

Climate induced declines in maternal size may come at a cost to embryonic investment and larval performance in the American lobster

Alexander Ascher^{a,b,*}, Maura Niemisto^c, Donaven Baughman^d, Grace Andrews^e,
Curtis Morris^a, Emily Patrick^a, Richard A. Wahle^a, David M. Fields^c

^a University of Maine, School of Marine Sciences 168 College Ave, Orono, ME 04469, United States

^b Woods Hole Oceanographic Institution 266 Woods Hole Rd, MS #33 Woods Hole, MA 02543, United States

^c Bigelow Laboratory for Ocean Sciences 60 Bigelow Dr, East Boothbay, ME 04544, United States

^d Florida State University 600 W College Ave, Tallahassee, FL 32306, United States

^e University of Oregon 1585 E 13th Ave, Eugene, OR 97403, United States

ARTICLE INFO

Handled by Ehud Spanier

Keywords:

Larval ecology
Reproductive biology
Ocean warming
Space-for-time substitution

ABSTRACT

Many crustacean taxa mature at a smaller size in warmer thermal regimes. Over the past four decades, female lobsters American lobster (*Homarus americanus*) in the rapidly warming Gulf of Maine have also been reported to be maturing at significantly smaller sizes over time. Smaller females have lower fecundity, but whether they also produce lower quality eggs and larvae has been unclear. Here we examine the hypothesis that smaller females invest less energy per larva than larger females, thereby compromising post-hatch performance and survival. This study used a combination of laboratory and field studies to assess the maternal size effect on embryos and larvae. In a space-for-time comparison of lobsters from contrasting thermal regimes along the coast of New England, we also investigated how lobster collected from populations in cooler northern regions may respond to future warming. We found smaller females not only are less fecund, but their embryos are smaller and generally less well invested with lipids than those from larger females. Furthermore, stage I larvae from smaller females are smaller and have less energy reserves needed to survive starvation. Our geographic comparison also revealed that female lobsters living in the warmer thermal regime of southern New England are more fecund and produced larger eggs than females of the same size from colder regimes in the Gulf of Maine, and we cautiously interpret this novel finding as evidence of a counter-gradient adaptation that could compensate for smaller maturation size at lower latitudes, a phenomenon requiring further investigation. These results help to reveal the cascading effects warming can have on important reproductive and larval survival traits on an economically important species.

1. Introduction

How marine invertebrates react to climate warming over their native range, depends in part on how temperature affects key life-history traits. Since 1980, NW Atlantic seawater temperature has increased 0.3 °C per decade (Nixon et al., 2004; Mills et al., 2013; Seidov et al., 2021). In response to the considerable post-industrial increases in CO₂, global temperatures have been, and are predicted to rise at an unprecedented rate in the coming decades (Andrews et al., 2014; IPCC, 2021). Depending on future greenhouse gas emissions, conservative estimates of surface ocean (<100 m) temperature predict an increases of 0.6° to 2.4 °C by 2100 (Blunden and Arndt, 2013). As a result of this warming,

marine organisms are forced to adapt in place (Calosi et al., 2016; Palumbi et al., 2019), migrate (Pinsky et al., 2013; Allyn et al., 2020), or face extinction (Barnosky et al., 2011; Dulvy et al., 2003).

The body size at onset of maturity is one trait impacted by temperature that has broad implications for survival and reproduction (Peters, 1983; Attard and Hudon, 1987; Moland et al., 2010; Garrido et al., 2015; Barneche et al., 2018). In ectotherms, maturation tends to occur at smaller sizes in warmer regimes (Deevey, 1960; Precht et al., 1973), a relationship which has been termed the “Temperature Size Rule” (Forster and Hirst, 2012). Less well understood are the fitness consequences of temperature-induced phenotypic shifts in maternal size for the investment in and performance of their offspring. “Space-for-time”

* Corresponding author at: University of Maine, School of Marine Sciences 168 College Ave, Orono, ME 04469, United States.

E-mail address: alexander.ascher@whoi.edu (A. Ascher).

<https://doi.org/10.1016/j.fishres.2024.107059>

Received 21 December 2023; Received in revised form 18 April 2024; Accepted 13 May 2024

Available online 20 May 2024

0165-7836/© 2024 Elsevier B.V. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

comparisons of geographically separated subpopulations residing in differing thermal regimes add additional insight into evaluating how populations will respond to a changing environment (Blois et al., 2013).

The native range of the American lobster (*Homarus americanus*) spans one of the steepest known latitudinal thermal gradients for a marine species, with average summer surface sea temperatures roughly 12° C in the northern extent of the range to 20° C in the southern extent (Fogarty, 1995). This creates a natural laboratory to conduct a space-for-time substitution (sensu Lovell et al., 2023); comparing how range-related temperature differences affect life history traits, such as size at maturity and fecundity, embryo size and energy investment that ultimately influence reproductive success. While it is well known that lobsters in warmer, southern zones mature at a smaller size (Estrella and McKiernan, 1989), recent surveys show that sustained warming over the species' range has induced a decrease in female size at maturity in all locations (Waller et al., 2021). For example, Long Island Sound (Landers et al., 2001), the Gulf of Maine (ASMFC, 2020; Pugh et al., 2013), and the Bay of Fundy (Gaudette et al., 2014) all report steady declines in size at maturity since the 1990s. In Maine, the mean size at maturity of reproductive females has decreased by nearly 20% over the past two decades (Waller et al., 2021). Despite initially faster growth rates in warmer water, the earlier maturation of gonadal tissues taxes somatic growth, causing adult lobsters to be smaller in warmer water (Aiken and Waddy, 1976).

Maternal size is widely regarded as a governing factor in embryonic and larval development, typically through greater investment in embryo size and quality (Mousseau and Fox, 1998). Greater embryo size and quality is broadly linked to greater survival rates (Vance, 1973) across many different taxa including, polychaetes (Smith and Bolton, 2007) lobsters (Moland et al., 2010), sea urchins (McAlister and Moran, 2013), and fish (Hixon et al., 2014). From a fishery management standpoint, the implications of smaller reproducing females on recruitment to the lobster fishery is not fully understood. In lobsters, maternal body size is significantly correlated to fecundity (Attard and Hudon, 1987, Waddy et al., 1995, Koopman et al., 2014, Goldstein et al., 2022), and may limit embryo production under future warming conditions. What is less well known is how maternal body size specifically relates to embryo and larval quality and performance.

The present study investigated the quantity and quality of embryos, as well as the performance of larvae originating from female lobsters collected over a naturally occurring range of sizes from three locations along the east coast of the United States spanning a steep latitudinal gradient in summer temperatures. In southern New England, the warmer extent of the species' range, females mature earlier and at smaller sizes than those in the cooler, northeastern Gulf of Maine and Bay of Fundy (Estrella and McKiernan, 1989, Waller et al., 2021). This latitudinal gradient allowed the comparison among sexually mature lobsters from sub-populations residing in different thermal regimes to determine how maternal body size relates to fecundity, embryo size, energy content, fatty acid profile, and total lipid content. In the context of a space-for-time substitution, differences in lobsters from the warmest regime may help predict expected changes in lobsters originating from cooler water under future warming. Furthermore, laboratory experiments were used to assess growth and survival under starvation of larvae from females collected from Boothbay harbor and Casco Bay in Midcoast Maine, where there was access to reproductive females that spanned a relatively large range of sizes. From these observations, inferences were made regarding the effects of future warming on key life-history traits in the American lobster.

2. Methods

2.1. Study areas and lobster collection

The relationship between maternal body size and embryo metrics such as fecundity, embryo volume, dry weight, and energy content

(maternal investment) was investigated at three study regions: Downeast, ME (DE), Midcoast, ME (MC), and Rhode Island (RI) (Fig. 1). These regions differ in their thermal regime, with RI, the southernmost study area, having the warmest summer temperatures and becoming deeply stratified during the warm growing season with average summer temperatures exceeding 20° C. DE in the eastern Gulf of Maine, by contrast, has the coldest summer temperatures where proximity to the Bay of Fundy and the Eastern Maine Coastal Current ensures the water column remains well mixed and cool throughout the year, and average summer temperatures tend not to exceed ~12° C. MC represents the intermediate conditions typical of the western Gulf of Maine (GoM). MC is separated from the eastern GoM by the Penobscot River discharge and is not as strongly influenced by the Eastern Maine Coastal Current. A lower degree of mixing allows for some degree of thermal stratification in the MC during the summer and average surface temperatures reach ~16–18° C. Although RI once had a thriving lobster fishery, rising temperatures coupled with a high rate of shell disease resulted in the lobster population center shifting northward and offshore (Le Bris et al., 2018, Casey et al., 2022), leading to lower rates of recruitment and a decline in lobster landings (Wahle et al., 2009, Oppenheim et al., 2019).

2.2. Fecundity, embryo size, and calorimetry

Ovigerous female lobsters were collected at three study sites along the New England coast of the USA: RI (n=65), MC (n=60), and DE (n=60). Lobsters from RI were collected via the state's inshore trawl survey, while those collected within the GoM (MC+DE) were provided opportunistically by lobstermen. Lobsters from DE were collected from the Machias Bay area in Maine's Lobster Management Zone A, roughly between 44.4° N and 44.7° N. Lobsters from MC were collected from the Casco Bay area in Lobster Management Zone F, roughly between 43.4° N and 43.7° N. Egg extrusion is temperature dependent, and begins first in warmer southern waters, and then progresses up the coast. Lobsters from RI were therefore sampled first during September 2018, followed by MC in October and DE in November.

The total number of embryos carried by each female was estimated using a non-invasive technique to calculate the volume of the brooded clutch (Currie et al., 2010). The clutch of embryos is assumed to approximate the shape of a half cylinder. Briefly, the length and depth (averaged from five measurements along the length of the embryo mass) of each clutch was measured at the dock and the volume calculated using the equation for a half cylinder: $\frac{\pi D^2 L}{2} * 0.535$ where D is the average depth of the egg mass (cylinder radius), L is the length of the clutch, and 0.535 is the packing efficiency of loosely packed spheres which accounts for interstitial space between individual embryos (Currie et al., 2010).

