Warming of subtropical coastal waters accelerates *Mnemiopsis leidyi* growth and alters timing of spring ctenophore blooms

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ABSTRACT: Shifts in the size, frequency, or timing of gelatinous zooplankton blooms in response to climate variability and climate change have become a concern in many coastal marine ecosystems worldwide. When abundant, gelatinous zooplankton can induce trophic cascades as well as alter energy flows to upper-level consumers. To quantify the role water temperature plays in regulating bloom development of the ctenophore *Mnemiopsis leidyi* in subtropical coastal waters, we experimentally determined the effects of increases in temperature and rates of warming on growth rate (mg C d^{-1}). Conditions were representative of those occurring during late winter and early spring (January to April) in the northern Gulf of Mexico. *M. leidyi* growth rates increased exponentially with temperature (9, 13, 16, and 22°C) and rates of warming (+1, +2, and +3°C wk^{-1}). A biologically important temperature threshold (15.0°C, delineating negative and positive growth) as a proxy measure for bloom initiation was applied to a time-series of sea surface temperature (1975 to 2013) from Mobile Bay (Alabama, USA) and indicated climate-related warming of northern Gulf of Mexico has likely advanced the timing of the spring *M. leidyi* bloom over the past 39 yr. Results have implications for ecosystem-based approaches to fisheries management since larger ctenophore blooms, occurring earlier in the year, would be expected to intensify potential competitive and predatory interactions between *M. leidyi*, zooplankton, and planktivorous juvenile fish utilizing nearshore waters as nursery habitat during the late winter and early spring.

KEY WORDS: Marine zooplankton · Jellyfish · Ctenophore · *Mnemiopsis leidyi* · Temperature · Growth rates · Phenology · Subtropical waters

INTRODUCTION

Changes in the size, frequency, or timing of gelatinous zooplankton blooms in response to favorable biophysical conditions have become a primary ecological concern in many marine ecosystems worldwide. Concerns have been heightened because gelatinous zooplankton can considerably alter marine food web structure and energy flows (Deason & Smayda 1982, Kideys 2002, Ruzicka et al. 2012) and, when abundant, negatively affect human industries such as fisheries and tourism (Purcell 2012). Among gelatinous zooplankton taxa, the ctenophore *Mnemiopsis leidyi* has received considerable attention due to the detrimental effects associated with its invasion of the Black Sea (Kideys 1994, 2002, Niermann et al.

1994) and subsequent expansion to other European ecosystems such as the Adriatic (Shiganova & Malej 2009), Aegean (Shiganova et al. 2001), and Caspian Seas (Finenko et al. 2006), and independent introduction into northern European waters (Reusch et al. 2010), such as the North Sea (Faasse & Bayha 2006), the Baltic Sea (Oliveira 2007) and adjacent waters (Riisgård et al. 2012). *M. leidyi* is native to the Atlantic coasts of North and South America (including the subtropical waters of the Gulf of Mexico) and is tolerant of a wide range of environmental conditions (Costello et al. 2012).

Mnemiopsis leidyi is a voracious consumer of plankton (Deason 1982, Sullivan & Gifford 2004, Finenko et al. 2013), including fish early life stages (Cowan & Houde 1993, Purcell et al. 1994, Shiganova et al. 2001). *M. leidyi* can induce trophic cascades and potentially compete with planktivorous forage fish during blooms by depleting zooplankton stocks (Deason & Smayda 1982, Feigenbaum & Kelly 1984, Sullivan et al. 2001, Roohi et al. 2010). It can also reduce coastal food web energy transfer efficiencies to higher-order consumers by shunting carbon to microbial communities (Condon et al. 2011). For these reasons, understanding the factors regulating *M. leidyi* bloom development is necessary for ecosystem-based approaches to fisheries management.

Mnemiopsis leidyi in temperate, coastal marine ecosystems are sensitive to changes in biophysical conditions. Observational field studies suggest *M. leidyi* abundance and reproduction increase with increasing water temperature, salinity, and prey availability (Costello et al. 2006a, Haraldsson et al. 2013, van Walraven et al. 2013). Empirical work similarly shows *M. leidyi* growth and egg production are dependent on prey density (Reeve et al. 1989, Kremer & Reeve 1989, Sullivan & Gifford 2007), dissolved oxygen concentration (Grove & Breitburg 2005), and salinity (Jaspers et al. 2011a). Recent modeling studies also imply that temperature and prey availability strongly control *M. leidyi* blooms (Salihoglu et al. 2011). Thus, shifts in water temperature and freshwater discharge can alter bloom size and timing, potentially intensifying predatory and competitive interactions between *M. leidyi*, zooplankton, and planktivorous fish.

The effect of temperature on spring *Mnemiopsis leidyi* bloom development is particularly important to consider, given concerns about the response of coastal marine ecosystems to climate variability and change. Climate-driven warming of coastal waters in the northern reaches of *M. leidyi*'s native range is thought to be the primary driver of a shift in bloom

timing that led to greater overlap with zooplankton and ichthyoplankton (Sullivan et al. 2001, Costello et al. 2006b, Condon & Steinberg 2008, McNamara et al. 2010). The relatively faster rate of warming of protected coves in comparison to adjacent open waters is the proposed mechanism that allows overwintering *M. leidyi* populations to bloom and then expand along onshore–offshore gradients in temperate ecosystems (Costello et al. 2006b, 2012).

