradient (Fig. 3).

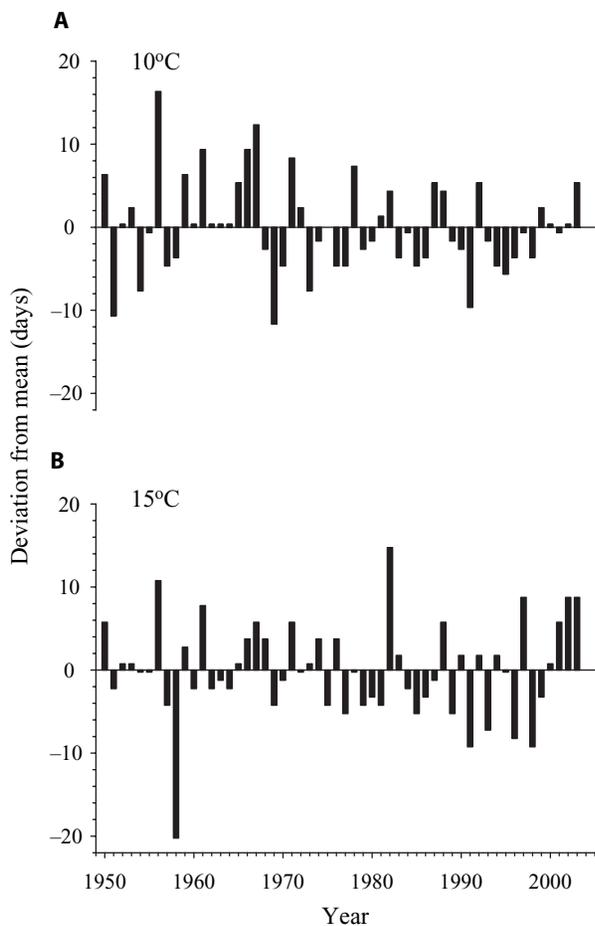
These interspecific differences in spatial dynamics of seasonal zooplankton growth are important because climate warming in temperate coastal systems is expressed unevenly on both spatial and temporal scales. Although there is a significant annual warming trend since 1970 of 1.2°C (Nixon *et al.*, 2004), the most substantial average warming occurred during the winter months (December–February), and there was no significant change since 1950 of the dates at which spring warming reached the temperature thresholds of 10 and 15°C (Fig. 4). Thus, although climatic warming is a demonstrated and significant phenomenon in Narragansett Bay (Hawk, 1998; Sullivan *et al.*, 2001; Oviatt, 2004), there has been no change in the biologically important temperature thresholds for spring population growth of either *A. tonsa* or *M. leidy* based on thermal patterns characteristic of waters in the open regions of the Bay. In contrast to the open regions of the Bay, shallow embayments are more affected by spring warming of air temperatures than deeper stations near the ocean boundary where interannual differences are comparatively conservative. Our weekly sampling regime during 2001–03 encompassed unusually warm (2002) and cold (2003) winters relative to historical average temperatures according to National Climate Data Center/NESDIS/NOAA (NOAA, 2006). We used the temperature differences between these years to demonstrate the impact of climate change at different locations within Narragansett Bay. During a warm winter, average water temperatures of inshore embayments remained relatively high and



**Fig. 3.** Average annual population concentrations at three sites in the Narragansett Bay estuary during 2002–03. (A) *Acartia tonsa* copepodites and adults and (B) *Mnemiopsis leidy* of total length >1.0 cm. Error bars represent SEM. Negative bars (not shown) are symmetrical with positive bars. Note that population centers for the two species are located in different regions of the Bay. *Mnemiopsis leidy* population concentrations are greatest in the shallow, near shore embayments, whereas *A. tonsa* concentrations tend to be greatest in the deeper, central portion of the estuary.