The average volume of an individual embryo was calculated from a subsample of embryos collected from one pleopod from each female and frozen in a -80° C freezer to preserve them for lipid analysis and calorimetry. Diameters of embryos were measured on the short and long axis of 10 embryos using ImageJ software (Schindelin et al., 2012). Embryo volume was calculated as a sphere with the equation $\frac{4\pi r^3}{3}$ where r is $\frac{1}{2}$ the average of the short and long radius of the embryo diameter. The number of embryos, or fecundity, was calculated by dividing the volume of the clutch by the average embryo volume for each female.

Embryo dry weight was measured from a subsample of 10 lobsters (30 embryos per lobster) from each of the three regions. Ovigerous females were chosen to represent the full size spectrum of lobsters sampled in the region. A single, extra-large female was included in the DE dataset, this female had the largest CL of lobsters sampled in any region (CL=165 mm). This individual was included to investigate whether a significantly larger female produced embryos of significantly higher quality. Embryos were placed into tins and left in a drying oven for a minimum of 48 h at 60° C and then weighed (Mettler Toledo ML204 scale) to determine dry weight. The same embryos were then combusted in a mini-bomb calorimeter (Parr 6200 Isooperibol Calorimeter) to

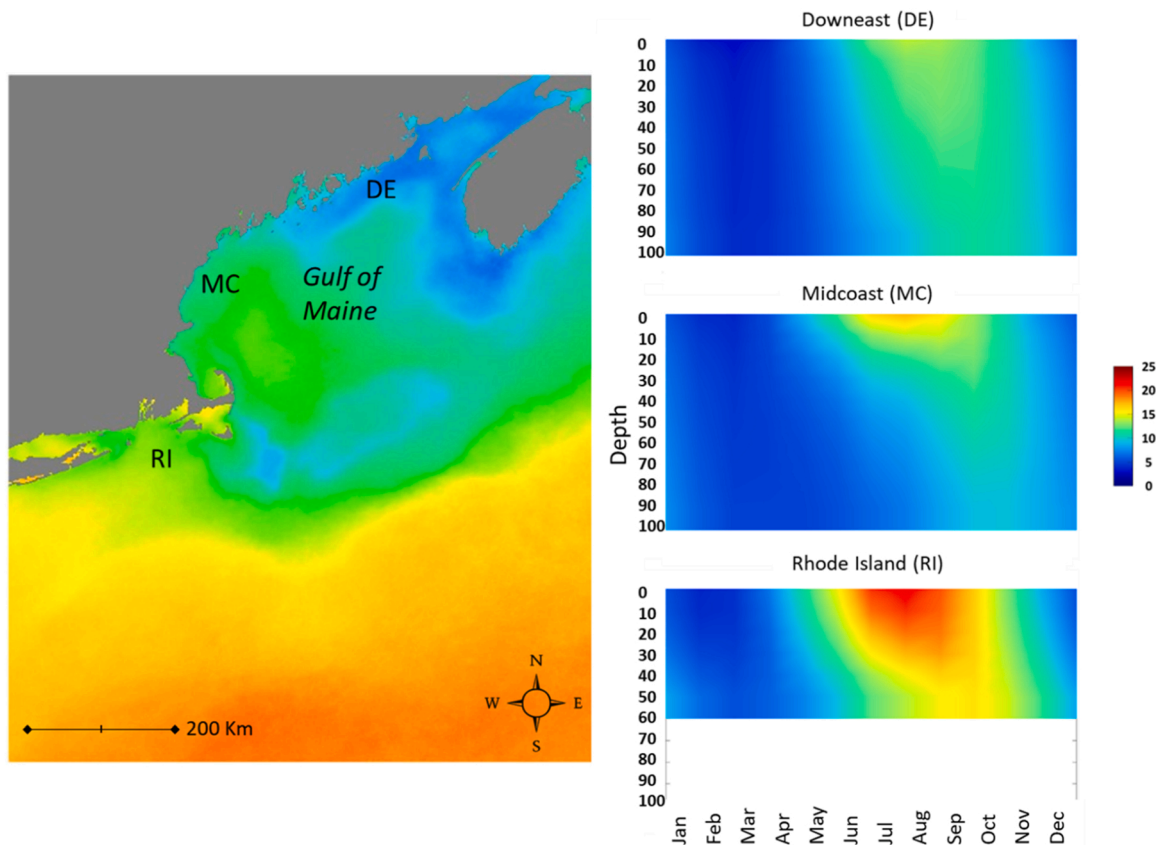


Fig. 1. Summer sea surface temperature and seasonal climatology of thermal depth profiles to 100 m averaged from 2011 to 2020 for each of the three study regions. Nearshore waters of Rhode Island do not exceed 60 m. Data source: FVCOM (<https://www.fvcom.org>), scale bar is approximate.

determine energy in Joules (J) or kiloJoules (kJ) depending on magnitude. The total amount of energy a female invests (EI) in her brood was calculated as:

$$EI = \#embryos * (J/embryo)$$

To statistically evaluate maternal size and regional effects on the response variables fecundity, embryo size, dry weight and energy content we conducted an analysis of covariance with region as a categorical variable with three levels (RI, MC, DE) and maternal carapace length (CL) as a continuous variable. All statistical analyses were conducted in JMP Pro statistical software (v.15.2.0). Data for these response variables and carapace length were log transformed prior to analysis. If we found a significant interaction between region and maternal size, separate regressions for each region were performed.

2.3. Embryo lipid and fatty acid content

For lipid and fatty acid profiling we adopted a different sampling approach. It was not cost effective to assess embryo lipid content for individual mothers as we did for fecundity, embryo volume, and dry weight. Instead, embryos from multiple females were pooled within selected size classes and compared. We used three non-overlapping maternal size classes: Small (80–90 mm CL), Medium (100–110 mm CL), and Large (130–140 mm CL). All three size classes were available in MC and DE, but the medium and large size classes were not available in RI. Seven females were selected for each of the size classes available in each region. Therefore, we subsampled 7 females from RI, and 21 each from MC and DE, for a total of 49 females. From each female we sampled 30 embryos, which were pooled by size class and region to homogenize the embryos from the females in each group for a total of 210 embryos (7 females*30 embryos per female) for each region and size class available.

The pooled embryos were then further subdivided into three replicate subsamples each containing 70 embryos.

Total lipid content and fatty acid profiles were analyzed by Bigelow Analytical Services (Bigelow Laboratory for Ocean Sciences, East Boothbay, ME). Briefly, embryos were oven dried (60 °C) and weighed to the nearest microgram. Lipids were extracted using a slightly modified Folch et al. (1957) method, as described in McMeans et al. (2012). Samples were extracted 3X using 2 mL of 2:1 (v/v) chloroform:methanol and pooled, after which polar impurities were removed by adding 1.6 mL NaCl solution (0.9% w/v) and discarded following centrifugation. The resulting lipid-containing solvent was concentrated to 2 mL and 2 aliquots (100 µL each) were removed and evaporated to dryness to quantify total lipid gravimetrically. Fatty acids in the lipid extracts were derivatized to fatty acid methyl esters (FAME) using sulfuric acid as the catalyst (Christie and Han, 2012). The FAME were then extracted 2X using hexanes: diethyl ether (1:1; v/v), after which they were dried under a gentle stream of extra dry nitrogen gas. The FAME were separated and analyzed using a gas chromatograph (GC) (Shimadzu-2010 Plus, Nakagyo-ku, Kyoto, Japan) equipped with an SP-2560 column (Sigma-Aldrich, St. Louis, Missouri). All solvents used in the extraction and FAME derivatization procedures were of high purity HPLC grade (>99%). The FAME were identified and quantified by retention time matching and a 5-point calibration curve, respectively, using a reference standard (GLC-463, Nu-Chek Prep, Inc., Waterville, Minnesota). A known concentration of 5 alpha-cholestane (C8003, Sigma-Aldrich, St. Louis, Missouri) was added to each sample prior to extraction to act as a surrogate internal standard to estimate extraction and instrument recovery efficiency. Individual fatty acid contents were expressed as percent (molar) of total quantified fatty acid methyl esters (FAME).

For statistical analysis, maternal size was treated as a categorical variable with three size levels, rather than a continuous variable as it

had been in the previous analysis. In the analysis of MC and DE all three maternal size levels were represented and were tested with a full 2-way ANOVA followed by a Tukey's HSD post-hoc test. Individual 2-way ANOVA factor results for each dependent variable can be found in Table 3. For RI however, the medium and large sizes were absent, necessitating a separate single factor ANOVA comparing all three regions using only females in the small maternal size category (supplementary material Fig. S1, and S2) in order to test for a regional effect.

2.4. Larval growth experiment

Experiments to determine maternal size effects on larval size and growth were carried out at the Bigelow Laboratory for Ocean Sciences. We only evaluated maternal size effects on larval performance for lobsters originating from MC. Ovigerous lobster with embryos near hatching were collected opportunistically by local harvesters, and held in a flow through tank at ambient temperature in the hatchery at the University of Maine's Darling Marine Center. Lobsters were held 2–3 per tank until hatch (typically no longer than 2 weeks), with larger/more aggressive individuals being isolated.

For these experiments, two size categories of ovigerous females were used "Smaller" (80–93 mm CL) and "Larger" (107–136 mm CL). Due to the availability of egg bearing females, the size ranges differ from those used for the analyses of embryos, but nonetheless provide an assessment of maternal size effects over a similar range of female sizes (Fig. 2). Larvae from at least three mothers in each size class were combined. For each size class approximately 1000 larvae were divided about equally into four communal rearing tanks. Rearing tanks were maintained at 16°C and kept well-aerated and circulated to keep planktonic food well mixed and reduce the probability of cannibalism. Each day larvae were fed to saturation with nauplii of *Artemia salina* (1–3 days post hatch). During larval stages I (SI) and II (SII), five larvae from each rearing tank were selected randomly and photographed (Canon EOS Rebel T3i, Japan) under a dissecting microscope (Olympus SX 61). Carapace length was measured in profile from the back of the eye to the posterior edge of the carapace using NIH-ImageJ software (NIH, USA). For dry weights, five larvae from each rearing tank were removed, rinsed three times in deionized water to remove salt and then placed into pre-weighted tin boats. Samples were desiccated in a drying oven at 40 °C for 48+ hrs and weighed (dry weight). Effect of maternal size on the mean length and mass of the larval stages was evaluated using t-tests.