While the role temperature plays in controlling spring *Mnemiopsis leidyi* bloom development in native temperate ecosystems has received considerable attention, there is a paucity of information from subtropical waters such as the Gulf of Mexico. In fact, we are only aware of one study reporting specific growth rates across a range of temperatures in subtropical waters (Reeve & Baker 1975). Temperatures used in those experiments (21, 26, and 31°C) were higher than those experienced by ctenophores during spring in the Gulf of Mexico. This limited information makes it difficult to evaluate whether springtime blooms of *M. leidyi* in subtropical coastal waters will shift in magnitude or timing in response to climate variability or long-term climate change. Thus, the objectives of this study were to experimentally determine: (1) the effect of varying temperature on *M. leidyi* daily growth rates, and (2) whether differential rates of warming affect growth rates.

MATERIALS AND METHODS

Experiment A: Increased temperature

An experiment was run from 6 to 13 March 2011 to test the hypothesis that *Mnemiopsis leidyi* daily growth rates increase with temperature. Ctenophores were collected on 2 March 2011 from 2 sites in southern Mobile Bay, Alabama (USA), using a 0.5 m diameter, 1000 µm mesh ring net towed obliquely between 0.5 and 3.0 m depth for 2 to 3 min at an approx. vessel speed of 1.8 m s^{-1}. The daily minimum water temperature (DMWT) for southern Mobile Bay on the day of collection was 17.5°C. Water temperature was measured at the 'Dauphin Island' weather station (30.25° N, 88.07° W) maintained by the Mobile Bay National Estuary Program (www.mymobilebay.com). Ctenophores were carefully transferred to a bucket containing 13 l of surface water and immediately transported back to a climate-controlled facility at the Dauphin Island Sea Lab (DISL). Visual inspection of individuals upon returning to the laboratory revealed nearly all

(approximately 80%) were in the cydippid life-stage. Because we were interested in the response of lobate individuals, the start of the experiment was delayed 4 d until a sufficient number of individuals (approx. 50%) had metamorphosed into the adult, lobate stage. *M. leidyi* were maintained in gently aerated 19 l plastic containers filled with natural seawater at 20 psu and 22°C. Ctenophores were fed daily a 50:50 mixture of *Artemia* spp. nauplii and natural zooplankton collected each morning off the DISL dock using a 0.25 m diameter, 64 µm mesh ring plankton net. The composition of the natural zooplankton assemblage consisted primarily of cyclopoid and calanoid copepods, copepod nauplii, tintinnids, and mixotrophic dinoflagellates.

The experimental design was a 1-way ANOVA with temperature treatments (9, 13, 16, and 22°C). The 9, 13, and 16°C treatments were created using water baths and 0.25 horsepower aquarium chillers (AquaEuroUSA® Model AC25H) set at target temperatures. Conditions are representative of those in Mobile Bay from January to April (Fig. 1). The 22°C treatment was maintained using the ambient air temperature of the climate-controlled facility. Water was circulated using 1325 l h^{-1} submersible pumps (Danner® Model No. MD3). Temperature in each water bath was recorded at 10 min intervals by an Onset® Pendant Temperature logger (Model UA-001-08).

There were 4 replicates per treatment, for a total of 16 experimental units. Each experimental unit consisted of 2 ctenophores in a 3.79 l plastic bag filled

with 2 l filtered seawater at 20 psu. Natural seawater from Mobile Bay was treated with ultraviolet light, adjusted to the desired salinity using deionized water or artificial sea salt, and then gravity-filtered through a 0.7 µm Whatman glass fiber filter (GF/F). Individuals were acclimatized to experimental temperatures for 48 h prior to the start of the experiment to ensure they started from the same set of conditions.

Oral-aboral lengths ('length', cm) of *Mnemiopsis leidyi* individuals were measured prior to their addition to an experimental unit (range 0.5 to 1.0 cm, N = 32), as well as on a daily basis. Animals were transferred with a spoon or cup and individually measured in a transparent dish and ruler, ensuring minimal handling with maximum time out of water not exceeding ~3 to 5 s.

Mnemiopsis leidyi were fed ad lib. a 50:50 mixture of cultured *Artemia* spp. nauplii and natural zooplankton collected each morning for a minimum of 6 h after being returned to their respective treatments. A daily 100% water change was then performed for each experimental unit using filtered seawater at the appropriate temperature and salinity. Ctenophores did not appear to be food-limited at any time during the experiment as there was always prey visibly present prior to the water change. Water quality parameters (pH, NH_4^+, NO_3^- and NO_2^-) were checked on 12 Mar 2011 using a saltwater aquarium test kit.

