



## Early spring egg hatching by the American lobster (*Homarus americanus*) linked to rising water temperature in autumn

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Increasing ocean temperatures may affect life cycles of organisms whose biological processes are temperature-dependent. Our objective was to determine whether hatching time of American lobster (*Homarus americanus*), which has a 2-year reproductive cycle, has advanced in the southern Gulf of St Lawrence, Canada, in response to rising temperature. We investigated temporal trends in hatching time 1989–2014 using fisheries monitoring data. We considered two metrics: the first week of the year when ovigerous females with pre-hatch or hatching clutches were observed [onset-of-hatching (OH)] and the rate of change in the ratio of females with pre-hatch/hatching vs. developing clutches each spring fishing season [rate of clutch development (RCD)]. OH advanced by 5 weeks and RCD increased by 40% on average. Comparisons of OH and RCD to cumulative degree-days going back 2 years prior to hatching suggested an effect of higher fall temperatures during early ovarian and embryonic development. The advancement of hatching time in response to environmental conditions 6–18 months before hatching occurs could lead to a mismatch with larval prey species with shorter life cycles. These findings highlight the importance of monitoring phenology of fished species and the need for further research into potential impacts of phenological changes.

**Keywords:** American lobster, phenology, temperature, temporal trends, timing of hatching

### Introduction

Upper water (<75 m) temperature has increased by  $\sim 0.1^{\circ}\text{C}$  per decade since 1970 globally, and by  $1^{\circ}\text{C}$  per decade in the northwest Atlantic (Knudsen *et al.*, 2011; Galbraith *et al.*, 2012, 2015; Rhein *et al.*, 2013; Loder and Wang, 2015). Changes in temperature are particularly consequential to marine life, as most marine organisms are ectothermic. Metabolism generally increases exponentially with temperature within an organism's physiological limits, and thus rising water temperature will accelerate most physiological processes (Doney *et al.*, 2012), such as growth, sexual maturation, embryonic development, and larval development (Waddy *et al.*, 1995; Cha *et al.*, 1997; Heilmayer *et al.*, 2005). Such increases in physiological rates can in turn affect phenology, including the timing of reproductive events (Doney *et al.*, 2012; Gerber *et al.*, 2014). There is

ample evidence from terrestrial ecosystems that climate change is resulting in altered phenologies, such as advancing breeding, nesting, and flowering events (Parmesan and Yohe, 2003; Root *et al.*, 2003). There is also a growing body of evidence of phenological changes in marine ecosystems, such as shifts in seasonal peak abundance of zooplankton and larval fishes, phytoplankton blooms, and fish migrations (Edwards and Richardson, 2004; Sullivan *et al.*, 2007; Schlüter *et al.*, 2010; Asch, 2015; Asch *et al.*, 2019; Staudinger *et al.*, 2019).

Climate-driven phenological shifts related to larval phases may be common, given over 70% of marine organisms have pelagic larval phases (Gerber *et al.*, 2014). Changes in the timing of hatching may affect food availability during the larval phase (Vaughn and Allen, 2010; Gerber *et al.*, 2014), potentially leading to a temporal mismatch between predatory offspring and their

prey, and subsequent year-class failure (Cushing, 1990; Durant *et al.*, 2007). Altering the timing of spawning and larval release may also alter the temperature and currents experienced by the larvae, which can further affect their survival success, development rate, and associated dispersal (Cowen and Sponaugle, 2009; Gerber *et al.*, 2014). Investigating the relationship between water temperature and the timing of larval release is critical to understand the effects of climate change on the connectivity and recruitment of marine populations, as well as subsequent effects on conservation efforts and fisheries management.

The American lobster (*Homarus americanus*) supports the most valuable fishery on the east coast of North America, valued annually at 1.5 billion dollars and employing 10 000 licenced harvesters in Canada alone (see Fisheries and Oceans Canada: <https://www.dfo-mpo.gc.ca/fisheries-peches/sustainable-durable/fisheries-peches/lobster-homard-eng.html>). There is evidence that recent increases in ocean temperature are affecting this important fishery. In the southernmost part of the species' range, stress from high temperature and disease outbreak appears responsible for marked stock declines and collapses (Le Bris *et al.*, 2018). Shallow nearshore lobster nursery grounds are receding as summer water temperature has increased above physiological limits for benthic lobster ( $>20^{\circ}\text{C}$ ; Jury and Watson, 2013; Wahle *et al.*, 2015). In contrast, increasing abundances have been observed in the northern part of the species' range (DFO, 2016a). There is also evidence that rising water temperature does not only affect lobster at the species' range limits. In the Bay of Fundy, for example, size-specific female lobster fecundity has declined by  $\sim 30\%$  from 2008 to 2013, with increasing water temperature hypothesized as a possible cause (Koopman *et al.*, 2015). Further effects of climate change on American lobster reproductive biology and phenology are likely given that both reproduction and growth are primarily temperature regulated in the species (Waddy and Aiken, 1995; Tlusty *et al.*, 2008).

The timing of egg hatching for the American lobster is likely influenced by temperature during the female reproductive cycle. For small/young mature females, reproduction is typically a 2-year process, where a female moults and mates one summer, stores the sperm in its seminal receptacle until the following summer when spawning occurs, then carries the eggs under its abdomen for 9–12 months before hatching, and releasing larvae during the third summer (type 1a; Aiken and Waddy, 1982; Figure 1). A smaller proportion of mature females (type 1b) have a 1-year cycle, in which moulting, mating, and spawning all occur in the same season with hatching the following summer (Aiken and Waddy, 1982; Comeau and Savoie, 2002b; Figure 1). Larger/older females may skip moulting between spawnings and spawn in consecutive years (Waddy and Aiken, 1986).

Primary vitellogenesis, during which yolk is synthesized within the oocytes resulting in a slow increase in ovarian size, begins as early as three summers prior to hatching (Aiken and Waddy, 1980; Ennis, 1995; Waddy and Aiken, 1995; Comeau and Benhalima, 2018; Figure 1). It is only after moulting and mating that a female directs energy towards ovarian development, as prior to this she allocates energy to somatic growth (Adiyodi, 1985). Secondary vitellogenesis is shorter than primary vitellogenesis and begins in autumn in the southern Gulf of St Lawrence (sGSL) prior to the winter diapause and resumes in the spring before summer spawning (Comeau and Benhalima, 2018). It is regulated by an interaction between temperature and photoperiod (Aiken and Waddy, 1980; Waddy and Aiken, 1995). Embryonic

development is also temperature-dependent (Perkins, 1972). Embryos undergo rapid development after spawning in the summer/fall and can reach 50–80% of development before going into diapause in the winter (Gendron and Ouellet, 2009). They resume development in the spring, followed by hatching and larval release between May and September (Ennis, 1995; Gendron and Ouellet, 2009). The pelagic larvae go through three moults in the water column over a period of 2–8 weeks, depending on temperature, before becoming competent to settle on the benthos (Ennis, 1995).

The objective of this study was to determine whether there is evidence that increases in water temperature have modified the timing of hatching of American lobster in sGSL, Canada, from 1989 to 2014. We used a coupled ice-ocean hydrodynamic model to obtain bottom temperature, and fisheries monitoring data to assess temporal trends in (i) the rate of clutch maturation through spring and (ii) the onset of the hatching period, both at the population (i.e. site) level rather than for individual females/clutches. We compared interannual variation in the rate of clutch maturation and the onset of egg hatching each spring to seasonal (fall–winter and spring–summer) cumulative degree-days (CDDs) up to 2 years prior to hatching to determine (i) whether temperature has influenced hatching time and (ii) during which portion of the reproductive cycle, incorporating both ovarian and embryonic development, temperature is most influential.