2.5. Larval starvation experiments

The effect of maternal size on the rate of mass loss during starvation for larvae was determined by placing a random sample of 25 newly hatched larvae from smaller and larger mothers individually into 1 L Mason jars in filtered seawater. Jars were maintained at 16 °C for 5 days with no food supply. Salinity and temperature were measured daily to

ensure consistency. Each day, five larvae were randomly removed from each treatment and transferred to a drying oven (60 °C) for 48 hrs, after which dry mass was recorded. Rate of mass loss over time was evaluated for both maternal size classes using a homogeneity of regression.

An additional starvation experiment was carried out to determine whether a larva's ability to endure starvation depended on maternal size. 30 SI larvae from three mothers in each size class were placed individually into starvation chambers maintained at 18° C for a total of n=90 larvae from each size class. The larvae were monitored daily for changes in behavior related to starvation: cessation of active swimming followed by sinking to the bottom of their enclosure and remaining in a state of immobility. If larvae remained inactive after a gentle stirring of the chamber, the trial was discontinued for that individual and the time (days) to starvation recorded. The time to inactivity was analyzed using a survival analysis with a log-rank test comparing larvae from the different maternal size classes (JMP Pro statistical software; v.15.2.0).

A summary of sampling strategy and statistical treatment for the maternal size variable in all analyses can be found in Table 1.

3. Results

3.1. Embryo characteristics

Regional differences were evident in the smaller size of sexually mature lobsters from southern New England (mature females rarely exceeded 90 mm CL) compared to those from the Gulf of Maine which spanned a greater size-range. This phenomenon limited the degree to which it is possible to compare maternal size effects across regions for the entire range of possible sizes. Nonetheless, comparisons between the smaller size females across the three regions and the three size classes in the MC and DE regions show clear maternal size effects in embryo metrics and clutch size.

We found a significant positive relationship between maternal size and fecundity, as well as a significant regional effect, as depicted in Fig. 3A; Table 2. A post-hoc analysis of the regional effect using Tukey's HSD found that RI differed significantly from DE ($p=0.002$), but only marginally so from MC ($p=0.084$). This regional effect leads females from RI to produce more embryos than same-sized females from the other regions. In other words, an ovigerous female at 90 mm from RI is estimated to have a fecundity of 8763 embryos, some 25–51% higher than ovigerous females in MC (6989 embryos) or DE (5814 embryos), respectively. While there was no significant interactive effect detected- i. e. the slopes for all three fecundity curves were the same- there was a marginally significant difference detected (Table 2). A greater sample size may have been able to detect an interactive effect, leading to fecundity curves with separate slopes for each region. Supplemental Material Table S1 includes regression parameters for the relationship between egg number (fecundity) and CL for alternative versions of the relationship, one assuming parallel slopes but different intercepts

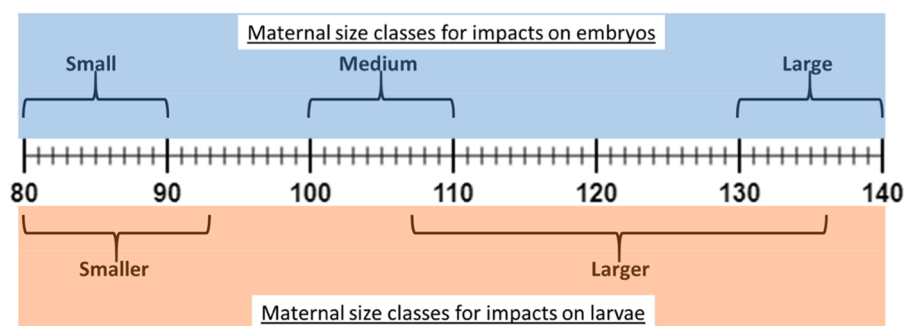


Fig. 2. Carapace length ranges of female lobsters sampled for embryos and larvae in this study. Because of limited larval availability, we used two wider maternal size classes for larval investigations than the three for embryos. And whereas the embryonic comparisons were made across three regions (Downeast, Midcoast and Rhode Island), the larval study was restricted to mid-coast Maine.

Table 1
Sampling strategy by region, sample size, and data collected.

Sample size, Lobster size/size class, [CL variable type]	Females collected from each region DE (n=60), MC (n=60), RI (n=65). [Continuous variable]	Subsample: 10 females per region representative of full size spectrum. [Continuous variable]	Subsample: Small (80-90 mm CL), Medium (100-110 mm CL) Large (130-140 mm CL) [Categorical variable]	Smaller (80-93 mm CL) Larger (107-136 mm CL) [Categorical variable]	Smaller (80-93 mm CL) Larger (107-136 mm CL) [Categorical variable]
Downeast, Maine	embryo quantity estimate, embryo volume	embryo mass, calories, Energetic investment	Lipids, EPA, DHA, DHA:EPA		
Midcoast, Maine	embryo quantity estimate, embryo volume	embryo mass, J/embryo, Energetic investment	Lipids, EPA, DHA, DHA:EPA	Larval length (SI, SII), Larval mass (SI, SII), Larval starvation mass (SI)	Larval starvation duration (SI)
Rhode Island	embryo quantity estimate, embryo volume	embryo mass, J/embryo, Energetic investment	Lipids, EPA, DHA, DHA:EPA		

among the three regions, as depicted in Fig. 3, and the other with independent slopes. By both analyses RI lobsters have higher fecundity in maternal sizes overlapping with the other two regions.

Embryo volume also increased significantly with maternal carapace length (Fig. 3B; Table 2) with a significant regional effect also being detected. A post-hoc analysis of the regional effect using Tukey’s HSD found that in the overlapping female size range embryos from RI were significantly larger than those from MC (p=0.014), but only marginally larger than those from DE (p=0.072). This suggests females from RI

produce larger embryos than same-sized females from the other regions. At 90 mm an ovigerous female from RI is expected to have embryos measuring 2.25 µL, roughly 6–7% larger than a similarly sized ovigerous female from MC (2.10 µL) and DE (2.12 µL) respectively. Again, a marginally significant interactive term was detected and the relevant exponential parameters for the relationship assuming parallel slopes and different slopes can be found in the supplementary material Table S2. Both versions of the model once more support the conclusion that size-for-size females from RI produced larger embryos than those from the

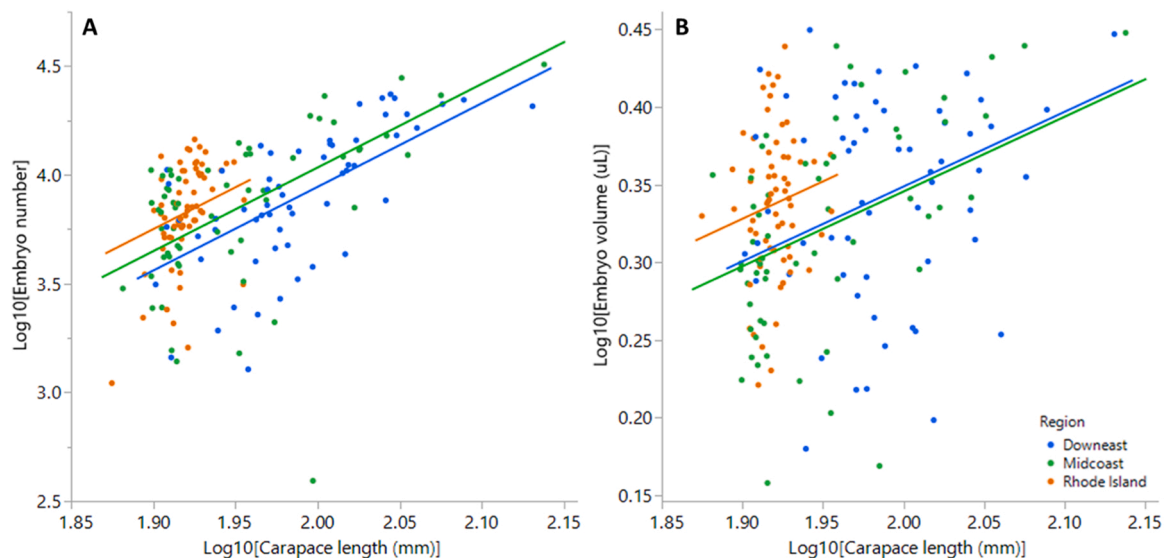


Fig. 3. A) The number of embryos, and B) average volume of individual embryos (µL) within a clutch of *Homarus americanus* as a function of female size. Colored lines represent the linear regression for each region. See Table 2 for statistical analysis.

Table 2
Summary of ANCOVA statistics for log-transformed egg metrics and carapace length in RI, MC, and DE depicted in Fig. 3+4. Significant relationships are marked with *, relationships which are marginally significant, i.e. α=0.1, are marked with ^.