Experiment B: Rate of change

An experiment was run from 27 March to 20 April 2011 to test the hypothesis that *Mnemiopsis leidyi* daily growth rates increase with the rate of change in water temperature (i.e. warming rate). To test this hypothesis in the context of current and future hydrographic conditions that *M. leidyi* spring blooms may experience, daily minima in water temperatures (DMWT) observed during March in coastal Alabama waters were used to estimate the historical mean, maximum, and 2× the maximum rate of change in temperature. These 3 rates were: +1, +2, and +3°C wk^{-1} (Table 1). Daily minima were extracted from a synthetic time-series created using surface (1.0 m) water temperature data collected at the NOAA National Data Buoy Center (NDBC) Station 'DPIA1' for 1987 to 2004 (30.25° N, 88.07° W; www.ndbc.noaa.gov/station_history.php?station=dpia1) and a calibrated instrument package maintained by the Dauphin Island Sea Lab for 2005 to 2007 (30.09° N, 88.22° W). The mean and maximum rate of change in DMWT was estimated using the slope of a least-squares lin-
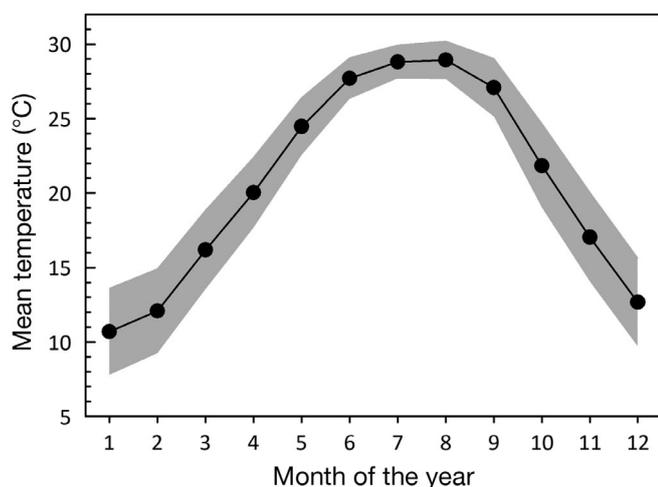

Fig. 1. Annual cycle of surface water temperature in Mobile Bay, Alabama (USA). Temperature expressed is the long-term (1975 to 2012) monthly mean (±1 SD, grey shading) of daily minima of surface water temperature observed at the Mobile Bay National Estuary Program 'Dauphin Island' station (30.25° N, 88.07° W)

Table 1. Treatments for Experiment B (rate of change). 'DOE + 1°C' refers to the day of the experiment when the temperature was increased by 1°C. SST: sea surface temperature

Treatment	March SST warming rate	Target (°C wk^{-1})	Actual (°C wk^{-1})	Duration (d)	Start Date	End Date	DOE + 1°C
+1°C wk^{-1}	Mean	1.12	1.12	25	27 Mar	20 Apr	2, 10, 17, 24
+2°C wk^{-1}	Maximum	1.54	1.47	19	27 Mar	14 Apr	2, 7, 14, 17
+3°C wk^{-1}	2× maximum	3.08	3.29	10	27 Mar	5 Apr	2, 5, 7, 9

ear regression relating the long-term mean and minima in DMWT to the number of days in March (Table 1). Daily warming rates were scaled up to °C wk^{-1} and rounded to the nearest integer. A range of 16 to 20°C was chosen because it represented the range between the long-term, monthly mean in DMWT for March (16°C) and April (20°C)—months when spring blooms of *M. leidyi* typically occur.

Ctenophores were collected on 17 March 2011 from 2 sites located in southwestern Mobile Bay using the same methods as described for Experiment A. The majority of *Mnemiopsis leidyi* individuals collected were still in the cydippid stage and the start of the experiment was delayed until 27 March 2011, when at least 30 ctenophores had metamorphosed into the lobate stage.

Experiment B treatments (+1, +2, and +3°C wk^{-1}) were created using water baths, submersible pumps, and aquarium chillers increased to a target temperature on pre-determined dates (Table 1). Temperature in each water bath was recorded every 15 min with an Onset Pendant Temperature logger. There were 5 replicates per treatment, for a total of 15 experimental units. Experimental units were the same as those in Experiment A. Seawater was diluted to the desired salinity with deionized water. *M. leidyi* in all treatments were acclimated to 16°C for 48 h prior to the start of the experiment to ensure all individuals started from the same set of conditions. We used the same feeding and aquaculture procedures as in Experiment A, with the addition of water quality parameters (pH, NH_4^+, NO_3^-, and NO_2^-) being checked weekly.

Estimating growth rates

Mnemiopsis leidyi growth was estimated as the difference in carbon biomass between successive days in both experiments. Daily measurement of ctenophore length (cm) was converted to carbon biomass (mg) using Eq. (1):

$$\text{Carbon biomass} = 0.15 \times \text{length}^{2.87}$$
$$(n = 13, R^2 = 0.92, p < 0.0001) \tag{1}$$

derived from *M. leidyi* originating in Mississippi and Alabama coastal waters during the spring, summer, and fall seasons of 2009 and 2010 (Robinson 2012; individual lengths ranged from 0.6 to 6.9 cm). In Robinson (2012), ctenophores were gently rinsed with deionized water to displace saltwater, patted dry with paper towels through 200 µm Nitex mesh to remove excess water, weighed to determine wet weight (mg), and then dried at 60°C for 3 wk until the difference between successive daily estimates of dry weight (mg) was <1%. *M. leidyi* carbon content was determined using an elemental combustion analyzer (Costech Analytical Technologies). Estimates of daily carbon biomass were averaged for each pair of ctenophores in experimental units because individuals were not considered to be true replicates.