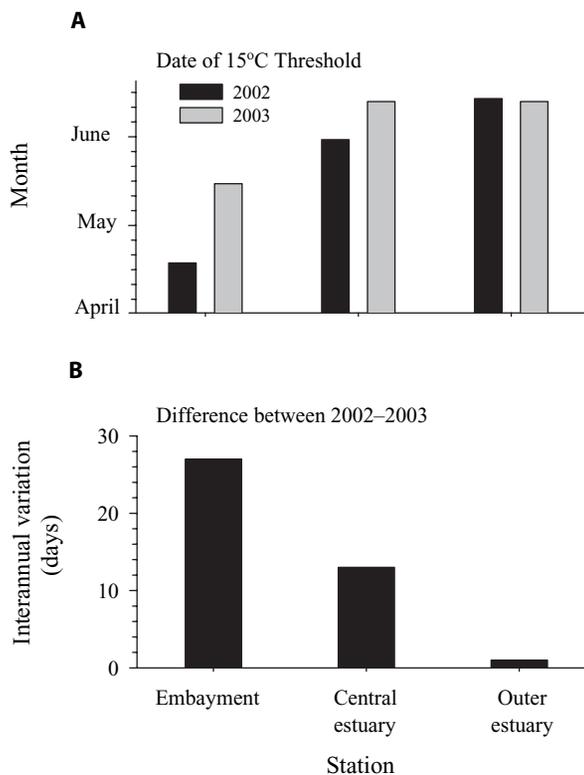
spring warming was amplified in comparison with stations in the open estuary areas (Fig. 5A). One result of this shoreward thermal amplification was that shallow embayments reached biologically significant temperatures weeks earlier in a warm year than did central and outer estuary stations (Fig. 5B). Such amplified spring warming of embayments during warm years has largely gone undetected because long-term temperature data sets with daily temporal resolution are rare for such inshore environments (Nixon *et al.*, 2004). Hence, local spatial and temporal variations in temperature accompanying larger scale climatic warming were not previously described.

These local spatial and temporal variations in temperature accompanying larger scale climatic warming are important ecologically because they directly affect the timing of spring population growth by overwintering animal populations. Most importantly for the *Acartia*–*Mnemiopsis* interaction, spatial characteristics of warming influence each species differently. Central and outer estuary stations characterizing *A. tonsa*'s population centers (Fig. 3A) have experienced no significant annual



**Fig. 4.** Annual variation in spring warming of surface waters in Woods Hole, MA, USA. Variations are depicted as deviations, in days, from the mean date at which the surface temperature surpassed the 10°C (**A**) and 15°C (**B**) thresholds. Analysis of variance indicates that the slope of lines regressed through the temperature threshold dates from 1950 to 2003 is not significantly different from zero (10°C,  $P > 0.32$ ; 15°C,  $P > 0.93$ ). Therefore, although average annual surface temperatures have increased by  $\sim 1.2^\circ\text{C}$  during this interval (Nixon *et al.*, 2004), the dates at which spring warming reaches the 10 and 15°C thresholds have not significantly changed during the period from 1950 to 2003.

difference in the temperature threshold necessary to initiate spring population growth (Figs 4B and 5). Consequently, owing to its life history and related estuary-wide population distribution, *A. tonsa* has retained relatively conservative timing of spring population growth between warm and cold years (Fig. 2). By contrast, shallow embayments experiencing shoreward thermal amplification during warm years also serve as source regions containing overwintering populations of the ctenophore *M. leidy* (Fig. 3). Populations of *M. leidy* have responded to these local warming disparities with earlier seasonal population growth and higher peak population levels during warm years. Higher peak populations can contribute to larger overwintering stocks that are the

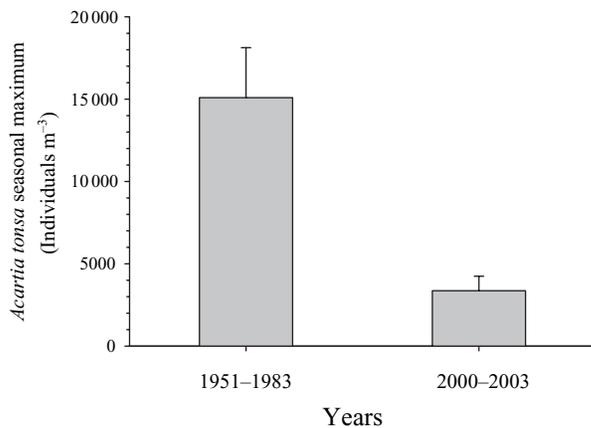


**Fig. 5.** Shoreward temperature amplification in the Narragansett Bay estuary. (**A**) Date at which the 15°C threshold was reached during the spring months of 2002 and 2003. (**B**) The advance, in days, of the 15°C threshold in the warm spring of 2002 relative to the colder spring of 2003. Note that whereas the timing of warming at the seaward most station is relatively unaffected between years, the shallow embayment is strongly affected. A similar but less pronounced pattern occurs for the 10°C threshold (Costello *et al.*, 2006).