Dependent variable	Embryo number	Embryo volume (µL)	Embryo dry weight (mg)	Energy (J)	Mass-specific energy (J/mg)	Total Energetic Investment (kJ)
ANCOVA results	Region: F= 6.14; p=0.003* CL: F= 74.53; p < 0.001* Region x CL Interaction: F=2.70; p=0.070^	Region: F= 4.38; p= 0.014* CL: F= 22.71; p<0.001* Region x CL Interaction: F=2.56; p=0.081^	Region: F=0.43; p=0.654 CL: F=6.04; p=0.021* Region x CL Interaction: F=0.30; p=0.743	Region: F= 0.437; p= 0.651 CL: F= 9.55; p= 0.005* Region x CL Interaction: F=0.25; p=0.779	Region: F=1.72; p= 0.197 CL: F= 5.40; p= 0.028* Region x CL Interaction: F=0.68; p=0.514	Region: F=1.58; p=0.225 CL: F=48.82; p<0.001* Region x CL Interaction: F=2.62; p=0.093^

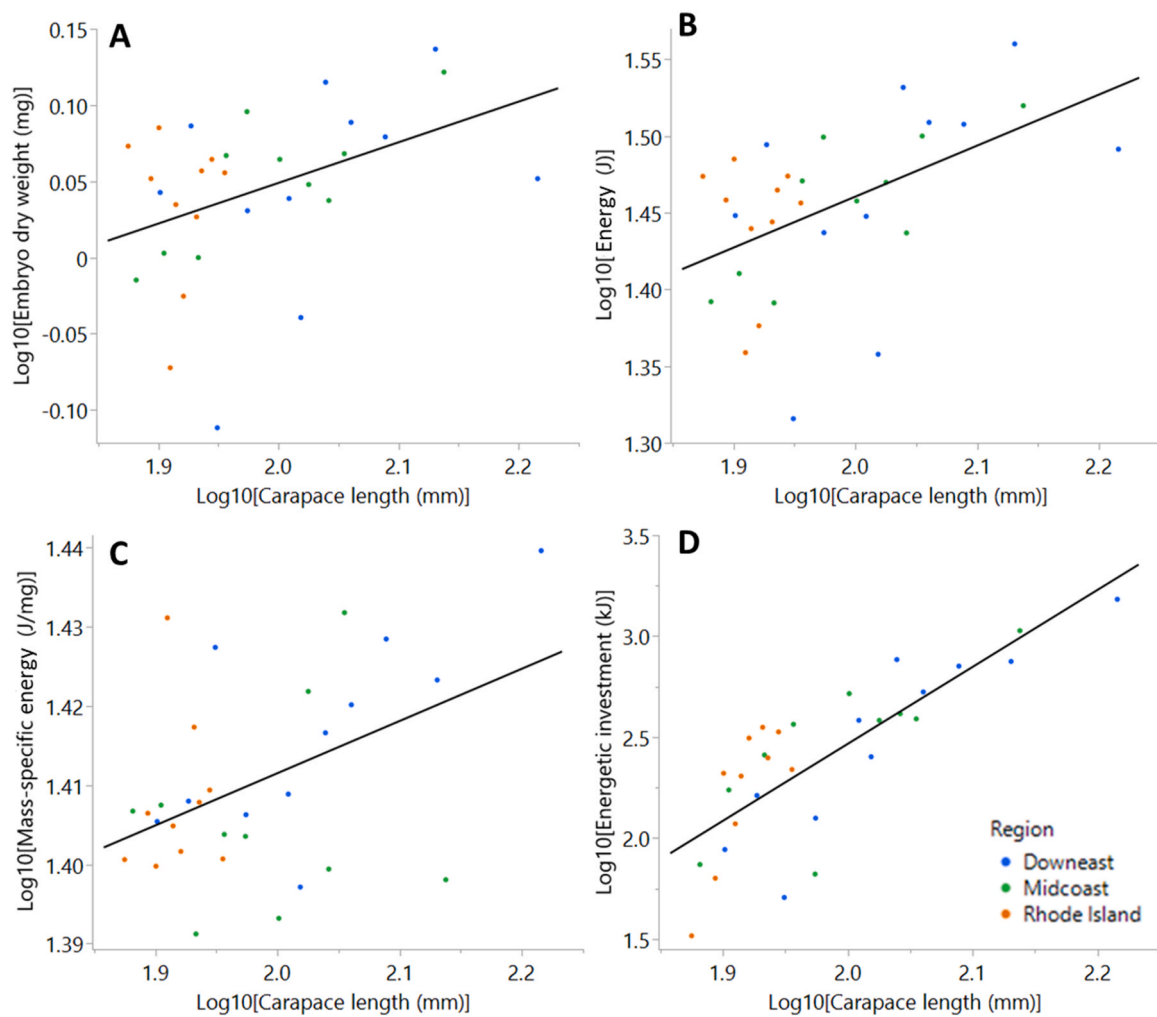


Fig. 4. A) Embryo dry weight (mg) B) energy content (J), C) mass-specific energy content of an individual embryo (J/mg) and D) total energy investment (kJ) in embryos of *Homarus americanus* as a function of female carapace length (mm). Each measurement represents an average of 30 embryos per female. See Table 2 for statistical analysis.

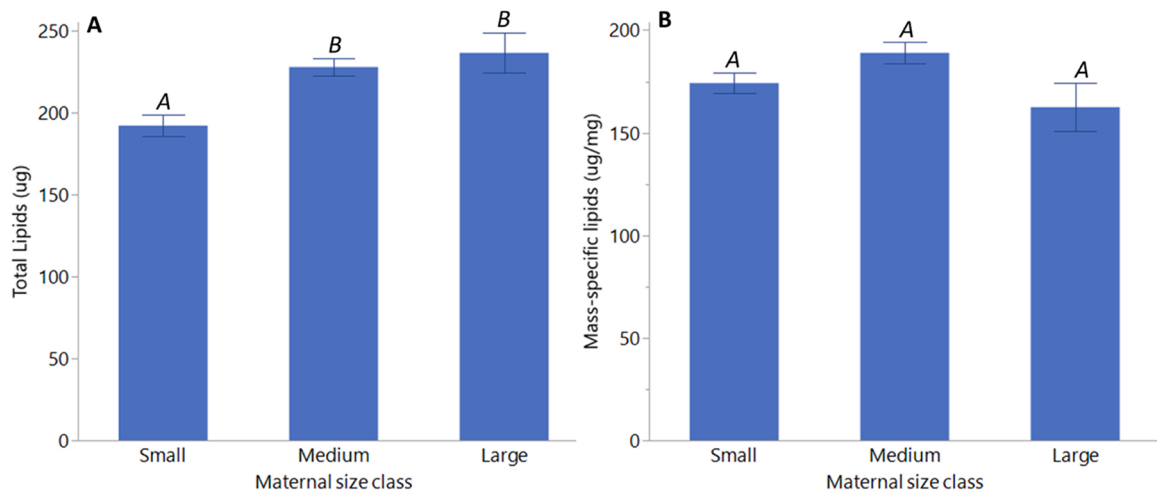


Fig. 5. Lipid content of *Homarus americanus* embryos as a function of maternal size class small (80–90 mm CL), medium (100–110 mm CL), and large (130–140 mm CL) A) Total lipid content of an average embryo (mg). B) Total lipid content in mg normalized to average embryo dry weight. Bars represent the mean response, and whiskers are standard error. Groups with different letters are significantly different.

other two regions.

In the further analyses of embryo mass and energetic content we consistently found significantly positive maternal size effects, but no regional effect or interaction (Fig. 4; Table 2). We therefore combined all females across regions for these analyses. Thus, embryo dry weight increased significantly with maternal size (Fig. 4A) with the average embryo weighing 1.11 (+/-0.02 SE) mg and increasing at an average rate of 0.003 mg per mm of maternal carapace length. Accordingly, whole-embryo energy content (J/embryo) (Fig. 4B), mass-specific energy content (Fig. 4C), and whole-clutch energy content (Fig. 4D), all scaled positively with maternal size. Thus the energetic content of an average embryo was 28.7 (+/- 0.63 SE) J increasing at a rate of 0.09 J per mm of maternal size. The mass-specific energy content averaged 25.7 (+/- 0.13 SE) J per mg of embryo dry weight changing at a rate of 0.02 J per mg with each added millimeter of maternal carapace length.

Using the product of the number of embryos in a clutch (fecundity) and embryo energy content, we calculated the energetic investment represented by a clutch. Not surprisingly larger females invested significantly more energy (kJ) per clutch than smaller females (Fig. 4D, Table 2). On average females invested roughly 360 (+/- 58.5 SE) kJ into a clutch with an increase of 14.5 kJ for each added millimeter of maternal carapace length.

For our analysis of maternal size effects on embryo lipid content we compared three size classes of ovigerous females across the two thermally contrasting regions of Maine, DE and MC. Total lipid content of the individual embryos was significantly greater in the larger maternal size classes (Fig. 5A; Table 3). Embryos of medium (Tukey's HSD, $p = 0.026$) and large (Tukey's HSD, $p = 0.006$) sized lobsters contained significantly more lipids than small lobsters, but no difference was detected between medium and large sized females (Tukey's HSD, $p = 0.757$). When normalized to the dry weight of the embryo, there was no significant relationship between maternal size and mass-specific lipid content of embryos (Fig. 5B; Table 3).

Eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) are two essential fatty-acids which are particularly important for larval development (Masuda, 2003). Our analysis revealed no significant relationship between maternal size and total EPA content of embryos (Fig. 6A; Table 3). When normalized to the mass of the embryo, there was still no significant relationship between maternal size and mass-specific EPA content (Fig. 6C; Table 3).

In contrast to EPA content, maternal size had a significant effect on total DHA content of embryos (Fig. 6B; Table 3). Embryos from large lobsters contained significantly more DHA than either small (Tukey's HSD, $p=0.017$) or medium (Tukey's HSD, $p=0.030$) sized lobsters. However, there was no significant relationship between mass-specific DHA content and maternal size (Fig. 6D; Table 3), but further analysis revealed a significant effect of region between DE and MC.

3.2. Larval characteristics

Maternal size had a significant effect on the mass (Fig. 7A) of the hatched larvae at both developmental stages. At stage I, larvae from larger females were roughly 18% heavier than larvae from smaller females ($t(360)=-3.15$, $p=0.002$), and 37% larger at stage II ($t(165)=-3.21$, $p=0.002$). Similarly maternal size had a significant effect on the

length (Fig. 7B) of larvae at both stages. Stage I larvae, hatched from larger females were 8% larger than larvae hatched from smaller females at both stage I ($t(366)=-14.78$, $p < 0.001$), and stage II ($t(181)=-4.35$, $p < 0.001$).