Mnemiopsis leidyi carbon growth rate (mg d^{-1}) in each Experiment A biomass treatment was estimated as the slope of a least-squares linear regression relating changes in mean daily carbon biomass (mg) to time. Slopes from all regressions were considered valid estimates of daily growth even if the coefficient did not significantly differ from zero (ANOVA, p > 0.05). The temperature threshold delineating negative and positive growth was identified as the intercept where growth rate was equal to zero from an exponential model fitted to growth rates and temperature. Growth in Experiment B treatments was described using the exponential equation Eq. (2):

$$y = b_0 e^{kx} \tag{2}$$

where *y* is the daily carbon biomass (mg), b_0 is a constant, *k* is the growth rate (d^{-1}) and *x* is time (d). Nonlinear models were fitted using the statistical software package SigmaStat v. 12 (Systat Software).

Differences in carbon biomass growth rates among treatments in both experiments were determined by comparing slopes of linear regressions (ANCOVA; Zar 1999). Carbon biomass estimates from Experi-

ment B treatments were square-root transformed prior to fitting least-squares linear regressions in order to meet the underlying assumptions of normality (Kolmogorov-Smirnov) and homoscedasticity (Levene median test). Regressions were fitted in the statistical software SigmaPlot v. 10.0 (Systat Software).

A Tukey HSD pair-wise comparison test was performed if an overall difference in slopes was identified by the ANCOVA. Hochberg's procedure was used to control experiment-wise error rate (Wright 1992; see also Legrendre & Legendre 1998). Significance for all analyses was determined at $\alpha = 0.05$.

Historical context

Daily growth rates from Experiment A (increased temperature) were also estimated as the change in ash-free dry weight (AFDW) over time (d) to put our rates in the context of those estimated at 21, 26 and 31°C by Reeve & Baker (1975) for *Mnemiopsis leidyi* from Biscayne Bay, Florida, USA. Oral-aboral length (cm) for each ctenophore was converted to AFDW using Eq. (3):

$$AFDW \text{ (mg)} = 4.30 \times length^{2.07}$$
$$(n = 13, R^2 = 0.91, p < 0.0001) \tag{3}$$

This equation was derived using the same set of ctenophores used to estimate carbon biomass. The tissue that remained after a portion was removed for carbon content analysis was dried at 60°C, weighed to the nearest milligram, and combusted at 500°C for 4 h. The resulting AFDW was then divided by the pre-ash weight of the sample to give the ash-free fraction. The original sample dry weight was multiplied by the ash-free fraction to obtain the total AFDW (mg). Growth rate was estimated as the slope from a least-squares linear regression relating the mean AFDW to time (d) following the method of Reeve & Baker (1975). Rates were compared with those estimated for ctenophores in size class B from Reeve & Baker (1975), since those individuals were similar in length (between 0.45 and 2.80 cm) to *M. leidyi* used in our Experiment A.

The possibility of a long-term shift in the timing of *Mnemiopsis leidyi* spring bloom was examined using the temperature threshold delineating negative and positive growth (see 'Results: Experiment A') and a historical time-series (1975 to 2013) of surface water temperature col-

lected daily by DISL personnel (Alabama, USA). For each year, the day of the year on which surface waters surpassed the identified temperature threshold was found and then expressed as an anomaly from the long-term mean day of the year on which the threshold was crossed. A Spearman Rank Correlation test was performed on the 5 yr running average of the annual anomaly (dependent) and year (independent) to determine if the timing of the threshold crossing each year had changed significantly during the 1975 to 2013 period.

RESULTS

Water quality parameters were within acceptable ranges. pH values ranged between 7.4 and 7.9 in Experiment A, and between 7.6 and 8.2 in Experiment B. All treatment temperatures were within ±1°C of experimental targets throughout both experiments.

Experiment A: Increased temperature

Ctenophore mortality throughout the experiment was 37.5% (9°C), 0% (13°C), 25% (16°C), and 0% (22°C), with only one replicate at 9°C lost entirely (on 12 March 2011).

Slopes representing daily growth rates differed from zero in the 9, 16, and 22°C, but not in the 13°C treatment (Table 2; Fig. 2). *Mnemiopsis leidyi* growth rates (mg C d⁻¹) varied significantly among temperature treatments (ANCOVA, $F_{3,12} = 23.22$, p < 0.0001). Growth rate increased with temperature, with negative growth at 9°C (–0.010 mg C d⁻¹) and 13°C (–0.001 mg C d⁻¹), slow, positive growth at 16°C (0.002 mg C d⁻¹) and highest growth at 22°C (0.039 mg C d⁻¹). Ctenophore growth was significantly faster in the 22°C treatment when compared to the other 3 temperature treatments. The same was true for animals in the 16°C treatment relative to those in the 9°C treat-

Table 2. *Mnemiopsis leidyi*. Growth rate (mg C d⁻¹) at 9, 13, 16, and 22°C. Standard errors (SE) of model parameters are shown in parentheses. The start of the experiment was denoted as 'Day 1'. Significant (p < 0.05) in **bold**

