

# Impact of Climate Change on Estuarine Zooplankton: Surface Water Warming in Long Island Sound Is Associated with Changes in Copepod Size and Community Structure

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Received: 2 August 2013 / Revised: 17 December 2013 / Accepted: 4 January 2014 / Published online: 31 January 2014  
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**Abstract** In coastal ecosystems with decades of eutrophication and other anthropogenic stressors, the impact of climate change on planktonic communities can be difficult to detect. A time series of monthly water temperatures in the Central Basin of Long Island Sound (LIS) from the late 1940s until 2012 indicates a warming rate of  $0.03\text{ }^{\circ}\text{C year}^{-1}$ . Relative to the early 1950s, there has been a concurrent decrease in the mean size of the dominant copepod species *Acartia tonsa* and *Acartia hudsonica*, an increase in the proportion of the small copepod *Oithona* sp., and the disappearance of the two largest-sized copepod genera from the 1950s. These changes are consistent with predictions of the impact of climate change on aquatic ectotherms. This suggests that even in eutrophic systems where food is not limiting, a continued increase in temperature could result in a smaller-sized copepod community. Since copepods dominate the zooplankton, which in turn link primary producers and upper trophic levels, a reduction in mean size could alter food web connectivity, decreasing the efficiency of trophic transfer between phytoplankton and endemic larval fish.

**Keywords** Climate change · Copepods · Estuaries · Community ecology · Body size

## Introduction

Climate change in the ocean entails multiple processes, such as temperature change, acidification, and invasions by non-native species (Stachowicz et al. 2002). Understanding the effects of climate change on organisms, populations, and communities in the ocean can thus be a fundamental challenge to marine ecologists. Zooplankton play a pivotal role in these communities, dominating pelagic food webs and linking primary producers to upper trophic levels. Zooplankton also play an important role in biogeochemical cycles in the ocean (Dam et al. 1995). In addition, because zooplankton are ectotherms with short generation times that allow for fast response to stressors through phenotypic plasticity or evolutionary adaptation, they are excellent sentinels for the response of the oceanic biota to climate change (Dam 2013).

The response of zooplankton to warming can be manifested at the individual, population, or community level. A common prediction is that long-term warming will result in a general decrease in the size of marine ectotherms (Moore and Folt 1993; Daufresne et al. 2009; Sheridan and Bickford 2011; Forster et al. 2012). Daufresne et al. (2009) outline mechanisms by which size reduction can occur. At the population level, a decrease in individual mean size can occur as juveniles mature more quickly and begin reproduction at smaller sizes. At the community level, two types of changes can occur: A change in proportion as endemic, smaller copepods become more relatively abundant and/or a shift in diversity as small warm-water species are gained or larger cool-water species are lost.

Within the marine zooplankton, copepods are the most dominant organisms, typically comprising between 50 and

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Communicated by Darcy Lonsdale

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80 % of the community by number (Wickstead 1976). In the Atlantic coastal environment, copepods from three orders (calanoid, cyclopoid, and harpacticoid) are critical links between primary producers and secondary consumers in aquatic food webs (Turner 1984; Johnson and Allen 2005). In Long Island Sound (LIS), a large, eutrophic, semi-enclosed estuary in the northern half of the Virginian biogeographic province (Fig. 1a, Capriulo et al. 2002; Pelletier et al. 2012), a few species of copepods dominate the copepod community. In the earliest survey of copepods in the Central Basin of LIS, Deevey (1956) showed that the calanoid copepod *Acartia clausi* (now *Acartia hudsonica*) numerically dominated the copepod community on an annual basis and the winter/spring assemblage in particular. During summer/fall, the calanoid copepod *Acartia tonsa* and the small cyclopoid copepod *Oithona* sp. alternated dominance. During this survey, calanoid copepods outnumbered cyclopoids annually. Others have consistently observed the same seasonal dominance patterns in LIS (Peterson 1985; Capriulo et al. 2002) and other systems along the northeast US Coast (Johnson and Allen 2005).

Warming of northeast US coastal waters is becoming evident. Woods Hole, MA, has experienced an annual warming trend of  $0.04\text{ }^{\circ}\text{C year}^{-1}$  over 1970–2002 (Nixon et al. 2004). Seekall and Pace (2011) have also found a warming trend of  $0.02\text{ }^{\circ}\text{C year}^{-1}$  over 1946–2007 in the Hudson River Estuary. Howell and Auster (2012) have found a significant ( $p < 0.05$ ) warming trend from 1976 to 2008 during March–June and August–October in the eastern basin of LIS. In this paper, we use a much longer time series (1948–2012) to show that the Central Basin of LIS has followed a similar pattern of warming and test if changes observed in copepod size and community composition are consistent with predictions of the effects of warming on ectotherms (Daufresne et al. 2009).

## Methods

### Temperature

We examined monthly surface water temperature means, for the period 1948–2012, provided by the National Oceanic and Atmospheric Administration (NOAA) at the Milford Laboratory, CT (Fig. 1b) to establish the long-term annual trend for the onshore surface temperature of the Central Basin of LIS. Measurements from 1948 to 1975 were made daily by a Bristol thermograph installed at the Milford Harbor dock whereas measurements from 1976 to 2012 were also made daily but with thermometer readings of sand-filtered harbor water pumped into the laboratory. Examination of the trend lines during the 1975–1976 transition between methods does not suggest a systematic error due to this methodological difference. More importantly, the same trends observed over

1948–2012 also exist in the 1976–2012 data. Daily measurements are consistently available from 1960 onward and are used to analyze trends in the number of days above or below certain temperatures. Data are available for download from the Milford Lab website (<http://mi.nefsc.noaa.gov/pubindex.html>). Biweekly (during summer) and monthly Central Basin offshore surface temperatures were recorded from 1994 to 2012 with a conductivity-temperature-depth (CTD) sensor by the Connecticut Department of Energy and Environmental Protection (CTDEEP) at stations H2, H4, H6, and I2 (Fig. 1b).