## Methods

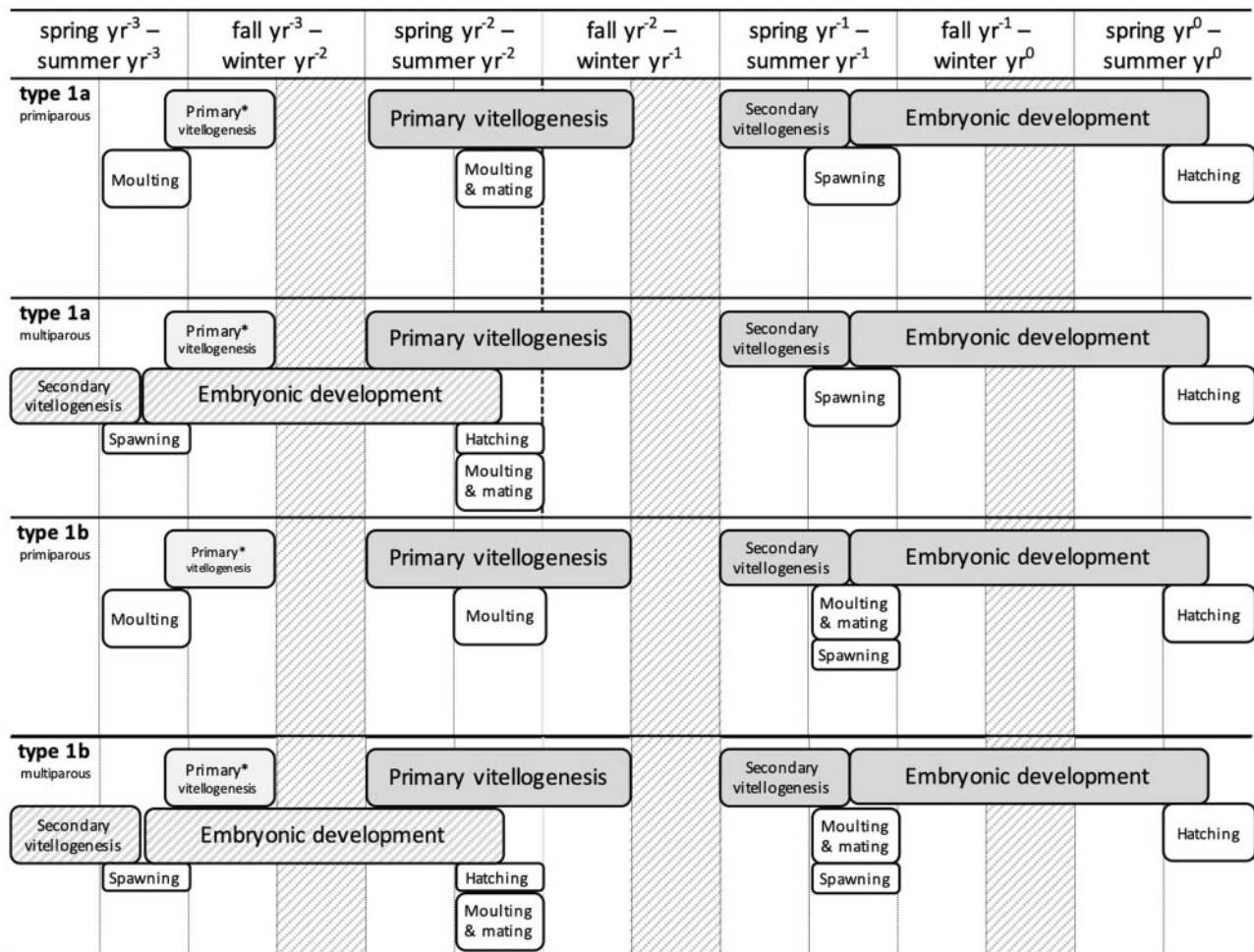
### Monitoring of ovigerous females in the sGSL

There are no available historical or time-series data that have been collected specifically to assess reproductive timing in American lobster, and therefore limited data with which to investigate potentially changing phenologies in the species. However, fisheries monitoring data from the sGSL do allow some investigation of this question. At-sea sampling has been carried out during the spring lobster fishing season (May–June) in areas 23, 24, and 26A (Figure 2) since 1989 (Mallet *et al.*, 2006). Data collected include sex, condition (missing claws, shell hardness), carapace length (CL), and location of capture for all lobsters, as well as clutch stage of ovigerous females (Mallet *et al.*, 2006). Clutch stage is based on embryo development and is categorized on a scale from 1 to 4 (Figure 3). During stage 4, eggs will hatch over several days to weeks (Tlusty *et al.*, 2008). From 1989 to 2003, stages 3 and 4 were not distinguished, but grouped as clutches with well-developed embryos. After 2004, all four stages were distinguished. Stage 3 clutches are typically within a week of commencing hatching (MLH and RR, unpublished data).

We used clutch stage data from 58 fishing ports (1126 sampling trips) to investigate temporal trends in the timing of hatching between 1989 and 2014. The exact timing of the at-sea sampling varied interannually because of factors such as ice coverage and storm days (Mallet *et al.*, 2006). There was a trend for sampling to extend slightly later (5 d) into the year as the study progressed from 1989 to 2014. We were generally able to assess temporal trends in spring clutch development of ovigerous females during the latter half of May until the end of June (Table 1).

### Study areas and temperature data

The sGSL was divided into four areas (Figure 2) based on spatial variation in seasonal CDDs (Table 1; J. Chassé, DFO, pers.



