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ORIGINAL ARTICLE

Multi-decadal (1972–2019) *Mnemiopsis leidy* (Ctenophora) abundance patterns in Narragansett Bay, Rhode Island, USA

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The influence of a warming climate on patterns of abundance and seasonality of the lobate ctenophore *Mnemiopsis leidy* is of interest worldwide, especially in regions where the species occurs at or near the limits of its thermal niche or is shifting its spatial distribution poleward. A 47-year (1972–2019) time series of weekly observations of *M. leidy* abundance in Narragansett Bay, the northern limit of its distribution in the Northwest Atlantic, was analyzed to identify links between abundance and environmental factors such as temperature. During this entire period, the species exhibited a striking degree of interannual variability with a gradual decline during the most recent years. Temperature influenced ctenophore abundance, with warmer winter and spring temperatures supporting higher abundances and longer bloom durations. Two blooms were typically observed each year, and both the summer and autumn bloom shifted earlier over time. Chlorophyll was an important factor in the abundance and bloom dynamics of reproductive stage ctenophores, where high levels of summer chlorophyll indicated lower autumn ctenophore abundance, suggesting top-down effects by *M. leidy*. These results suggest that multiple factors affect *M. leidy* abundance and phenology but that ctenophores in both native and introduced ranges may benefit from continued ocean warming.

KEYWORDS: *Mnemiopsis leidy*; ocean warming; population dynamics; phenology; Narragansett Bay

INTRODUCTION

The ctenophore, *Mnemiopsis leidyi*, has become a species of interest worldwide and has been intensively studied both in its native habitat (e.g. Kremer and Nixon, 1976) and in seas to which it has been introduced, including multiple locations in southern Eurasia (Purcell *et al.*, 2001; Kideys, 2002; Costello *et al.*, 2012) and northern Europe (e.g. Javidpour *et al.*, 2006; Riisgård *et al.*, 2007; Tendal *et al.*, 2007). The enormous range expansion, demonstrative of the adaptable nature of this species, is well summarized by Jaspers, Huwer, *et al.* (2018), who explain the role of ocean currents in spreading the species from marine source regions. As a result of its high reproductive capacity, *M. leidyi* rapidly increases in abundance when temperature and food availability are favorable and can significantly impact food web function. The first studies on *M. leidyi* reproduction, population growth rates and effects on prey populations in Narragansett Bay, Rhode Island, USA (Kremer and Nixon, 1976; Kremer, 1979; Deason and Smayda, 1982a) established the top-down control of lower trophic levels by this species. The ability of the species to control planktonic ecosystem dynamics where and when it occurs at high densities, acting as a top-down predator, continues to be documented in both native and now in introduced habitats (Deason and Smayda, 1982b; Shiganova, 1997; Ivanov *et al.*, 2000; Sullivan *et al.*, 2001; Costello *et al.*, 2006a, 2006b, 2012; Tiselius and Møller, 2017). Because of *M. leidyi*'s influence on ecosystems, understanding the drivers of ctenophore abundance is important in all regions in which it occurs.

Water temperature is a major driver of seasonal and interannual variability in *M. leidyi* abundances as seen by the strong association of population dynamics to seasonal heating and cooling (Kremer, 1994). In Narragansett Bay, for example, *M. leidyi* abundances are typically minimal in the cold winter months (November to April) but can quickly increase during bloom events that usually occur when the Bay warms between May and October (Deason and Smayda, 1982b; Sullivan *et al.*, 2001; Costello *et al.*, 2006a, 2006b, 2012; Beaulieu *et al.*, 2013). Most studies of the relationship of *M. leidyi* population abundances to temperature explain specific linkages to the life cycle, such as the impact of minimum winter temperatures on reproduction (Costello *et al.*, 2006b, 2012; Salihoglu *et al.*, 2011) or short-term shifts in bloom phenology (Sullivan *et al.*, 2001). While important, these studies do not explain broadscale patterns over decadal scales of interannual variability. An improved understanding of *M. leidyi*'s response to temperature, both in terms of abundance and bloom dynamics, is needed for predicting impacts in its native habitat and in northern Europe where winter warming has allowed the species to persist in previously colonized regions (Jaspers, Huwer, *et al.*, 2018).

While research in other habitats has also provided important insights into the ecology of *M. leidyi* (e.g. McNamara *et al.*, 2013; Breitburg and Burrell, 2014), Narragansett Bay, a large temperate estuary has proven to be an ideal study site with few confounding factors to investigate such lingering questions. First, the resident Narragansett Bay population is seeded from inshore waters rather than from yearly offshore invasions (Kremer and Nixon, 1976; Costello *et al.*, 2006b; Beaulieu *et al.*, 2013). Second, predators of *M. leidyi* have only rarely been reported. The predatory ctenophore *Beroë ovata*, for example, invades this system infrequently and only in late summer from southern waters (Kremer and Nixon, 1976; Beaulieu *et al.*, 2013). Third, Narragansett Bay is at the historic northern extreme of the *M. leidyi* range along the coast of North America (Mayer, 1912), a geographical region that has been experiencing rapid ocean warming, due to a combination of climate change and shifts in ocean circulation (Pershing *et al.*, 2015; Chen *et al.*, 2020), and subsequent spatial and phenological shifts in marine population distributions (Hare *et al.*, 2016). Studying the northern extent of *M. leidyi* populations has already proven useful in drawing inferences about changes in phenology of the species in response to climate change (Sullivan *et al.*, 2001, 2008; Costello *et al.*, 2006a). Finally, it is thought that introduction to northern Europe originated from invasion of *M. leidyi* from its northern Western Atlantic native habitat, rather than southern native Western Atlantic populations (Bayha *et al.*, 2015). This potential genetic similarity between Narragansett Bay ctenophores and the introduced populations in northern Europe may prove important to predicting behavior of the species there. Despite intensive studies of habitat requirements, predators, feeding and reproduction for Eurasian populations of *M. leidyi* (e.g. Tiselius and Møller, 2017; Jaspers, Marty, *et al.*, 2018), not all factors controlling its abundance and distribution have been resolved (Jaspers, Marty, *et al.*, 2018).