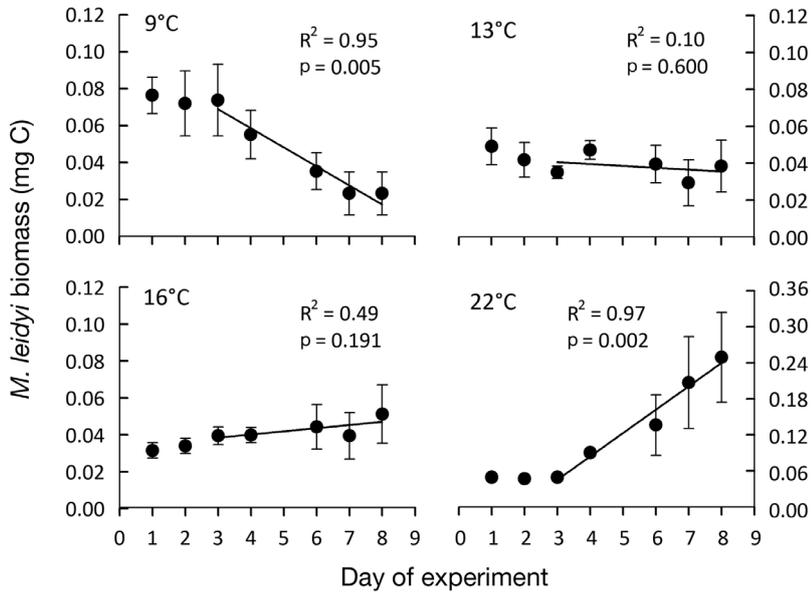| Treatment	n	R^2	Growth rate (SE)	Intercept (SE)	p
9°C	5	0.95	−0.010 (0.001)	0.079 (0.006)	**0.005**
13°C	5	0.10	−0.001 (0.002)	0.042 (0.010)	0.597
16°C	5	0.49	0.002 (0.001)	0.037 (0.004)	0.191
22°C	5	0.97	0.039 (0.004)	0.006 (0.016)	**0.002**

Fig. 2. *Mnemiopsis leidyi*. Mean (±1 SE) carbon biomass (mg) in the 9, 13, 16, and 22°C treatments over the course of Experiment A: increased temperature. Slopes from least squares linear regressions were used to estimate growth rates (mg C d^{-1}) at each temperature. Note the different *y*-axis scale for 22°C

ment (Table 3). *M. leidyi* grew exponentially faster as temperature increased (Fig. 3) and the relationship was described with Eq. (4):

$$\text{Growth (mg C d}^{-1}) = -0.0135 + 0.0008e^{(0.1879 \times [T°C])}$$
$$(n = 4, R^2 = 0.99, p = 0.09) \qquad (4)$$

Using this model, 15.0°C was identified as the temperature threshold delineating negative and positive growth for *M. leidyi*. To determine if the springtime bloom had possibly undergone a phenological shift,

Table 3. *Mnemiopsis leidyi.* Growth rates were significantly different among Experiment A (increased temperature) and Experiment B (rate of change) treatment pairs. Significant (p < 0.05) in **bold**

Treatment pairs		df$_{pooled}$	q	p
Experiment A				
9°C	13°C	12	3.83	0.078
9°C	16°C	12	5.17	**0.015**
9°C	22°C	12	17.36	**<0.001**
13°C	16°C	12	2.15	0.456
13°C	22°C	12	19.37	**<0.001**
16°C	22°C	12	19.12	**<0.001**
Experiment B				
+1°C wk^{-1}	+2°C wk^{-1}	48	8.76	**<0.001**
+1°C wk^{-1}	+3°C wk^{-1}	48	8.73	**<0.001**
+2°C wk^{-1}	+3°C wk^{-1}	48	3.68	**0.033**

we used this threshold as a proxy indicator for the timing of bloom initiation, and the day of year surface water temperatures surpassed this threshold each year from 1975 to 2013. Our analysis indicated there is a likelihood that the *M. leidyi* bloom is occurring earlier in the year. Inshore waters of the northern Gulf are tending to warm to 15.0°C sooner in recent times in comparison to decades past (Fig. 4; Spearman Rank, n = 35, ρ = −0.58, p < 0.0001).

Experiment B: Rate of change

No mortality occurred in the +1°C wk^{-1} treatment during the experiment. Ctenophore mortality was 20% in both the +2°C wk^{-1} and +3°C wk^{-1} treatments. All experimental units had a least one ctenophore throughout the duration of the experiment.

Mnemiopsis leidyi mean carbon biomass increased exponentially with time for all 3 treatments (Fig. 5). Estimates of growth rate (sample size, parameter standard error) derived from the exponential models for each treatment were: +1°C wk^{-1}: 0.12 d^{-1} (25,
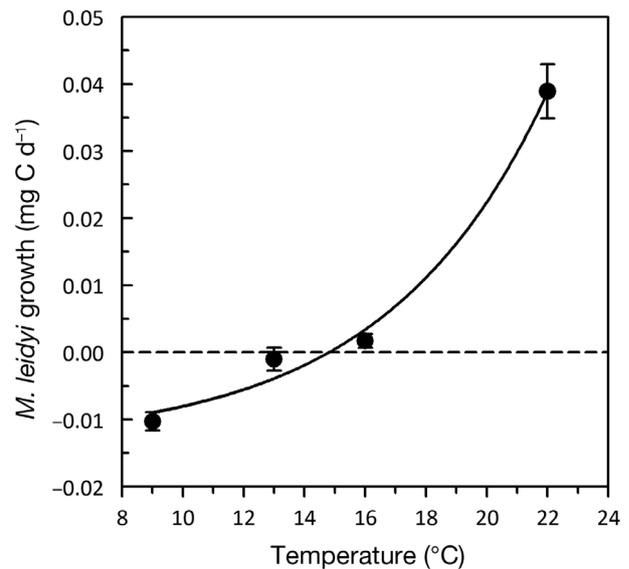

