SPATIOTEMPORAL VARIATION IN SEXUAL MATURATION AND HATCHING OF AMERICAN LOBSTER (*HOMARUS AMERICANUS*) IN EASTERN CANADA: PATTERNS, PROCESSES AND IMPLICATIONS TO FISHERIES

by

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GENERAL ABSTRACT

The American lobster supports the most valuable fishery in eastern North America, involving over 15,000 fishers and $1.5 billion in annual revenue. The species' range extends 10° latitude from North Carolina to Newfoundland, exposing lobster to considerable variation in environmental conditions. The lobster's environment also changes over time, for example in relation to rapid climate change, exploitation rates, and pronounced changes in lobster abundance (*e.g.*, record high last 3-4 decades). Consequently, spatiotemporal variability in life-history traits is expected, but has been investigated relatively little. In this thesis, I investigated spatiotemporal variation in female size-at-maturity (SM) and timing of hatching in eastern Canada, as well as inter- and intra-clutch variation in embryonic development at hatching. The most salient findings are: (1) SM of female lobster has declined by 1-3 moults over the past 10-80 years; (2) evidence that declines in SM are due to size-selective harvesting, based on the relationship between spatial variation in the magnitude of SM declines and the degree to which minimum legal size regulations have allowed harvesting of immature females; (3) hatching occurs in eastern Canada during weeks of the year (Jul-Sept) that are predicted (based on a larval dispersal model) to minimise larval drift time; (4) considerable geographic variation in timing of hatching (8-10 weeks), which does not seem related to local variation in when hatching would minimise drift time; (5) considerable variation within and among clutches in embryonic size at hatch, likely as a bet-hedging strategy; and (6) an advancement of ≈5 weeks in the start of the hatching period in the southern Gulf of St. Lawrence over 25 years, seemingly in response to an increase in cumulative degree days available in fall for gonadal development and early embryonic development. These findings show considerable variability in reproductive traits of lobster, and highlight the need to consider such variability in fisheries management and research.

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Specific contributions to data chapters

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LIST OF ABBREVIATIONS

CL – Carapace length. Measured from the back of the eye socket to the posterior end of the carapace.

CL_{50} – The size by which 50% of the population has reached maturity.

CL_{min} – The smallest SM in a population, or in this case at a sampling location.

DFO – Department of Fisheries and Oceans Canada

LFA – Lobster Fishing Area. Management units of the Canadian lobster fishery.

MLS – Minimum legal size. The smallest-sized individuals (min CL) that can be legally landed.

OH – Onset-of-hatching. The first week during the fishing season when an ovigerous female with a stage 3 (mature, hatching imminent) or 4 (in the process of hatching) clutch was observed.

PEI – Perkins Eye Index. The diameter of an embryo's eye, measured as the average of the shortest and longest axes of the pigmented eye spot, given in microns. PEI is proportional to embryo size and an indicator of the degree of embryonic development.

RCD – Rate of clutch development. The linear slope of the log ratio of ovigerous females with mature/hatching (stages 3 and 4) to immature (stages 1 and 2) clutches regressed against calendar week.

sGSL – The southern Gulf of St. Lawrence.

SM – Size-at-maturity. The size at which an individual reaches physical maturation, presented in mm carapace length. In the context of this thesis SM always refers to female lobsters as male SM was not considered. CL_{50} and CL_{min} are indicators of the population mean and minimum SM, respectively.