Time series of zooplankton data must be sufficiently long to resolve both interannual and longer-term responses of species to environmental factors such as temperature, but records of this consistency and duration are rare. Here, we examine a nearly continuous 47-year, weekly record of *M. leidyi* in lower Narragansett Bay using samples collected from a single location. During this time, Narragansett Bay has experienced shorter multi-decadal warming periods likely partially driven by climate oscillations (Hawk, 1998; Oviatt, 2004; Smayda *et al.*, 2004) as well as a long-term increase of mean annual water temperature on the order of 1.4–1.6°C, with even greater winter warming of ~2.0°C over the last 50 years (Fulweiler *et al.*, 2015). Not surprisingly, significant changes in composition of phytoplankton,

zooplankton and fish species have been documented over this time period (Li and Smayda, 1998; Collie *et al.*, 2008; Nixon *et al.*, 2009; Borkman *et al.*, 2018). With respect to *M. leidyi*, it was suggested more than a decade ago that the species was benefitting from warming winter and spring temperatures with altered phenology (an advance in the spring appearance) and increasing abundance (Sullivan *et al.*, 2001, 2008; Costello *et al.*, 2006a, 2006b; Beaulieu *et al.*, 2013). At the time, the data available was temporally sparse and collected as part of several different studies conducted at different stations in Narragansett Bay. The record compiled and analyzed here, spanning from 1972 to 2019, makes possible a novel reanalysis and update of the drivers of *M. leidyi* population dynamics. This work aims to (i) determine how long-term trends of *M. leidyi* annual abundance and bloom dynamics have changed over time; (ii) identify the major environmental drivers of interannual variance in *M. leidyi* abundance and (iii) characterize the influence of winter temperatures on *M. leidyi* population dynamics.

METHOD

Field methods and data collection

From 1972 to 2019, weekly research cruises recorded ctenophore abundance at Station 2, located in the lower West Passage of Narragansett Bay (41° 34' 07" N, 71° 23' 31" W; Fig. 1). Station 2 is an open bay station with a depth of 6–8 m. There was a 4-year break in data collection from June 1997 to October 2001. Between 1972 and 1983, collections occurred only between summer and late autumn, with sampling in summer beginning the week following observation of ctenophores in the water column in a weekly zooplankton tow that was also collected at this station. After 1983, samples were collected throughout the year. From 1972 to 1997, ctenophores were collected using a 1 m × 1 m square net hauled vertically from depth to the surface. The mesh size was 1 mm for 1976–1997, but was 6.4 mm in 1972, 153 µm in 1973–1974 and 1.8 mm in 1975. Once the net was on-board, the ctenophores were counted to yield number of ctenophores m⁻³. During the 2001–2019 sampling, ctenophores were collected with a 0.5 m diameter circular plankton net, also of 1 mm mesh size, by two vertical tows except when ctenophores were sufficiently dense to obtain a representative count from one tow. Compared to the earlier time series where ctenophore counts were made onboard the vessel, the combined samples from the 2001–2019 time series were returned to the lab. There, ctenophores were counted live under a dissecting scope to aid in detection of the smaller ctenophores, where ctenophores were measured for total length to

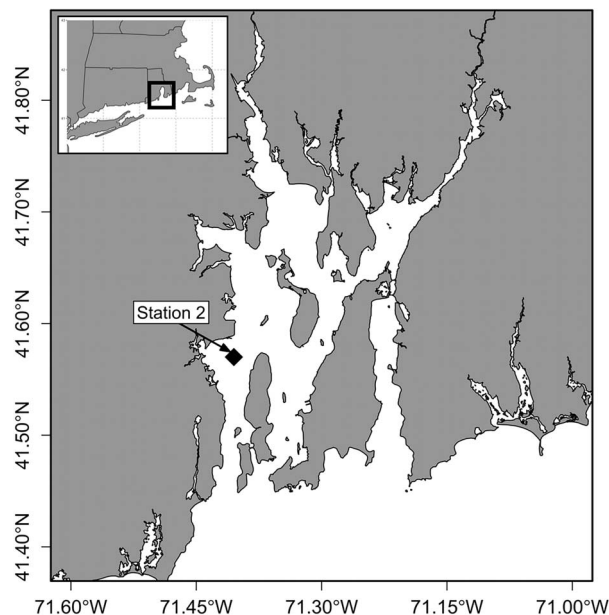


Fig. 1. Map of the location sampling station, Station 2, in Narragansett Bay, RI. The inset map shows the location of Narragansett Bay along the US East Coast.

distinguish primarily larval (<1 cm) from reproductive stage (>1 cm) individuals. The abundance of ctenophores m⁻³ was based on the volume sampled, calculated either from a flow meter (October 2001–January 2005; General Oceanics) or estimated from the depth of the vertical tows (February 2005–December 2019). The 1972–1997 data are available at and 2001–2019 data are available online at <https://web.uri.edu/gso/research/plankton>. It should be noted that the data for 2001–2003 in this study were first published in Costello *et al.* (2006b) and are included here to maintain consistency throughout the 47-year time series.

Statistical methods

Irregular sampling frequency and large week-to-week variability in observed ctenophore abundance throughout the entire time series, likely due in part to a patchy distribution or tidal dynamics, presented challenges in analyzing the raw data. To mitigate this, ctenophore samples for both time periods were first assigned to weeks of the year, and then 5-week running mean abundances (ctenophores m⁻³) were calculated to smooth the data and impute missing values using nearby measurements where available. The effects of sampling week and year were assessed to characterize the average seasonal cycle (intra-annual variability) and yearly time trend (inter-annual variability) of ctenophore abundance using generalized additive models (GAMs) with the R package

'mgcv' (Wood, 2013). Because the data were positively skewed, contained many zeros and exhibited nonlinear trends within and across years, and GAMs with Tweedie-distributed errors were well suited to evaluate seasonal and inter-annual trends. Due to the change in counting procedures between 1972–1997 and 2001–2019, there was concern that an apparent increase in abundance in the later time series compared to the earlier time series could be influenced by more thorough counting of < 1 cm ctenophores. Because of this concern, here, and in all subsequent analyses, data for 1972–1997 and 2001–2019 were considered separately. The larval and reproductive size classes of ctenophores were also analyzed separately for the 2001–2019 observations because preliminary tests showed potentially important phenological differences between the size classes. In order to evaluate patterns in the relative abundance of the size classes within and across year between 2001 and 2019, the proportion of reproductive stage ctenophores was calculated for each sample. The proportion data were then transformed to fall strictly within the (0,1) interval as in Smithson and Verkuilen (2006) and fit with a GAM with beta-distributed errors.

