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Growth of juvenile American lobster *Homarus americanus* in a changing environment

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ABSTRACT: In recent years, the abundance of American lobster *Homarus americanus* stocks has increased exponentially in coastal Maine, which is likely due to increased recruitment, enhanced growth rates, and decreased predation. This study analyzed the effects of lobster size (12–19.9, 20–29.9, and 30–39.9 mm carapace length, CL) and temperature on growth rates using an 18 yr mark–recapture study in coastal Maine during a period of considerable warming in the Gulf of Maine. Our results showed that the smallest size class of lobsters grew significantly faster than the 2 larger size classes. Peak molt incidence occurred in June and September for all size classes. Greater percent growth measurements were significantly more frequent in warm years for the 12–19.9 mm CL size class, and were also found to be significantly more frequent in the spring season during warm years for all size classes combined. In addition, time at 50% molt probability for the 20–29.9 mm CL and 30–39.9 mm CL size classes was significantly shorter in warm years. This study represents one of the first documentations of growth of small juvenile American lobsters (<20 mm CL) in the wild, and provides evidence of how juvenile growth varies between warm and cold years. Collectively, our findings have implications for how warming sea water temperatures may affect lobster stock productivity, and are of value to lobster stock assessment models and resource management efforts.

KEY WORDS: American lobster · Mark–recapture · Growth · Temperature · Molt probability · Gulf of Maine

INTRODUCTION

The Gulf of Maine (GOM) is warming at a rapid rate relative to the majority of the world's other oceans (Pershing et al. 2015). This climate-induced environmental forcing is restructuring marine communities and impacting system productivity (Mooney et al. 2009), increasing the need for efficient assessment of climate change impacts on local ecosystems. Identifying environmental changes that impact fisheries productivity is particularly important given the role of fisheries in the function of both ecological and social systems.

In marine ecosystems, moderate increases in temperature elevate metabolic rates and can impact key biological processes (Hoegh-Guldberg & Bruno 2010). Temperature is perhaps the most influential environmental variable affecting growth in ectotherms (reviewed in Angilletta et al. 2002). In particular, temperature directly influences intermolt interval (Templeman 1936, Waddy et al. 1995, Tremblay & Eagles 1997, Comeau & Savoie 2001) and molt increment (Wilder 1953, Aiken 1977, Campbell 1983, Waddy et al. 1995) in the American lobster *Homarus americanus* H. Milne-Edwards, 1837. Lobsters found in warmer waters, such as Long Island Sound, grow

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faster than lobsters from colder areas, such as the GOM (Aiken 1977, Waddy et al. 1995, Lawton & Lavalli 1995, Comeau & Savoie 2001). Towards the northern extent of the lobsters' range, molting incidence can decrease by almost 50% in particularly cold years compared to warmer years (Ennis 1983). Ovigerous lobsters are able to optimize the thermal regime that their eggs are exposed to by undergoing seasonal inshore-to-offshore migrations, thus influencing the rate of egg development (Cowan et al. 2007, Goldstein & Watson 2015). Juvenile lobsters are less mobile and more shelter-restricted (Wahle 1992, Wahle & Steneck 1992), and generally remain in nearshore waters where they may endure several months below the minimum temperatures at which lobsters molt (Waddy et al. 1995). Wahle et al. (2001) grew young-of-the-year lobsters in cages at 2 different nearshore field sites in Maine that differed in temperature by 2°C, and lobsters at the warmer site were 6 mm larger in carapace length (CL) on average at the end of 3 mo. Therefore, even slight changes in average water temperature in these areas could significantly impact the growth of juvenile lobsters.

The American lobster spans a wide geographic range, from Newfoundland to Cape Hatteras and from the low-tide mark to a depth of 400–600 m (Phillips et al. 1980). It is the third most valuable commercially fished species in the USA (NMFS 2014). Lobster landings in the GOM have steadily increased since 1990, and in 2015 the Atlantic States Marine Fisheries Commission stock report indicated record high lobster stock abundance and recruitment throughout most of the GOM (ASMFC 2015). Within the state of Maine, lobster landings were valued at over $495 million US dollars in 2015, comprising 81% of the total value of Maine's landings for all commercial species (MDMR 2016). Furthermore, the coastal GOM is currently dominated by crustaceans, and lobsters exert top-down forcing on the system (Jackson et al. 2001). Because of its economic and ecological importance, there is a strong need to understand the underlying mechanisms that control lobster abundance and that have led to such drastic increases in lobster populations and landings over the past ~25 yr.

Over the past 20 yr, water temperatures in nearshore mid-coast Maine have been increasing (data from Boothbay Harbor Sea Water Temperature Record, Maine Department of Marine Resources). How this increase has influenced the growth of juvenile lobsters in this area is currently unknown. However, if increasing water temperatures have accelerated the growth rates of lobsters, they likely are reaching harvestable size at a younger age, and consequently, warming may be contributing to the increase in lobster landings in the GOM in the last 25 yr.

Tagging studies provide a way to measure lobster growth in the wild and have become more reliable with the advent of tags that are anchored in the tissue and retained through ecdysis, such as sphyrion or streamer tags. Coded microwire tags (Northwest Marine Technology [NMT], Washington, USA) are also designed to be retained through ecdysis, and are much more suitable for juveniles because of their small size and complete internal placement (McMahan et al. 2012). Retention rates of coded microwire tags are high, and they have little to no influence on growth or survival of lobsters (Krouse & Nutting 1990, Uglem & Grimsen 1995, Linnane & Mercer 1998, James-Pirri & Cobb 1999, Sharp et al. 2000, McMahan et al. 2012). Thus, coded microwire tags (NMT) can be used to execute large-scale mark–recapture studies that produce unbiased growth measurements for juvenile lobsters (Cowan 1999, Cowan et al. 2001, McMahan et al. 2012).

The purpose of this study was to analyze and interpret juvenile growth data from an 18-yr, mark–recapture field study conducted in the GOM from 1993–2010 in an effort to expand our understanding of growth during early life history stages (Cowan 1999, Cowan et al. 2001, Solow et al. 2000, Ellis & Cowan 2001, Solow & Cowan 2012). Percent growth, seasonal molt incidence, and molt probability were analyzed as a function of size, time-at-large and temperature (i.e. warm vs. cold years) for tagged juvenile lobsters in 3 size classes. We hypothesized that growth rates (i.e. percent growth and molt probability) of smaller juveniles would be greater than larger juveniles, would accelerate during warm years, and that molt incidence would occur earlier in the season during warm years.