3.3. Starvation experiments

During starvation, Stage 1 larvae lost a significant amount of mass over a 5-day period (Fig. 8A; $F_{2, 56}=15.22$; $p < 0.001$, $R^2=0.35$). There was no evidence that maternal size affected the rate of absolute mass loss during starvation. The average mass loss for larvae from both maternal size classes was 0.08 (+/- 0.02 SE) mg per day over the course of 5 days. But because of their lower average starting weight, after 5 days larvae from smaller mothers lost a larger percent of their weight (~38%) than those from larger mothers (~30%).

In a separate experiment larvae from larger mothers took significantly longer to reach a state of starvation (as determined by a behavioral endpoint) (Fig. 8B; $X^2_{1, 180}=3.86$; $p=0.049$). Larvae from smaller mothers had an LD₅₀ (time until half of larvae were starved) of 7.39 (+/- 0.33 SE) days, while those from larger mothers had an LD₅₀ of 8.08 (+/- 0.37 SE) days. Additionally, the larva which remained in treatment the longest from small mothers lasted 14 days, while its counterpart from large mothers lasted 15 days.

4. Discussion

This study found a significant positive impact of maternal body size on fecundity, energy content and size of the individual embryos and larvae, and, in turn, the ability of larvae to endure starvation. As in most invertebrates (Peters, 1983) and fishes (Barneche et al., 2018), the size at onset of maturity in the American lobster is highly responsive to temperature which is well documented along the thermal gradient of the species range (Estrella et al., 1989), and more recently in the Gulf of Maine after decades of rapid ocean warming (Waller et al., 2021). These changes have important implications for reproductive performance, but are poorly understood, revealing the necessity for ongoing monitoring of life-history traits which may be impacted by a changing environment. For instance, population models relying on estimates of average fecundity may need these parameters updated to reflect declining maternal size associated with warming. Our study of maternal size effects on embryonic and larval traits under three contrasting thermal regimes allowed for a space-for-time substitution through regional comparisons, giving new insight into how life history traits may change under future conditions.

Fecundity, for example, is well known to increase with the size of female clawed lobsters (e.g., *H. americanus* - Herrick, 1911; Attard and Hudon, 1987; Koopman et al., 2014; *H. gammarus* - Lizárraga-Cubedo et al., 2003). Our results agree, but the space-for-time substitution adds new insight in finding that lobsters at the warmer southern end of the species' range not only mature at a smaller size and do not achieve the large sizes seen to the north, but they also produce more eggs and larger eggs than their northern counterparts of the same size. We address this phenomenon in more depth under *Regional Effects* below.

We also found that larger females produce not only larger eggs, but more energy rich ones. This combination enhances the probability that

Table 3

Summary of ANOVA statistics for lipid content and fatty-acid profile in MC, and DE depicted in Fig. 5+6. Significant relationships are marked with *, relationships which are marginally significant, i.e. $\alpha=0.1$, are marked with ^. Additional comparison of RI, MC, and DE can be found in Figs S1+2.

Dependent variable	Total lipids (µg)	Mass-specific lipids (µg/mg)	Total EPA (µg)	Total DHA (µg)	Mass-specific EPA (µg/mg)	Mass-specific DHA (µg/mg)
2-Way ANOVA results	Region: $F=0.04$; $p=0.849$ CL: $F=7.04$; $p=0.008^*$	Region: $F=1.92$; $p=0.187$ CL: $F=2.87$; $p=0.090^*$	Region: $F=0.41$; $p=0.53$ CL: $F=3.03$; $p=0.081^*$	Region: $F=1.34$; $p=0.266$ CL: $F=6.21$; $p=0.012^*$	Region: $F=1.03$; $p=0.328$ CL: $F=2.11$; $p=0.158$	Region: $F=6.51$; $p=0.023^*$ CL: $F=1.26$; $p=0.314$

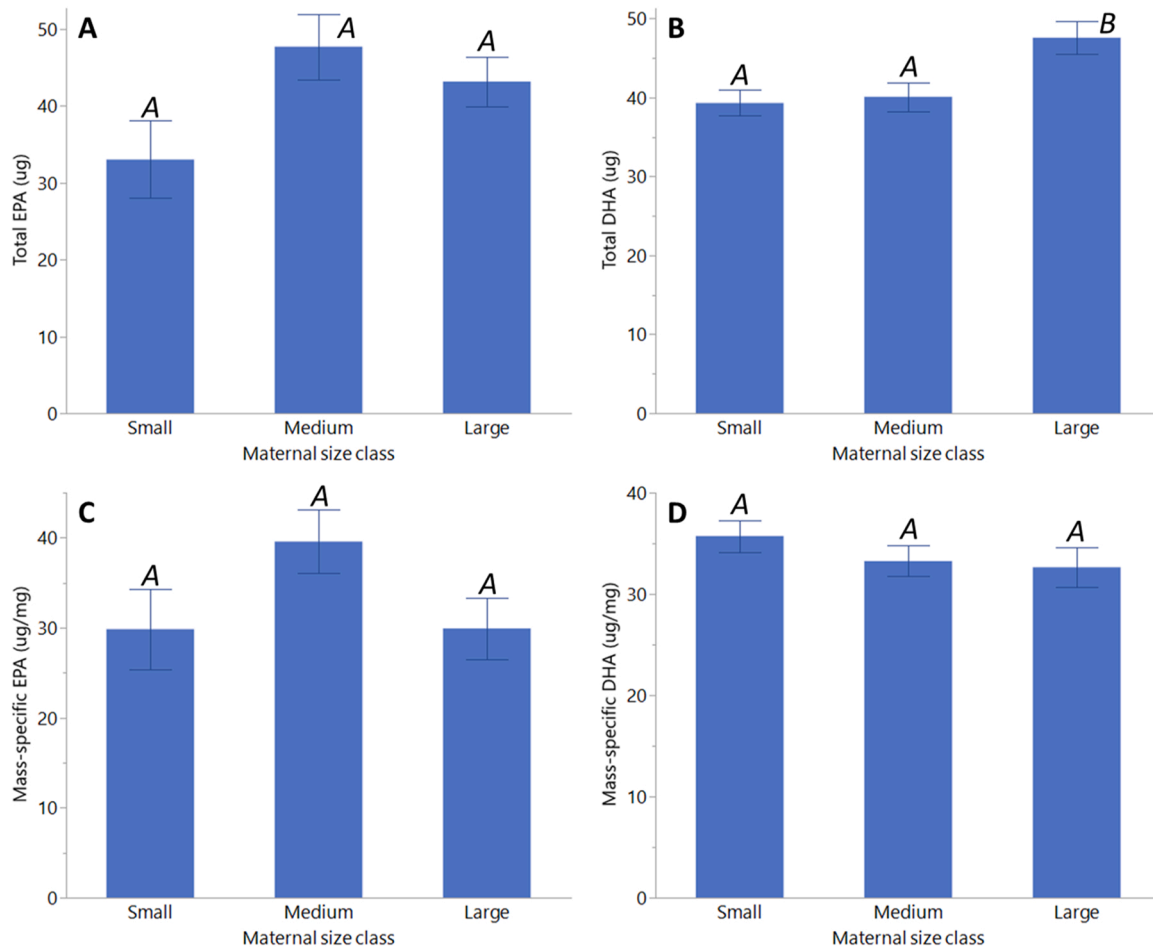


Fig. 6. Essential fatty-acid content of *Homarus americanus* embryos as a function of maternal size class A) Total Eicosapentaenoic acid (EPA) content of an average embryo in μg . B) Total Docosahexaenoic acid (DHA) content of an average embryo in μg . C) EPA content normalized to average embryo dry weight. D) DHA content normalized to average embryo dry weight. Bars represent the mean response, and whiskers are standard error. Groups with different letters are significantly different. Maternal size classes as in Fig. 5.

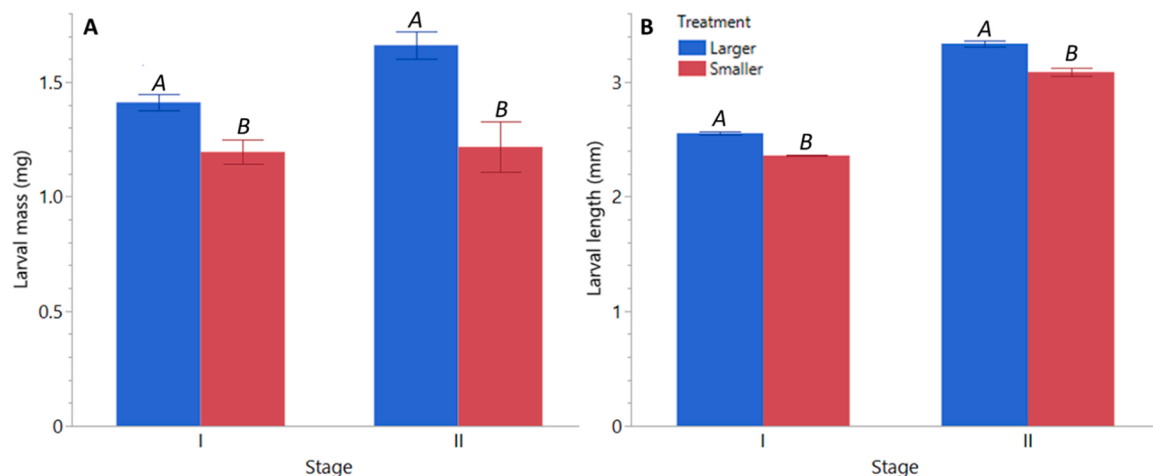


Fig. 7. A) Mass and B) Carapace length of *Homarus americanus* larvae by maternal size class and developmental stage. Smaller mothers: 80–93 mm; larger mothers: 108 – 136 mm. Bars represent the mean response, and whiskers are standard error. Within each stage, the different letters demark significant differences due to maternal size.