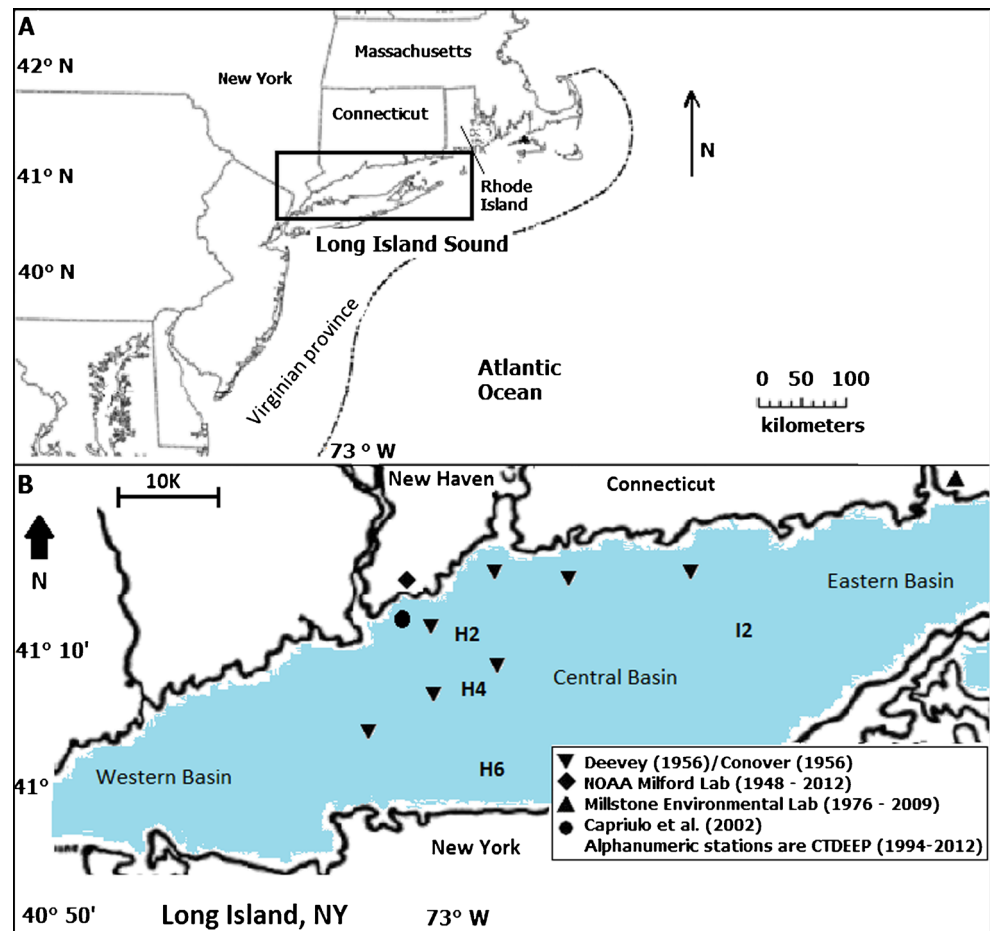
Time series data can be subject to autocorrelation error and non-normal distributions, making analysis via ordinary least squares linear regression inappropriate. Following the method of Seekall and Pace (2011) for their analysis of long-term warming in the Hudson, we used a non-parametric Kendall test for annual temperature trend analysis. The test was run in R version 2.11.1, a free user-supported statistical software package available at <http://cran.r-project.org/bin/windows/base/>. Specific R sub-routines written by the R community are noted in italics where used. Outliers due to possible instrument error were identified with a Bonferroni test from the *car* package. For trend analysis, we used the *kendall* package to calculate tau (correlation) and *p* values (significance). The slope of the warming trend was estimated using the Theil-Sen approach in the R package *zyp*. The Theil-Sen estimator is a robust, distribution-free non-parametric method of analyzing linear trends (Sen 1968). A Breusch-Godfrey test for serial autocorrelation was passed for annual temperature values, indicating that these methods were appropriate.

### Zooplankton Surveys

In order to establish historical context for analysis of copepod size and community composition percentages, previous inter-annual surveys of the Central Basin (Fig. 1b, Table 1) were obtained from archival and published sources. Although the surveys varied somewhat in intensity, scope, and specific location, they provide the only baseline data to compare to current trends. The earliest surveys of copepod size, diversity, and community proportion were reported by Conover (1956) and Deevey (1956) and took place from March 1952 to May 1953 (Table 1). Surveys sampled four stations equally divided between onshore and offshore in the Central Basin of LIS (Fig. 1b). Both surveys visited two of the four stations every week, whereas the other two were visited on alternate weeks. This resulted in 12 observations per month or 192 observations in total. Zooplankton tows were oblique and conducted with a single-opening 153- $\mu\text{m}$  mesh net via a Clarke-Bumpus sampler.

The next survey was conducted across LIS, with one station in the Central Basin, also with oblique tows, but using

**Fig. 1** **a** The location of Long Island Sound in relation to the Virginian marine biogeographic zone. **b** The locations of survey and time series data referenced in this paper. The Connecticut Department of Energy and Environmental Protection (CTDEEP) surveys (1994–2012) of the Central Basin are represented by *alphanumeric characters*. The station used in the Rice survey (March 2010–September 2011) was collocated with the Deevey (1956) survey station 2, which is the station directly northeast of CTDEEP station H4



a 202- $\mu\text{m}$  mesh net (Capriulo et al. 2002). This station was near an inshore Deevey (1956) station next to the NOAA Milford Laboratory (Fig. 1b) and was visited monthly, totaling 35 observations. The CTDEEP performed the most recent large-scale survey of zooplankton (divided into three periods: August 2002 to October 2004, March 2007 to April 2008, and January to November 2011), with 2002–2004 and 2007–2008 results analyzed in Dam and McManus (2009). The CTDEEP survey also used oblique tows, with a 202- $\mu\text{m}$  mesh net, from two stations within the Central Basin, H4 and I2 (Fig. 1b). In the CTDEEP survey, with the exception of summer and hypoxia surveys, H4 and I2 were visited once per month

(during summer they were visited twice per month). The CTDEEP survey contains 93 observations. In terms of sampling intensity, the Deevey (1956) survey is roughly twice as intensive as the CTDEEP, but roughly half as extensive (16 vs. 29 months). Samples from Conover (1956), Deevey (1956), Capriulo et al. (2002), and the CTDEEP were preserved in 10 % formalin.