MATERIALS AND METHODS

Tagging data

The Lobster Conservancy began a mark–recapture study tagging juvenile lobsters in 1993 at Lowell's Cove (43° 45′ 30″ N, 69° 58′ 24″ W) in Harpswell, ME (Cowan 1999, Cowan et al. 2001; our Fig. 1). Sampling occurred on a monthly year-round basis at the intertidal–subtidal interface (~0.3 m below mean low water). As of 2010, a total of 12 015 lobsters (≥12 mm CL) had been tagged by injecting a coded microwire tag (NMT) in the medial muscle tissue of the propodus of the second right walking leg with a single shot

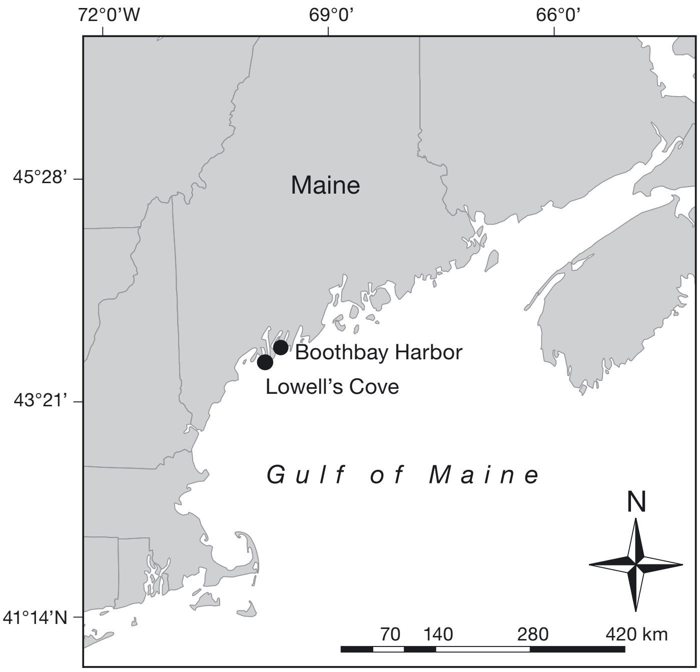

Fig. 1. Location of juvenile *Homarus americanus* census and mark–recapture site at Lowell's Cove in Harpswell, ME (43° 45′ 30″ N, 69° 58′ 24″ W). Water temperature was measured at Boothbay Harbour (43° 50′ 40″ N, 69° 38′ 30″ W)

injector (NMT; Cowan 1999, Cowan et al. 2001, McMahan et al. 2012). These tags are biologically inert and measure 0.25 mm in diameter by 1.0 mm in length. Before each lobster was tagged, it was passed over a V-Detector (NMT) to determine if it was a recapture. Recaptured lobsters had the tip of the leg containing the tag excised and saved for tag identification; lobsters were re-tagged to continue following the same individual over time. Tagged lobsters were also v-notched in the uropod to externally mark them and identify which leg had been tagged. All lobsters were immediately replaced within the quadrat from where they were captured, allowing for repeated sampling of the same individuals over time. McMahan et al. (2012) evaluated this tagging method using a field cage experiment and found there was no significant effect on growth, survival or autotomy of the tagged leg.

Temperature data

The Boothbay Harbor (BBH) Sea Water Temperature Record (data provided by Mark Lazzari, Maine Department of Marine Resources) was used to analyze temperature during the time period when mark–recapture data was collected. We used the BBH time series because it is the longest running seawater time series in the GOM (extending over more than a century) and the temperature probe is located roughly 30 km northeast of Lowell's Cove (Fig. 1). Temperature readings were collected hourly by data loggers located at a fixed point on the seabed, approximately 1.7 m below mean low water. Analyses of the effects of temperature on growth utilized average annual temperature as well as average temperature during warm months (May–October), when the majority of molting occurs. Temperature was further categorized into warm and cold years in order to analyze differences in growth between warm and cold periods. Average annual temperature during May–October was sorted from coldest to warmest, and the largest temperature difference between years that would allow for at least 5 yr in either category was used as the splitting point. Regression analysis was used to analyze the change in average temperature for both warm (May–October) and cold months (November–April) from 1993–2010.

Temperature readings were also collected hourly at Lowell's Cove starting in 2002. Data loggers were located underneath a rock within the sampled transects. Regression analysis was used to compare average daily temperature from BBH and Lowell's Cove in warm and cold months from 2002–2010 to examine the degree to which temperature at the 2 sites is correlated.

Analysis of growth

Percent growth and molt incidence

A total of 1004 recaptured lobsters (roughly 90%) had 12–40 mm CL. Within this size range, lobsters were grouped into 3 size classes for analysis; 12–19.9 mm CL (small), 20–29.9 mm CL (medium), and 30–39.9 mm CL (large). Although growth is a continuous process, perceived growth in crustaceans is measured by the time interval and change in size increment (i.e. CL) between ecdysis (Aiken 1980). To measure growth, lobsters that molted between subsequent captures were classified by number of days-at-large. We calculated growth during 1 molt cycle for individuals recaptured between 25 and 45 days-at-large (N = 157). This duration reflects the range of time between sampling periods and is short enough to exclude lobsters that may have molted more than once. Percent growth between captures during 1 molt cycle was used for all growth calculations. The effect of initial size on percent growth within warm and cold years was tested using ANCOVA with initial size as a covariate. Regression analysis was used to determine the effect of average annual temperature and average temperature during May–October on average percent growth measurements within each year. Linear regression and quantile regression were used to analyze percent growth over time (1993–2010). The Kolmogorov-Smirnov (K-S) test was used to compare the cumulative frequency distribution of percent growth between warm and cold years as well as between size classes for all years pooled. Seasonal percent growth (spring: May/June, summer: July/August, and fall: September/October) was also compared within size classes for all years pooled. We also examined whether seasonal percent growth differed between warm and cold years, but there were not enough recaptured lobsters within each season and temperature period to test between size classes. Therefore, seasonal percent growth within warm and cold years was tested for all size classes pooled using K-S tests.

Molt incidence (%) was determined using molt condition and month of capture for all captured lobsters between 12–40 mm CL from 1993–2010 (N = 11,609). Molt condition was assessed in the field using external criteria such as shell hardness and color (sensu Aiken 1980). Condition was categorized as premolt (dark limb buds, presence of new shell growth in clipped pleopods), molt (shell is soft, lobster is lethargic), newly molted (shell has begun to harden and is bright) and hard shell (no flexibility of the shell when finger pressure is applied, color is muted, presence of abrasions or epizoa). The frequency of molting within each month was calculated by dividing the number of lobsters captured that had recently molted by the total number of lobsters captured within that month. The K-S test was used to compare the cumulative frequency distribution of monthly molt incidence between warm and cold years as well as between size classes for all years pooled.