larger larvae will survive low food concentrations during early development (Anderson, 1988; Moland et al., 2010). However, while variables related to embryo quality, such as embryo volume (Fig. 3B), dry weight (Fig. 4A), caloric content (Fig. 4B+C) and lipid profile (Figs. 5, 6)

showed significant relationships with maternal size, the correlations were significantly weaker than the relationship between maternal size and fecundity. Therefore, the data suggest that embryo quality is more constrained than fecundity. In other words, it appears that resources

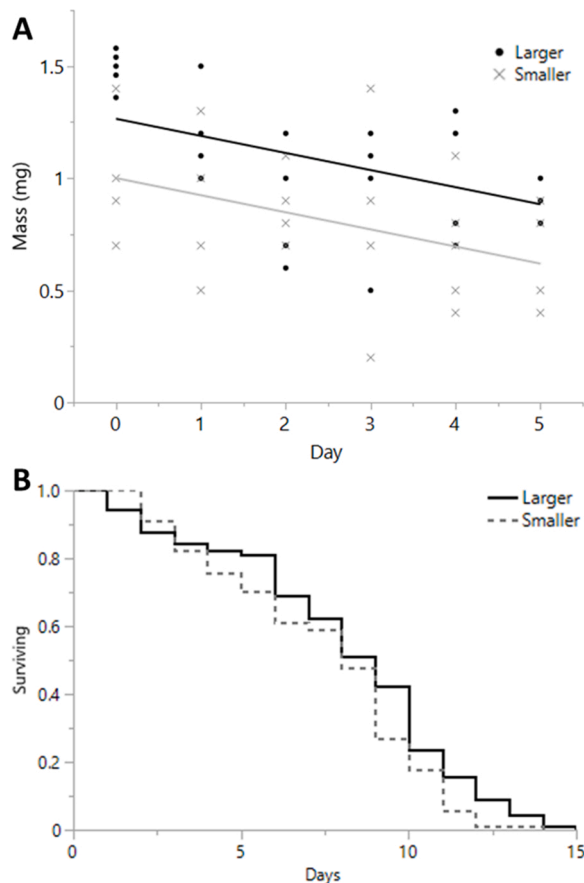


Fig. 8. A) Mass of larvae from smaller (80–93 mm) and larger (108–136 mm) female *Homarus americanus* over the course of five days of starvation. B) Survival plot showing proportion of larvae from smaller and larger mothers still active after consecutive days of starvation.

are partitioned preferentially towards producing a greater quantity of moderately provisioned embryos, rather than fewer well provisioned embryos.

4.1. Maternal size effects on embryo quality

In general, we found larger female lobsters produced embryos with a greater amount of total lipids and one essential fatty acid (DHA) (Figs. 5, 6). Lipids and fatty-acids provide high-density bioenergetic fuel and the structural components for the growth of larval and juvenile crustaceans (Watanabe, 1993; Bascur et al., 2018). In addition, the larger lipid content provides an energetic buffer during times of low food supply or high metabolic cost. Of the suite of fatty acids measured, the essential omega-3 fatty acids EPA (eicosapentaenoic acid, 20:5w3) and DHA (docosahexaenoic acid, 22:6w3) are of particular importance (Masuda, 2003). These specific long-chain polyunsaturated fatty acids (LC-PUFAs) molecules must be obtained from dietary sources, although there is some small amount of chain elongation from the omega-3 parent ALA (alpha-linolenic acid, 18:3w3), but this pathway represents only a small percentage of the total LC-PUFAs available to the animal (Arts et al., 2001). The significant increase in total DHA within the embryos with increased maternal size suggests that larger females produce higher quality embryos (Fig. 6B). Previous studies on American lobster larvae (*Homarus americanus*) have found them to be reliant on LC-PUFAs in the diet (Tlusty et al., 2005; Beltz et al., 2007). Tlusty et al. (2005) observed higher survival and growth rates in lobster larvae fed diets enriched with omega-3 fatty acids compared with those fed unenriched diets. Deficiencies in DHA and EPA have been further linked to a change in the

level and temporal pattern of neuronal proliferation in the brains of lobsters (Beltz et al., 2007; van der Meer et al., 2009) and reduced developmental rates in crustacean larvae (Siu et al., 2007; Andres et al., 2010; Beder et al., 2018). When normalized for mass of the embryos, mass-specific lipid, EPA, and DHA quantities did not scale significantly to maternal size (Figs. 5, 6). Since maternal size had a significant effect on total quantities, the absence of a significant maternal size effect in these mass-specific lipid values means that relative fatty acid investment into embryos remains roughly constant over the range of female size. In short, **larger females are able to maintain mass-specific investment in embryo quality, even while producing a greater quantity of embryos.** That the concentration of lipids was not found to scale with maternal size suggests that other sources of energy may account for the higher caloric concentration per unit weight of the embryo. This difference between lipid and caloric content may mean that lobsters store a significant amount of energy in molecules other than fatty acids, such as carbohydrates, or glycogen, which have been demonstrated to be important energy stores in other crustaceans (Sanchez-paz et al., 2006).

4.2. Maternal size effects on larval traits

Consistent with the patterns observed for embryos, our results indicate that larger ovigerous lobsters produce larger larvae that are better able to survive periods of starvation. Length and mass can have important implications for the survival of larvae (Anderson, 1988; Garrido et al., 2015). For example, larger larvae have higher movement efficiency allowing them to travel further with the same energy reserves (Peters, 1983). Size can also impact the breadth of prey size that a planktonic predator such as lobster larvae can handle (Vucic-Pestic et al., 2010). Conversely, greater size serves as a refuge from predation by other planktonic predators, as a larger larva may have outgrown their predator's preferred prey size (Nowlin et al., 2006; Almeida et al., 2011; Zhang et al., 2017).

The ability to withstand starvation is important for the survival of lobster larvae. The reliance of recruitment on the overlap between the timing of larvae hatching and the timing of peak abundance of their prey suggests that food limitation may play an important role in recruitment for this species (Carloni et al., 2018, 2024). Larger larvae with more energy stores are more likely to survive starvation than smaller ones. This was supported by our starvation experiments showing that although the rate of mass loss during starvation does not differ, larvae from smaller mothers are themselves smaller, and so may reach a critically low mass earlier during starvation (Fig. 8A). Importantly, during starvation lobster larvae reach a "point of no return" beyond which they will be unable to survive even if fed to satiation (Abrunhosa and Kittaka, 1997). Results from behavioral experiments showed that after just a few days of starvation, active swimming stops and the larva sinks to the bottom of their enclosure. Larvae from larger mothers maintained active swimming for a greater amount of time than larvae from smaller mothers (Fig. 8B). With such high mortality rates during planktonic stages, small changes in survival can have measurable impacts on larval recruitment (Thorson, 1950; Grosberg and Levitan, 1992).

4.3. Regional effects

The geographical regions used in this study reflect the broad thermal regime occupied by this species allowing for a space-for-time substitution. In the process of conducting this study, the widely recognized trend that lobsters in southern warmer regions tend to be smaller than their counterparts in cooler thermal regimes to the north was confirmed (Estrella and McKiernan, 1989; Goldstein et al., 2022). Warming over the recent decades has also been linked to a decrease in the size at maturity of adult females (Waller et al., 2021; Aiken and Waddy, 1976). Because of their smaller size, lobsters in southern regions tend not to be as fecund as their northern counterparts.

However, when normalized to carapace length, the smaller lobsters

in RI were actually more fecund than the same sized females in cooler DE (and marginally so for MC as well). Moreover, the individual embryos from mothers of the same size were larger in RI than those in MC (and marginally so for DE). We speculate that these regional effects provide evidence for counter-gradient adaptation in lobster that may genetically pre-dispose lobsters to compensate for the more limited egg production associated with smaller adult size in warmer waters (Levins, 1968; Conover and Schultz, 1995). Another potential source for the greater reproductive capacity of RI females at a given size could be age and reproductive experience (Herrick, 1911). As the onset of maturity induces a decrease in growth-rate for female lobster, small females from an early-maturing population (RI) may in fact be older and have more reproductive experience than females from later-maturing populations of a similar size (MC+DE) (Aiken and Waddy, 1976). In American lobster (Ouellet and Plante, 2004) and fish (Trippel et al., 1997) primiparous (first time breeder) females have been shown to produce undersized larvae, and maternal age has been linked to offspring quality in many other species (Benton et al., 2008; Plaistow et al., 2015; Coakley et al., 2018). Maternal size, therefore, may only play a partial role in embryo size and fecundity. It is important to keep in mind, however, that adult lobster are not static, and have the ability to move and follow a preferred thermal envelope (constrained of course by their regional climate). Thermally motivated movement represents a potential confounding factor beyond the scope of this paper.

Larvae die for a number of reasons: predation, starvation, disease, physiological stress etc. (Anderson, 1988). Species responses to these pressures often involve adaptive trade-offs. For example, starvation and predation may be overcome through production of larger larvae with greater energy reserves, the trade-off being reduced fecundity or diminished dispersal potential (Allen et al., 2008). A widely held explanation for why a large diversity of marine invertebrates and fish tend to produce large numbers of planktonic offspring relates to bet-hedging - the advantage of spreading risk over several potential outcomes in a variable environment difficult to predict (Winemiller and Rose, 1993). Within its own phyletic constraints, there is evidence that the life history traits of *Homarus americanus* represent adaptations consistent with that hypothesis. For example, among clawed lobsters and crayfishes (clade Astacidea) the shallow coastal dwelling lobsters (e.g., *Homarus* spp.) have relatively high fecundity and planktotrophic larvae, whereas their freshwater (e.g., *Orconectes* spp.) and deep sea (e.g., *Metanephrops* spp.) counterparts have lecithotrophic larvae and abbreviated development (Wahle et al., 2012). At the extreme end of the scale, tropical spiny lobsters (clade Palinuridae) produce embryos smaller than those of *Homarus* and in numbers 1–2 orders of magnitude greater, a suite of traits which allow spiny lobsters to exploit a mild environment with more constant conditions and food supply (Wahle et al., 2020). Still, geographic differences in these traits among subpopulations (e.g., southern and northern) reveal plasticity in the response to environmental variability, providing a natural experiment in the form of a space-for-time substitution that is useful in the context of understanding the impacts of a climate that is changing rapidly relative to the generation time of the species.