As noted above, the latter two surveys collected zooplankton samples with a 202- $\mu\text{m}$  mesh while the early survey (Deevey 1956) used a smaller mesh (158  $\mu\text{m}$ ). Hopcroft et al. (2001) note that in temperate regions, a 200- $\mu\text{m}$  mesh net samples the 550–1,600- $\mu\text{m}$  size range most effectively.

**Table 1** Relevant zooplankton surveys occurring in the Central Basin of LIS, 1952–2011, including the mesh size of plankton nets and inclusive dates

Survey	Dates	Mesh size ( $\mu\text{m}$ )	Zooplankton parameters
Conover (1956)	1 March 1952–1 May 1953	158	<i>Acartia tonsa</i> and <i>Acartia hudsonica</i> size
Deevey (1956)	1 March 1952–1 May 1953	158	Zooplankton diversity. Zooplankton abundance for major species only
Capriulo et al. (2002)	1 June 1992–1 April 1995	202	Copepod diversity and copepod abundance
CTDEEP	1 August 2002–1 October 2004	202	Zooplankton diversity and abundance
CTDEEP	1 March 2007–12 April 2008	202	Zooplankton diversity and abundance
Rice	15 March 2010–1 November 2011	150	Copepod diversity and abundance

For copepods <550  $\mu\text{m}$ , Harris et al. (2000) report that at tow speeds >1  $\text{m s}^{-1}$ , a 158- $\mu\text{m}$  net is four times as effective as a 202- $\mu\text{m}$  mesh net at capturing copepods with a width less than or equal to 150  $\mu\text{m}$ . Thus, these three surveys may not provide the same information regarding zooplankton abundance and community composition. Specifically, since small cyclopoids (such as *Oithona* sp.) are more likely than larger calanoids to have a width less than 150  $\mu\text{m}$  and have an overall length less than 550  $\mu\text{m}$ , their proportional abundance was likely underestimated by Capriulo et al. (2002) and the CTDEEP copepod survey. In order to provide a valid comparison of copepod community to the 1950s survey, we collected samples (Rice survey, Table 1) with the same mesh size, at the same locations, and in the same manner as the Deevey (1956) and Conover (1956) surveys of copepods of the Central Basin of LIS.

The Rice survey samples were collected from March 2010 to November 2011 at the CTDEEP Central Basin stations (H2, H4, H6, and I2) and also at station 2 from the Deevey (1956) and Conover (1956) surveys. This station is northeast of H4 (Fig. 1b). We conducted vertical tows with a single-opening 150- $\mu\text{m}$  mesh net from the CTDEEP R/V *John Dempsey* and *Patricia Lynn* as well as the NOAA R/V *Victor Loosanoff*. Two to three stations (from those above) were visited during each monthly or biweekly (during summer) trip, for 41 observations. The end result is that there are 169 total observations represented by the three most recent surveys (CTDEEP, Capriulo et al. (2002), and the Rice survey).

During the Rice survey, the contents of the net were rinsed with on-site water into a 10-l container, passing through a 2-mm sieve. The resulting contents were gently stirred, and sub-samples were drawn with a 50-ml pipette until 500 ml was collected. Sub-samples were preserved in 5 % Lugol's iodide, kept in coolers in the field, and transferred to a 10 °C incubator upon return. These sub-samples were enumerated by transferring known volumes to a petri dish and counting all copepods present in the petri dish. Final abundance was estimated by accounting for the aliquot size. Between 100 and 150 copepods were generally present and counted per sub-sample. This range is similar to that used by Capriulo et al. (2002) for their analysis of the copepod community of the Central Basin. For comparison of our Rice survey monthly means in copepod proportion with Deevey (1956) monthly means, we averaged the data from all of our Central Basin stations. The counting error in community percentage was estimated from Harris et al. (2000),  $\text{CL}_{95} (\%) = \pm 2(100/\sqrt{n})$  for each monthly or biweekly (during summer) survey, and ranged from 9.3–20 %.

#### Taxonomic Identification

Enumeration and identification of the 150- $\mu\text{m}$ -mesh copepod samples from the Rice survey were carried out via a dissecting microscope within 1 year of collection, the recommended time

frame for identification of samples preserved in Lugol's (Harris et al. 2000). Line drawings and key taxonomic features identified in Johnson and Allen (2005) were used to guide identification. Positive identification of *A. tonsa* vs. *A. hudsonica* species during the Rice survey was carried out using the recommendation of Conover (1956) for rapid identification of large numbers of *Acartia* sp. Relative lengths of outermost caudal bristles were examined, and copepods with the longer bristles (more fanlike) were determined to be *A. tonsa*. Since there are significant gender differences in length, for later size measurements, *Acartia* sp. females were confirmed by antenna length and orientation, after the recommendations of Sabatini (1990).

Annual and monthly proportional abundance of the most dominant cyclopoid copepod (*Oithona* sp.) was also analyzed. Cyclopoids are the smaller of the two dominant orders of copepods in LIS (Deevey 1956). With the exception of *Paracalanus crassirostris*, endemic calanoids are generally twice as long as the most prevalent endemic cyclopoid, *Oithona* sp. The criteria for identifying *Oithona* sp. in LIS were adapted from Johnson and Allen (2005): size (adults <550  $\mu\text{m}$ ), short antenna, articulation behind the fourth thoracic segment, and a prosome wider than the urosome.