Molt probability

Intermolt interval cannot directly be measured from mark–recapture studies; however, molting probability can be used to replace intermolt interval (Chang et al. 2012). Molt probability is estimated using the proportion of individuals that have molted within a given period and size class. We utilized the days-at-large between captures for individuals exhibiting a size increase within the 95% confidence interval corresponding to one molt (calculated from individuals at large for 25 to 45 d) to estimate molt probability. Only data ranging from 1994–2010 was used to calculate time at large between captures. The study began in mid-1993, therefore all 1993 interval estimates were less than 6 mo in length, and potentially would bias the results if included. The probability of molting in relation to time was calculated, similar to Chen & Kennelly (1999), using a logistic equation:

$$p = 1 / (1 + e^{-r(t - t_{50})})$$

where p is proportion of lobsters that have molted in time duration t, t_{50} is the time duration when 50% of lobsters have molted, and r is a slope parameter estimated by nonlinear least squares method. Estimated molt probability was compared between warm and cold years and between size classes for all years pooled using an F-test. All of the above analyses were performed in Matlab R2014b.

RESULTS

Tagging data

Of the 12 015 lobsters tagged, 1172 individuals were recaptured at least once, 922 of which had grown while at large. Many lobsters were recaptured multiple times (n = 124), some as many as 3 (n = 24), 4 (n = 3), or 5 (n = 2) times, and one as many as 6 times. Recaptured lobsters ranged from 12 to 61.5 mm CL.

Temperature data

Bottom temperature at BBH fluctuated seasonally with average monthly temperatures in cold months (November–April) ranging from 1.1 to 12.1°C, and average monthly temperatures in warm months (May–October) ranging from 8.3 to 20.2°C. Bottom temperature significantly increased during warm months by an average of 0.13°C yr^{-1} between 1993 and 2010 ($F_{1,16}$ = 9.53, r^2 = 0.37, p = 0.007; Fig. 2A); although there was also an increasing trend in temperature during cold months over this period, it was not significant ($F_{1,16}$ = 1.9, r^2 = 0.11, p = 0.19). Average annual temperature from May–October was divided into warm and cold years, with cold years (1993–1998, 2007 and 2009) ranging from 12.7 to 14.3°C, and warm years (1999–2006, 2008 and 2010) ranging from 14.7 to 17.0°C.

It is important to note that the location where lobsters were captured (transects at 0.3 m depth) was predominantly subtidal and exposed to air <2% of the month; however, sampling was conducted when

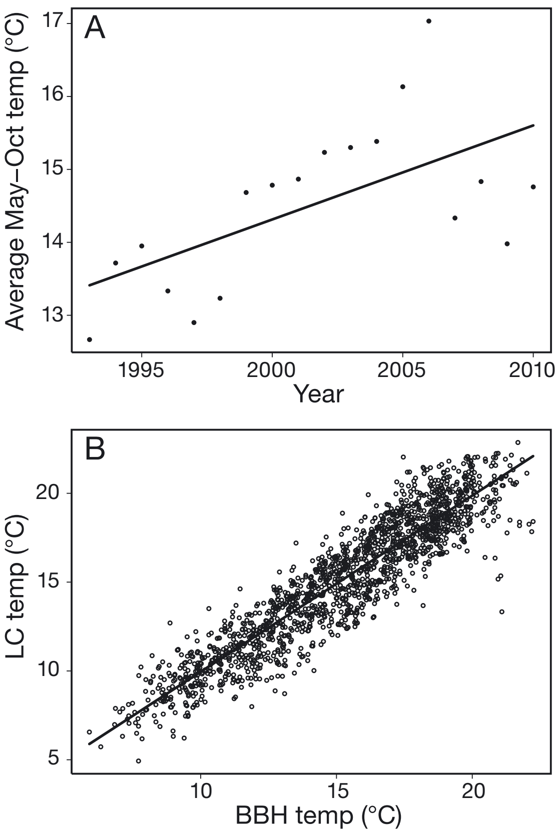

Fig. 2. (A) Time trend of temperature increase from 1993 to 2010 during the growing season. Regression of average bottom temperature for May–October at Boothbay Harbor (BBH; 1.7 m below mean low water). Linear trend in annual variability has a slope of 0.13°C yr^{-1} ($r^2 = 0.37$, $p = 0.007$). (B) Regression of average daily temperature at BBH, and Lowell's Cove (LC) between 2002 and 2010 during the warm season (May–October: *y*-intercept = 0.04, $r^2 = 0.87$, $p < 0.0001$)

the area was exposed for a few hours each month during the lowest spring tides. Therefore, there were brief windows of time when Lowell's Cove experienced greater temperature extremes than the BBH temperature data logger, which is completely submerged (BBH measured at 1.7 m depth). However, there was a strong, significant correlation between average daily temperature observed at BBH and Lowell's Cove from 2002–2010, during both warm and cold months (warm: $r^2 = 0.87$, *y*-intercept = 0.04, $p < 0.0001$; cold: $r^2 = 0.79$, *y*-intercept = –0.03, $p < 0.0001$; Fig. 2B). In particular, the *y*-intercept value resulting from the regression of daily temperature at BBH and Lowell's Cove in warm months indicates a minimal offset of temperature (i.e. slightly warmer at Lowell's Cove) between the 2 sites when the majority of growth is occurring. Therefore, we used the BBH time series for all temperature analyses rather than extrapolating temperature data from observations at Lowell's Cove.

Percent growth and molt incidence

Percent growth of lobsters of 12–39.9 mm CL over 1 molt cycle (25–45 days-at-large) ranged from 3.03 to 19.57 % (mean ± SE = 12.60 ± 0.45 %, n = 77) in cold years and from 6.35 to 21.05 % (14.39 ± 0.36 %, n = 80) in warm years. Initial CL did not significantly affect percent growth ($F_{1,153} = 0.67$, $p = 0.57$), and the interaction between initial CL and warm and cold periods was also not significant ($F_{1,153} = 0.11$, $p = 0.73$). Average annual temperature and average temperature from May–October did not significantly influence average percent growth measurements for all size classes combined (annual: $F_{1,12} = 0.08$, $p = 0.78$; May–October: $F_{1,12} = 0.77$, $p = 0.40$). The size classes were not tested independently because there were too few data points within most years. Regression of percent growth over time for all lobster size classes combined was not significant ($F_{1,155} = 3.04$, $p = 0.08$); however, quantile regression (StataCorp 1995, Scharf et al. 1998) of the lower (25th quantile) bound of the data revealed a significant increase in percent growth over time ($r^2 = 0.11$, $F_{1,37} = 4.32$ $p = 0.04$; Fig. 3). There was no significant difference in the cumulative distribution of percent growth between size classes (K-S test, $p > 0.05$). Yet, greater percent growth measurements were significantly more frequent in warm years for the small size class (mean ±

