Marine Environmental Research 120 (2016) 154–165

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

# Decadal changes in zooplankton abundance and phenology of Long Island Sound reflect interacting changes in temperature and community composition

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ARTICLE INFO

*Article history:*
Received 29 April 2016
Received in revised form
3 August 2016
Accepted 5 August 2016
Available online 8 August 2016

*Keywords:*
Long Island Sound
Zooplankton
Phenology
Warming
Copepods
Ctenophores

ABSTRACT

Between 1939 and 1982, several surveys indicated that zooplankton in Long Island Sound, NY (LIS) appeared to follow an annual cycle typical of the Mid-Atlantic coast of North America. Abundance peaked in both early spring and late summer and the peaks were similar in magnitude. In recent decades, this cycle appeared to have shifted. Only one large peak tended to occur, and summer copepod abundance was consistently reduced by ~60% from 1939 to 1982 levels. In other Mid-Atlantic coastal systems such a dramatic shift has been attributed to the earlier appearance of ctenophores, particularly *Mnemiopsis leidyi*, during warmer spring months. However, over a decade of surveys in LIS have consistently found near-zero values in *M. leidyi* biomass during spring months. Our multiple linear regression model indicates that summer *M. leidyi* biomass during this decade explains <25% of the variation in summer copepod abundance. During these recent, warmer years, summer copepod community shifts appear to explain the loss of copepod abundance. Although *Acartia tonsa* in 2010–2011 appeared to be present all year long, it was no longer the dominant summer zooplankton species. Warmer summers have been associated with an increase in cyanobacteria and flagellates, which are not consumed efficiently by *A. tonsa*. This suggests that in warming coastal systems multiple environmental and biological factors interact and likely underlie dramatic alterations to copepod phenology, not single causes.

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## 1. Introduction

In coastal and marine systems, a key link between primary producers and higher trophic levels are the zooplankton (Wickstead, 1976). The zooplankton of the Mid-Atlantic is numerically dominated by copepods - microcrustaceans that graze upon phytoplankton, microzooplankton and juveniles (nauplii) of their own species as well as nauplii of other copepod species (Turner, 2004). Copepods dominate the gut contents of larval cod, haddock, and anchovy, and thus serve as an important link in aquatic foodwebs from phytoplankton and microzooplankton to larval fish (Turner, 1984). In Mid-Atlantic coastal systems, copepod abundance has historically been bimodal, with peak summer (July, August, September) abundance equaling or exceeding that in the spring (April, May, June) (Kremer, 1994).

However, zooplankton can also respond very quickly to physical forcings associated with climate change, such as changes in temperature, salinity, or stratification (Richardson, 2008). Such changes appear to be occurring in Northeast and Mid-Atlantic coastal systems. Annual regional warming of surface waters at the rate of 0.03–0.04 °C $yr^{-1}$ has been reported for Long Island Sound (LIS), Narragansett Bay, and Massachusetts Bay (Sullivan et al., 2001; Nixon et al., 2004; Rice and Stewart, 2013) (Fig 1A, Williams, 1981, Fig 1B; Lewis and Needall, 1987).

In Narragansett Bay, this warming has been associated with a unimodal zooplankton abundance pattern of reduced summer copepod abundance and a single spring copepod abundance peak (Oviatt, 2004; Costello et al., 2006; Beaulieu et al., 2013). These changes were attributed to greater overlap between copepod prey and the ctenophore *Mnemiopsis leidyi* (a gelatinous secondary consumer), increased grazing by zooplankton of primary

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http://dx.doi.org/10.1016/j.marenvres.2016.08.003
0141-1136/Published by Elsevier Ltd.