#### Copepod Sizing

Prosome lengths of adult female *A. tonsa* and *A. hudsonica* were reported by Conover (1956). These lengths provide the baseline against which 2010–2011 data on prosome lengths for the same congeners were compared. Conover (1956) did not report individual male sizes; hence, in our analysis of long-term differences in size between *Acartia* sp. from 1952–1953 and from 2010–2011, we also examined only mature adult females. Seasonal temperature effects were minimized by comparing the 1952–1953 and 2010–2011 size distributions during the same months of each year (August, September, and November for *A. tonsa* and March and May for *A. hudsonica*).

Conover (1956) measured *Acartia* sp. size using an ocular micrometer from samples preserved in buffered formalin within 2–4 years of collection. We made our *Acartia* sp. size measurements within the same time frame and using the same method from buffered formalin-preserved samples. These samples were collected by the CTDEEP at the same locations and times as those of our Rice survey. Preservation in formalin may result in a 20 % reduction in mass, and likely size, for the copepod *A. tonsa* (Pöllupüü 2007). We have assumed that preservation biases are equivalent and that we can compare sizes of *Acartia* sp. between those measured by Conover (1956) and those more recently collected by the CTDEEP. Reported prosome lengths of *Acartia* collected by Deevey (1956) and measured by Conover (1956) were converted from graphical to numerical format using the shareware program

DataThief©—which allowed scanned images to be converted into numeric format after applying the appropriate scales.

### Diversity Analysis

Calanoid genus richness was chosen as a standard for testing the hypothesis that there would be a shift toward smaller genera at the community level (Daufresne et al. 2009). We specifically focused on calanoids since the only cyclopoid genus in LIS named by Deevey (1956) was *Oithona* sp. and it was consistently found in all surveys. Deevey (1956) also referred to a category of “other cyclopoids” in the 1952–1953 species list, making it difficult to conclusively quantify change in cyclopoid richness. Other researchers on the effect of climate change on marine invertebrate diversity have used richness along with more robust measures (Margalef’s index, Shannon’s index, and evenness) that we cannot calculate (since abundance for non-major genera was not provided by Deevey (1956)), and they achieved similar results among all methods (e.g., Danovaro et al. 2004). In addition, since 1980, the endemic calanoid *P. crassirostris* was renamed *Parvocalanus crassirostris* (Johnson and Allen 2005). Since this would mistakenly add a genus relative to the 1950s, for comparative analysis, we have considered *Paracalanus crassirostris* equivalent to *Parvocalanus crassirostris*.

### Statistics

Bayesian credible intervals were used to establish whether there were significant differences in the size of *Acartia* sp. and the community percentage of *Oithona* sp. between 1952–1953 and 2010–2011. Since a flat prior was chosen, our credible intervals can be essentially interpreted as frequentist 95 % confidence intervals. Bayesian credible intervals do not require a normal distribution (Balazs and Chaloupka 2004) and are ideal for analyzing relatively smaller datasets and/or analyzing plankton time series (Boyce et al. 2010). Credible intervals were calculated using the quantile method within the *laplacesdemon* package in R. An observation was considered significantly different if it fell outside the credible interval.

We chose the largest sources of variation from all prior surveys as the basis of our credible intervals. This minimized the chances of finding a significant difference where none actually exists. For *Acartia* sp. mean prosome length, interannual variation was the greater source of variation than spatial variation and was thus used as the basis for all credible intervals. For *Oithona* sp. community percentage, spatial variation among stations in the Rice survey was larger than interannual variation from 1952 to 1953, 1992 to 1995, 2002 to 2004, 2007 to 2008, and 2010 to 2011. Spatial variation in the 2010–2011 Rice survey was thus chosen as the basis for

our comparison with the 1952–1953 data (Deevey 1956) for *Oithona* sp. community percentage.