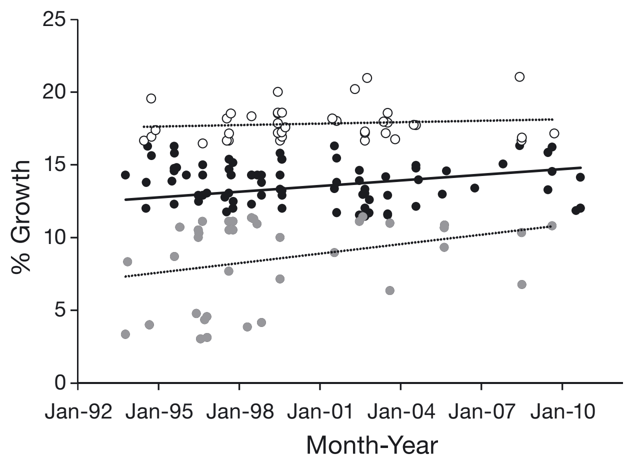

Fig. 3. Percent growth of *Homarus americanus* recaptured between 25–45 days-at-large (n = 185) at Lowell's Cove from 1993–2010. Each symbol represents an individual lobster. Solid trend line = linear regression of percent growth over time (all circles, $r^2 = 0.0182$, $p > 0.05$). Dashed trend lines = quantile regression of percent growth and time for 25th quantile (gray circles, $r^2 = 0.11$, $p < 0.05$) and 75th quantile (white circles, $r^2 = 0.01$, $p > 0.05$)

SE: cold years = 11.64 ± 1.01 %, warm years = 13.93 ± 0.59 %; K-S test, p < 0.05; Fig. 4A). There was also a trend of greater percent growth being more frequent in warm years for both the medium and large size classes (medium size class mean ± SE: cold years = 12.52 ± 0.58 %, warm years = 14.14 ± 0.60 %; large size class mean: cold years = 13.04 ± 0.89 %, warm years = 15.48 ± 0.60 %); however, neither relationship was significant (K-S tests, p > 0.05; Fig. 4B,C). There was no seasonal difference in percent growth across all years within the medium and large size classes (K-S tests, p > 0.05). The small size class was not tested independently because there were too few data points within each season and year. Dividing the percent growth data by size class, season, and warm and cold years, resulted in too few data points to compare; therefore, we compared seasons within warm and cold years for all size classes combined. Greater percent growth measurements were significantly more frequent in the spring in warm years compared to cold for all size classes combined (spring mean ± SE: cold years = 12.55 ± 0.78 %, warm years = 15.21 ± 0.60 %; K-S test, p < 0.05; Fig. 5). There was no significant difference in summer and fall percent growth between warm and cold years (K-S tests, p > 0.05).

During the 18-yr sample period, 1726 out of 1741 individuals molted between May and October, with peak molt incidence in June and September (Fig. 6A). Less than 1 % of molt incidence occurred between November and April (n = 15). There was no significant difference in monthly distribution of molt incidence among size classes or between warm and cold years (K-S tests, p > 0.05 for all tests; Fig. 6A). However, further examination of the 4 coldest (1993, 1996–1998) and 4 warmest (2002, 2004–2006) years did reveal a significant increase in the frequency of molt incidence in May in warm years for the small size class (K-S test, p < 0.05; Fig. 6B).

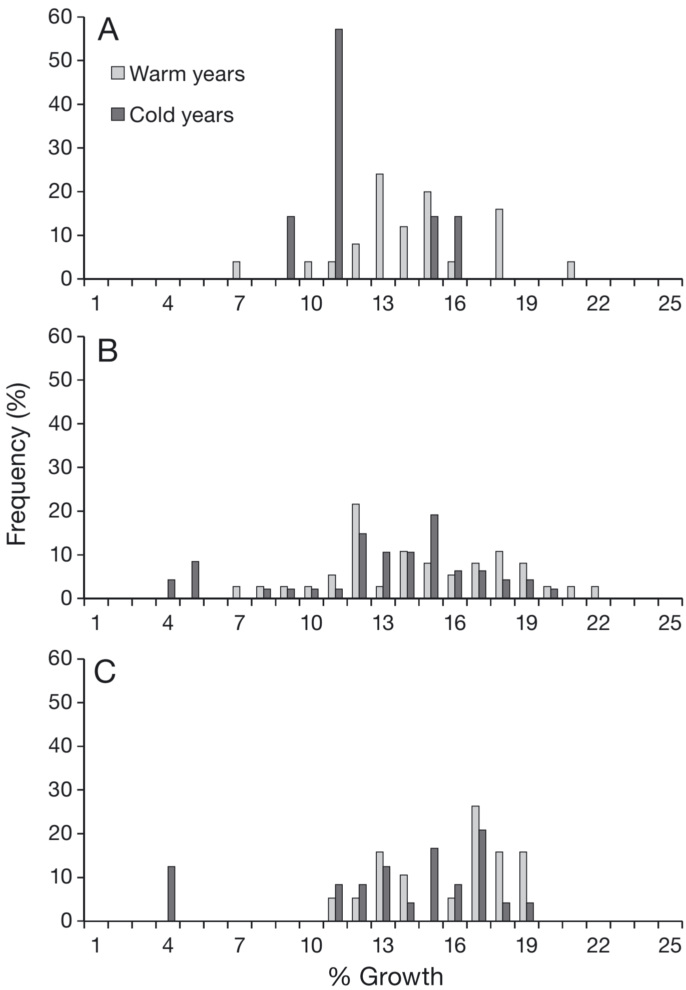

Fig. 4. Frequency distribution of percent growth of *Homarus americanus* recaptured after 25–45 days-at-large in warm and cold years for (A) 12–19.9 mm CL size class, (B) 20–29.9 mm CL size class, and (C) 30–39.9 mm CL size class

Molt probability

The time at which 50 % of the population had molted(t_{50}, i.e. intercept of 0.5 probability and days-at-large) was significantly shorter for the small size class (t_{50} = 44 d) compared to both the medium (69 d) and large (75 d) size classes (*F*-tests, p < 0.05; Fig. 7A) but not between the medium and large size classes (*F*-test, p > 0.05; Fig 7A). There was also a significant difference in molt probability between warm and cold years for the medium (warm: t_{50} = 50 d; cold: t_{50} = 83 d) and large (warm: t_{50} = 51 d; cold: t_{50} = 94 d) size classes (*F*-tests, p < 0.05; Fig. 7B,C).