Fig. 3. *Mnemiopsis leidyi.* Growth rates (±1 SE) (mg C d^{-1}) at 9, 13, 16, and 22°C. Dashed line at zero on *y*-axis is the temperature threshold (15.0°C) at which northern Gulf of Mexico *M. leidyi* switched from negative to positive growth. Growth rates increased exponentially with temperature and were best described by Eq. (4)
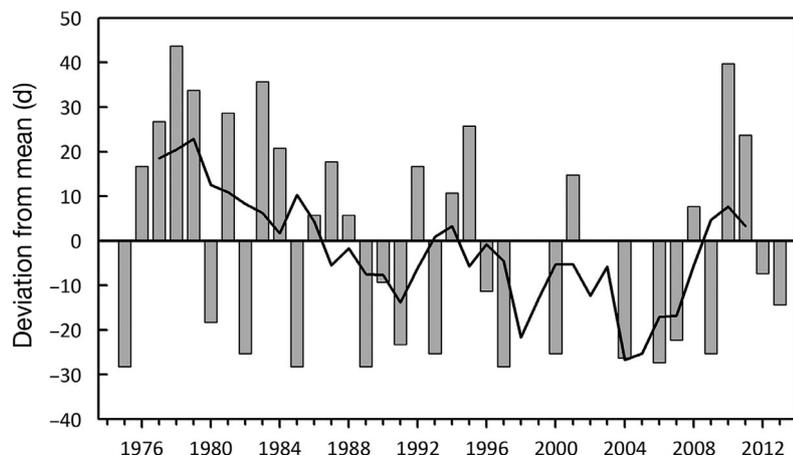
Fig. 4. Annual variation in warming of surface waters of Mobile Bay, Alabama, USA (1975 to 2013). Variations are shown as deviations (grey bars), in days, from the long-term mean day of year (29) at which daily minimum water temperature (DMWT) exceeded 15.0°C. Negative deviations occurred when DMWT surpassed 15.0°C on an earlier date than the long-term mean. A negative correlation between time (year) and the 5 yr running average of the annual deviation (solid line) indicates the crossing of this biologically important threshold is tending to occur earlier in recent years in comparison to decades past (Spearman Rank, n = 35, ρ = −0.58, p < 0.0001)

0.004), +2°C wk^{-1}: 0.16 d^{-1} (19, 0.005), and +3°C wk^{-1}: 0.23 d^{-1} (10, 0.001). Growth rates significantly differed from zero and were positive for all treatments (p < 0.0001; Fig. 5). Comparison of daily growth using square-root transformed carbon biomass estimates revealed differences among treatments (ANCOVA, $F_{2,48}$ = 50.24, p < 0.0001). *M. leidyi* experiencing warming rates of +2°C wk^{-1} and +3°C wk^{-1} grew significantly faster than those at +1°C wk^{-1}, with highest growth rates attained at the largest temperature increase per week (Table 3).

DISCUSSION

Mnemiopsis leidyi from the northern Gulf of Mexico showed a stronger growth response to increases in water temperature than those from Biscayne Bay, Florida (Fig. 6). Though the range of temperatures used by Reeve & Baker (1975) and this study were similar (10 and 13°C, respectively), examination of *M. leidyi* growth rates (mg C d^{-1}) among all temperature treatments indicates ctenophore growth rates increase exponentially from 9 to 22°C, peak at 26°C, and then begin to slow at 31°C (Fig. 6). This empirically-derived relationship validates the strong control of temperature on *M. leidyi* life stages implied by a population-based model of blooms in the Black Sea, and confirms the non-linear increase in biomass

and abundance observed at simulated (10 to 30°C) and *in situ* (12 to 17°C) temperatures for populations in the Black and Dutch Wadden Seas (Salihoglu et al. 2011, van Walraven et al. 2013). The identification of 15.0°C as significant biological threshold for bloom development for native, subtropical populations corroborates the finding that likelihood of juvenile *M. leidyi* being present in the Dutch Wadden Sea (where it is an invasive species) is near 100% when water temperature exceeds 15°C (van Walraven et al. 2013).

One methodological issue ought to be noted regarding the 9°C treatment in Experiment A. The acclimation period (48 h) should have been longer given the change in temperature endured. Ctenophores in Mobile Bay can be exposed to rapid drops in temperature (range: −8.8 to 0°C, mean ±1SD: −1.60 ± 1.54°C) over 48 h, particularly during the passage of northerly cold fronts during winter and spring (Schroeder & Wiseman Jr. 1985). Animals in the 9°C treatment experienced a 13°C change; thus, the mortality (37.5%) may have been due, in part, to thermal stress. Despite this issue, we believe the negative growth rate at 9°C is an accurate representation response of *M. leidyi* since the reduction in biomass was consistent over the course of the experiment (Fig. 2).

The acceleration of *Mnemiopsis leidyi* growth with rising temperatures and rates of warming in the northern Gulf of Mexico has potential implications for coastal food webs and predator–prey interactions. Both consumption rates and egg production rates scale with ctenophore size (Reeve et al. 1989, Purcell & Decker 2005, Jaspers et al. 2011a). Thus, an exponential increase in ctenophore biomass in response to climate-related warming would result in greater predation pressure on their prey, including ichthyoplankton (Niermann et al. 1994, Costello et al. 2006b). Larger ctenophore blooms in terms of both biomass and abundance would also be expected to reduce energy transfer efficiencies to high-order consumers, such as piscivorous fishes and sea birds, in coastal food webs. *M. leidyi* can be a significant carbon shunt when it is abundant, with most carbon consumed ultimately respired by microbial communities (Condon et al. 2011).