GENERAL INTRODUCTION

0.1 Prologue

This thesis comprises work that has been a part of the "Lobster Node" of the Natural Sciences and Engineering Research Council of Canada (NSERC) Canadian Fisheries Research Network (CFRN) (www.cfrn-rcrp.ca; Rochette *et al.* 2018). The CFRN was a 6-year research network launched in 2010, which embraced a unique tri-partite collaboration between academia, government and industry to increase knowledge to enhance ecological sustainability, socio-economic viability and management of Canadian fisheries. This thesis was a part of project 1.2: "Metapopulation dynamics, management areas and biological units of lobster in eastern Canada", which sought to advance our understanding of lobster stock structure in eastern Canada and the interconnectedness of lobster (*i.e.,* connectivity) among management zones, known as Lobster Fishing Areas (LFAs). This overarching objective was addressed through five integrated research activities centered around different stages of the lobster life cycle (Fig. 0.1): (1) investigations of egg production and the input of larvae into the system, (2) biophysical modeling of larval drift, (3) studies of larval settlement behaviour to inform the model, (4) tagging studies to investigate the contributions of benthic movement to connectivity, and (5) the development of a large quantity of genetic markers to further our understanding of population genetics and stock structure. This thesis is a primary contribution to the first research activity, assessing patterns of egg production and larval supply.

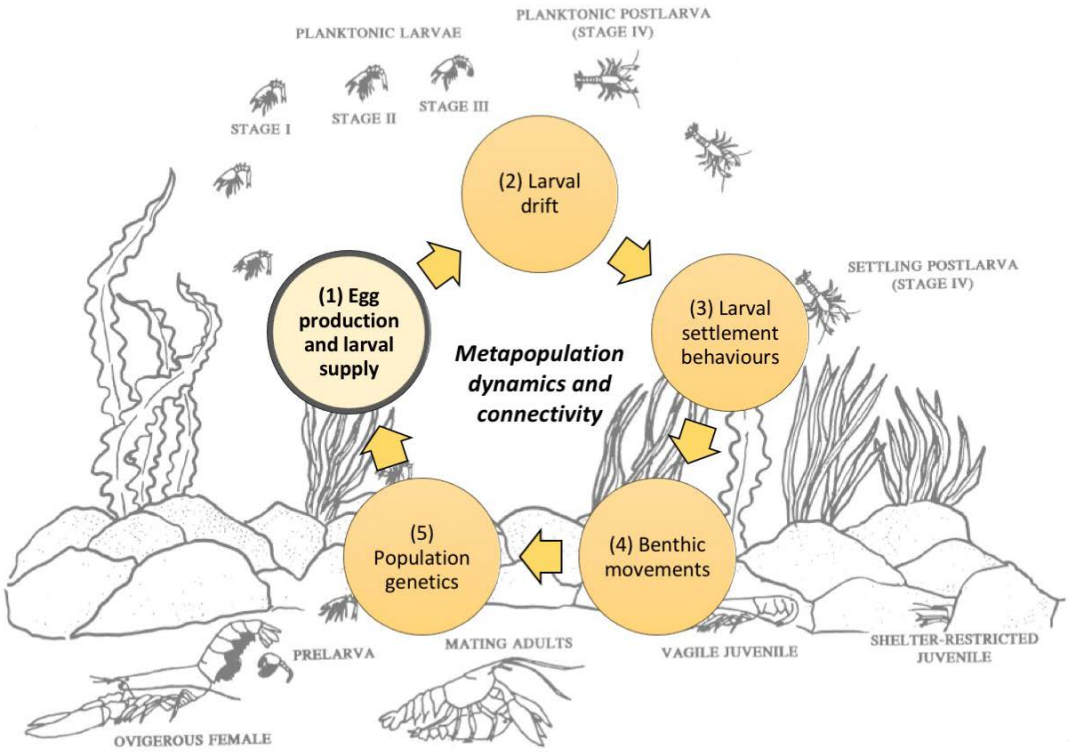

Figure 0.1: *An illustration of the objectives and research activities of the "Lobster Node" of the Canadian Fisheries Research Network. This thesis contributes to research activity 1 (highlighted). The background graphic showing the lobster life cycle is adopted from Factor 1995.*