## Results

### Temperature

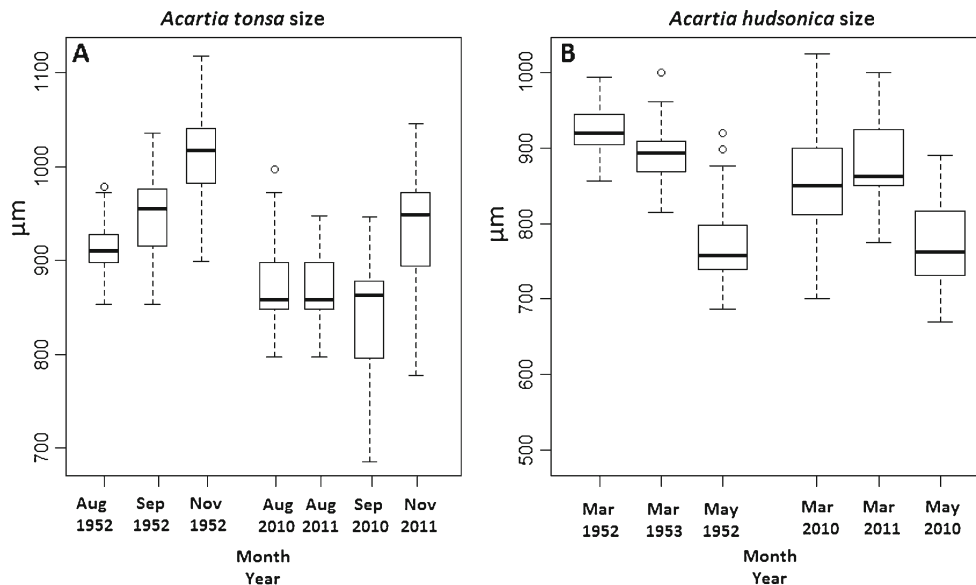
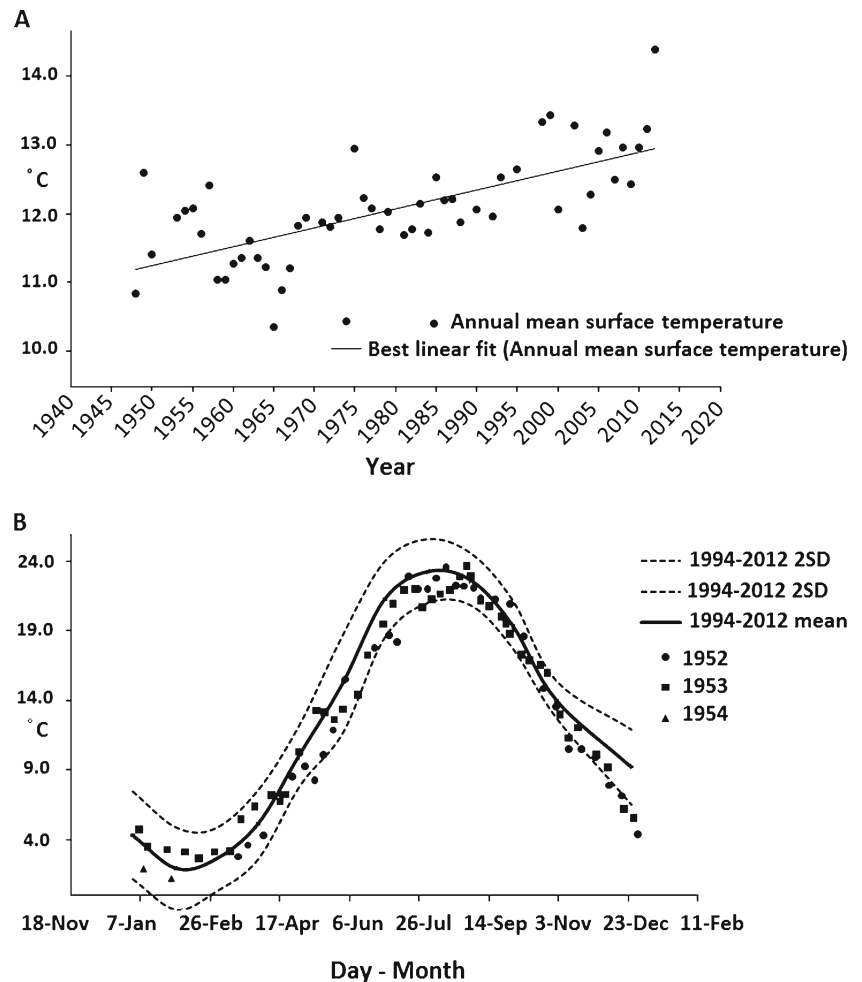
From 1948 to 2012, average annual surface water temperatures increased in the Central Basin of LIS from roughly 11 to almost 13 °C (Fig. 2a). The best-fit line yielded a rate of increase of 0.03 °C year<sup>-1</sup> ( $\tau=0.49$ ,  $p<<0.01$ , Fig. 3a). Surface temperature values for the offshore stations in the Central Basin of LIS surveyed by Deevey (1956) and reported by Riley et al. (1956) were generally distributed below the monthly surface temperature mean values measured during the 1994–2012 CTDEEP surveys in that area (Fig. 2b). During late spring to mid-summer, 78 % of the observations were below the 1994–2012 mean. This pattern reoccurs in late fall (November–December), with all observations below the mean and six observations significantly ( $\alpha=0.05$ ) cooler. From winter to mid-spring (January–May), however, values appeared evenly distributed above and below the mean. Warming was also apparent in the number of summer days with surface water temperatures >21 °C. The latest (2001–2010) decade had significantly ( $p<<0.05$ ) more days >21 °C relative to the earliest decade of measurements in which daily temperatures were reported consistently (1960–1969, data not shown).

### Size of *A. tonsa* and *A. hudsonica*

During the months when *A. tonsa* dominated the copepod community (August, September, and November), *A. tonsa* showed a significant reduction in mean individual size from 1952–1953 to 2010–2011 (Fig. 3a). The Bayesian credible interval for interannual size differences was 42.7 µm; therefore, any size differences exceeding this interval could be considered a significant difference at the  $\alpha=0.05$  threshold. The mean prosome lengths of *A. tonsa* in August 2010 ( $873\pm 4.0$  µm) and August 2011 ( $872\pm 5.4$  µm) were 50.5 and 51.5 µm smaller, respectively, than the length in August 1952. *A. tonsa* in September 2010 ( $841\pm 7.5$  µm) was almost 100 µm smaller than *A. tonsa* in September 1952. In November 2010, *A. tonsa* measured  $935\pm 5.8$  µm, 77.0 µm smaller than *A. tonsa* in November 1952.

During months when *A. hudsonica* dominated the community (March, May), there was a reduction in the mean individual size of *A. hudsonica*, but the reduction was not always significant. *A. hudsonica* in March 2010 and 2011 was significantly smaller than *A. hudsonica* in March 1952 by 43.8 and 56.9 µm, respectively (Fig. 3b). *A. hudsonica* prosome length in March 1953 was not significantly different from mean

**Fig. 2 a** Inshore Central Basin trend of temperature over 1948–2012. Correlation coefficient ( $\tau$ )=0.49,  $p < 0.01$ . Line shown is the best fit, slope=0.03, intercept=-43.2.  $N=63$ . Data from the NOAA Milford Laboratory, <http://mi.nefsc.noaa.gov/pub/index.html>. **b** Offshore surface temperatures for Central Basin stations (mean and 2SD) for 1994–2012 and reported values from Riley et al. (1956) for 1952–1954



**Fig. 3 a** Box-and-whisker plot of mean prosome lengths ( $\mu\text{m}$ ) of *A. tonsa* in August, September, and November 1952, 2010, and 2011. The thick, center line in each box is the median; upper and lower solid lines of the box represent the first and third quartiles, respectively; dashed lines represent the range; and open circles are outliers. **b** Box-and-whisker plot