5. Conclusion

In a rapidly warming ocean it is important to parameterize species' responses to the changing environment (Pershing et al., 2015). For commercial species such as the American lobster, understanding how climate change affects life history traits is especially important because changes in these traits can affect the sustainability of current fishing rates. The impact of thermal regime on lobster size of maturity has long been evident in geographic comparisons among subpopulations along New England's steep thermal gradient (Estrella and McKiernan, 1989) and within single populations over time (Waller et al., 2021). These biological changes may have important demographic consequences. Our results suggest that larger maternal size confers reproductive benefits

not only in terms of fecundity, but also to individual embryos and their resulting larvae. At a population level, declining embryo production per female due to smaller size could be balanced by rapid maturation under warmer temperatures bolstering the number of reproductive individuals. The addition of declines in embryonic and larval quality reported here, suggests that the larvae of these smaller individuals may experience greater mortality rates prior to settlement, leading to a net loss in productivity for the population. However, there is also evidence for significant phenotypic variability with a presumed genetic underpinning. Whether this is evidence of counter-gradient variation, or the effect of age/reproductive experience in the American lobster remains a question for further study. Therefore, when considering how other marine crustaceans may adapt to future warming conditions, it is important to consider the effect of warming waters on body size, maturation and their cascading effect on important traits related to reproduction and larval survival.

CRedit authorship contribution statement

Maura Niemisto: Writing – review & editing, Methodology, Investigation. **Alexander Ascher:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **David Fields:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Curtis Morris:** Investigation. **Grace Andrews:** Investigation. **Richard Wahle:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Emily Patrick:** Investigation. **Donaven Baughman:** Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgments

The authors would like to thank the lobstermen of the South Bristol coop, Scott Olszewski of RI-DEM, Curt Brown of Ready Seafood, and Jordan Drouin for providing the ovigerous lobsters which made this study possible. We would also like to thank Craig Burnell of Bigelow analytics for help with sample analysis. Funding for this project was provided by NOAA grant # NA18NMF4270184 awarded to DMF and RW.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2024.107059](https://doi.org/10.1016/j.fishres.2024.107059).

References

- Abrunhosa, F.A., Kittaka, J., 1997. Effect of starvation on the first larvae of *Homarus americanus* (Decapoda, Nephropidae) and phyllosomas of *Jasus verreauxi* and *J. edwardsii* (Decapoda, Palinuridae). *Bull. Mar. Sci.* 8.
- Aiken, D.E., Waddy, S.L., 1976. Controlling growth and reproduction in the American lobster. *Proc. Annu. Meet. - World Maric. Soc.* 7, 415–430.
- Allen, R.M., Buckley, Y.M., Marshall, D.J., Clarke, A.E.A., Whitlock, E.M.C., 2008. Offspring size plasticity in response to intraspecific competition: An adaptive maternal effect across life-history stages. *Am. Nat.* 171, 225–237.
- Allyn, A.J., Alexander, M.A., Franklin, B.S., Massiot-Granier, F., Pershing, A.J., Scott, J. D., Mills, K.E., 2020. Comparing and synthesizing quantitative distribution models and qualitative vulnerability assessments to project marine species distributions under climate change. *PLOS ONE* 15, e0231595.

- Almeida, M.J., González-Gordillo, J.I., Flores, A.A.V., Queiroga, H., 2011. Cannibalism, post-settlement growth rate and size refuge in a recruitment-limited population of the shore crab *Carcinus maenas*. *J. Exp. Mar. Biol. Ecol.* 410, 72–79.
- Anderson, J.T., 1988. A Review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *J. Northwest Atl. Fish. Sci.* 8, 55–66.
- Andrés, M., Estévez, A., Hontoria, F., Rotllant, G., 2010. Differential utilization of biochemical components during larval development of the spider crab *Maja brachydactyla* (Decapoda: Majidae). *Mar. Biol.* 157, 2329–2340.
- Andrews, A.E., Kofler, J.D., Trudeau, M.E., Williams, J.C., Neff, D.H., Masarie, K.A., Chao, D.Y., et al., 2014. CO₂, CO, and CH₄ measurements from tall towers in the NOAA Earth System Research Laboratory's Global Greenhouse Gas Reference Network: instrumentation, uncertainty analysis, and recommendations for future high-accuracy greenhouse gas monitoring efforts. *Atmos. Meas. Tech.* 7, 647–687.
- Arts, M.T., Ackman, R.G., Holub, B.J., 2001. 'Essential fatty acids' in aquatic ecosystems: A crucial link between diet and human health and evolution. In: *Canadian Journal of Fisheries and Aquatic Sciences*, 58. Canadian Science Publishing NRC Research Press, Ottawa, Canada, pp. 122–137, 16 pp.
- ASMFC. 2020. American Lobster stock assessment for peer review.
- Attard, J., Hudon, C., 1987. Embryonic development and energetic investment in egg production in relation to size of female lobster (*Homarus americanus*). *Can. J. Fish. Aquat. Sci.* 44, 1157–1164.
- Barneche, D.R., Robertson, D.R., White, C.R., Marshall, D.J., 2018. Fish reproductive-energy output increases disproportionately with body size. *Science* 360, 642–645.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., et al., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57.
- Bascur, M., Guzmán, F., Mora, S., Espinoza, P., Urzúa, Á., 2018. Temporal variation in the fatty acid composition of ovigerous females and embryos of the squat lobster *Pleuroncodes monodon* (Decapoda, Munididae). *J. Mar. Biol. Assoc. U. Kingd.* 98, 1977–1990 (Cambridge University Press).
- Beder, A.M., Copeman, L.A., Eckert, G.L., 2018. The effects of dietary essential fatty acids on the condition, stress response, and survival of the larvae of the red king crab *Paralithodes camtschaticus* Tilesius, 1815 (Decapoda: Anomura: Lithodidae). *J. Crustace Biol.*
- Beltz, B.S., Tlusty, M.F., Benton, J.L., Sandeman, D.C., 2007. Omega-3 fatty acids upregulate adult neurogenesis. *Neurosci. Lett.* 415, 154–158.
- Benton, T.G., St Clair, J.J.H., Plaistow, S.J., 2008. Maternal effects mediated by maternal age: from life histories to population dynamics. *J. Anim. Ecol.* 77, 1038–1046.
- Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., and Ferrier, S. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences*, 110: 9374–9379. *Proceedings of the National Academy of Sciences*.
- Blunden, J., Arndt, D.S., 2013. State of the climate in 2012. *Bull. Am. Meteorol. Soc.* 94 (8), S1–S258.
- Calosi, P., De Wit, P., Thor, P., Dupont, S., 2016. Will life find a way? Evolution of marine species under global change. *Evolut. Appl.* 9, 1035–1042.
- Carloni, J.T., Wahle, R., Geoghegan, P., Bjorkstedt, E., 2018. Bridging the spawner-recruit disconnect: trends in American lobster recruitment linked to the pelagic food web. *Bull. Mar. Sci.* 94, 719–735.
- Carloni, J.T., Wahle, R.A., Fields, D.M., Geoghegan, P., Shank, B., 2024. Diverging phenology of American lobster (*Homarus americanus*) larvae and their zooplankton prey in a warming ocean (In press.). *ICES J. Mar. Sci.* <https://doi.org/10.1093/icesjms/fsae051>.
- Casey, F., Churchill, J.H., Cowles, G.W., Pugh, T.L., Wahle, R.A., Stokesbury, K.D.E., Glenn, R.P., 2022. The impact of ocean warming on juvenile American lobster recruitment off southeastern Massachusetts. *Fish. Oceanogr.* 32, 229–244.
- Christie, W.W., Han, X., 2012. Lipid analysis: isolation, separation, identification and lipidomic analysis. Oily Press lipid library. WP, Woodhead Publishing, Oxford Cambridge Philadelphia New Delhi, p. 428.
- Coakley, C.M., Nestoros, E., Little, T.J., 2018. Testing hypotheses for maternal effects in *Daphnia magna*. *J. Evolut. Biol.* 31, 211–216.
- Conover, D.O., Schultz, E.T., 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends Ecol. Evol.* 10, 248–252.
- Currie, J.J., Schneider, D.C., Wilke, K.M., 2010. Validation of a noninvasive technique for estimating fecundity in the American lobster *Homarus americanus*. *J. Shellfish Res.* 29, 1021–1024.
- Deevey, G.B., 1960. Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bull. Bingham Oceanogr. Collect.* 17, 54–84.
- Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine populations. *Fish Fish* 4, 25–64.
- Estrella, B.T., and McKiernan, D.J. 1989. Catch-per-unit-effort and Biological Parameters from the Massachusetts Coastal Lobster (*Homarus americanus*) Resource: Description and Trends. NOAA Technical Report, 81. NMFS.
- Fogarty M.J. 1995. Chapter 6. Populations, fisheries and management. In *Biology of the Lobster Homarus americanus*, pp. 111–137. Ed. By J.R. Factor.
- Folch, J., Lees, M., Stanley, G.H.S., 1957. A simple method for the isolation and purification of total lipides from animal tissues. *J. Biol. Chem.* 226, 497–509.
- Forster, J., Hirst, A.G., 2012. The temperature-size rule emerges from ontogenetic differences between growth and development rates. *Funct. Ecol.* 26, 483–492.
- Garrido, Ben-Hamadou, S., R, Santos, A.M.P., Ferreira, S., Teodósio, M.A., Cotano, U., Irigoien, X., et al., 2015. Born small, die young: Intrinsic, size-selective mortality in marine larval fish. In: *Scientific Reports*, 5. Nature Publishing Group.
- Gaudette, J., Tremblay, M.J., Silva, A.M., Denton, C., Pezack, D.S., 2014. Reproductive status of the American lobster in southwest Nova Scotia and the Bay of Fundy. *Lobster Fish. Areas* 34–38.
- Goldstein, J.S., Zarrella-Smith, K.A., Pugh, T.L., 2022. Recent declines in American lobster fecundity in southern New England: drivers and implications. *ICES J. Mar. Sci.* 79, 1662–1674.
- Grosberg, R.K., Levitan, D.R., 1992. For adults only? Supply-side ecology and the history of larval biology. *Trends Ecol. Evol.* 7, 130.
- Herrick, F.H., 1911. *Natural History of the American Lobster*. U.S. Government Printing Office, p. 308.
- Hixon, M.A., Johnson, D.W., Sogard, S.M., 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* 71, 2171–2185.
- IPCC, 2021: *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, In press, <https://doi.org/10.1017/9781009157896>.
- Koopman, H.N., Westgate, A.J., Siders, Z.A., 2014. Declining fecundity and factors affecting embryo quality in the American lobster (*Homarus americanus*) from the Bay of Fundy. *Can. J. Fish. Aquat. Sci.* 72, 352–363.
- Landers Jr, D.F., Keser, M., Saila, S.B., 2001. Changes in female lobster (*Homarus americanus*) size at maturity and implications for the lobster resource in Long Island Sound. *Conn. Mar. Freshw. Res.* 52, 1283.
- Le Bris, A., Mills, K.E., Wahle, R.A., Chen, Y., Alexander, M.A., Allyn, A.J., Schuetz, J.G., et al., 2018. Climate vulnerability and resilience in the most valuable North American fishery. *Proc. Natl. Acad. Sci.* 115, 1831–1836.
- Levins, R., 1968. *Evolution in changing environments: Some theoretical explorations*. (MPB-2. Princeton University Press).
- Lizárraga-Cubedo, H.A., Tuck, I., Bailey, N., Pierce, G.J., Kinnear, J.A.M., 2003. Comparisons of size at maturity and fecundity of two Scottish populations of the European lobster, *Homarus gammarus*. *Fish. Res.* 65, 137–152.
- Lovell, R.S.L., Collins, S., Martin, S.H., Pigot, A.L., Phillimore, A.B., 2023. Space-for-time substitutions in climate change ecology and evolution. *In: Biol Rev*, 98, pp. 2243–2270. <https://doi.org/10.1111/brv.13004>.
- Masuda, R., 2003. The critical role of docosahexaenoic acid in marine and terrestrial ecosystems: from bacteria to human behavior (Ed. by). In: *Browman, H.I., Skiftesvik, A.B. (Eds.), The big fish bang: proceedings of the 26th annual Larval Fish Conference*. Institute of Marine Research, Bergen, Norway.
- McAlister, J., Moran, A., 2013. Effects of variation in egg energy and exogenous food on larval development in congeneric sea urchins. *Mar. Ecol. Prog. Ser.* 490, 155–167.
- McMeans, B.C., Arts, M.T., Rush, S.A., Fisk, A.T., 2012. Seasonal patterns in fatty acids of *Calanus hyperboreus* (Copepoda, Calanoida) from Cumberland Sound, Baffin Island, Nunavut. *Mar. Biol.* 159, 1095–1105.
- Mills, K., Pershing, A., Brown, C., Chen, Y., Chiang, F.-S., Holland, D., Lehuta, S., et al., 2013. Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* 26.
- Moland, E., Moland Olsen, E., Stenseth, N., 2010. Maternal influences on offspring size variation and viability in wild European lobster *Homarus gammarus*. *Mar. Ecol. Prog. Ser.* 400, 165–173.
- Mousseau, T., Fox, C.W., 1998. The adaptive significance of maternal effects. *Trends Ecol. Evol.* 13, 403–407.
- Nixon, S.W., Granger, S., Buckley, B.A., Lamont, M., Rowell, B., 2004. A one hundred and seventeen year coastal water temperature record from Woods Hole. *Mass. Estuaries* 27, 397–404.
- Nowlin, W.H., Drenner, R.W., Guckenberger, K.R., Lauden, M.A., Alonso, G.T., Fennell, J.E., Smith, J.L., 2006. Gape limitation, prey size refuges and the top-down impacts of piscivorous Largemouth bass in shallow pond ecosystems. *Hydrobiologia* 563, 357–369.
- Oppenheim, N.G., Wahle, R.A., Brady, D.C., Goode, A.G., Pershing, A.J., 2019. The cresting wave: larval settlement and ocean temperatures predict change in the American lobster harvest. *Ecol. Appl.* 29, e02006.
- Ouellet, P., Plante, F., 2004. An investigation of the sources of variability in American Lobster (*Homarus americanus*) eggs and larvae: female size and reproductive status, and interannual and interpopulation comparisons. *J. Crustace Biol.* 24, 481–495.
- Palumbi, S.R., Evans, T.G., Pespeni, M.H., and Somero, G.N. 2019. Present and future adaptation of marine species assemblages: DNA-based insights into climate change from studies of physiology, genomics, and evolution. *Oceanography*, 32: 82–93. *Oceanography Society*.
- Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Bris, A.L., Mills, K.E., Nye, J.A., et al., 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350, 809–812.
- Peters, R.H., 1983. *The Ecological implications of body size*. Cambridge University Press, p. 348.
- Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., Levin, S.A., 2013. Marine taxa track local climate velocities. *Science* 341, 1239–1242 (American Association for the Advancement of Science).
- Plaistow, S.J., Shirley, C., Collin, H., Cornell, S.J., Harney, E.D., 2015. Offspring provisioning explains clone-specific maternal age effects on life history and life span in the water flea, *Daphnia pulex*. *Am. Nat.* 186, 376–389 (The University of Chicago Press).
- Precht, H., Christophersen, J., Hensel, H., Larcher, W., 1973. *Temperature and life*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- Pugh, T.L., Goldstein, J.S., Lavalli, K.L., Clancy, M., Watson, W.H., 2013. At-sea determination of female American lobster (*Homarus americanus*) mating activity: Patterns vs. expectations. *Fish. Res.* 147, 327–337.