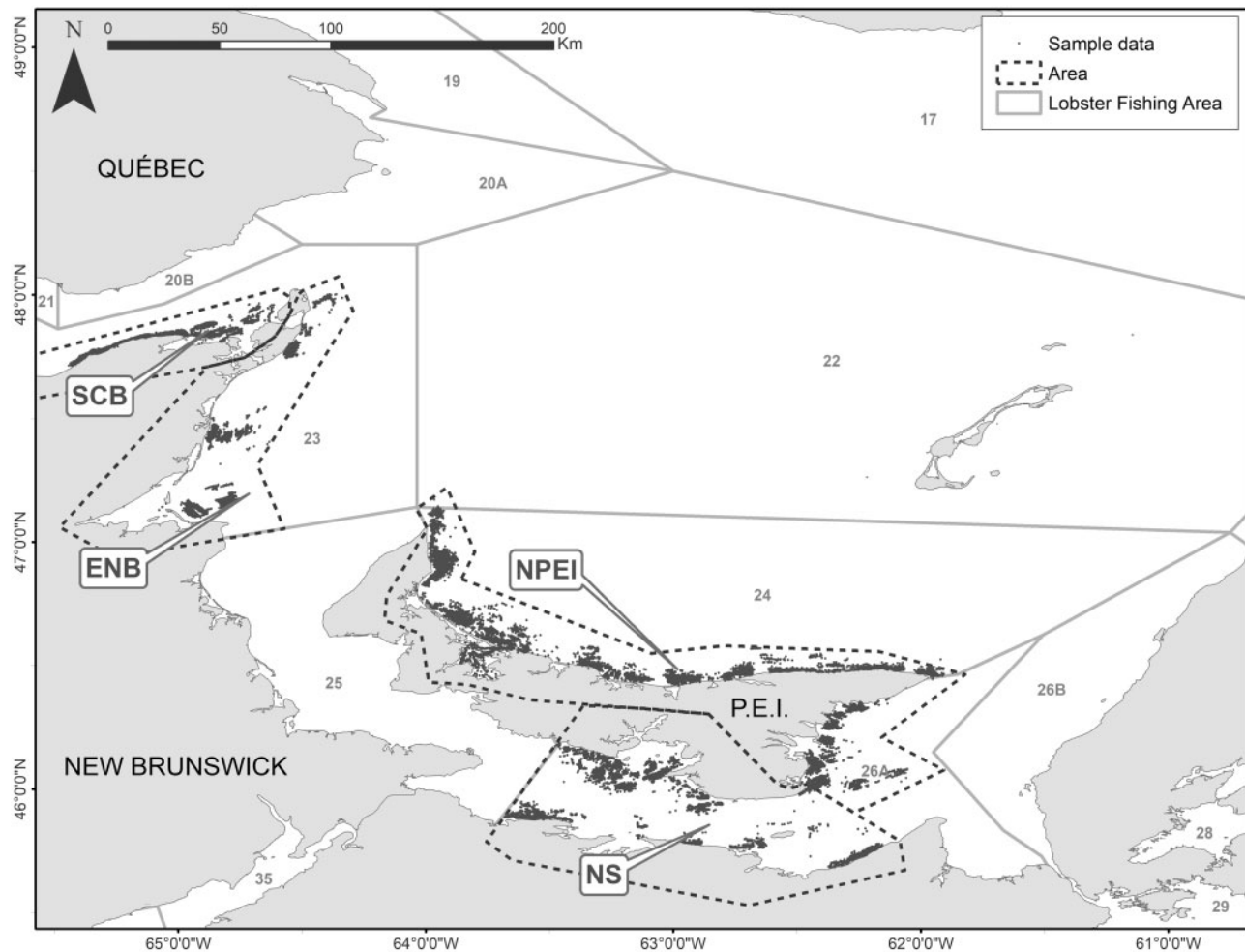
**Figure 1.** Gantt chart showing a conceptual model of the female American lobster typical 2-year (type 1a) and less common 1-year (type 1b) reproductive cycles between moulting and egg hatching. Processes shaded in dark grey are those under consideration in this study; the dotted vertical line indicates the point after which energy reserves are used for gonad development, rather than somatic growth, until the end of secondary vitellogenesis for type 1a females. Important events in the reproductive cycle are in white, whereas the onset of primary vitellogenesis in year 3 and mating of type 1b multiparous females are less certain and marked by an asterisk (\*). The striped vertical bars indicate time periods of physiological diapause (i.e. in winter with temperatures  $<0^{\circ}\text{C}$  in the southern Gulf of St. Lawrence).

comm. 2015), with outer boundaries of each area (distance from shore) being determined by the locations from which ovigerous females were sampled (Comeau *et al.*, 2008). The four areas were the south shore of Chaleur Bay (SCB), eastern New Brunswick (ENB), the Northumberland Strait (NS), and the north shore of Prince Edward Island (NPEI; Figure 2). All data originating from a same area were pooled. In the two largest areas (NS and NPEI), 4–13 ports were sampled annually, whereas in the two smaller areas (SCB, ENB), 2–3 ports were sampled annually.

Between 600 and 1100 traps were hauled weekly for an average 4–7 weeks annually in the different areas. For each area, years with fewer than 3 weeks sampled were excluded from analyses. An average of 250 and 1300 ovigerous females were sampled weekly and annually, respectively. Although the range of years sampled was 1989–2014, not every year was sampled in each area; the total number of years sampled ranged from 8 to 25 (Table 1). The average travelled distance for lobsters in the sGSL is  $<10\text{ km}$  a year (Comeau and Savoie, 2002a; Bowlby *et al.*, 2007), thus significant movement of females between study areas was likely not a frequent occurrence.

Ocean temperature data were obtained from a coupled ice-ocean modelling system. The ocean circulation model is based on the Nucleus for European Modelling of the Ocean (Madec, 2016) and the setup is described in Brickman and Drozdowski (2012). The ice model is LIM2 (Madec *et al.*, 1998; Goosse and Fichefet, 1999) and includes thermodynamic and rheology components. The coupled model domain covers the Gulf of St Lawrence at a horizontal resolution of  $1/12^{\circ}$  and 46 layers of variable thickness in the vertical. It is a prognostic model, meaning that the temperature and salinity fields are free to evolve with time and are only constrained through open boundary conditions, freshwater run-off, and surface forcing. Monthly temperature and salinity climatologies were used to initialize the model and set the open boundary conditions. The model is driven with the National Centers for Environmental Prediction atmospheric forcing (winds, heat fluxes), as well as tides and river runoff from the 78 main rivers discharging within the model domain. The model was calibrated to reproduce the main features of the system, like the seasonal cycle of temperature, circulation, and sea ice (Chassé *et al.*, 2014a). Simulations have been carried out for 1948–2015





**Figure 2.** Map of the southwestern Gulf of St. Lawrence located in eastern Canada showing the four study areas (grey polygons) divided based on lobster sampling locations (black circles) and mean summer temperatures. The map also indicates the boundaries of different lobster fishing areas (black line).

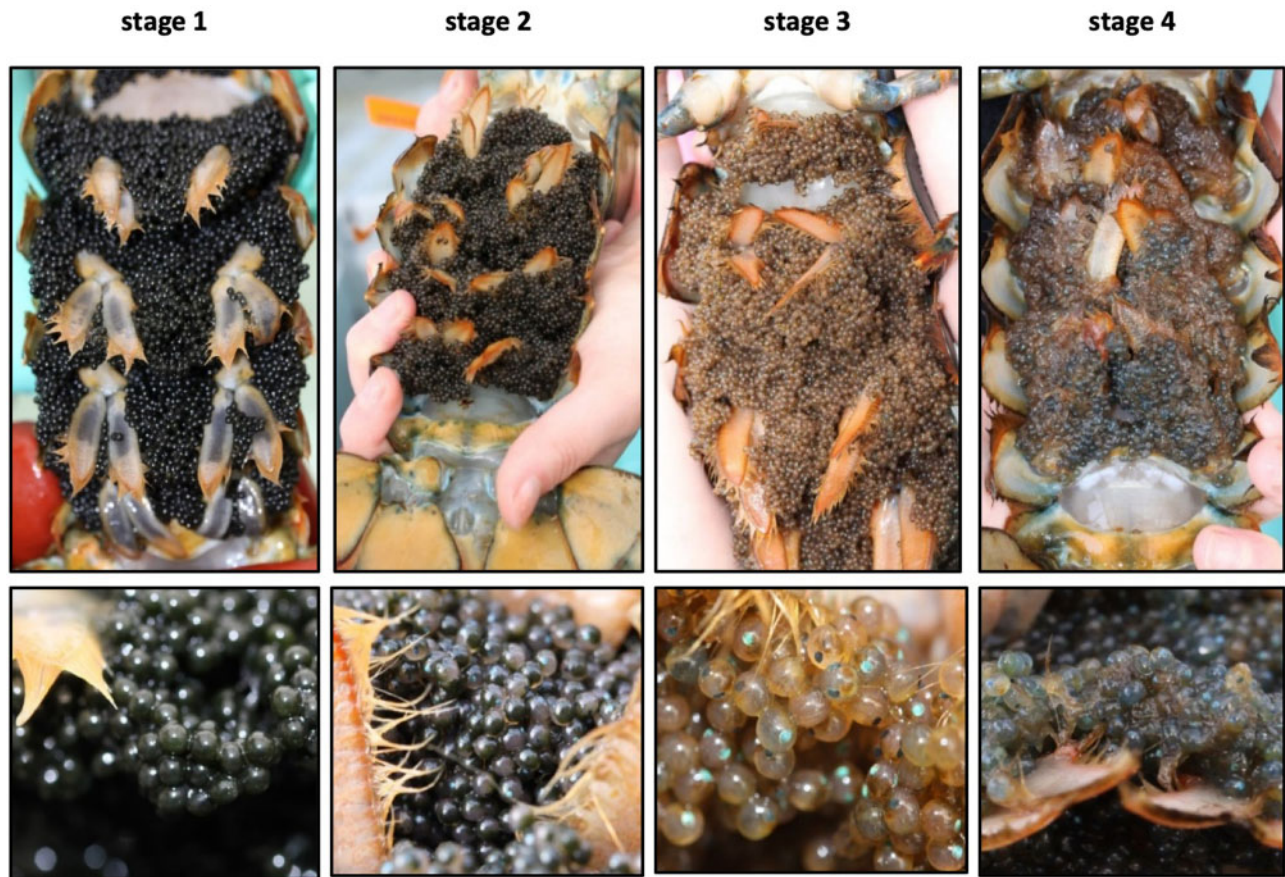
and provide a long time-series of simulated ocean variables over the domain. For our analysis, bottom temperatures were averaged daily within each study area (one datum per day per study area) to provide time-series starting 2 years prior to the biological data and cover different time periods potentially consequential to hatching time.