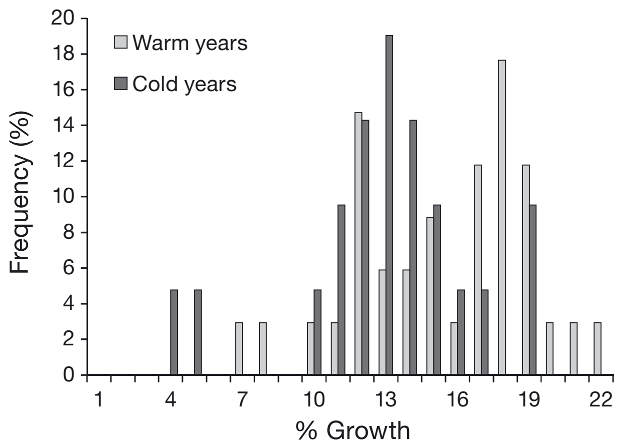

Fig. 5. Frequency distribution of percent growth of *Homarus americanus* in the spring (May–June) in warm and cold years for all size classes combined (spring mean ± SE: cold years = 12.55 ± 0.78 %, warm years = 15.04 ± 0.63 %; p < 0.05)

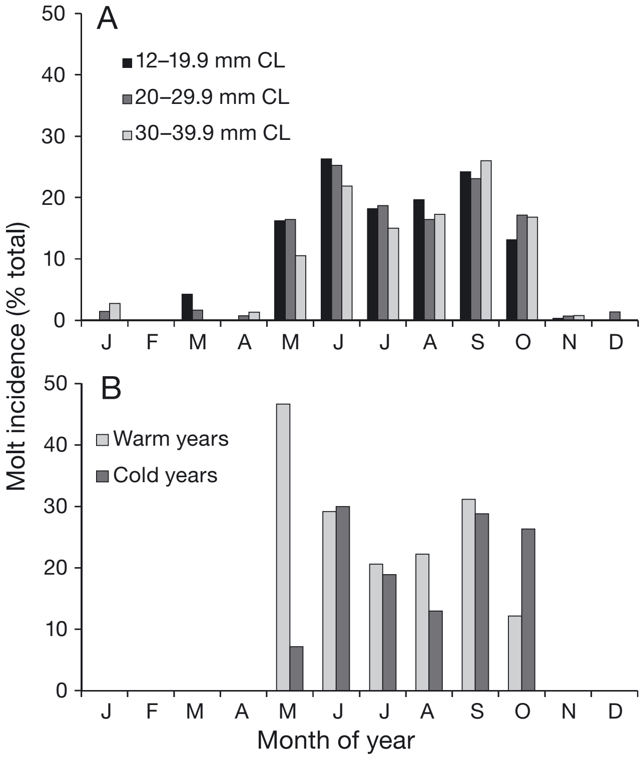

Fig. 6. Molt incidence by month for (A) 3 size classes (12–19.9, 20–29.9 and 30–39.9 mm CL) of juvenile *Homarus americanus* during 1993–2010 ($p > 0.05$ for all tests), and (B) the 12–19.9 mm CL size class in the 4 warmest (2002, 2004–2006) and coldest (1993, 1996–1998) years

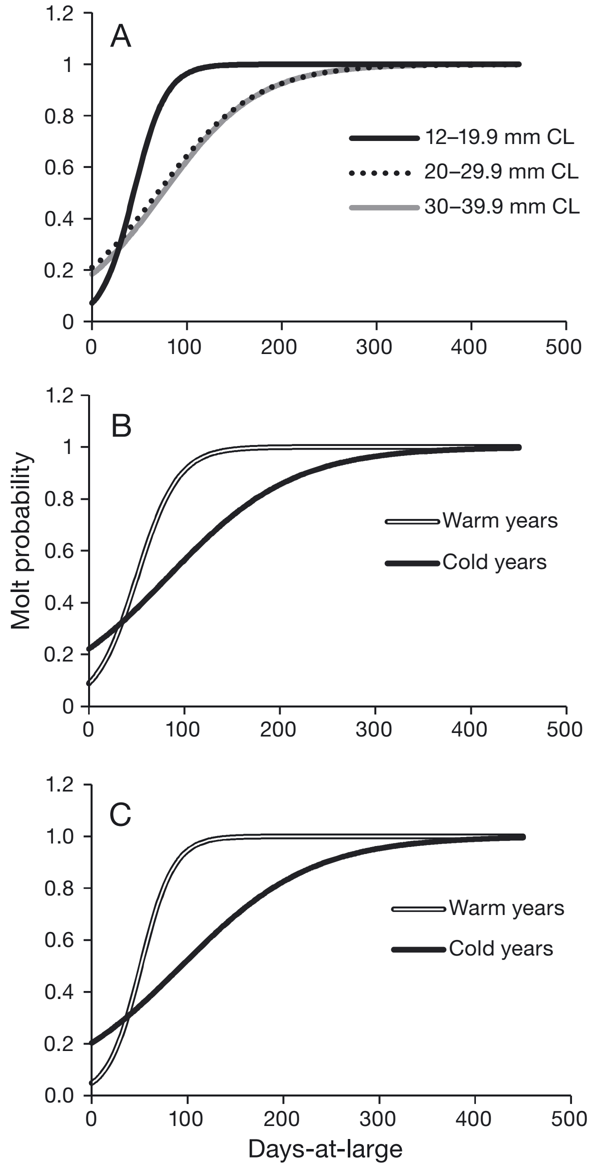

Fig. 7. Molt probability for *Homarus americanus* estimated from days-at-large (A) compared between 3 size classes (12–19.9, 20–29.9, 30–39.9 mm CL) for 1993–2010, (B) for the 20–29.9 mm CL size class in cold years and warm years, and (C) for the 30–39.9 mm CL size class in cold years and warm years

DISCUSSION

This study directly measured individual juvenile American lobster *Homarus americanus* (12–39.9 mm CL) growth rates in the field through multiple molt cycles spanning 2 decades during a period of considerable warming in the GOM (Mills et al. 2013). Growth rates (i.e. molt probability) were significantly faster for small (12–19.9 mm CL) juveniles compared to larger (>20 mm CL) juvenile lobsters (Fig. 7A). There was no difference between size classes in the timing of molt incidence. The majority (99%) of molting occurred between May and October, with peaks in both June and September. There was no direct correlation between average annual temperature or average temperature in May–October and percent growth, but percent growth was greater in warm years for the smallest size class (Fig. 4A), and percent growth of all size classes combined was greater during the spring in warm years compared to cold (Fig. 5). We also found that the duration of 50% molt probability of medium and large-sized juvenile lobsters (20–29.9 and 30–39.9 mm CL) was reduced by almost half in warm years (Fig. 7B,C). Collectively, these results suggest that growth differs between small and large juveniles, and that growth has fluctuated during warm and cold years over the course of the 18-yr study.

Previous studies have estimated juvenile lobster growth rates from observing size distributions of hatchery reared or wild juveniles (Hudon 1987, James-Pirri et al. 1998), from manipulative laboratory or field experiments using hatchery reared juveniles

(Hughes et al. 1972, Wahle et al. 2001, Tlusty & Metzler 2012), and through the use of mark–recapture data from larger juveniles (i.e. >20 mm CL; e.g. Wilder 1953, Tremblay & Eagles 1997, Comeau & Savoie 2001, Bergeron 2011). The novelty of our study stems from the use of mark–recapture data of small juveniles in the field to measure growth, and subsequently estimate growth rates, over 2 decades. By taking advantage of juvenile lobster use of the shallow subtidal (0.3 m below mean low water), thousands of individuals were marked and recaptured over the course of 18 yr. Thus, the growth rates estimated in this study are derived from a large sample size of juvenile lobsters in the wild.