The sensitivity of *Mnemiopsis leidyi* growth to changes in temperature makes bloom development
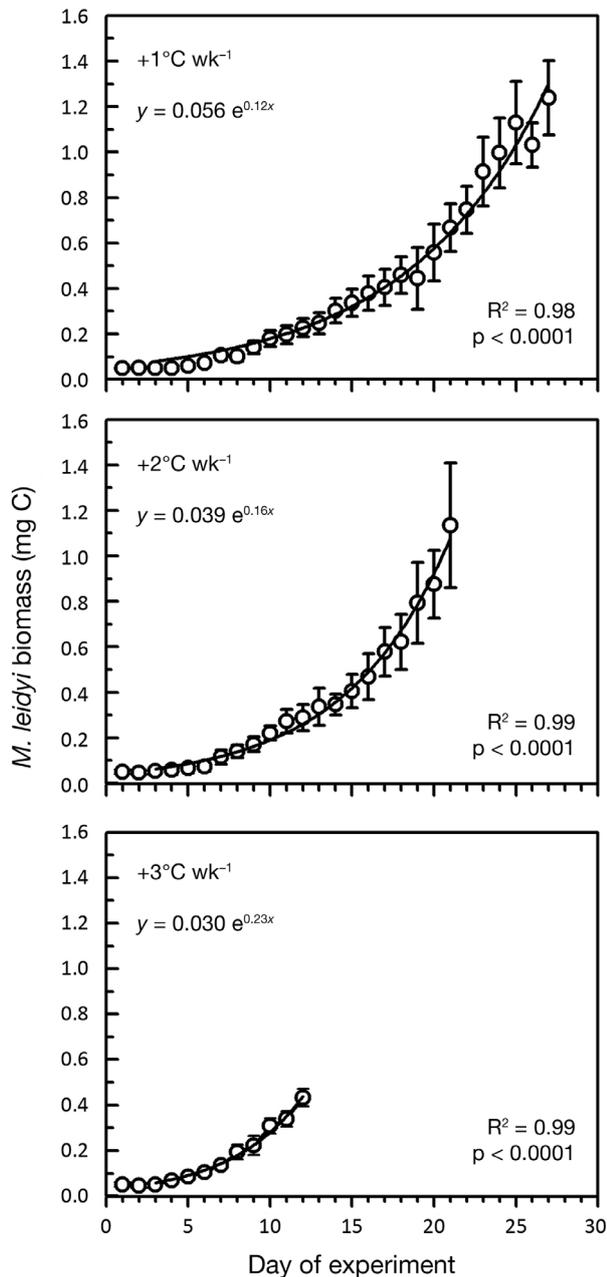
Fig. 5. *Mnemiopsis leidyi.* Carbon biomass (mg) in the +1, +2, and +3°C wk^{-1} treatments over the duration of the experiment. Lines represent the best-fit of an exponential model ($y = b_0 e^{kx}$) where k is the growth rate (d^{-1}). Mean (±1 SE) ctenophore carbon biomass in each treatment during the initial 2 d acclimation period are shown. Only biomass values from experiment Day 3 onwards were used to fit exponential models in each treatment
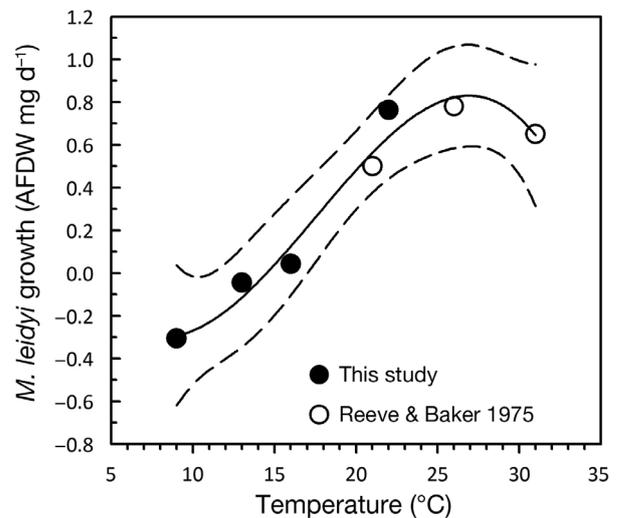
Fig. 6. *Mnemiopsis leidyi.* Growth rate (ash-free dry weight [AFDW] mg d^{-1}) increased significantly with temperature from 9 to 31°C. Growth appeared to slow once water temperatures reached 26°C. Growth response to temperature (T) was best fit with a 3rd order polynomial equation: AFDW (mg d^{-1}) = $-0.554 - (0.690 \times T) - (0.018 \times T^2) - (0.001 \times T^3)$; R^2 = 0.99, $F_{3,6} = 33.15$, p = 0.008. Model 'goodness of fit' was determined using coefficient of determination values. Dashed lines represent the 95% confidence limits

similar to northern populations (Costello et al. 2006b, Condon & Steinberg 2008, McNamara et al. 2010). The consequences of earlier ctenophore blooms in the northern Gulf of Mexico are not fully understood. However, if similar to those observed in ecosystems such as Narragansett Bay, Rhode Island, USA (Sullivan et al. 2001, Costello et al. 2006b), effects would include higher maximum population biomass, larger overwintering stocks inshore where blooms originate, and increased pressure on copepod populations which previously may have had a temporal refuge from predation.