### Indices for the timing of egg hatching

Given that sampling was restricted to the commercial fishing season, we were unable to directly assess temporal changes in the peak larval hatching period of July and August (Ennis, 1995; Waddy and Aiken, 1995; Miller et al., 2016) as the fishing seasons end prior to this. As such, we assessed temporal changes in the timing of hatching through two indirect metrics: (i) the change in ratio of ovigerous females with stages 3 + 4 (prehatch and hatching) to stages 1 + 2 (developing) clutches each spring and (ii) the first week in spring when females with prehatch/hatching clutches were observed. The latter is a coarse measure of hatching time and will be referred to as the “onset-of-hatching” (OH). This index was corrected for year–area combinations with prehatch/hatching clutches observed on the first sampling date by adjusting

to first sampling week minus one and for year–area combinations with no hatching observed by adjusting to the final sampling week plus one.

The rate of increase in the occurrence of females with prehatch/hatching clutches relative to females with developing clutches (i.e. the slope of the ratio prehatch/hatching: developing vs. date) was used as an indicator of the site-level “rate of clutch development” (RCD) in the spring following the winter diapause each year. Based on the premise that a more rapid progression from developing to prehatch/hatching clutches in the spring should result in earlier hatching of larvae, we suggest that change in RCD across years reflects population-level changes in the hatching period. For each year, we calculated the ratio of ovigerous females with prehatch/hatching to developing clutches for each sampling week in each area, and then took the slope of log-transformed ratios over time as the RCD for that particular area and year. For weeks when only prehatch/hatching clutches were observed, we substituted a value of 1 for the zero count of developing clutches to allow a ratio to be estimated. Similarly, for weeks when no prehatch/hatching clutches were observed we substituted 0 counts with 0.5 to ensure a ratio  $>0$ ; 0.5 was chosen rather than 1 as a single female with a prehatch/hatching clutch



**Figure 3.** Visual clutch staging scheme. A stage 1 clutch is newly spawned; clutch appears black or olive green, and no part of the embryo is visible (i.e. eggs consist primarily of yolk). A stage 2 clutch is further developed but still immature (i.e. not close to hatching); the overall appearance of the clutch is lighter, the embryo's eye spots are visible within the eggs and individual eggs are clearly two toned in colour with one portion consisting of the embryo and the other of yolk. Stage 3 clutches are mature and close to hatching; overall the clutch appears tan to orange in colour, and the embryos now take up most of the space inside the eggs (i.e. very little to no yolk is visible). A stage 4 clutch is in the process of hatching and can be recognized by primarily dark eggs without yolk and clearly visible embryos, the presence of prezoeae (newly hatched prelarvae), and (later in the hatching period) empty egg casings and adhesive material (the clutch appears "mossy").

was observed several times in the dataset and the substituted value needs be smaller than the range of observed values. The earliest sampling week in any given year was week 18 (early May), but we added week 15 (mid-April) as a forced zero to reflect the fact that all clutches are in diapause in the developmental phase (stage 2) through winter. Week 15 was chosen as modelled bottom temperature then consistently averaged  $\sim 0^{\circ}\text{C}$  ( $-1.7^{\circ}$  to  $0.9^{\circ}$ ), that is no embryonic development would be occurring. We set the ratio of prehatch/hatching to developing clutches at this forced zero to 0.0010, to be just below the lowest observed ratio of 0.0011. We only calculated the RCD for year–area combinations with a minimum of three sampling weeks and  $R^2 > 0.4$ ; the latter excluded 6 of 70 data points.

### Statistical analyses

Evidence of an advancing hatching period between 1989 and 2014 was investigated using linear regressions, where RCD and OH were the dependent variables regressed against year, with geographic area set as a random factor. Effects of temperature were compared using similar linear models with additional

parameters reflecting CDDs experienced by lobsters over four broad time periods that may be important to ovarian and embryonic development: (i) fall–winter 1.5 years preceding hatching (primary vitellogenesis with a transition to secondary vitellogenesis), (ii) spring–summer the year preceding hatching (late secondary vitellogenesis and spawning), (iii) fall–winter the year preceding hatching (early embryonic development), and (iv) spring prior to hatching (late embryonic development). We built and compared 32 models (including a null model with no temperature term) for each of the 2 hatching metrics, based on all combinations of the 4 temperature parameters and an area term. Models were compared using the corrected akaike information criterion (AICc) to determine which thermal periods (if any) are the most influential on hatching time. Area was used as a random term in these models as well (intercepts assumed random, slopes assumed fixed) as our aim was to assess general trends for the sGSL, and grouping the data in areas enabled us to account for some of the variability in our dependent variables that might be related to differences in biotic and abiotic conditions in these areas. We used  $3.4^{\circ}\text{C}$  as the threshold for degree-days, given embryonic development

**Table 1.** Summary of sampling conditions in each of our four study areas, including the number of years with adequate data to estimate the two metrics of the timing of hatching (OH and RCD), the timing of the sampling period, as well as temperature conditions in terms of CDDs (3.4°C threshold) in spring–summer (April–September) and fall–winter (October–March) months, showing both average conditions and temporal trends.