A key novelty of this thesis is that it investigated aspects of reproductive biology of lobster across nearly all its Canadian range; studies of such scale are exceedingly rare. Most research to date has focused on individuals from a single location (see General Discussion for a review). Naturally, one of the primary reasons for this is logistical challenges given the time-consuming and expensive nature of such research; however, the local studies invariably fail to consider possible spatial variation in reproductive traits, which is expected given the wide range in environmental conditions experienced by lobster across its range. Summer temperatures in the Canadian portion of the range alone vary from over 20°C to less than 12°C (Larouche and Galbraith 2016). I overcame some of the major challenges of a large-scale study by collaborating with fishermen through the "Lobster Node" and investigated patterns in female

size-at-maturity (SM) and the timing of hatching in more than 20 locations spread across most of eastern Canada. To my knowledge, only two studies have been conducted to date at a comparable spatial scale (Currie and Schneider 2011 [female fecundity]; Raper and Schneider 2013 [growth rates]), and both collected limited new data, relying instead on historic data where data from different locations were also from different time periods, thus confounding spatial with potential temporal variation in these traits. In addition to the large geographic scope, I also utilised a combination of new and historic data to investigate variability in SM and hatching time over the past 1-8 decades. Consequently, this thesis investigates aspects of lobster egg production at spatial and temporal scales rarely seen in ecological studies.

0.2 The Canadian lobster fishery

The American lobster (*Homarus americanus*) supports Canada's most valuable fishery (Rochette *et al.* 2018). The fishery generates approximately one billion dollars annually in exports, $600-700 million in landed value, employs over 10,000 harvesters and supports over 500 licensed buyers, 400 shippers and 40 processors (Fisheries Resource Conservation Council 2007; DFO 2015a). The fishery comprises 45 Lobster Fishing Areas (LFAs) (Fig. 0.2), 43 of which support owner-operated small-boat inshore fisheries; of the remaining two LFAs, one is closed to fishing as a conservation measure (LFA 40) and the other is an enterprise allocation offshore fishery (LFA 41) (DFO 2015a). Most fishing activities take place within 15 km of shore and in water shallower than 40 m deep. The exceptions to this are the Bay of Fundy and southwest Nova Scotia (LFAs 34-38), where fishing activities often take place further from shore, and in waters up to 200 m deep (DFO 2015a). The fishery is largest in the Bay of Fundy (LFAs 34-38), along the Scotian Shelf (LFAs 27-33) and in the southern Gulf of St. Lawrence (LFAs 23-26B). These areas account for more than half the national landings (Fisheries Resource Conservation

Council 2007). Since the 1990s, and the collapse of groundfish fisheries, the dependence of fishermen and communities on the lobster fishery has increased, and many now rely exclusively on lobster for economic viability (Fisheries Resource Conservation Council 2007).