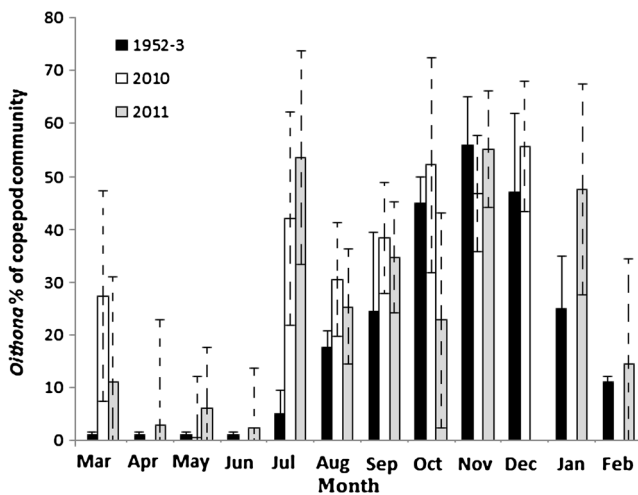
of mean prosome lengths ( $\mu\text{m}$ ) of *A. hudsonica* during March and May 1952, 2010, and 2011. The thick, center line in each box is the median; upper and lower solid lines of the box represent the first and third quartiles, respectively; dashed lines represent the range; and open circles are outliers

prosome length in March 2010 and 2011 (size differences were only 22.0 and 35.2  $\mu\text{m}$ , respectively). May 1952 and May 2010 *A. hudsonica* lengths were nearly identical ( $777 \pm 4.84$  vs.  $772 \pm 3.83$   $\mu\text{m}$ , respectively).

#### Percentage of *Oithona* sp. in Copepod Community

Monthly *Oithona* sp. percentages throughout most of the Rice survey in 2010–2011 were greater than those reported by Deevey (1956) in her 1953–1954 survey. During March 2010, July 2010, and July 2011 (Fig. 4), the percentage of *Oithona* sp. in the copepod community exceeded the 95 % Bayesian credible interval, indicating a significant increase in the relative abundance of *Oithona* during those months. In March 2010, *Oithona* sp. comprised 27.4 % of the copepod community. This is well above the credible interval, counting error, and range of values from March 1952 and March 1953. In contrast, in March 2011, *Oithona* sp. declined to 11.0 % of the community. This was still greater than *Oithona* sp. percentage in March 1952 (<1.0 %) and March 1953 (5.5 %) but within the credible interval for that month. In July 2010, the percentage of *Oithona* sp. ranged from 12.0 to 62.0 % (mean 42.0 %) at our Central Basin stations. In July 2011, *Oithona* sp. community percentage was 53.6 % (Fig. 4). Both July 2010 and 2011 percentages were well above the credible interval calculated for July 1952–1953.

During May 2010, November 2010 and 2011, and October 2011, the *Oithona* sp. percentages from the 1952–1953 survey were larger than the *Oithona* sp. percentages from the Rice survey but within the Bayesian credible intervals for those



**Fig. 4** Mean monthly percentage of *Oithona* sp. within the copepod community during the 2010–2011 Rice survey and the 1952–1953 Deevey (1956) survey. Dashed lines represent 2010 and 2011 error bars which are 95 % Bayesian credible intervals. Solid lines represent 1952–1953 error bars which indicate the range of values for their respective month (maximum and minimum). There are no error bars for values for April, May, or June in 1952–1953 because the percentage of *Oithona* was always near zero during those months

months, thus not significantly different. In 2010 and 2011, the primary peak in *Oithona* sp. community percentage occurred in November (59.6 and 55.1 %, respectively) but was accompanied in both years with secondary peak values in July of similar magnitudes (51.2 and 55.1 %, respectively). In the 1950s, the single peak in *Oithona*'s community percentage was in November.

#### Calanoid Genus Richness

The 2010–2011 survey of calanoid diversity by Rice (Table 2) matched the results of the pooled 2002–2004 and 2007–2008 CTDEEP survey data reported by Dam and McManus (2009). The contemporary surveys all report ten genera of calanoid copepods: *Acartia*, *Calanus*, *Centropages*, *Eurytemora*, *Labidocera*, *Paracalanus*, *Pseudocalanus*, *Pseudodiaptomus*, *Temora*, and *Tortanus* (Dam and G.B. McManus 2009). The only genera which were present in the 1952–1953 survey but did not appear in any of the contemporary (1993+) surveys were the two largest-sized genera, *Metridia* and *Candacia*. These genera appeared in at least one station during 5 months of the 1952–1953 survey (Deevey 1956). *Metridia* was found in November 1952 and April 1953 and *Candacia* in November and December 1952, as well as June 1953. All other genera (including those that appeared even less frequently than either *Metridia* or *Candacia* in 1952–1953) were recorded in either the 2002–2004 or 2007–2008 survey or both.

#### Discussion

In the present study, we found clear evidence of a steady warming of the Central Basin of LIS for the last five decades. Along with this warming, we observed reductions in body size in the dominant copepod species during the winter-spring

**Table 2** Annual calanoid genus richness reported for the Central Basin of LIS. Differences in mesh size, dates, and number of genera reported are noted

Annual calanoid genus richness			
Year	Survey	Mesh ( $\mu\text{m}$ )	Number of genera
1953–1954	Deevey (1956)	153	12 <sup>a</sup>
1993–1995	Capriulo et al. (2002)	202	7
2002–2004	CTDEEP	202	8
2007–2008	CTDEEP	202	8
2002–2004+2007–2008	CTDEEP	202	10
2010–2011	Rice	150	10

<sup>a</sup> Missing species from 1953–1954 in later studies: *Metridia lucens* (2,500  $\mu\text{m}$ ), *Candacia armata* (2,700  $\mu\text{m}$ )

(*A. hudsonica*) and summer-fall (*A. tonsa*), an increase in the relative proportion of the small copepod *Oithona*, and the disappearance of the two largest-sized copepod genera, *Candacia* and *Metridia*. These changes are consistent with predictions of global warming on ectotherms (Daufresne et al. 2009).