The fitted mean seasonal cycles from the GAMs of ctenophore abundance were used to define the approximate timing and number of the annual bloom period(s) for both time series (1972–1997 and 2001–2019). Based upon preliminary analyses of the data, up to two blooms per year, following a winter–spring abundance minimum, were hypothesized. Where two blooms were present in the GAM fits, the density minimum between estimated modes was used as a boundary of potential bloom periods. While the GAM fits to ctenophore abundance provided information on the average number and timing of ctenophore blooms throughout the two time series, two-component Gaussian mixture models were used to identify the number of blooms and when they occurred in each individual year of sampling. Here, ctenophore density observations of at least 10 ctenophores m^{-3} were considered to represent a bloom condition. Because the average proportion of reproductive stage ctenophores in samples was 0.22 between 2001 and 2019, bloom thresholds of 7.8 and 2.2 ctenophores m^{-3} were used for the larval and reproductive stages, respectively. A threshold of 2.2 ctenophores m^{-3} was also used for the 1972–1997 data because it was assumed that visual counts would primarily sample ctenophores in the reproductive stage. The data were subset to density observations at or above the corresponding bloom threshold and fit using the R package 'mixtools' (Benaglia *et al.*, 2009). A year was considered to have two blooms if the fitted modes were on either side of the time-averaged bloom period boundary defined by the GAM of ctenophore abundance and there

was a local minimum in abundance between them. In such cases, the week of minimum abundance between the two modes was considered the true boundary between bloom events in a given year. Specifically, the average bloom peak timing in the GAM fit to the 1972–1997 data was 4 weeks later than the first bloom period in the 2001–2019 data, so the boundary between the prospective bloom periods in the Gaussian mixture model was set 4 weeks later (week 38) for the 1972–1997 data than for the more recent time series (week 34). The week of the start and end of the blooms identified by the Gaussian mixture model fits was then quantified to estimate ctenophore abundances during the bloom. This was achieved by fitting an 80% highest density interval (HDI), which identifies the narrowest time interval in which 80% of ctenophores were collected during a bloom period, to the weekly densities. For each HDI, a suite of bloom metrics were recorded, including the bloom duration (weeks between bounds), mean abundance, peak abundance and week of peak abundance.

The calculated bloom metrics for each year from the HDIs were evaluated for time trends and relationships with environmental factors to investigate patterns in ctenophore abundance. In addition to year, environmental covariates including surface water temperature, salinity and chlorophyll, and indices of the North Atlantic Oscillation (NAO) and ocean circulation were tested. Temperature, salinity and chlorophyll data were obtained from NABATS.org (<https://www.nabats.org/>) for 1972–1997 and from the University of Rhode Island Graduate School of Oceanography plankton survey (<https://web.uri.edu/gso/research/plankton>) for 2001 to 2019. Seasonal means of each were calculated for winter (January–March; the coldest quarter of the year in Narragansett Bay), spring (April–June), summer (July–September; the warmest quarter of the year in Narragansett Bay) and autumn (October–December). Minimum winter surface temperature was also considered. The winter (December–March mean) NAO Index, which has been shown to impact the winter wind field and coastal circulation of Rhode Island (Luo *et al.*, 2013), was obtained from the National Weather Service Climate Prediction Center (<https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao>). Due to past observations of correlations between Gulf Stream dynamics and water temperatures in Narragansett Bay (Borkman and Smayda 2009), the Regional Slope Water Temperature Index was calculated as in Pershing *et al.* (2001) and included in the analysis.

Relationships between bloom metrics were analyzed to determine if conditions of the first bloom affected the conditions of the second bloom. Such patterns, along with relationships between bloom metrics and environmental

covariates, were investigated separately using generalized linear models (GLMs). Metrics for each bloom were only tested against environmental covariates describing conditions since the prior bloom period, where it was assumed any relationships with conditions earlier than the prior bloom would be mediated through, or complicated by, that event. Data prior to 1984 and in 1995 were omitted from the GLMs due to low and irregular sampling frequency. Because blooms did not occur in every year, resulting in small sample sizes, and could be highly variable, the GLM residuals were modeled with a student's *t*-distribution with the R package 'heavy' (Osorio, 2019) to decrease the impact of extreme values. Forward model selection to identify selected covariates to include in the GLMs was also performed via the likelihood ratio test due to small sample sizes. For selected models where multiple covariates were included, collinearity was checked among covariates to ensure correlated predictors were not influencing the interpretation of the results. All analyses were conducted in R (version 3.6.2; R Core Team 2019).

RESULTS

Annual abundance

From 1972 to 2019, 1492 zooplankton tows were made with ctenophores present in 904 collections (61% of tows). With all years pooled, *M. leidy* was found during every week of the year, but its abundance was usually greatest during the summer from July through September. On average, 0.9 ctenophores m^{-3} were recorded between January and March, increased during April through June (13.4 ctenophores m^{-3}) and reached peak abundances (41.7 ctenophores m^{-3}) between July and September. From October to December, abundance declined to an average 16.1 ctenophores m^{-3} . Higher average abundances for the summer and autumn seasons reflect the frequency of summer and autumn blooms present throughout the data set. Mean annual ctenophore abundance was highly variable throughout the entire time series (Table I; Figs 2A and 3). In general, the number of ctenophores was higher for the 2001–2019 time series than for the 1972–1997 time series (Table I). This is very likely an artifact of the post collection counting process. While samples for all years were counted live and very shortly after collection (ctenophores cannot be preserved), the 2001–2019 samples were counted in the laboratory under a dissecting scope allowing for a greater number of small ctenophores to be detected than for the 1972–1997 samples counted on board the vessel without the aid of a scope. Counts of reproductive stage ctenophores between 2001 and 2019, meanwhile, were similar to the observations made between 1972 and

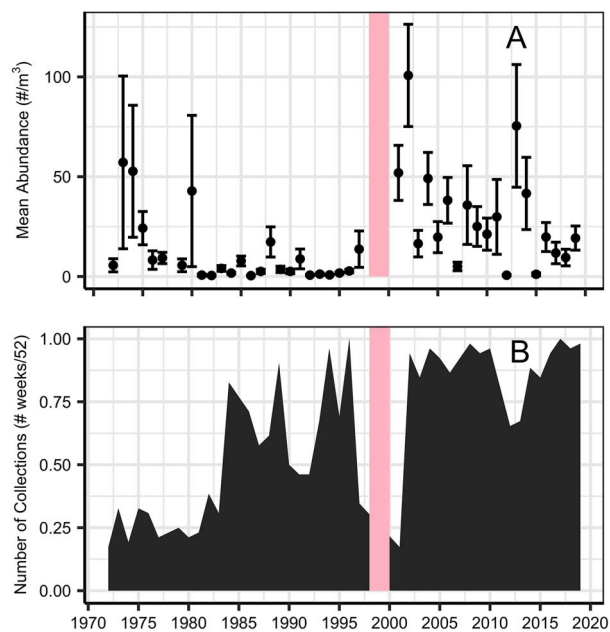


Fig. 2. The interannual variability in total ctenophore abundance is shown with annual trends in density and collection frequency plotted per year with (A) the annual ctenophore abundance (mean \pm S.E.) and (B) the annual proportion of samples (number of sampling weeks divided by 52 weeks in year) for all ctenophore collections (1972–2019). Sampling frequency markedly increased after 1984. The pink (gray in print) bar indicates the period where sampling stopped (1997–2000).

1997 (Table I). Comparisons between the 1972–1997 and 2001–2019 time series refer to the larger >1 cm reproductive stage ctenophores.