Our results build on previous studies of juvenile lobster growth. For instance, Bergeron (2011) developed growth models for juvenile lobsters in the GOM measuring 20–39 mm CL and found an estimated time at 50% molt probability of 92 d. Our study estimated growth for 2 size classes (i.e. medium = 20–29.9 mm CL, large = 30–39.9 mm CL) within this range and found that molt probability estimates for lobsters were shorter (medium = 69 d, large = 75 d) for 1993–2010 than Bergeron's estimates for 1975–2003. Furthermore, we found significant variation in molt probability over time within size classes. These results emphasize the importance of utilizing multiple size classes when estimating juvenile lobster growth, and advocate for the use of stock assessment models that incorporate variation in growth over relatively short periods of time to account for variability in factors that influence lobster growth, such as temperature.

Our results of lobster growth in warm and cold years are consistent with field and laboratory studies documenting the effect of temperature on crustacean growth rates (reviewed in Hartnoll 1982, 2001, Chang et al. 2012). Field studies have documented faster juvenile growth in warmer seasons for spiny lobsters *Panulirus argus* (Forcucci et al. 1994) and blue crabs *Callinectes sapidus* (Ju et al. 2001), and also increased growth, or earlier molting, for American lobsters found in warmer geographic areas, or during warm seasons or years (e.g. Templeman 1936, Tremblay & Eagles 1997, Comeau & Savoie 2001). Laboratory studies have also shown that increased temperature increases juvenile growth rates for many crustacean species, including Dungeness crab *Cancer magister* (Kondzela & Shirley 1993), spiny lobster *Panulirus argus* (Lipcius & Herrnkind 1987), red and blue king crabs *Paralithodes camchaticus* and *Paralithodes platypus* (Stoner et al. 2013), and American lobsters (Hughes et al. 1972, Aiken & Waddy 1976, Tlusty & Metzler 2012). However, it is less clear why our documented effects of temperature differed between size classes. For instance, molt increment in warmer years was only greater for the smallest lobsters, whereas t_{50} decreased for both medium and large-sized lobsters in warmer years. It is possible that the intermolt interval of the smallest size class is already at the minimum duration necessary to complete the energetic requirements of the molt cycle. Our results suggest that changes in growth of the smallest juveniles may instead manifest as an increase in magnitude of molt increment. Meanwhile, the decrease in the time at which both medium and large-sized juveniles reached 50% molt probability during the warm years suggests that medium and large-sized juvenile lobsters may have responded to increases in water temperature by decreasing intermolt interval.

We divided warm and cold years using mean temperature for May–October; however, temperature variation within those months, and across years, may have also impacted juvenile lobster growth. Temperature variation may have equal or stronger effects on growth and development in ectotherms compared to mean temperature (Thorp & Wineriter 1981, Bozinovic et al. 2011, Niehaus et al. 2012, Quinn & Rochette 2015). Further investigation into the relative importance of mean temperature and temperature variability in a controlled environment, as opposed to a field study, is warranted to partition the relative importance of each potential driver of growth and how they interact.

Although there was no significant correlation between average temperature and average percent growth, the extremely low percent growth values (i.e. <5%) seen in cold years were not observed in warm years (Fig. 3) and there was a significant increase in molt increment for the smallest juveniles (Fig. 4A) during the warmer period. Furthermore, percent growth in the spring for all size classes combined was greater in warm than in cold years. This result is consistent with controlled field studies that have found that lobsters from warmer waters (sometimes differing by only 2°C) experience larger growth increments than those from colder waters (Wilder 1953, Aiken 1977, Campbell 1983, Waddy et al. 1995, Wahle et al. 2001). However, Little & Watson (2005) found that female lobsters matured at smaller sizes in warmer water, and, along with Landers et al. (2001), hypothesized that females in warmer water may experience smaller molt increments. We did not test female and male lobsters separately, and thus cannot conclusively say whether or not temperature impacted percent growth of females and males differently in warm and cold years. In general, the lack of correlation between percent growth and temperature suggests that multiple factors are likely influencing percent growth of wild juvenile lobsters. Although physical factors such as temperature and photoperiod play a major role in influencing crustacean growth, biological factors including shelter and food availability, density, inter- and intra-specific competition, and predation levels all influence lobster population dynamics (Nelson et al. 1980, Steneck 2006, Grabowski et al. 2009, 2010, McMahan et al. 2013, Oppenheim & Wahle 2013). Further observation of, and experiments examining, interactions among juvenile lobster growth rates and abundance, shelter and prey resource availability, predation, and seawater temperature changes will help reveal how abiotic and biotic factors couple to influence lobster growth rates and stock productivity.

Molt incidence peaked for all size classes in June and again in September, similar to field observations that have documented spring and autumn molting peaks in juvenile and adult lobsters (reviewed in Waddy et al. 1995, Tremblay & Eagles 1997, Comeau & Savoie 2001). However, we did not find a significant difference in the distribution of monthly molt incidence between warm and cold years. We expected to see molting occurring earlier in the season during warmer years, similar to Tremblay & Eagles (1997), who found that adult lobsters molted earlier in the season when spring and early summer temperatures were higher than average. The influence of temperature on lobster molt incidence was further revealed during the 2012 warm water temperature anomaly in the GOM that induced an early molt and caused landings to rise rapidly (Mills et al. 2013). The warmest year within the 1993–2010 data we analyzed was in 2006, when the average annual temperature reached 12.4°C. The 2012 temperature anomaly exceeded the 2006 average annual temperature by >1.5°C. Had the mark–recapture data set extended through 2012, we may have observed a similar shift in juvenile molt incidence. However, a deeper probe of the molt incidence data that compared the 4 warmest and 4 coldest years in the data set did find a significant difference in molt timing for the smallest size class (Fig. 6B). There was a 40% increase in the frequency of molt incidence in May during the 4 warmest years, and molt incidence in May was greater than any other month. Goldstein & Watson (2015) suggested that the rate of temperature increase in the spring had a greater impact on when lobster eggs hatch than cumulative degree days experienced throughout egg development. Our results similarly suggest that extremely warm spring temperatures induce earlier and more frequent molting of small juvenile lobsters on the coast of Maine. This effect was only apparent in the smallest lobsters, emphasizing that temperature impacts small juveniles differently than large juveniles. It is important to note that analyzing the effect of temperature on molt incidence using finer resolution data (i.e. seasonal or monthly temperature trends and/or daily molt incidence) may have revealed further shifts in molt incidence beyond what was observed for the smallest juveniles in the warmest years in this study.