Area	Number of years adequate data OH <sup>a</sup>	Number of years adequate data RCD <sup>b</sup>	Annual sampling intensity (# weeks)	Start annual sampling (week #) <sup>c</sup>	End annual sampling period (week #) <sup>c</sup>	CDD spring/summer <sup>d</sup>	CDD fall/winter <sup>d</sup>
SCB	14	13	$x = 5.4$ Min = 2 Max = 9	$x = 19.0$ Min = 18 Max = 20	$x = 25.7$ Min = 24 Max = 27	$x = 690$ Slope = $-0.68$ $x = 896$	$x = 150$ Slope = $3.12$ $x = 234$
ENB	14	8	$x = 4.2$ Min = 1 Max = 9	$x = 19.6$ Min = 18 Max = 23	$x = 25.3$ Min = 23 Max = 27	$x = 1\,308$ Slope = $-2.05$ $x = 1\,308$	$x = 329$ Slope = $3.53$ $x = 329$
The eastern NS	24	21	$x = 5.2$ Min = 2 Max = 10	$x = 19.9$ Min = 18 Max = 22	$x = 26.6$ Min = 25 Max = 28	$x = 721$ Slope = $-2.65$ $x = 721$	$x = 257$ Slope = $3.69$ $x = 257$
The NPEI	25	23	$x = 6.9$ Min = 2 Max = 9	$x = 19.0$ Min = 18 Max = 21	$x = 26.3$ Min = 25 Max = 28	$x = 721$ Slope = $-2.02$ $x = 721$	$x = 257$ Slope = $3.40$ $x = 257$

<sup>a</sup>OH was the first calendar week when ovigerous females with prehatch and/or hatching clutches were observed.

<sup>b</sup>RCD was the rate of increase in the ratio of ovigerous females with prehatching/hatching: developing clutches through the spring each year.

<sup>c</sup>The start and end of the sampling period are given in calendar weeks.

<sup>d</sup>Slopes show the interannual trends in seasonal CDDs.

SCB: southern Chaleur Bay.

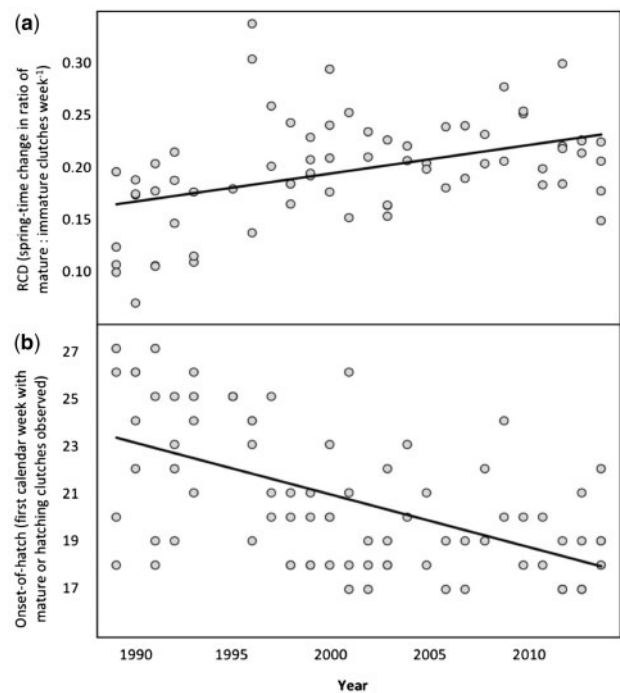
below this temperature is limited (Perkins, 1972). Model residuals were tested for normality using Shapiro–Wilk  $W$  goodness-of-fit tests and generally did not violate this assumption ( $p < 0.05$ ).

## Results

Our results suggest that female lobsters have been hatching their eggs earlier in the season between 1989 and 2014 in the sGSL, as there has been a significant increase in the spring RCD ( $F_{1,86.95} = 14.52$ ;  $R^2 = 0.12$ ,  $p = 0.0003$ ; Figure 4a) and a significant advancement of the OH ( $F_{1,79.32} = 35.16$ ;  $R^2 = 0.34$ ,  $p < 0.0001$ ; Figure 4b) over the study period. Based on the model slopes, RCD occurred 1.4 times more rapidly, and OH 5 weeks earlier in 2014 compared to 1989.

Modelled bottom temperature in the sGSL shows a significant increase in the number of degree-days in the fall between 1989 and 2014 (year:  $F_{1,96} = 64.62$ ,  $p < 0.0001$ ; area:  $F_{3,96} = 160.24$ ,  $p < 0.0001$ ; area  $\times$  year:  $F_{3,96} = 0.08$ ,  $p = 0.97$ ). In contrast, the number of degree-days in the spring has not changed over the same period (year:  $F_{1,96} = 0.0025$ ,  $p = 0.96$ ; area:  $F_{3,96} = 86.94$ ,  $p < 0.0001$ ; area  $\times$  year:  $F_{3,96} = 0.28$ ,  $p = 0.84$ ), and the number of degree-days in the summer has actually somewhat decreased (year:  $F_{1,96} = 8.23$ ,  $p = 0.005$ ; area:  $F_{3,96} = 541.08$ ,  $p < 0.0001$ ; area  $\times$  year:  $F_{3,96} = 0.79$ ,  $p = 0.50$ ; Figure 5; Table 1). The temperature increase during the fall has been pronounced, representing 20–60% more CDDs from 1989 to 2014 in different areas, in contrast to a 5–15% reduction in the summer. As temperatures during winter consistently did not surpass 3.4°C, the resulting in constant zero-valued CDDs was not included as model predictors.

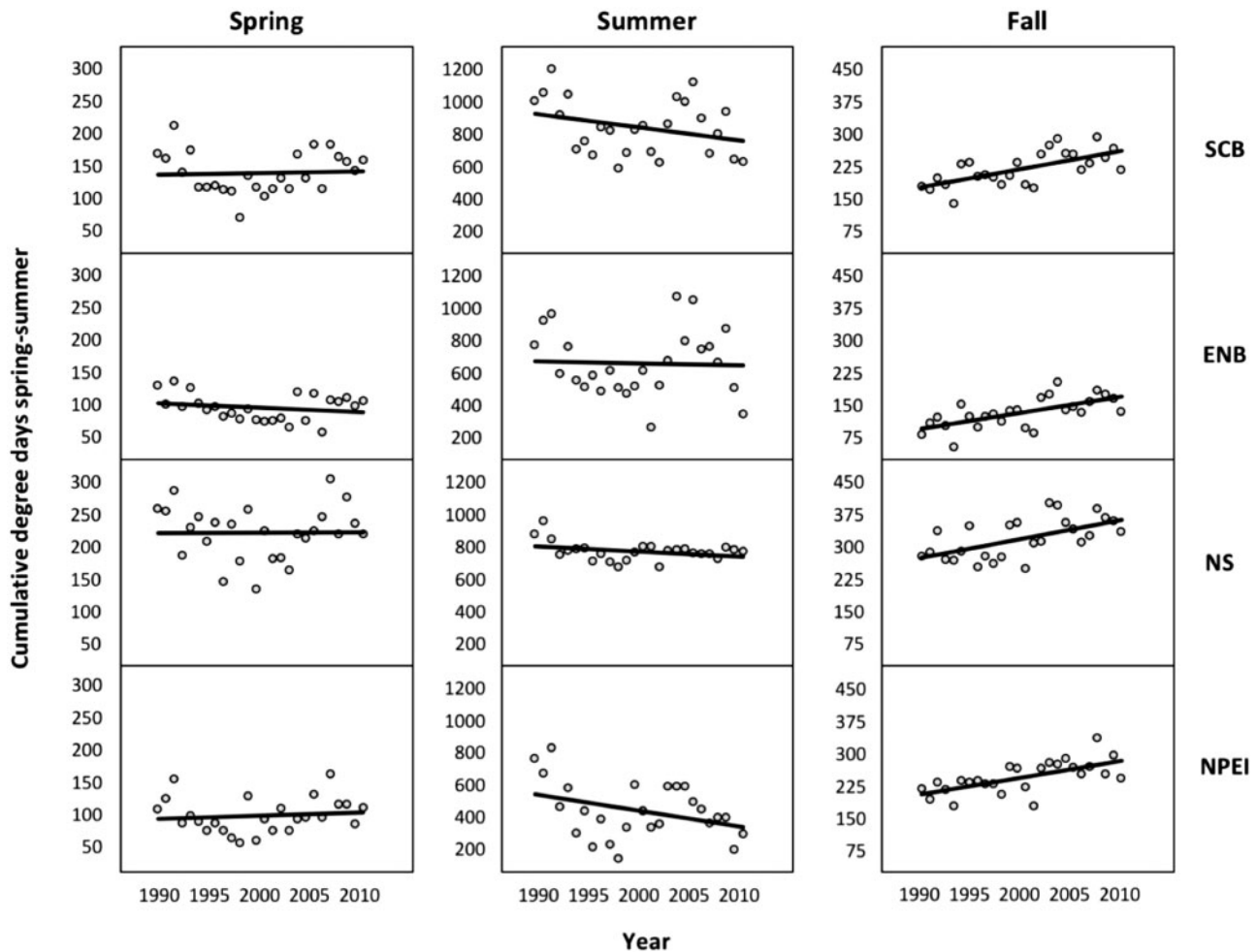
The model that best explained interannual variation in RCD included the parameters CDD during spring–summer 1 year prior to hatching (i.e. secondary vitellogenesis and spawning) and CDD during fall–winter prior to hatching (i.e. early embryogenesis). This model composed 21% of the AICc