Seasonal bloom dynamics

The GAM fit to 1972–1997 data indicated that there was a variable trend in ctenophore abundance over time that initially decreased before stabilizing (Fig. 3A; Supplementary Table I). The increase in abundance in 1997 is based upon a partial year of data and therefore may not represent a true change in density. On average for the 1972–1997 time series, abundance reached an annual minimum in late February (\sim week 9) and peaked in a single August bloom (\sim week 32; Fig. 4A). A second GAM fit to data from 1984–1997 only, when sampling effort was more frequent throughout the year, produced similar results. Between 2001 and 2019, inter-annual and intra-annual abundance patterns differed by size class. Across years, larval stage ctenophores declined in abundance over time (Fig. 3B) while exhibiting two blooms per year (Fig. 4B). Following an abundance minimum in early April (\sim week 15), the first bloom, referred to herein as the summer bloom, generally started in July (\sim week 27) and was characterized by higher

Table I: For each year of collection, the number of samples, mean (s.e.), median, maximum value (week of maximum value) and first week of occurrence (week of occurrence at bloom threshold) are reported for (a) 1972–1997 and (b) 2001–2019 time series.

(a)					
Year	# of sampling dates (n)	Mean abundance (std. error)	Median abundance	Maximum value (week of year)	Week of first occurrence (week of occurrence > 2.2 ctenophores m ⁻³)
1972	9	5.62 (3.29)	0.43	30.65 (38)	27 (36)
1973	17	57.16 (43.26)	0.00	735.00 (29)	29 (29)
1974	10	52.72 (33.06)	2.00	328.00 (33)	27 (29)
1975	17	24.23 (8.34)	6.81	100.00 (34)	30 (31)
1976	16	8.24 (4.63)	0.82	73.56 (35)	31 (32)
1977	11	9.29 (2.82)	5.01	25.12 (38)	32 (32)
1978	N.D.	N.D.	N.D.	N.D.	N.D.
1979	13	5.20 (3.20)	0.50	39.81 (34)	3 (32)
1980	11	42.84 (37.88)	2.50	421.00 (33)	31 (31)
1981	12	0.71 (0.52)	0.00	6.38 (39)	39 (39)
1982	20	0.52 (1.52)	0.00	6.63 (32)	32 (32)
1983	16	4.05 (1.43)	2.56	23.13 (38)	33 (34)
1984	43	1.71 (0.43)	0.38	11.19 (34)	4 (5)
1985	40	7.79 (2.47)	1.53	80.41 (40)	1 (1)
1986	37	0.45 (0.11)	0.12	2.99 (46)	1 (4)
1987	30	2.56 (1.08)	0.09	27.13 (51)	1 (33)
1988	32	17.32 (7.55)	1.84	207.94 (30)	2 (2)
1989	47	3.57 (1.60)	0.06	60.94 (33)	1 (31)
1990	26	2.57 (1.18)	0.00	26.46 (33)	13 (27)
1991	24	8.81 (4.96)	0.03	88.38 (37)	13 (36)
1992	24	0.69 (0.28)	0.06	4.94 (32)	22 (32)
1993	35	1.20 (0.58)	0.13	16.13 (22)	1 (1)
1994	50	0.81 (0.23)	0.00	7.63 (16)	8 (13)
1995	36	1.73 (0.51)	0.25	12.50 (3)	1 (3)
1996	52	2.77 (0.85)	0.25	32.50 (52)	1 (16)
1997 ^a	18	13.71 (9.11)	0.16	162.5 (15)	1 (1)

(b)					
Year	# Of sampling dates (n)	Mean abundance (std. error)	Median abundance	Maximum value (week of year)	Week of first occurrence (week of occurrence > 10.0 ctenophores m ⁻³)
2001 ^b	9	51.92 (13.79)	41.41	144.02 (43)	43 (43)
2002	49	100.73 (25.61)	1.95	720.48 (25)	1 (24)
2003	44	16.47 (6.64)	0.07	200.78 (29)	2 (27)
2004	50	49.12 (13.04)	2.19	395.13 (43)	25 (25)
2005	48	19.73 (7.79)	2.52	323.03 (42)	1 (21)
2006	45	38.18 (11.45)	0.36	279.40 (26)	1 (26)
2007	48	5.04 (2.16)	0.00	95.31 (44)	33 (38)
2008	51	35.79 (19.71)	0.00	933.61 (27)	15 (25)
2009	49	25.08 (9.96)	0.36	335.63 (32)	24 (28)
2010	50	21.24 (8.04)	1.82	311.27 (28)	1 (11)
2011	42	29.88 (18.76)	0.73	701.09 (24)	1 (23)
2012	34	0.66 (0.28)	0.00	8.00 (29)	22 (na)
2013	35	75.45 (30.72)	4.07	844.44 (27)	2 (27)
2014	46	41.62 (18.09)	1.85	622.22 (36)	1 (2)
2015	44	1.11 (0.75)	0.00	31.85 (43)	18 (43)
2016	49	19.78 (7.27)	1.48	333.33 (26)	7 (23)
2017	52	11.81 (5.39)	0.37	255.56 (42)	1 (5)
2018	50	9.50 (4.16)	0.00	133.33 (39)	1 (39)
2019	51	19.26 (6.04)	1.11	261.11 (34)	5 (26)

^a Data collection in 1997 was ended early (May 5), so this only comprises part of a year of sampling.

^b Sample collection for 2001 was initiated late in the year (October 24), so this does not comprise of a full year of sampling. Mean and median abundances are ctenophores m⁻³

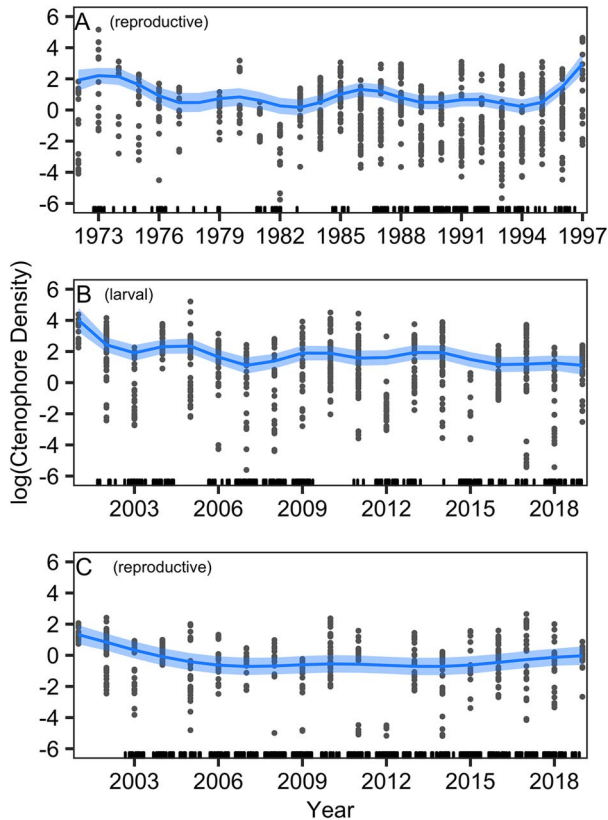


Fig. 3. The inter-annual trends (solid blue line) and 95% confidence interval (blue shading) for ctenophore abundance estimated by GAMs show (A) ctenophore abundance from 1972–1997 decreases and then stabilizes during the late 1980s, and (B) larval stage ctenophore and (C) reproductive stage ctenophore abundances from 2000–2019 have a slight decreasing trend. The jittered rug plot on the *x*-axis of each panel indicates zeros in the data. The gray points are the $\log(\text{ctenophore abundance})$ from the raw data. The average seasonal cycles were removed from both the raw data and GAM estimates for plotting.