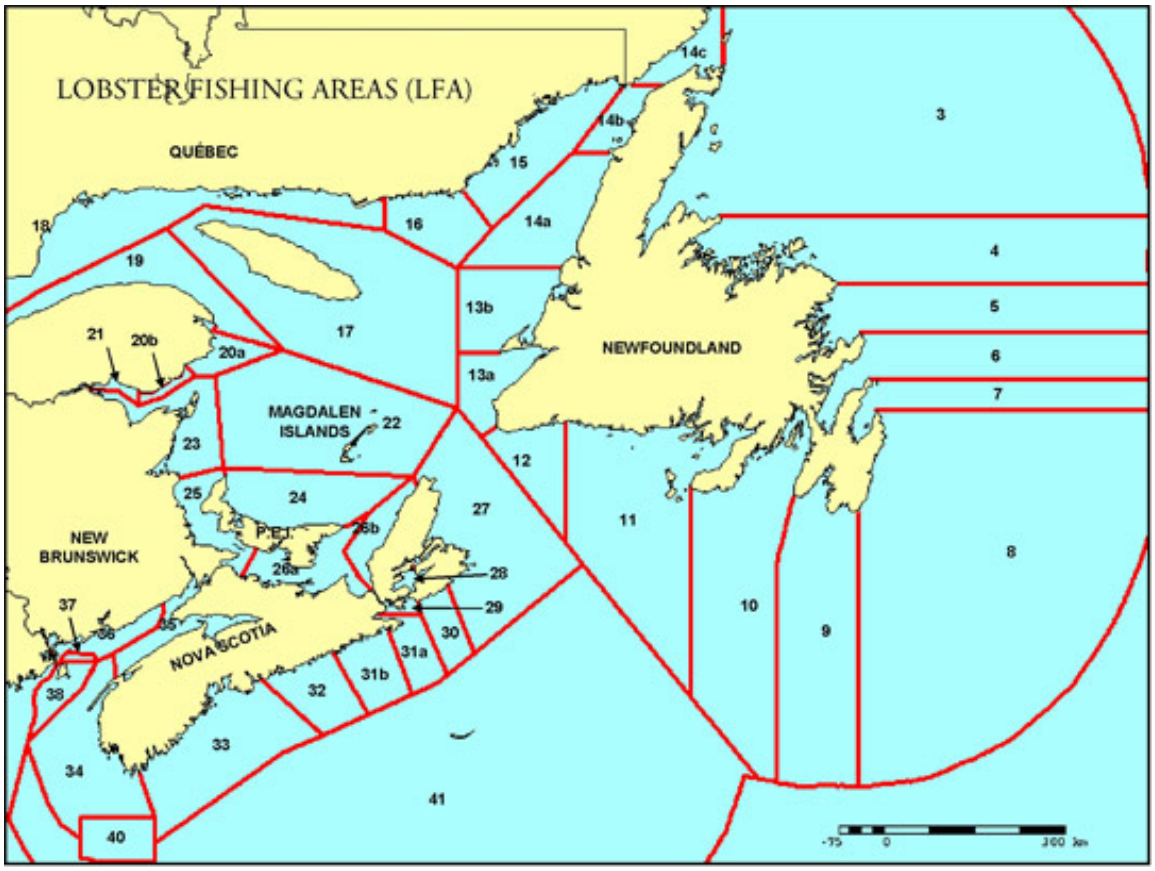

Figure 0.2: *Map of Canadian Lobster Fishing Areas (LFAs). Adopted from DFO (2015a).*

The commercial lobster fishery began in Canada in the 1800s. Reported landings were modest at first, with only 1,360 mt landed in 1870, but increased rapidly to a peak of 44,450 mt in 1886 (Rutherford *et al.* 1967). This rapid increase was followed by over 30 years of declining landings and considerable reductions in the average size of lobsters caught, as the resource was increasingly "fished down" (Rutherford *et al.* 1967). Landings stabilised in the early 1920s at approximately 15,000 mt annually, and began increasing again in the 1980s. It reached record highs in the past 15 years, peaking at nearly 75,000 mt in 2012 and 2013 (DFO 2015a). Reasons

for the current record landings are unclear, but reduced predation on juveniles due to the collapse of groundfish stocks and increased productivity due to warming oceans have been suggested as contributors (Campbell *et al.* 1991; Elner and Campbell 1991; Boudreau and Worm 2010). Despite this overall increase in lobster landings, however, some areas of Newfoundland and the southern Gulf of St. Lawrence have levelled off or even experienced recent declines (DFO 2013a, b). Landings in the central Northumberland Strait (parts of LFAs 25 and 26A) have decreased dramatically, threatening the economic viability of fishing enterprises in the area (Rondeau *et al.* 2015; DFO 2015b). Exploitation rates are high, with over 75% of legal-sized individuals fished out annually in many regions, even exceeding 90% in some areas (Fisheries Resource Conservation Council 2007).