**Figure 4.** Temporal trends in two indices of the timing of hatching 1989–2014 in four study areas in the southern Gulf of St Lawrence: (a) RCD, indicated by the rate of change in ratios of ovigerous females with mature vs. immature clutches (stages 3–4 vs. 1–2) through the spring fishing season each year ( $F_{1,86.95} = 14.52$ ;  $p = 0.0003$ ); (b) onset-of-hatching, indicated by the first calendar week when ovigerous females with mature or hatching clutches were observed each year ( $F_{1,79.32} = 35.16$ ;  $p < 0.0001$ ).

weight of the 32 models compared (Table 2). Overall, the model was significant ( $F_{2,68} = 3.86$ ,  $p = 0.026$ ) with  $R^2 = 0.10$ . It showed a positive relationship between CDD during





**Figure 5.** Temporal trends (1989–2014) in CDDs  $> 3.4^{\circ}\text{C}$  in spring (April–June), summer (July–September), and fall (October–December); winter (January–March is not shown as CDD never exceeded 0). There are clear spatial differences in CDD in all three seasons (spring:  $F_{5,144} = 70.67$ ,  $p < 0.0001$ ; summer:  $F_{5,144} = 318.00$ ,  $p < 0.0001$ ; fall:  $F_{5,144} = 168.48$ ,  $p < 0.0001$ ), but only fall CDD shows an increase over the study period ( $F_{1,144} = 87.44$ ,  $p < 0.0001$ ); spring CDD shows no temporal trends ( $F_{1,144} = 0.21$ ,  $p = 0.65$ ); summer CDD shows a slight negative trend ( $F_{1,144} = 13.81$ ,  $p = 0.0003$ ); all these temporal trends, or lack thereof, are consistent among areas (i.e. no significant areas  $\times$  year interaction term; spring:  $F_{5,144} = 0.32$ ,  $p = 0.90$ ; summer:  $F_{5,144} = 0.78$ ,  $p = 0.56$ ; fall:  $F_{5,144} = 0.39$ ,  $p = 0.86$ ).

early embryogenesis and RCD ( $F_{1,68} = 2.76$ ,  $p = 0.007$ ), indicating warmer water during the first months after spawning results in a more rapid RCD leading to hatching the following spring. The model also showed a negative relationship between CDD during secondary vitellogenesis and spawning and RCD ( $F_{1,68} = -1.61$ ,  $p = 0.11$ ), suggesting a warmer summer the year of spawning results in slower RCD, and presumably later hatching, the following year (Table 2). CDD during early embryogenesis accounted for considerably more of the variation in RCD explained by the model than did CDD during spawning (75 and 25%, respectively). The second-best model (AICc weight = 17%, Delta  $< 2$ ) included only CDD during early embryogenesis (Table 2).

The model that best explained variation in OH included the parameters CDD during the fall–winter prior to spawning (i.e. primary vitellogenesis with a transition to secondary vitellogenesis  $\sim 1.5$  years prior to OH) and CDD during the spring–summer 1 year prior to hatching (i.e. secondary vitellogenesis and spawning; Table 3). This model composed 50% of the AICc weight of the 32 models compared (Table 3). Overall, the

model was highly significant ( $F_{2,79} = 9.94$ ,  $p < 0.0001$ ) with  $R^2 = 0.20$ . The model showed a negative relationship between OH and CDD during primary vitellogenesis with a transition to secondary vitellogenesis ( $F_{1,79} = -4.26$ ,  $p < 0.0001$ ), indicating that higher temperature during the fall–winter prior to spawning results in earlier OH. The model also showed a positive relationship between OH and CDD during secondary vitellogenesis and spawning ( $F_{1,79} = 3.82$ ,  $p < 0.0001$ ), indicating that higher temperature at this time delays OH the following year (Table 3). CDD during primary vitellogenesis with a transition to secondary vitellogenesis accounted for slightly more of the variance in OH explained by the model than did CDD during secondary vitellogenesis and spawning (57 and 43%, respectively).

## Discussion

### Timing of egg hatching in the sGSL

Results of this study provide strong evidence that female American lobsters in the sGSL have been releasing their larvae progressively earlier since 1989. First, the change in ratio of pre hatch/hatching

**Table 2.** AIC model selection for spatial and temporal variation in the RCD in relation to temperature during different phases of the reproductive cycle.

Models <sup>a</sup>	Parameter estimate <sup>b</sup>	k <sup>c</sup>	AICc	$\Delta^d$	AICc weight <sup>e</sup> (%)
CDD spawning	-4.646e-5	3	-219.61	0.00	20.9
CDD early embryogenesis	0.000283				
CDD early embryogenesis	0.000017	2	-219.19	0.42	16.9
CDD early embryogenesis	0.000242	3	-218.37	1.25	11.2
CDD late embryogenesis	-0.000121				
CDD gametogenesis	0.000144	2	-217.52	2.10	7.3
CDD spawning	-5.570e-5	4	-217.35	2.26	6.7
CDD early embryogenesis	0.000282				
CDD late embryogenesis	4.024e-5				

<sup>a</sup>The RCD was indicated by the change in ratios of ovigerous females with prehatch/hatching (stages 3–4) vs. developing (stages 1–2) clutches through the spring each year. Temperature considered was CDDs > 3.4°C over 6-month periods spring/summer (April–September) and fall/winter (October–March) starting from the spring of sampling immediately prior to larvae hatching (summer months excl.) and going back to the fall/winter 3 years prior when the onset of ovarian development began.

<sup>b</sup>Parameter estimates (coefficients) are given for temperature indices only; intercepts are not shown.

<sup>c</sup>k indicates the number of parameters in each model (the number of variables plus intercept).

<sup>d</sup>The best-fit model is indicated by the lowest AICc value ( $\Delta = 0$ ).

<sup>e</sup>AICc weights indicate the relative support received by the different models based on the data. Only the top 5 out of the 32 models compared are shown, yet weights were calculated in relation to all 32 models compared (all combinations of 4 seasons and area terms).

**Table 3.** AIC model selection for trends in OH in relation to temperature during different phases of the reproductive cycle.