abundances on average than the second bloom, referred to herein as the autumn bloom, in October (~week 40). Reproductive stage ctenophores declined in abundance during the early 2000s before stabilizing and increasing again beginning in the mid-2010s (Fig. 3C). This size class reached an annual abundance minimum in mid-April (~week 17) and displayed two blooms per year at approximately the same times as the larval stage (Fig. 4C). However, the abundances of reproductive stage ctenophores were approximately equal in both blooms. It should also be noted that because sampling only occurred at a single fixed location, increases in either size class of ctenophore could also be an artifact of advection from the upper bay locations where reproduction can begin earlier (Costello *et al.* 2006b). The between-bloom abundance minimum occurred in late August (~week 34) for both stages. The GAM fit to ctenophores size composition between 2001 and 2019

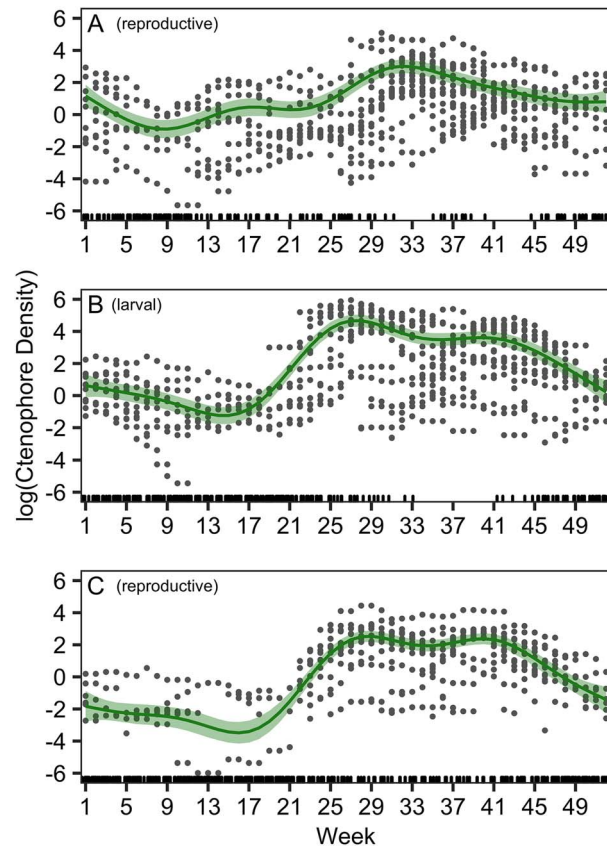


Fig. 4. The seasonal cycles (solid green line) and 95% confidence intervals (green shading) for ctenophore abundance estimated by the GAMs show a unimodal bloom period for (A) ctenophore abundance from 1972 to 1997 and a two-bloom mode for (B) larval stage ctenophore and (C) reproductive stage ctenophore abundances from 2000 to 2019. The summer bloom (i.e. first bloom) has shifted earlier in the year from the 1972–1997 to the 2000–2019 data. The jittered rug plot on the *x*-axis of each panel indicates zeros in the data. The gray points are the $\log(\text{ctenophore abundance})$ from the raw data. The average inter-annual trends were removed from both the raw data and GAM estimates for plotting.

suggested that relative abundance of reproductive-to-larval stage ctenophores was highest in the early 2000s and late 2010s (Fig. 5B; Supplementary Table II). In addition, the reproductive-to-larval stage ctenophore ratio reached a seasonal maximum during the between-bloom abundance minimum (Fig. 5C), suggesting a maturation of the larvae, although this cannot be directly measured from our data.

The Gaussian mixture model fits revealed that most years in both time series exhibited summer and autumn ctenophore blooms (Fig. 6A–C; Supplementary Table III), suggesting the time-averaged unimodal pattern fit by the GAM for the 1972–1997 data was comprised of two variable annual bloom events. Only one bloom was recorded in nearly all years prior to 1984, but this appears

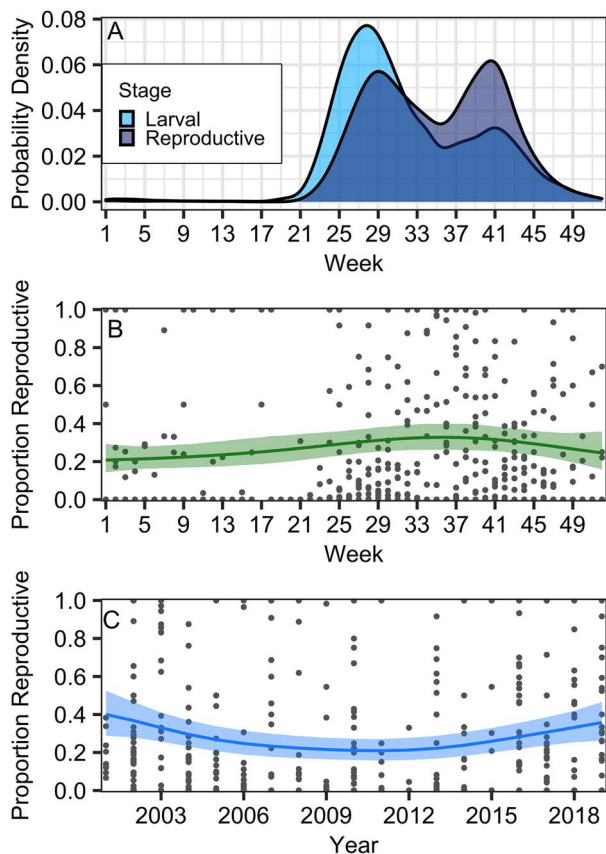


Fig. 5. The proportion of reproductive stage ctenophores varied annually both during and across years. (A) The distribution of collections of larval and reproductive stage ctenophores by week of the year. On average, there is a two-bloom pattern, with larval ctenophores dominating the summer bloom and reproductive stage ctenophores dominating the autumn bloom. The results of the GAM fit to the proportion of each sample made up by reproductive stage ctenophores (B and C), where the model fit and 95% confidence interval are indicated by solid lines and shading, respectively. (B) The change in relative abundance of reproductive stage ctenophores by week, where they made up the highest proportions of samples collected during the late summer. The average inter-annual trend was removed from the data and GAM estimates for plotting. (C) The change in relative abundance of reproductive stage ctenophores over time, showing a declining trend until 2010. The average seasonal cycle was removed from the data and GAM estimates for plotting. The gray points for both (B) and (C) are the proportion reproductive stage from the raw data.