Currently, the ASMFC lobster stock model uses growth rates for lobsters measuring ≥53 mm CL (ASMFC 2015). The size range we tested (12–39.9 mm CL) revealed growth rates of lobsters during early, critical life history stages when post-settlement processes influence lobster population dynamics, and our study revealed that their growth rates vary with size. These results are important given that stock projections for the species are currently being conducted with gaps in basic biological metrics for early life history stages. Furthermore, we found that environmental variables, such as temperature, may influence the growth of smaller juveniles differently than larger juveniles and adult lobsters. Given that the American lobster inhabits waters that are warming faster than 99% of the world's other oceans (Pershing et al. 2015), our results have implications for how this species may respond to future changes in seawater temperatures.

Evaluating juvenile lobster growth using a long-term mark–recapture time series has enhanced our understanding of their growth in the wild and the apparent influence of ocean temperature on growth rates. An increase in lobster growth in warmer years, whether it results from larger molt increments or a decrease in intermolt interval, could cause juveniles to reach harvestable size at a younger age. The overall economic impact of accelerating lobster growth rates is potentially immense since lobsters represent the third most valuable fishery in the USA (NMFS 2014).With sea water temperatures predicted to continue to rise, it is likely that lobster growth rates will also continue to increase. However, warming water temperature has also been linked to increased occurrence of epizootic shell disease in lobsters (Glenn & Pugh 2006), further underscoring the vital importance of continuing to monitor growth in wild populations. The data collected from this study can improve management of the lobster resource by providing empirical data that can be used to parameterize lobster stock assessment models (Chen et al. 2005, ASMFC 2015) that account for changes in seawater temperature and other important post-settlement processes.

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LITERATURE CITED

Aiken DE (1977) Molting and growth in decapod crustaceans with particular reference to the lobster *Homarus americanus*. Div Fish Oceanogr Circ No. 7, CSIRO, Canberra ACT, p 41–73

Aiken DE (1980) Molting and growth. In: Cobb JS, Phillips BF (eds) The biology and management of lobsters. Academic Press, New York, NY, p 91–164

Aiken DE, Waddy SL (1976) Controlling growth and reproduction in the American lobster. J World Aquacult Soc 7: 415–430

Angilletta MJ, Niewiarowski PH, Navas CA (2002) The evolution of thermal physiology in ectotherms. J Therm Biol 27:249–268

ASMFC (Atlantic States Marine Fisheries Commission) (2015) American lobster benchmark stock assessment and peer review report. ASMFC American Lobster Stock Assessment Review Panel, Woods Hole, MA

Bergeron CE (2011) Research on lobster age-size relationships: developing regionally specified growth models from meta-analysis of existing data. MS thesis, The University of Maine, Orono, ME

Bozinovic F, Bastías DA, Boher F, Clavijo-Baquet S, Estay SA, Angilletta MJ Jr (2011) The mean and variance of environmental temperature interact to determine physiological tolerance and fitness. Physiol Biochem Zool 84: 543–552

Campbell A (1983) Growth of tagged lobsters (*Homarus americanus*) off Port Maitland, Nova Scotia, 1946–80. Can Tech Rep Fish Aquat Sci 1232:1–10

Chang YJ, Sun CL, Chen Y, Yeh SZ (2012) Modelling the growth of crustacean species. Rev Fish Biol Fish 22: 157–187

Chen Y, Kennelly S (1999) Growth of spanner crabs, *Ranina ranina*, off the east coast of Australia. Mar Freshw Res 50: 319–325

Chen Y, Kanaiwa M, Wilson C (2005) Developing and evaluating a size-structure stock assessment model for the American lobster, *Homarus americanus*, fishery. NZ J Mar Freshw Res 39:645–660

Comeau M, Savoie F (2001) Growth increment and molt frequency of the American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. J Crustac Biol 21: 923–936

Cowan DF (1999) Method for assessing relative abundance, size distribution, and growth of recently settled and early juvenile lobsters (*Homarus americanus*) in the lower intertidal zone. J Crustac Biol 19:738–751

Cowan DF, Solow AR, Beet A (2001) Patterns in abundance and growth of juvenile lobster, *Homarus americanus*. Mar Freshw Res 52:1095–1102

Cowan DF, Watson WH III, Solow AR, Mountcastle AM (2007) Thermal histories of brooding lobsters, *Homarus americanus*, in the Gulf of Maine. Mar Biol 150:463–470

Ellis SL, Cowan DF (2001) Volunteer-based monitoring of juvenile American lobster, *Homarus americanus*. Mar Freshw Res 52:1103–1112

Ennis GP (1983) Annual variations in standing stock in a Newfoundland population of lobsters. N Am J Fish Manage 3:26–33

Forcucci D, Butler MJ, Hunt JH (1994) Population dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida Bay, Florida. Bull Mar Sci 54:805–818

Glenn RP, Pugh TL (2006) Epizootic shell disease in American lobster (*Homarus americanus*) in Massachusetts coastal waters: interactions of temperature, maturity, and intermolt duration. J Crustac Biol 26:639–645

Goldstein JS, Watson WH III (2015) The influence of natural inshore and offshore thermal regimes on egg development and time of hatch in the American lobster, *Homarus americanus*. Biol Bull 228:1–12

Grabowski JH, Clesceri EJ, Gaudette J, Yund PO (2009) The role of food limitation in lobster population dynamics throughout the Gulf of Maine. NZ J Mar Freshw Res 43: 185–193

Grabowski JH, Clesceri EJ, Gaudette J, Baukus A, Weber M, Yund PO (2010) Use of herring bait to farm lobsters in the Gulf of Maine. PLOS ONE 5:e10188

Hartnoll RG (1982) Growth. In: Abele LG, Bliss DE (eds) The biology of crustacea, Vol 2: Embryology, morphology, and genetics. Academic Press, New York, NY, p 111–196

Hartnoll RG (2001) Growth in crustacea: twenty years on. Hydrobiologia 449:111–122

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328: 1523–1528

Hudon C (1987) Ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Îles de Madeleine (Quebec). Can J Fish Aquat Sci 44:1855–1869

Hughes JT, Sullivan JJ, Shleser R (1972) Enhancement of lobster growth. Science 177:1110–1111

Jackson JBC, Kirby MX, Berger WH, Björndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637

James-Pirri MJ, Cobb JS (1999) Influence of coded microwire tags on postlarval lobster (*Homarus americanus*) behavior. Mar Freshw Behav Physiol 32:255–259

James-Pirri MJ, Cobb JS, Wahle RA (1998) Influence of settlement time and size on post settlement growth in the American lobster (*Homarus americanus*). Can J Fish Aquat Sci 55:2436–2446