Models <sup>a</sup>	Parameter estimate <sup>b</sup>	k <sup>c</sup>	AICc	$\Delta^d$	AICc weight <sup>e</sup> (%)
CDD gametogenesis	-0.022914	3	401.43	0.00	49.7
CDD spawning	0.005620				
CDD gametogenesis	-0.023081	4	403.60	2.16	16.9
CDD spawning	0.005012				
CDD late embryogenesis	0.002822				
CDD gametogenesis	-0.021342	4	403.65	2.21	16.5
CDD spawning	0.005716				
CDD early embryogenesis	-0.002032				
CDD gametogenesis	-0.019378	3	405.71	4.27	5.9
CDD late embryogenesis	0.017390				
CDD gametogenesis	-0.021637	5	405.88	4.45	5.4
CDD spawning	0.005127				
CDD early embryogenesis	-0.001857				
CDD late embryogenesis	0.002695				

<sup>a</sup>OH was indicated by the first calendar week with ovigerous females with prehatch/hatching (stages 3–4) observed each year. Temperature considered was CDDs > 3.4°C over 6-month periods spring/summer (April–September) and fall/winter (October–March) starting from the spring of sampling immediately prior to larvae hatching (summer months excl.) and going back to the fall/winter 3 years prior when the onset of ovarian development began.

<sup>b</sup>Parameter estimates (coefficients) are given for temperature indices only; intercepts are not shown.

<sup>c</sup>k indicates the number of parameters in each model (the number of variables plus intercept).

<sup>d</sup>The best-fit model is indicated by the lowest AICc value ( $\Delta = 0$ ).

<sup>e</sup>AICc weights indicate the relative support received by the different models based on the data. Only the top 5 out of the 32 models compared are shown, yet weights were calculated in relation to all 32 models compared (all combinations of 4 seasons and area terms).

(stages 3–4) to developing (stages 1–2) clutches through the spring fishing season, which we refer to as the RCD, occurs on average 40% faster across the study domain now than it did 25 years ago. Second, we showed that the first appearance of ovigerous females with prehatch or hatching clutches, which we refer to as the OH, was observed on average 5 weeks earlier.

Both the RCD and OH metrics were subject to limited sampling intensity and the constraint of the relatively short time window of the spring fishing season. This was particularly true for OH. For example, OH was recorded as the first week of sampling in 30–60% of years sampled in different areas. The frequency with which this occurred increased later in the study period [33%, 46%, and 67% of cases (year–area combination) in 1989–

1997, 1998–2005, and 2006–2014, respectively], which means that we likely underestimated the true advancement in OH. Also, there were five instances from 1989 to 1991 when no females with prehatch/hatching clutches were reported during the fishing season. This was consistent with later hatching during the earlier part of our survey and further suggests that our data likely underreport the true advancement of hatching.

### Temporal trends in temperature and their effect on the timing of hatching

We found evidence that temperature during the female reproductive cycle influences the timing of hatching of lobster larvae in the



sGSL, which is not surprising given that several aspects of lobster biology and reproduction are under thermal regulation (Waddy and Aiken, 1995). The rate of embryonic development increases with temperature (Perkins, 1972), and up to 80% of the embryogenesis can be completed prior to winter (Gendron and Ouellet, 2009). Because CDD in the fall has increased over the past 25 years, early embryonic development following spawning (and prior to winter diapause) is expected to have been accelerated over the this time period, which is supported by our results.

Temperature during vitellogenesis also seems to play a role in regulating hatching time. Rising temperature in the fall may affect not only early embryonic development but also ovarian development, as suggested by the relationship between OH and CDD 1.5 years prior to hatching. Primary vitellogenesis occurs over several months in the spring, summer, and fall the year before spawning, resulting in a slow increase in ovarian size before the ovary enters a winter diapause period (Aiken and Waddy, 1980; Comeau and Benhalima, 2018). It has been assumed that secondary vitellogenesis only begins the following spring, prior to summer spawning (Aiken and Waddy, 1980; Waddy and Aiken, 1995), but recent monitoring of ovarian development in the sGSL indicates that secondary vitellogenesis is well underway in the fall prior to spawning (Comeau and Benhalima, 2018). We propose that the mechanism behind the relationship between temperature during the fall prior to spawning and an early OH  $\sim 1.5$  years later is an increase in fall CDD allowing the earlier completion of primary vitellogenesis and greater progression of secondary vitellogenesis prior to the winter diapause. Furthermore, warmer water during the transition from primary vitellogenesis to secondary vitellogenesis may lead to an earlier spawning, amplifying the effects of more CDD available for embryonic development in the fall a year later.

In contrast with the CDD observed in fall that positively influence the ovarian and embryonic development, higher spring–summer temperature the year of spawning was associated with slower RCD and later OH the following year. It was expected that lower CDD in spring–summers results in delayed secondary vitellogenesis and spawning (Aiken and Waddy, 1980, 1982), and thus delayed hatching as well. The observation that hatching is earlier despite cooler springs–summers may suggest that temperature at this time has limited effect on spawning time, which is consistent with the fact that it was the weakest contributor to model predictive ability. As the onset of secondary vitellogenesis has been observed in fall prior to the winter diapause in the sGSL (Comeau and Benhalima, 2018), our findings suggest that CDD in fall rather than in spring/summer has a greater influence on spawning and hatching.

Given the positive relation shown in the lab between temperature and late development of lobster embryos (Perkins, 1972; Gendron and Ouellet, 2009), as well as the ability to predict hatching in nature based on spring temperature and temperature-based embryonic development functions (Miller *et al.*, 2016), the lack of a relationship between interannual variation in spring temperature and our two metrics of hatching time was unexpected. The lack of relationship may be because of an imperfect temporal and/or spatial match between our temperature (daily from April to June over entire area) and biological (ovigerous females sampled in May and June in parts of each area) data and/or errors in the modelled temperature data in shallow coastal areas. Alternatively, it may reflect an adaptation to unpredictable spring temperature. Temperature is considerably

more variable in June than in September in the sGSL (Chassé *et al.*, 2014b). Modelled temperature in our study showed inter-annual variation of 30% around the mean CDD in spring, compared to only 10% in the fall. The ability for embryos to progress to hatching independently of spring temperature may be an adaptive response to unpredictable spring conditions. This interpretation is supported by the observation that American lobster embryos may hatch anytime from 50% development onwards, based on observations of the Perkins Eye Index (Perkins, 1972) of prezoaeae (hatchlings not yet moulted to stage I larvae) in relation to the embryonic moult cycle documented by Helluy and Beltz (1991). This suggests that embryos may have the ability to deplete their yolk reserves and proceed to hatching irrespective (to some degree) of the degree-days available for embryogenesis during spring.

Given that many aspects of lobster biology are regulated by temperature to some degree, including size-at-maturity and moulting (Waddy *et al.*, 1995), it is not inconceivable that changes to temperature-mediated processes other than vitellogenesis have contributed to the temporal trends in lobster hatch documented in this study. Female size-at-maturity has in fact declined in large parts of eastern Canada and the Gulf of Maine over the past 20–80 years (Haarr *et al.*, 2018; Le Bris *et al.*, 2018). However, such declines have not occurred in the sGSL during the time period of this study (Haarr *et al.*, 2018). There was evidence of a small decrease ( $\approx 4$  mm in CL) in average size of ovigerous females over our study period (results not shown), but this is unlikely to explain the advancement in hatching time we documented as smaller females consistently release their larvae later (not earlier) than larger females in hatcheries in the sGSL (M. Mallet, Maritime Fishermen Union, Shediac, Canada, pers. comm.). Nor does it seem likely that the temporal trend in hatching time is related to changes to the moulting cycle, as the cold spring temperatures in the sGSL [ $-1.6^{\circ}\text{C}$  from December to April (Hanson and Courtenay, 1996)] leave little opportunity for advancement of moulting; soft-shelled lobsters have never been encountered in the past 35 years of the spring fishery survey (ends  $\approx 30$  June) upon which this study is based (M. Comeau, Fisheries and Oceans Canada, unpublished data).