to be a result of sampling frequency, and thus these years were omitted from further analyses of bloom dynamics. Data for 1997 and 2001 were also omitted because collection only occurred in portions of the year. Both the summer and autumn blooms were undetectable in some years, and no blooms were observed for either size class in 2012. For the summer bloom, there was not a significant difference between the 1984–1996 and 2002–2019 reproductive stage ctenophore data for both the mean and peak abundance measures (Wilcoxon Rank Sum test, $P > 0.05$). There was also not a significant difference

between the two time series for the mean and peak abundances of the autumn bloom (Wilcoxon Rank Sum test, $P > 0.05$). Both of these metrics were significantly higher during the summer bloom compared to the autumn bloom for larval ctenophores during the later time series (Wilcoxon Rank Sum test, $P < 0.01$). The start and end of the bloom and week of peak abundance for both the summer and autumn blooms occurred 2–5 weeks earlier for reproductive stage ctenophores between 2002 and 2019 than for the 1984–1996 data (Supplementary Table III; Wilcoxon Rank Sum test, $P < 0.05$). As suggested by the GAMs, there were no differences between the bloom phenologies of larval and reproductive stage ctenophores from the 2002–2019 time series (Wilcoxon Rank Sum test, $P > 0.05$). Therefore, it can be hypothesized that the phenology of bloom timing has shifted earlier for all stages of ctenophores in the 2002–2019 time series when compared to the 1984–1996 time series.

The fitted GLMs assessing the potential effects of the summer bloom on the autumn bloom identified inter-relationships among bloom metrics for the 1984–1996 data and reproductive stage ctenophores from the 2002–2019 data. Both duration and ctenophore abundance of the 1984–1996 autumn bloom were related to the timing and abundance of the summer bloom. Thus, from 1984–1996, autumn ctenophore abundances were higher when the summer bloom ended later and when summer abundances were higher (Table II). Also, the duration of the autumn bloom was longer when summer ctenophore abundances were lower. For the reproductive stage ctenophores from 2002 to 2019, all autumn bloom metrics relating to phenology (e.g. start, end, duration, peak week) were all correlated with phenology of the summer bloom (Table II). Overall, the phenology of the autumn bloom was positively correlated with phenology of the summer bloom (i.e. an earlier end of the summer bloom would lead to an earlier autumn bloom). However, for larval ctenophores, there was no summer bloom metrics correlated with the autumn bloom.

There were also detectable shifts in the phenology of ctenophore blooms over time. The start of the autumn blooms shifted later over time in the 1984–1996 data and in the 2002–2019 reproductive stage ctenophore data (Table III). However, overall, there were earlier autumn blooms occurring in 2002–2019 when compared to 1984–1996, even if time trends in both data sets exhibited similar patterns. Combined with a negative trend in summer bloom end in the earlier time series, these correlations indicate a lengthening of the annual period of elevated ctenophore abundance defined by the summer and autumn blooms over both datasets.

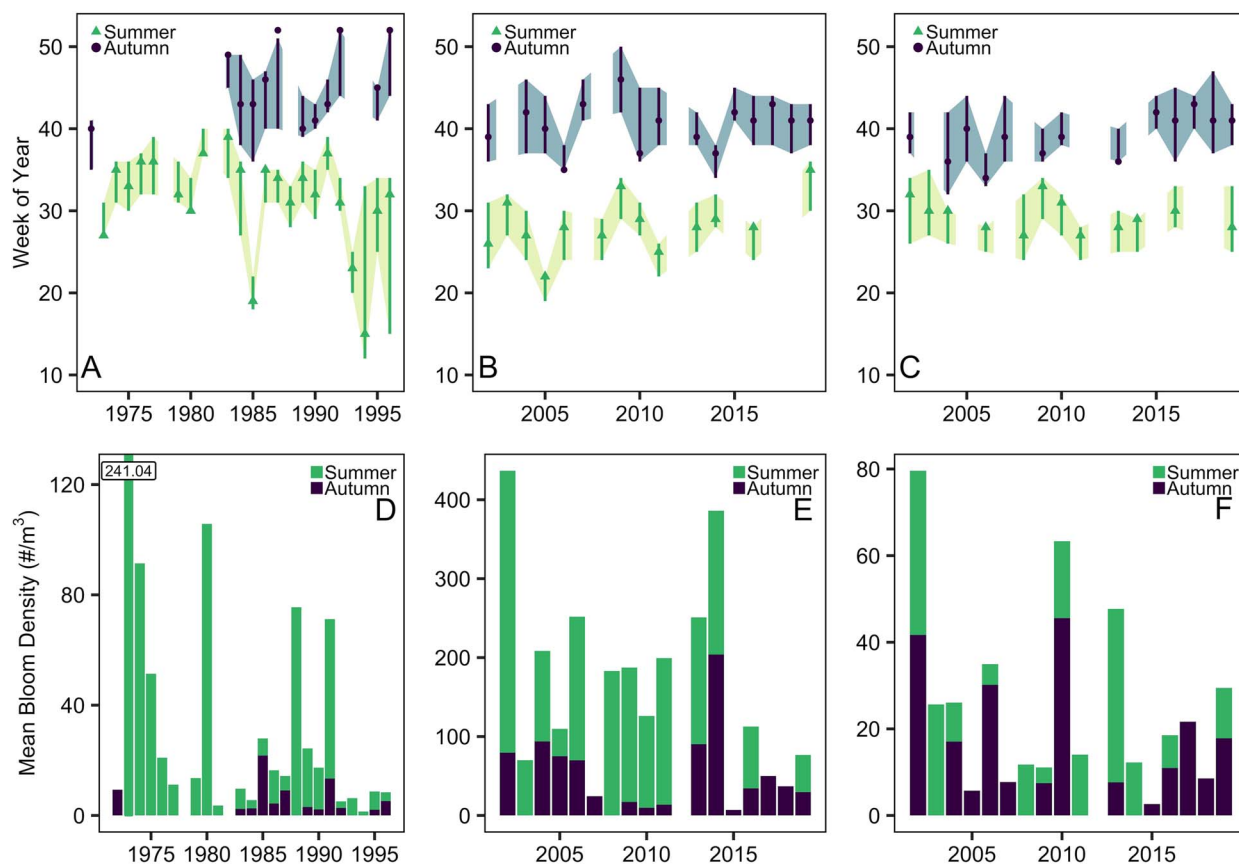


Fig. 6. The bloom duration fit from the 80% highest density intervals (shading) and week of peak abundance are shown for both the summer (green triangles, print gray triangles) and autumn blooms (purple circles, print black circles) for the (A) 1972–1997 ctenophores, (B) 2001–2019 larval ctenophores and (C) 2001–2019 reproductive ctenophores. The mean bloom density calculated throughout the bloom duration with summer (green, print gray) and autumn (purple, print black) blooms are shown in D–F (D, 1972–1997 ctenophores; E, 2001–2019 larval ctenophores; F, 2001–2019 reproductive ctenophores). In panels A–C, the years without blooms, either summer and/or autumn, appear as breaks between the filled regions, and for D–F, years with no blooms are denoted as a break between bars on the x-axis. Note for D–F, the bars are stacked, not cumulative and the different scales for the mean bloom density. For D, the mean bloom density for 1973 was 241.04 ctenophores m^{-3} , and the bar for this year was cut off to scale the y-axis to the other mean bloom densities. Estimated values for the bloom metrics are in the supplemental table (Supplementary Table III).