- Sanchez-paz, A., Garcíacarreño, F., Muhliaalmazan, A., Peregrinourarte, A., Hernandezlopez, J., Yepizplascencia, G., 2006. Usage of energy reserves in crustaceans during starvation: status and future directions. *Insect Biochem. Mol. Biol.* 36, 241–249.
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., et al., 2012. Fiji: an open-source platform for biological-image analysis. *Nat. Methods* 9, 676–682 (Nature Publishing Group).
- Seidov, D., Mishonov, A., Parsons, R., 2021. Recent warming and decadal variability of Gulf of Maine and Slope Water. *Limnol. Oceanogr.* 66, 3472–3488.
- Smith, B.L., Bolton, T.F., 2007. Consequences of natural variation in maternal investment and larval nutrition on larval growth of a marine polychaete. *Mar. Freshw. Res.* 58, 1002.
- Sui, L., Wille, M., Cheng, Y., Sorgeloos, P., 2007. The effect of dietary n-3 HUFA levels and DHA/EPA ratios on growth, survival and osmotic stress tolerance of Chinese mitten crab *Eriocheir sinensis* larvae. *Aquaculture* 273, 139–150.
- Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25, 1–45.
- Thlusty, M.F., Fiore, D.R., Goldstein, J.S., 2005. Use of formulated diets as replacements for Artemia in the rearing of juvenile American lobsters (*Homarus americanus*). *Aquaculture* 250, 781–795.
- Trippel, E.A., Kjesbu, O.S., Solemdal, P., 1997. Effects of adult age and size structure on reproductive output in marine fishes (Ed. by). In: Chambers, R.C., Trippel, E.A. (Eds.), *In Early Life History and Recruitment in Fish Populations*. Springer Netherlands, Dordrecht, pp. 31–62.
- van der Meeren, G., Thlusty, M.F., Metzler, A., van der Meeren, T., 2009. Effects of dietary DHA and EPA on neurogenesis, growth, and survival of juvenile American lobster, *Homarus americanus*. *N. Z. J. Mar. Freshw. Res.* 43, 225–232.
- Vance, R.R., 1973. On reproductive strategies in marine benthic invertebrates. *Am. Nat.* 107, 339–352.
- Vucic-Pestic, O., Rall, B.C., Kalinkat, G., Brose, U., 2010. Allometric functional response model: body masses constrain interaction strengths. *J. Anim. Ecol.* 79, 249–256.
- Waddy, S., Aiken, D., and Kleijn, D. 1995. Chapter 10. Control of growth and reproduction. *In Biology of the Lobster Homarus americanus*, pp. 217–266. Ed. By J.R. Factor.
- Wahle, R., D. Tshudy, J.S. Cobb, J. Factor, M. Jaini. 2012. Astacidea (Marine Lobsters). *In Treatise on Zoology: Crustacea Decapoda*, Vol. 9B (66) pp 3-108. Ed. By F.R. Schram & J.C. von Vaupel Klein. Brill, Netherlands.
- Wahle, R.A., Wilson, C., Parkhurst, M., Bergeron, C.E., 2009. A vessel-deployed passive postlarval collector to assess settlement of the American lobster *Homarus americanus*. *N. Z. J. Mar. Freshw. Res.* 43, 465–474.
- Wahle, R.A., Linnane, A.J., Harrington, A.M., 2020. Lobster Fisheries. In: Lovrich, G., Thiel, M. (Eds.), *Fisheries and Aquaculture*. Oxford University Press, pp. 56–90.
- Waller, J.D., Reardon, K.M., Caron, S.E., Jenner, B.P., Summers, E.L., Wilson, C.J., 2021. A comparison of the size at maturity of female American lobsters (*Homarus americanus*) over three decades and across coastal areas of the Gulf of Maine using ovarian staging. *ICES J. Mar. Sci.: fsab034*.
- Watanabe, T., 1993. Importance of docosahexaenoic acid in marine larval fish. *J. World Aquac. Soc.* 24, 152–161.
- Winemiller, K.O., Rose, K.A., 1993. Why do most fish produce so many tiny offspring? *Am. Nat.* 142, 585–603.
- Zhang, H., Tian, F., Harvim, P., Georgescu, P., 2017. Effects of size refuge specificity on a predator–prey model. *Biosystems* 152, 11–23.