There are no other empirical data on changes in hatching time of American lobster over a similar time period with which to compare our results. The most comparable data are from a recent study in the Magdalen Islands, in the central Gulf of St Lawrence, in which hatching time of lobster was retro-calculated based on estimated settlement date and water temperature during the larval period. This study suggested that hatching may have moved to later in the season between 1997 and 2013, opposite to what was documented in this study, although the relationship was weak ( $R^2 = 0.18$ ) and not statistically significant ( $p = 0.09$ ; Gendron *et al.*, 2019). There is also uncertainty associated with this retro-estimation of hatching time related to factors other than temperature that may affect interannual variability in larval development (e.g. differences in larval food supply). The seemingly contradictory results are nevertheless surprising. Fall temperatures have increased around the Magdalen Islands 1994–2013, just as in the sGSL, but spring temperatures have also increased and there has been no trend in summer temperatures (Galbraith *et al.*, 2014), neither which was the case for the sGSL. Consequently, the thermal changes around the Magdalen Islands differ somewhat from those in the sGSL, which may explain this evidence for opposite temporal trends in lobster hatching time in these two regions.

Further research is clearly needed to confirm and explain these phenological changes.

### Effects of an earlier timing of hatching

Based on the presence of stage I larvae in the water column, hatching is generally thought to peak between mid-July and mid-August in the sGSL (Chassé and Miller, 2010). There are considerable potential ecological implications if hatching peaks earlier in the season in response to environmental conditions that occur 6–18 months prior to hatching. Survival of larvae is assumed to be very low, generally <2% (Harding *et al.*, 1982; Incze, 2000; Chassé and Miller, 2010), and thus likely important to benthic recruitment. Rising water temperature, within the bounds of physiological limits, is likely positive during the pelagic larval phase as it results in more rapid development and settlement, and hence reduced exposure to pelagic predators and offshore drift (MacKenzie, 1988; Xue *et al.*, 2008; Pershing *et al.*, 2012). However, we documented an earlier larval release that does not appear to be associated with an increase in spring–summer temperature, suggesting that larvae may now be released into colder water (there was a significant negative temporal trend in average temp during the week of OH in two of our four study areas, results not shown), and hence might experience slower development, greater dispersal, and greater mortality than 25 years ago. To the best of our knowledge, these three hypotheses cannot be tested directly, given the sparse data on lobster larvae in the sGSL. The third of these hypotheses is not consistent with the high levels of lobster settlement in certain regions of the sGSL over the past 5–6 years (DFO, 2016b). It must be noted, however, that the linkage between the pelagic and benthic phases of lobsters is complex (Carloni *et al.*, 2018), and the changes in hatch time documented in this study may ultimately have little incidence on the successful settlement and early survival of stage IV postlarvae relative to other processes.

An earlier timing of hatching driven by thermal conditions many months prior to hatching may also have ramifications for larval food supply. Mismatches between prey abundance and larval needs can occur if there are asynchronous changes in phenology across different trophic levels (Cushing, 1990; Visser *et al.*, 1998; Edwards and Richardson, 2004; Durant *et al.*, 2007). American lobster larvae are active predators feeding on a variety of zooplankton and phytoplankton (Ennis, 1995). Given lobster larvae appear to be hatching earlier in the summer mostly because of temperature affecting ovarian and early embryonic development, they may face a temporal mismatch with other zooplankton upon which they prey. It seems unlikely that the lobster prey would have a similar early presence in the plankton, given the shorter life cycles of most zooplankton prey species [~1 month generation time in copepods (Fransz *et al.*, 1991)]. The phenology of plankton most commonly correlates positively with water temperature immediately prior to and during their growing season (Mackas *et al.*, 2012), and as there is less evidence of warming during spring and summer compared to the fall in the sGSL, plankton may not currently be undergoing the same phenological shift as lobster. A loss of synchronicity between the timing of hatching of lobster larvae and their prey is therefore possible, and similar scenarios have been documented and predicted in various zooplankton, crustaceans, fishes, and birds (Gotceitas *et al.*, 1996; Visser *et al.*, 1998; Edwards and Richardson, 2004; Durant *et al.*, 2007; Asch, 2015; Asch *et al.*, 2019). Food limitation is generally

not believed to be an important factor in the mortality of lobster larvae (Ennis, 1995). However, if the timing of hatching is altered, resulting in a decoupling between peak prey abundance and lobster larval release, starvation from food limitation could result in high mortality and jeopardize benthic recruitment. Further research into the plankton dynamics of the sGSL is necessary to investigate this possibility.

An earlier OH also has the potential to affect larval drift trajectories and connectivity patterns, not only through altering the duration of the pelagic phase, and thus drift time, but also by exposing the larvae to different currents (Xue *et al.*, 2008; Chassé and Miller, 2010; Quinn, 2014). Larval drift modelling in the sGSL predicts significantly lower survival for larvae released in locations where the peak hatching period occurs earlier in summer (Chassé and Miller, 2010), and there is some empirical evidence of lower survival of early hatched larvae (Miller, 1997). Wind and weather patterns also vary seasonally and earlier hatching may expose larvae to different wind-driven surface currents not otherwise experienced during the pelagic phase, which has been shown to have a great effect on spatial and temporal patterns in postlarval supply and settlement (Harding *et al.*, 1982; Wahle and Incze, 1997; Incze, 2000; Pershing *et al.*, 2012; Quinn *et al.*, 2017). Seasonal variation in temperature and currents in the sGSL is predicted to result in variation in drift time and distance up to 1 month and 100 km, respectively, for larvae released at different times in a 5-week window during the summer, and up to >2 months and >300 km over a 10-week window (B. Quinn and M.L. Haarr, unpublished data). Thus, it seems clear that even relatively modest changes in the timing of hatching have the potential to alter connectivity patterns and survival of larvae.

This study provides compelling evidence that the timing of hatching for American lobster larvae in the sGSL has advanced over the past ~25 years (1989–2014). The relatively narrow annual at-sea sampling during the spring fishery (May–June) likely masked the extent of the temporal shift to earlier hatching in the sGSL. The implications of the changes in phenology we document are not clear but could produce adverse effects for the fishery. Hatching earlier in the season most likely results in larvae being exposed to colder water, causing prolonged development and potentially reduced larval survival (MacKenzie, 1988; Quinn *et al.*, 2013). Such an effect could be amplified if larval survival is further reduced by changes in food availability following a possible loss of synchronicity with prey species. Earlier hatching will also result in increased catch rates and handling of females with more loosely attached embryos, as the clutches of a greater proportion of ovigerous females will reach prehatch/hatching stages before the end of the spring fishing season. Given that eggs are more readily lost from a female's abdomen in prehatch clutches than from developing ones (Talbot *et al.*, 1984), increased handling of females whilst their clutches are close to hatching may result in increased egg loss and negatively affect larval supply (Tang *et al.*, 2018). Further research into effects of climate change on lobster phenology is clearly warranted, particularly with respect to the potential effects of earlier hatching on larval survival and benthic recruitment.

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