Table II: Selected covariates and associated coefficient values of interrelationships for summer and autumn ctenophore blooms from the best fit GLMs. For 2001–2019, L = larval and R = reproductive stage

Data set	Bloom period	Bloom metric	Selected covariate	Coefficient value ^a
1984–1996	Autumn	Duration	Summer peak abundance	–0.07
			Summer mean abundance	–0.11
1984–1996	Autumn	Peak abundance	Summer end	–1.95
			Summer peak week	–1.27
			Summer end	–1.7
1984–1996	Autumn	Mean abundance	Summer peak abundance	0.13
			Summer mean abundance	0.2
			–	–
2002–2019 L	Autumn	–	–	–
2002–2019 R	Autumn	Start	Summer end	0.7
			Summer duration	0.9
2002–2019 R	Autumn	End	Summer end	0.68
2002–2019 R	Autumn	Duration	Summer duration	0.33
2002–2019 R	Autumn	Peak week	Summer end	0.89
			Summer duration	1.03

^aA positive coefficient value for the start and end of a bloom indicates a later start and end date, respectively, and for bloom duration, mean or peak abundance can be interpreted as an increase in the magnitude of each metric (i.e. longer duration, higher abundance).

Table III: Selected environmental covariates and associated coefficient values for bloom metrics for both summer and autumn blooms from the best fit GLM models. For 2002–2019, L = larval and R = reproductive stages. For the selected covariates, T = temperature, S = salinity and Chl. = chlorophyll

Data set	Bloom period	Bloom metric	Selected covariate	Coefficient value
1984–1996	Summer	Start	Winter T	7.51
1984–1996	Summer	End	Year	–0.16
			Winter S	1.19
1984–1996	Summer	Peak week	Min. Winter T	1.51
1984–1996	Summer	Peak abundance	Summer Chl.	0.09
1984–1996	Summer	Mean abundance	Min. Winter T	1.28
1984–1996	Autumn	Start	Year	0.6
			Autumn S	–1.99
1984–1996	Autumn	Peak abundance	Autumn T	–5.47
1984–1996	Autumn	Mean abundance	Autumn T	–2.85
2002–2019 L	Summer	Start	Summer T	–2.84
2002–2019 L	Summer	End	Summer T	–2.45
2002–2019 L	Summer	Duration	Min. Winter T	0.53
2002–2019 L	Summer	Peak week	Summer T	–2.44
2002–2019 L	Autumn	Duration	Autumn T	–1.39
2002–2019 R	Summer	End	Spring Chl.	0.12
2002–2019 R	Autumn	Start	Year	0.24
2002–2019 R	Autumn	End	Summer Chl.	0.17
2002–2019 R	Autumn	Duration	Summer Chl.	0.15
2002–2019 R	Autumn	Peak week	Year	0.28
2002–2019 R	Autumn	Peak abundance	Summer Chl.	–0.65
2002–2019 R	Autumn	Mean abundance	Summer Chl.	–0.69

Environmental covariates and ctenophore blooms

Measures of ctenophore bloom phenology and abundance had significant relationships with the tested environmental covariates (Table III). Between 1984 and 1996, several characteristics of the summer bloom were related to conditions of the preceding winter. Summer abundance was higher following a warm winter, yet the bloom occurred later after a warm, more saline winter. The summer bloom peak abundance also exhibited a positive relationship with summer chlorophyll. For the autumn bloom, abundances were higher during cooler autumn temperatures, and the timing of the bloom was later during less saline autumn conditions.

Bloom metrics for larval stage ctenophores between 2002 and 2019 also had several relationships to temperature (Table III). The summer bloom occurred later during cool summers and persisted longer following a warm winter. For the autumn bloom, the duration was longer during cool autumn temperatures. In reproductive stage ctenophores, estuary chlorophyll was significantly related to bloom dynamics (Table III). High spring chlorophyll was correlated with a delayed end of the summer bloom. Similarly, high summer chlorophyll was associated with a delayed end of the autumn bloom and an increased autumn bloom duration. Summer chlorophyll was also negatively correlated to autumn bloom abundance, indicating ctenophore autumn bloom abundance was lower following a summer of high chlorophyll.

DISCUSSION

Despite infrequent years without blooms, *Mnemiopsis leidyi* has been a persistent component of the Narragansett Bay plankton throughout the entire period of 1972–2019. This has been a period of gradual warming waters due to climate change (Fulweiler *et al.*, 2015) as well as shifts in species composition of phytoplankton (Nixon *et al.*, 2009; Anderson and Rynearson, 2020; Rynearson *et al.*, 2020), zooplankton (Borkman *et al.*, 2018) and nekton (Collie *et al.*, 2008, Tableau *et al.* 2019) and anthropogenically altered reduction in nutrient input into Narragansett Bay (Oviatt *et al.*, 2017; Oczkowski *et al.*, 2018). While the species has maintained a striking degree of interannual variability during this entire time period, a slight decline in abundance of *M. leidyi* is apparent throughout the 2000s. Throughout both time series, we also found that there were usually two bloom periods per year, the first being in early to late summer and followed by an autumn bloom. Where ctenophore size data were present in the 2001–2019 time series, larval stage ctenophores exhibited a larger bloom in summer than in autumn, while blooms of reproductive stage ctenophores were approximately the same in magnitude. There was not one specific environmental covariate that acted as a main driver of the interannual variability, but instead a suite of environmental factors, including seasonal temperature and chlorophyll, influenced *M. leidyi* abundance and bloom phenology.