The likelihood of these consequences occurring in the northern Gulf of Mexico is supported to some extent by previous work. Drastic reductions in zooplankton abundance concomitant with a rise in *Mnemiopsis leidyi* numbers have been noted in Mississippi Sound (Phillips et al. 1969). *M. leidyi* and dominant copepod populations in Mobile Bay and adjacent coastal waters exhibit the same life history characteristics and similar spatial and temporal patterns in abundance and production that led to the phenological shifts that altered plankton production dynamics elsewhere (Costello et al. 2006b, 2012). *M. leidyi* overwinter in shallow, protected coves where waters warm more rapidly in late winter and early spring than those in the relatively more open bays

vulnerable to phenological shifts. The earlier warming of coastal waters to 15.0°C, an important physical threshold for *M. leidyi* growth, over the past 39 yr (Fig. 4) strongly suggests northern Gulf of Mexico *M. leidyi* have undergone a change in their phenology

and sounds (Robinson 2012). In contrast, copepods such as *Acartia tonsa*, *Labridocera aestiva*, and *Parvocalanus* (formerly *Paracalanus*) *crassirostris* are distributed throughout the estuaries during winter and spring (Booker 1980, Albright 2002). Zooplankton biomass peaks in February and *Acartia tonsa* production reaches its maximum in March (Albright 2002). Thus, if *M. leidyi* population growth peaks earlier than copepod production, then copepod populations could be subjected to greater predation pressure when ctenophores are advected from their source regions to waters throughout the estuary (Costello et al. 2006b, 2012).

Altered bloom timing can also negatively affect fish early life stages if it leads to greater temporal overlap between ctenophores and these fish, and ctenophores are sufficiently abundant to reduce prey populations (Monteleone & Duguay 1988, Purcell et al. 1994, Purcell & Decker 2005, McNamara et al. 2010). *Mnemiopsis leidyi* populations in Mobile Bay and adjacent Mississippi Sound can reach densities during late winter/early spring blooms (149.96 ± 14.27 ind. m^{-2}) that could impact prey species, particularly in the semi-enclosed, shallow (1.6 to 2.5 m) embayments (Robinson 2012). The northern Gulf of Mexico is home to a number of winter-spawning fish populations; eggs and larvae from these populations using nearshore nursery habitats would have a potential predator and competitor not previously encountered. Species potentially affected include the 2 herring species *Brevoortia patronus* and *Etrumeus teres*, anchovies *Anchoa* spp., mullets *Mugil cephalus*, the 2 drum species (also called croakers) *Leiostomus xanthurus* and *Micropogonias undulatus*, gobies *Gobiesox strumosus*, cods *Urophycis* spp., butterfish *Peprilus burti*, and flatfish (Achiridae) (Ditty et al. 1988, Rakocinski et al. 1996, Carassou et al. 2012). Planktivorous, juvenile fish which co-occur with *M. leidyi* during early spring, including those directly and indirectly supporting fisheries such as Gulf menhaden *Brevoortia patronus* and the bay anchovy *Anchoa mitchilli* (Roithmayr & Waller 1963, K. Robinson unpubl. data), potentially will have to compete with a large number of ctenophores for shared prey resources.

Determination of the exact consequences of a phenological shift in late winter and early spring *Mnemiopsis leidyi* blooms in nearshore, northern Gulf of Mexico waters requires additional study, including *in situ* zooplankton (including ichthyoplankton) prey composition and abundance, estimates of *M. leidyi* clearance rates at representative water temperatures, and the effects of climate change-related

warming on the timing of the zooplankton spring bloom. The predatory impact of *M. leidyi* on fish eggs and larvae is especially critical to ascertain since reports on the importance of *M. leidyi* as a consumer of fish early life stages are conflicting (Purcell et al. 2001, Oguz et al. 2008, Hamer et al. 2011, Jaspers et al. 2011b). The strong likelihood of a phenological shift identified for northern Gulf of Mexico coastal waters sets the stage for these questions and those related to the role long-term temperature changes play in altering food web dynamics in coastal waters, including the intensity of trophic interactions between gelatinous predators and their prey.

We demonstrated here that *Mnemiopsis leidyi* in a riverine-dominated subtropical bay are sensitive to increases in temperature and rates of warming. Specifically, we found: (1) carbon biomass growth rates exponentially increase with temperature between 9 and 22°C, (2) spring blooms likely cannot start developing until temperatures reach 15.0°C, a threshold associated with positive growth, and (3) bloom development (i.e. changes in individual growth and reproduction rates leading to a true increase in population density) will accelerate if the rate at which coastal waters warm during spring increases. Moreover, climate-driven warming of the northern Gulf coastal waters over the past 39 yr has likely caused a shift in the timing of spring ctenophore blooms. These changes have implications for fisheries management since larger ctenophore blooms, occurring earlier in the year, would be expected to alter food web dynamics, including intensifying trophic interactions between *M. leidyi* and fish species, in nearshore waters during the late winter and early spring.

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