Ju SJ, Secor DH, Harvey HR (2001) Growth rate variability and lipofuscin accumulation rates in the blue crab *Callinectes sapidus*. Mar Ecol Prog Ser 224:197–205

Kondzela CM, Shirley TC (1993) Survival, feeding, and growth of juvenile Dungeness crabs from southeastern Alaska reared at different temperatures. J Crustac Biol 13:25–35

Krouse JS, Nutting GE (1990) Evaluation of coded microwire tags inserted in legs of small juvenile American lobsters. Am Fish Soc Symp 7:304–310

Landers DF Jr, Keser M, Saila SB (2001) Changes in female lobster (*Homarus americanus*) size at maturity and implications for the lobster resource in Long Island Sound, Connecticut. Mar Freshw Res 52:1283–1290

Lawton P, Lavalli KL (1995) Postlarval, juvenile, adolescent, and adult ecology. In: Factor JR (ed) Biology of the lobster: *Homarus americanus*. Academic Press, San Diego, CA, p 47–88

Linnane A, Mercer JP (1998) A comparison of methods for tagging juvenile lobsters (*Homarus gammarus* L.) reared for stock enhancement. Aquaculture 163:195–202

Lipcius RN, Herrnkind WF (1987) Control and coordination of reproduction and molting in the spiny lobster *Panulirus argus*. Mar Biol 96:207–214

Little SA, Watson WH (2005) Differences in the size at maturity of female American lobsters, *Homarus americanus*, captured throughout the range of the offshore fishery. J Crustac Biol 25:585–592

McMahan MD, Cowan DF, Sherwood GD, Grabowski JH, Chen Y (2012) Evaluation of coded microwire tag retention in juvenile American lobster, *Homarus americanus*. J Crustac Biol 32:497–502

McMahan MD, Brady DC, Cowan DF, Grabowski JH, Sherwood GD (2013) Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*). Can J Fish Aquat Sci 70:1625–1634

MDMR (Maine Department of Marine Resources) (2016) Commercial Maine Landings, West Boothbay Harbor, Maine. www.maine.gov/dmr/commercial-fishing/landings/documents/11-15LandingsBySpecieswithBonus.Table.pdf (accessed 28 July 2016)

Mills KE, Pershing AJ, Brown CJ, Chen Y and others (2013) Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave in the northwest Atlantic. Oceanography (Wash DC) 26:191–195

Mooney H, Larigauderie A, Cesario M, Elmquist T and others (2009) Biodiversity, climate change, and ecosystem services. Curr Opin Environ Sustain 1:46–54

NMFS (National Marine Fisheries Service) (2014) Fisheries of the United States. NOAA Office of Science and Technology, Silver Spring, MD. www.st.nmfs.noaa.gov/commercial-fisheries/fus/fus14/index (accessed 28 July 2016)

Nelson K, Hedgecock D, Borgeson W, Johnson E, Daggett R, Aronstein D (1980) Density-dependent growth inhibition in lobsters, *Homarus* (Decapoda, Nephropidae). Biol Bull 159:162–176

Niehaus AC, Angilletta MJ Jr, Sears MW, Franklin CE, Wilson RS (2012) Predicting the physiological performance of ectotherms in fluctuating thermal environments. J Exp Biol 215:694–701

Oppenheim NG, Wahle RA (2013) Cannibals by night? *In situ* video monitoring reveals diel shifts in inter- and intra-specific predation on the American lobster. Can J Fish Aquat Sci 70:1635–1640

Pershing AJ, Alexander MA, Hernandez CM, Kerr LA and others (2015) Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science 350:809–812

Phillips BF, Cobb JS, George RW (1980) General biology. In: Cobb JS, Phillips BF (eds) The biology and management of lobsters. Academic Press, New York, NY, p 1–82

Quinn BK, Rochette R (2015) Potential effect of variation in water temperature on development time of American lobster larvae. ICES J Mar Sci 72:i79–i90

Scharf FS, Juanes F, Sutherland M (1998) Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. Ecology 79:448–460

Sharp WC, Lellis WA, Butler MJ, Herrnkind WF, Hunt JH, Pardee-Woodring M, Matthews TR (2000) The use of coded microwire tags in mark–recapture studies of juvenile Caribbean spiny lobster, *Panulirus argus*. J Crustac Biol 20:510–521

Solow AR, Cowan DF (2012) A test for space limitation with an application to recently settled lobsters. Mar Biol 159: 467–470

Solow AR, Beet A, Cowan DF (2000) Optimal seasonal sampling for estimating an interannual trend. Isr J Zool 46: 351–354

StataCorp (1995) Stata Statistical Software: Release 4.0. Stata Corporation, College Station, TX

Steneck RS (2006) Possible demographic consequences of intraspecific shelter competition among American lobsters. J Crustac Biol 26:628–638

Stoner AW, Copeman LA, Ottmar ML (2013) Molting, growth, and energetics of newly-settled blue king crab: effects of temperature and comparisons with red king crab. J Exp Mar Biol Ecol 442:10–21

Templeman W (1936) Local differences in the life history of lobster on the coast of the maritime provinces of Canada. J Biol Board Can 2:41–88

Thorp JH, Wineriter SA (1981) Stress and growth response of juvenile crayfish to rhythmic and arrhythmic temperature fluctuations. Arch Environ Contam Toxicol 10: 69–77

Tlusty MF, Metzler A (2012) Relationship between temperature and shell disease in laboratory populations of juvenile American lobsters (*Homarus americanus*). J Shellfish Res 31:533–541

Tremblay MJ, Eagles MD (1997) Molt timing and growth of the lobster, *Homarus americanus*, off northeastern Cape Breton Island, Nova Scotia. J Shellfish Res 16:383–394

Uglem I, Grimsen S (1995) Tag retention and survival of juvenile lobsters, *Homarus gammarus* (L.), marked with coded wire tags. Aquacult Res 26:837–841

Waddy SL, Aiken DE, DeKleijn DPV (1995) Control of growth and reproduction. In: Factor JR (ed) Biology of the lobster: *Homarus americanus*. Academic Press, San Diego, CA, p 217–266

Wahle RA (1992) Body size-dependent anti-predator mechanisms of the American lobster. Oikos 65:52–60

Wahle RA, Steneck RS (1992) Habitat restrictions in early benthic life: experiments on habitat selection and *in situ* predation with the American lobster. J Exp Mar Biol Ecol 157:91–114

Wahle RA, Tully O, O'Donovan V (2001) Environmentally mediated crowding effects on growth, survival and metabolic rate of juvenile American lobsters (*Homarus americanus*). Mar Freshw Res 52:1157–1165

Wilder DG (1953) The growth rate of the American lobster (*Homarus americanus*). J Fish Res Board Can 10:371–374

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