Surface water temperatures have warmed at a rate of  $0.03\text{ }^{\circ}\text{C year}^{-1}$  from 1948 to 2012 in the Central Basin of LIS (Fig. 2a). This rate is similar to what has been reported for nearby systems:  $0.04\text{ }^{\circ}\text{C year}^{-1}$  the period 1970–2002 in coastal Massachusetts (Nixon et al. 2004) and  $0.02\text{ }^{\circ}\text{C year}^{-1}$  for the period 1946–2007 in the Hudson River Estuary (Seekall and Pace 2011). Although there appear to be interseasonal differences in this rate of warming in LIS (data not shown), these differences were not statistically significant. Mean surface temperature values for 1994–2012 in the Central Basin of LIS, however, appeared consistently higher than the 1952–1954 measurements only from June to December (Fig. 2b). This result is also consistent with the changes in nearby Woods Hole (MA), where the observed warming primarily occurred from June to August and from December to February (Nixon et al. 2004).

It has been argued that global warming selects for smaller organisms in aquatic systems (Moore and Folt 1993; Daufresne et al. 2009; Sheridan and Bickfords 2011). For non-food-limited aquatic ectotherms, greater respiratory demands at higher temperatures are a possible mechanism for size reduction (Moore and Folt 1993; Sheridan and Bickfords 2011). Shifts toward smaller primary prey organisms, however, cannot be ruled out (Daufresne et al. 2009) and likely exacerbate the impact of increased energy loss due to higher respiration rates.

During late summer and fall, the dominant copepod species, *A. tonsa*, was significantly smaller in 2010–2011 than it was in 1952–1953. Likewise, the dominant species during winter-spring, *A. hudsonica*, appeared to be smaller in 2010–2011 than during winter in the 1950s, but not during spring (when it normally reaches maximum proportion of the community). This difference could reflect greater variation in the spring warming trend relative to summer and fall. Comparison of temperatures recorded by the CTDEEP during 2010–2011 and the Deevey (1956) survey during the months we examined *Acartia* sp. for size differences highlights this possibility. Surface temperatures during each month in which we saw significant size differences in *A. tonsa* (August, September, and November) were also  $1.4\text{--}2.5\text{ }^{\circ}\text{C}$  warmer relative to 1952, a significant (Student's *t* test,  $\alpha=0.05$ ) increase. During months that we did not see a significant change in the size of *A. hudsonica* (March and May), temperatures were not significantly different ( $p=0.87$  and  $0.72$ , respectively).

Higher temperatures affect copepod size via the Temperature-Size Rule (TSR), which states that an increase in temperature decreases development time and final adult size (Huntley and Lopez 1992; Daufresne et al. 2009;

Forster et al. 2012). Although growth rate and development rate (progressing from stage to stage) in copepods are both sensitive to temperature, development rate increases faster relative to growth rate; thus, adult stage is reached before the largest potential size is achieved (Forster and Hirst 2012).

A variety of other factors have also been demonstrated to affect copepod size, including food availability and season. A primary food source for *Acartia* sp. in a Long Island coastal embayment is microzooplankton (Lonsdale et al. 1996). Unfortunately, no data exist on abundance of microzooplankton in LIS during 1952–1953; furthermore, we did not measure microzooplankton during our survey. Microzooplankton in eutrophic systems may increase in abundance in response to increasing surface water temperatures (Chen et al. 2012). In addition, a comparison of chlorophyll concentration from 1952 to 1953 (Riley and Conover 1956) and during recent surveys by the CTDEEP indicates that phytoplankton abundance has not decreased with warming. That is, during the months when we saw the largest reduction in size of *A. tonsa*, September 1952 ( $4.74\text{ }\mu\text{g l}^{-1}$ ) vs. 2010 ( $3.13\text{ }\mu\text{g l}^{-1}$ ) and November 1952 ( $3.32\text{ }\mu\text{g l}^{-1}$ ) vs. 2011 ( $3.10\text{ }\mu\text{g l}^{-1}$ ), chlorophyll concentrations were not significantly different. In conclusion, it is not readily apparent that food was any more limiting to copepods during 2010–2011 relative to 1952–1953.

A seasonal decrease in copepod body size from winter to summer has been previously reported (Conover, 1956; Deevey 1960; Evans 1981; Dam and Peterson 1991; Durbin et al. 1992; Viitasalo et al. 1995). This seasonal decrease in body size appears to be related to the increase in temperature, although some change may be related to a decrease in food availability as the year progresses (see discussion in Dam and Peterson 1991). There is also some evidence that the seasonal changes in *A. tonsa* size from summer to fall may not be related to temperature (Durbin et al. 1983; Dam et al. 1994). In order to control for the effect of season on copepod size, we only compared the lengths of *Acartia* sp. during the same months in 1952–1953 vs. 2010–2011 and found significant interannual differences.

Interannual variation in body size for seasonal congeners such as *A. tonsa* and *A. hudsonica* in an estuarine system has not yet been previously reported. Our results indicate that interannual decreases in *Acartia* sp. body size were more consistently linked to interannual increases in temperature than changes in food availability. This suggests that consistent, long-term warming conditions could lead to consistently smaller copepods via the physiologically based TSR, which could be applied to other systems undergoing warming.

In the present study, the cyclopoid *Oithona* sp. (a summer-fall species) increased in annual percentage of the community from 21.3 % ( $\pm 4.9$ ) in 1952 to 32.6 % ( $\pm 4.9$ ) in 2010–2011. Deevey (1956) noted that *Oithona* sp. had such low numbers in winter that it was not worth reporting. However, we found



*Oithona* sp. to be a significant member of the late winter and early summer community in recent years (Fig. 4). In 1953, *Oithona* sp. did not increase in proportion until August, when it reached 28 % of the copepod community (Deevey 1956). In our survey, this increase occurred in July but was not sustained. *Oithona* sp. declined in August 2010 and 2011 to levels that were higher relative to 1952 but within the credible interval.