source of subsequent spring population growth (Costello *et al.*, 2006).

The shift in seasonal timing of population growth by *M. leidy* relative to *A. tonsa* has dramatically altered summer plankton dynamics within the central region of Narragansett Bay (Sullivan *et al.*, 2001; Sullivan *et al.*, in press). The relative advance in *M. leidy*'s seasonal appearance has shifted the predator's peak abundance into a time period during which *A. tonsa* has historically enjoyed a temporal refuge from ctenophore predation (Fig. 1). *Mnemiopsis leidy* is capable of causing dramatic predatory decreases of copepod populations (Shiganova, 1998; Purcell and Decker, 2005), and peak seasonal concentrations of *A. tonsa* have declined significantly in Narragansett Bay since 2000 (Fig. 6). Because this copepod was historically the dominant secondary producer in the plankton (Durbin and Durbin, 1981), this decline is a substantial alteration of planktonic production dynamics.

The consequences of species-specific phenological responses to climate change are not limited to the



**Fig. 6.** Decline in maximum seasonal concentrations of the copepod *Acartia tonsa* in the Narragansett Bay estuary during the period 2000–03 ( $n = 4$ ) relative to years between 1951 and 1983 ( $n = 7$ ). All data have been collected from the same site and historical data (pre-2000) from a variety of sources (as in Fig. 2). Error bars represent SEM, and although not shown, negative bars are symmetrical with positive bars. Average values for the two time periods are significantly different (Mann–Whitney test,  $P = 0.008$ ).

*Mnemiopsis–Acartia* predator–prey relationship and may not readily be reversed. Summer copepods such as *A. tonsa* are important prey to other consumers such as fish larvae, and *M. leidy* can be an important fish egg predator (Monteleone and Duguay, 1988). Therefore, alterations in the *Mnemiopsis–Acartia* relationship can cascade through the planktonic community and potentially influence observed estuary-wide community changes (Oviatt, 2004) associated with warming. Historic phenological patterns may not easily be restored by a series of cold winters because low summer abundances of *A. tonsa* since 2000 may diminish the supply of *A. tonsa* resting eggs available in the upper sediment layers for initiation of spring population growth. Although resting eggs of marine copepods may remain viable for tens of years (Marcus *et al.*, 1994), mortality due to exposure to anoxia, infaunal predators and deep burial probably decrease viability over time (Marcus and Boero, 1998). A long succession of warm years accompanied by low resting egg production may diminish the overwintering egg concentrations at the sediment–water interface to levels that decrease availability for spring recruitment. Such a series of warm winters would simultaneously support larger overwintering stocks of *M. leidy* with which to initiate rapid spring population growth. This combination of climate-related alterations in population dynamics may be self-reinforcing among vulnerable species and resist return to historical phenological patterns.

Although we propose that the different responses of *A. tonsa* and *M. leidy* are based on an interaction between

physical (shoreward thermal amplification) and biological (different life histories resulting in different population centers within Narragansett Bay) factors, these may interact with physiologically based differences known to affect phenological responses of other species (Harrington *et al.*, 1999; Stenseth and Mysterud, 2002; Stenseth *et al.*, 2002). However, the phenological alterations and their ecological impacts in Narragansett Bay may require no more complex explanation than the physical–biological interaction we describe. These types of interactions are important because differing life histories are common among species inhabiting estuaries, and shifts in historic patterns of relationships among species such as the one identified here may be expected to arise frequently in response to climatic warming. Our ability to understand and predict these changes may depend upon the depth of our knowledge about the links between life history patterns and temperature changes in population centers of these organisms.

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