Temperature was an important environmental covariate that had a notable correlation with interannual changes in abundance and a long-term change in the phenology of the species. Interannual variation in bloom abundance was related to temperature, with warm winters leading to high abundance in the 1972–1997 time period. There was also a shift in phenology resulting in a pattern that would be expected in response to warming winters and earlier springs due to climate change. Costello *et al.* (2006a, 2006b) suggested winter warming would increase winter ctenophore abundance by expanding the extent of warmer, shallow embayments, which act as refugia for over-wintering ctenophore populations. Because the shallow embayments warm earlier in the year, *M. leidyi* populations in upper Narragansett Bay reproduce earlier and reach a higher maximum abundance (Kremer and Nixon, 1976; Deason and Smayda, 1982b; Costello *et al.*, 2006b). These upper bay sites serve as a source population for *M. leidyi* because ctenophores can be transported down-Bay through advection (Costello *et al.*, 2006b). Our analysis for 2001–2019 showed that the first bloom of the year occurred on average 4 weeks earlier than in the 1972–1997 period. The start, end and week of peak abundance for both summer and autumn blooms shifted 2–5 weeks earlier for reproductive stage ctenophores. Although warm temperatures in spring and summer clearly favored early ctenophore blooms with higher abundance, minimum winter temperatures also appeared to influence the phenology and abundance of the following blooms in both data sets. Here, warmer winters led to a later bloom start and peak week in the 1972–1997 time series and a longer bloom duration for the 2001–2019 larval ctenophores. These results could be in agreement with Costello *et al.* (2006b) where, following a warm winter, the longer summer bloom duration for larval ctenophores is an effect of increased abundance and advection from the upper Bay sites.

While temperature was an important abiotic environmental factor affecting ctenophore abundance, there also appeared to be an important relationship between reproductive stage *M. leidyi* and chlorophyll in the 2001–2019 time series. The summer ctenophore blooms ended later when spring chlorophyll was high. When summer chlorophyll was high, autumn ctenophore bloom abundances were lower, and the bloom ended later. However, a later bloom end does not necessarily equate to a longer bloom duration. In our data, the autumn bloom start and end were positively correlated with the summer bloom end (Table II), so it could be surmised that in this case the autumn bloom duration was unchanged due to similar shifts in both of its bounds. These relationships are best interpreted through well-documented trophic cascades between ctenophores, copepods and

phytoplankton. Reproductive stage ctenophores have the largest impact on their zooplankton prey, copepods (Kremer, 1979). When ctenophore predation on copepods is high, grazing pressure of copepods on phytoplankton is released, leading to an increase in phytoplankton abundance (Tiselius and Møller 2017). Top-down control of phytoplankton was first documented for Narragansett Bay by Deason and Smayda (1982a). The ctenophore top-down control hypothesis supports a positive relationship between chlorophyll and ctenophore abundance—high ctenophore abundance leads to low zooplankton abundance and thus high chlorophyll abundance (released from grazing pressure). Yet, in the current data, the top-down control hypothesis needs to be interpreted with these cause-and-effect events occurring at different time periods. Specifically, increased ctenophore abundances during the summer bloom could lead to increased summer chlorophyll concentrations, and without recovery in copepods abundances in the fall, a smaller autumn ctenophore bloom that is constrained by reduced food abundances. Corroborating this hypothesis, analysis of *Acartia tonsa* abundance collected alongside the ctenophore samples between 1972 and 1990 indicated a significant negative relationship between annual mean square root copepod abundance and mean summer chlorophyll (Supplementary Table IV; GLM with *t*-distributed errors, $P < 0.05$).

While temperature and chlorophyll were clearly important variables correlated with ctenophore abundance, there are other potential variables to consider such as predation. *Beröe ovata*, a warm water species of ctenophore, is a predator of *M. leidyi* and has occasionally been observed in Narragansett Bay (Kremer and Nixon, 1976). Beaulieu *et al.* (2013) reported that *B. ovata* was present in the estuary during August and September of 2006. The following year, 2007, *M. leidyi* were completely absent from the samples until September. It is possible that the presence of *B. ovata* had a delayed impact on *M. leidyi* by reducing abundance of overwintering ctenophores during the winter of 2006–2007. Before and since that time, *B. ovata* was not found in any samples collected for this time series. There were other years, particularly in the later part of the time series, for which there was only an autumn bloom; however, there was no evidence that *B. ovata* were present in Narragansett Bay in those years.

Another important factor that may explain the gradual decline in abundance of *M. leidyi* in the latter part of the time series is the planned oligotrophication of Narragansett Bay, in which nitrogen has been decreased due to upgrades to wastewater treatment facilities (Oviatt *et al.*, 2017, Oczkowski *et al.*, 2018). The upgrades began in 2005 and by late 2013 had resulted in over a 50%

reduction in nitrogen inputs to upper Narragansett Bay. The decreased loading of nitrogen could affect phytoplankton abundances and/or species composition, leading to changes in zooplankton abundance, and thus available food to support a ctenophore bloom. While this change in nutrient loading is localized in the upper Bay, the changes in ctenophore abundance there likely would be reflected in abundances at Station 2 because the upper Bay is known to seed to the lower Bay where Station 2 resides (Costello *et al.*, 2006b). This framework would suggest the dynamics controlling ctenophore abundance would be bottom-up during the latter part of the time series. Therefore, ctenophore annual abundances may be mediated by both top-down and bottom-up processes over long-time scales.

CONCLUSION

The hypothesis that *M. leidy* population in Narragansett Bay is responding to climate-induced warming proposed by Sullivan *et al.* (2001) and Costello *et al.* (2006a) is supported by this updated time series in one respect: the occurrence of shifting phenology. The summer bloom started earlier in the 2001–2019 data set when compared to the 1972–1997 data set. Shifts in bloom phenologies throughout marine ecosystems can have ecologically significant impacts if the timing of bloom events between predator and prey can now overlap (Edwards and Richardson, 2004). As ctenophore blooms shift earlier in their endemic range, they can coincide with annual copepod blooms (Sullivan *et al.*, 2007) and predate on larval ichthyoplankton (i.e. winter flounder *Pseudopleuronectes americanus*; Kolesar *et al.*, 2017), which can have substantial downstream effects on fisheries. The devastating effects ctenophore predation can have on fisheries have also been documented in European waters (e.g. Kamakin and Khodorevskaya, 2018). However, another expected response to temperature, that of increasing abundance of *M. leidy*, as has been observed by Link and Ford (2006), has not materialized in Narragansett Bay. Rather, long-term abundance has shown some evidence of decline, contrary to what would be expected with long-term warming. This suggests that the controls on annual and long-term variability of *M. leidy* abundance are complex. Nevertheless, warming temperatures were shown to positively correlate with ctenophore abundance, especially when warming occurred during the winter. Our data for Narragansett Bay *M. leidy* supports the hypothesis that warming winters in Northern Europe are likely to favor *M. leidy* or permit introductions in cooler water than it has previously inhabited, promoting the invasion of this ctenophore (David *et al.*, 2015; Jaspers,

Marty, *et al.*, 2018b). In conclusion, while the factors that influence ctenophore abundance in Narragansett Bay are complicated, the impacts of climate change appear to have affected *M. leidy* most significantly through altered bloom phenology.

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