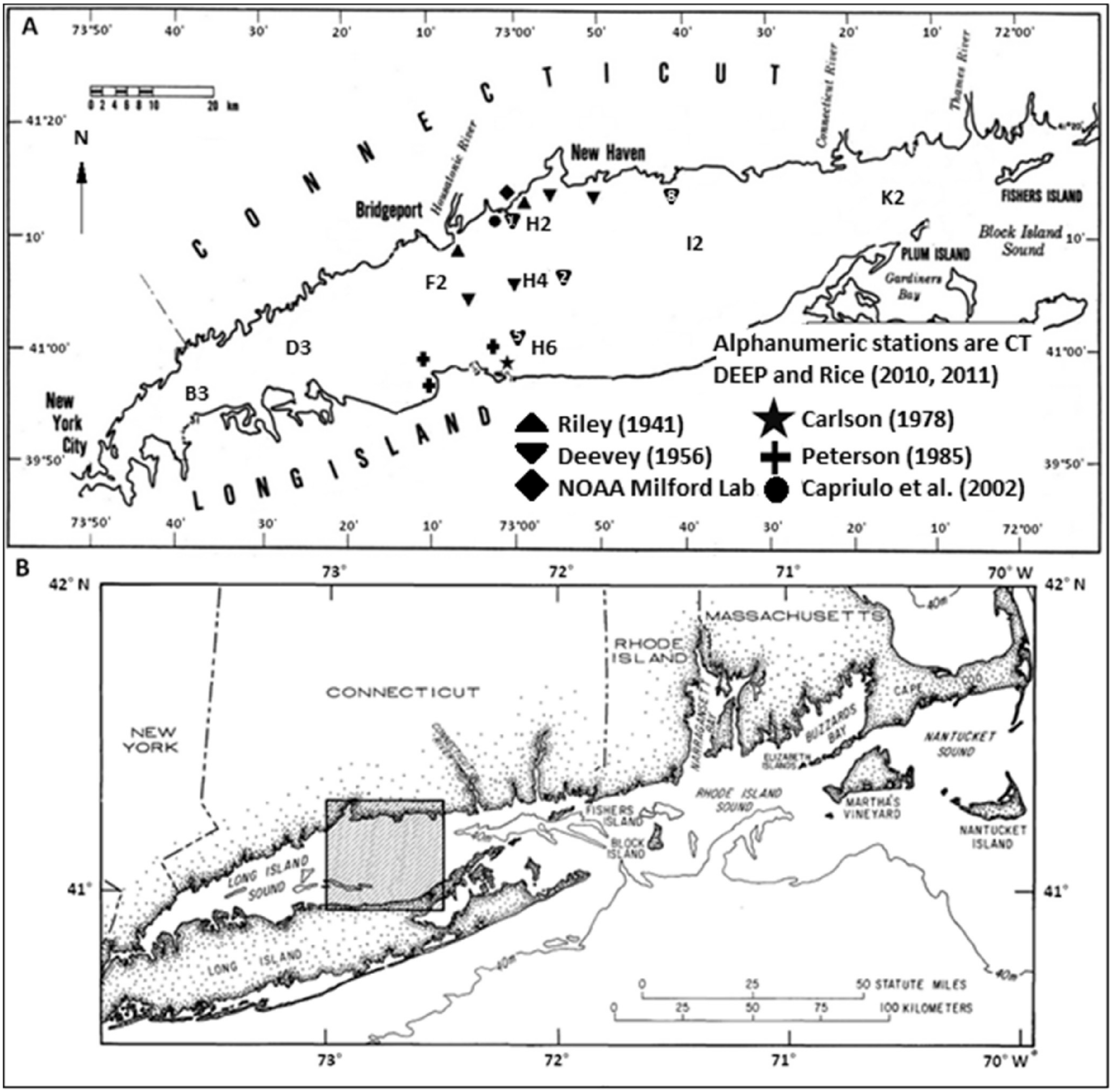


**Fig. 1.** **A**. LIS locations and survey stations referenced in this article. Deevey (1956) stations referenced elsewhere are numbered (where indicated). Base map is from Williams (1981). The Central Basin extends from 73°10′ (Bridgeport) to roughly 72°35′ (The mouth of the Connecticut River). **B.** Location of the Central basin of LIS (1A stations are in the shaded box) in relation to coastal systems referenced in this article. Narragansett Bay is between Rhode Island and Massachusetts. The Thames River Estuary is north of Fisher's Island. Base map is from Lewis and Needall (1987).

producers, and greater respiration losses by producers during warmer winter and spring months (Oviatt, 2004).

Several aspects of *M. leidyi* life history support the hypothesis that *M. leidyi* can cause the loss of summer zooplankton: 1) it is a key predator of copepods during summer along Mid-Atlantic coasts 2) *M. leidyi* is tolerant of a wide range of environmental conditions, and 3) *M. leidyi* is able to feed on a large size range of particles and organisms (Purcell, 2009). However, estimates of *M. leidyi* predation rates on copepods can range widely, from 0.3% to 58.7% $d^{-1}$ (Purcell, 2009). In coastal Rhode Island, Kremer (1979) found that *M. leidyi* could typically remove 10–11% of daily copepod abundance during summers. In Chesapeake Bay, Purcell et al. (1994) found that the rate of copepod production was an order of magnitude higher than the predation rate, and ctenophore predation alone was unable to control copepod populations. More recent research by Vliestra (2014) in the Thames River estuary (adjacent to LIS) found that the predation impact of *M. leidyi* on copepods was a maximum of 2.2% of the standing stock of copepods per day.

Other hydrodynamic, biotic and climatic factors may resolve the discrepancy. During years in which cnidarian predators of *M. leidyi* are absent from the Chesapeake Bay estuary, Purcell and Decker (2005) found *M. leidyi* predation impact increased to 45% of the copepod community per day. The climatic factors that appeared to increase *M. leidyi* predation on copepods were low salinity (which