Some of the increase in relative abundance of *Oithona* sp. can be explained by its small size and feeding ecology. In nearby coastal Massachusetts, *Oithona similis* grazes heavily on ciliates and heterotrophic dinoflagellates (microzooplankton) during the summer (Nakamura and Turner 1997). Rice and Stewart (2013) found that flagellates and small cells were associated with warmer summer and fall temperatures in the Central Basin of LIS. This suggests that the increase in *Oithona* sp. community percentage may reflect their ability to graze on and preference for flagellates and smaller prey that thrive under warmer conditions.

We also observed changes in calanoid community diversity that conform to predictions of the impact of climate change on aquatic systems. Daufresne et al. (2009) projected that large ectotherms would be lost from systems as they exceed thermal tolerances. The largest calanoid copepods reported by Deevey (1956), *Metridia lucens* and *Candacia armata*, did not appear in any of the modern surveys, contributing to a possible reduction in the average copepod size within the community. No specific data could be found on temperature thresholds for *Metridia* and *Candacia*, but Kane (2003) notes that during summer in the Mid-Atlantic Bight, *Metridia* tends to concentrate off the shelf in cooler waters. *C. armata* is also a more neritic species, but other than occurring preferentially over the shelf break, it is relatively cosmopolitan in mid-Atlantic waters (Beaugrand et al. 2002). Since other neritic, smaller, rarer genera (such as the harpacticoids, *Microsetella* and *Clytemnestra*) appear to have been retained in the system since 1953 (Dam and G.B. McManus 2009), the larger size of *Candacia* and *Metridia* is their most distinguishing characteristic.

Alternative explanations for a local loss of species that prefer the shelf break as opposed to an estuary would be a reduction in salinity and/or dissolved oxygen concentrations. Kimmel et al. (2006) found that interannual variations in freshwater discharge to the Chesapeake during spring altered salinity and contributed to interannual variations in the size spectra of zooplankton biomass. Long-term changes in freshwater inputs were thus investigated as a possible variable in LIS as well. Summer (July–September) river discharge for the Connecticut River (the source of 70 % of LIS freshwater) was highly variable over the 1991–2009 period but displayed a significant increase over time ( $r^2=0.22, p=0.025$ ) at the rate of  $356 \text{ cu.ft s}^{-1} \text{ year}^{-1}$ . Average summer discharge during 1950–1960 was  $5,804 \text{ cu.ft s}^{-1}$  ( $\pm 852 \text{ SE}$ ), significantly lower

(Student's  $t$  test,  $p=0.0394$ ) than the summer discharge during 2000–2009 of  $8,924 \text{ cu.ft s}^{-1}$  ( $\pm 1,493 \text{ SE}$ ). However, unlike the results of Kimmel et al. (2006) for the Chesapeake, surface and bottom salinity during the summer and fall of the Capriulo et al. (2002) surveys and CTDEEP surveys were not significantly different from salinity during the Deevey (1956) survey (data not shown).

Surface dissolved oxygen does appear to be different, with surface values significantly ( $\alpha=0.05$ ) higher during the last decade relative to values reported by Riley et al. (1956) for 1952–1954. Bottom dissolved oxygen is also higher in the CTDEEP record, except during summer (data not shown). Since both of these changes could be expected to favor larger copepods relative to smaller ones (which would have a lower oxygen demand), they are not consistent with our observations.

Another possible explanation for community changes could be a change in nutrients. Interannual trends in eutrophication in several lakes were related to mesozooplankton community changes (Pinto-Coelho 1998). Moreover, eutrophication in estuaries has been shown to stimulate abundance of microzooplankton and decrease the proportion of mesozooplankton (Park and Marshall 2000). In contrast, in a mesozooplankton survey of Japanese brackish water systems, Uye et al. (2000) found that decades of eutrophication (40 years) resulted in increased copepod biomass, but no change in community structure. Within the mesozooplankton of LIS, Capriulo et al. (2002) found no significant difference in community structure between the more nutrient-rich Western Basin and the less nutrient-rich Central Basin of LIS. We made the same comparison during the Rice survey and also found no significant difference in terms of community proportion of *Oithona* sp. (data not shown). Our results thus suggest that the observed changes in community structure and size may be more related to temperature differences than to eutrophication.

All of the abovementioned changes—a decrease in size of the most dominant copepod genus, an increase in the proportion of one of the smallest copepod genera, and a loss of the largest copepod genera—fit the predictions of Daufresne et al. (2009) for the impact of climate change on an aquatic ecosystem. If temperatures continue to rise, *Acartia* sp. may be smaller, *Oithona* sp. may increase its abundance relative to other species, and more cool-water larger calanoid species may be lost as they exceed thermal tolerances during more frequent, warmer days. A general decrease in mean size for copepods in LIS, and potentially other eutrophic coastal systems, is thus possible. Since commercial larval fish such as Atlantic herring (e.g., *Clupea harengus*) have been demonstrated to select prey on the basis of both type and size (Checkley 1982), a shift in the community toward dominance by smaller species could disrupt the traditional predator-prey dynamics between larval fish and their primary copepod prey.

This in turn could lead to ecological changes that would affect community structure and ecosystem function such as secondary production and nutrient cycling.

**Acknowledgments** We thank the NMFS/NOAA Milford Laboratory for providing the temperature data. We thank Matthew Lyman and Katie O'Brien-Clayton of the CTDEEP for their assistance in collecting zooplankton samples. We thank the captains of the R/V *John Dempsey* and R/V *Patricia Lynn*, Rodney Randall and Kurt Gotschall, as well as the captain of R/V *Victor Loosanoff*, Robert Alix, and his crewmate, Werner Schreiner. For assistance with statistical analysis, Professor Jeff Bird of Queens College and Professor Stephen Baines of SUNY Stony Brook were invaluable. We thank Lydia Norton, University of Connecticut, for the assistance in sizing copepods. Lastly, we would like to thank the thesis committee members of the first author, Professor John Waldman, Professor Greg O'Mullan, Professor John Marra, and especially Dr. Julie Rose, for their patience and insightful comments. Analysis of the zooplankton samples by Dam and McManus and of copepod sizes for the years 2010–2011 was funded by a contract with the CTDEEP.

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