The lobster life cycle is characterised by two distinct phases: a benthic juvenile and adult phase, and a planktonic larval phase (Fig. 0.3) (Ennis 1995). Most females follow a two-year reproductive cycle, where moulting and mating occur in one summer, sperm is stored in the seminal receptacle until the following summer when spawning occurs, and eggs are carried attached to the female's abdomen for 9-12 months before larvae hatch during the third summer (Ennis 1995). A smaller proportion of females have what is considered a one-year cycle, during which moulting, mating and spawning all occur in the same season (Comeau and Savoie 2002). These females are typically smaller, primiparous females (first-time spawners), that spawn and hatch their eggs somewhat later than females exhibiting the more typical two-year cycle (Comeau and Savoie 2002; Gendron and Ouellet 2009). Large females (>120 mm carapace length [CL]) may skip moulting between spawnings and spawn in consecutive years (Waddy and Aiken 1986). Embryonic development is temperature-dependent (Perkins 1972). Embryos undergo rapid development after spawning in the fall, reaching 50%-80% of development before going into winter diapause (Gendron and Ouellet 2009). Development

resumes in the spring, and hatching occurs sometime 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 weeks to months, depending on temperature, before becoming competent to settle on the bottom (Ennis 1995). Biophysical modeling suggests larvae may drift up to 100s of km before settling (Xue *et al.* 2008; Quinn *et al.* 2017). Larval drift is generally believed to be the primary contributor to dispersal and connectivity (Ennis 1995), although benthic movements undoubtedly contribute to this process (Morse 2017). Survival during the larval phase is assumed to be very low, generally <2% (Harding *et al*. 1982; Incze *et al*. 2000; Chassé and Miller 2010).

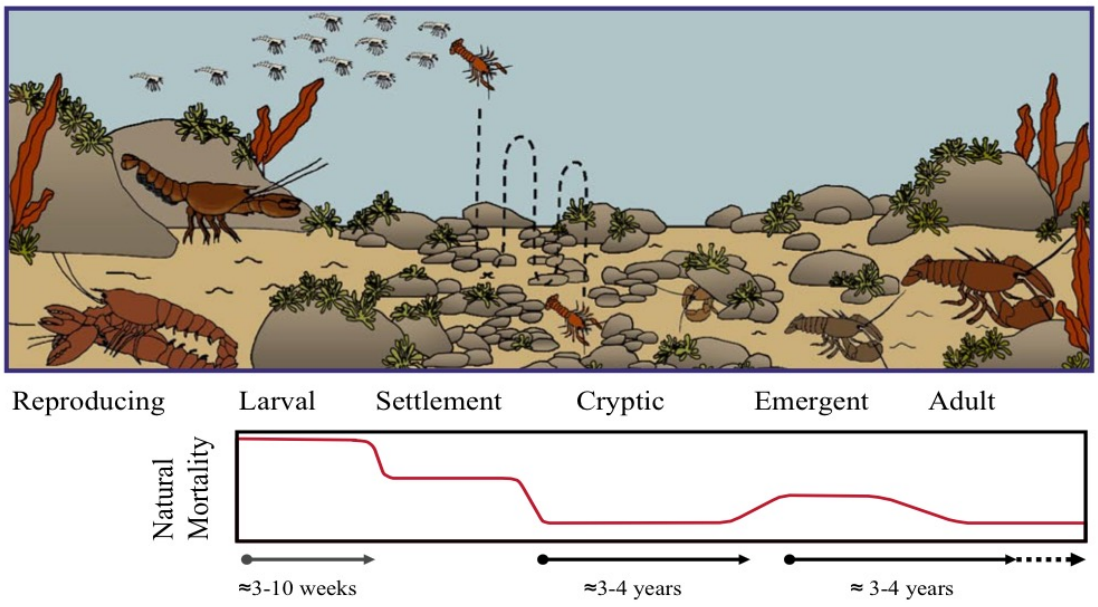

Figure 0.3: *The lobster life cycle, adapted from Fisheries Resource Conservation Council (2007). Females mate primarily in association with moulting during the summer, subsequently store the sperm, and spawn and fertilise eggs one year later, after which eggs are carried on the abdomen for 9-12 months before hatching (reproducing). Larvae are pelagic and drift in the water column while undergoing three moults to reach the postlarval stage (larval). Postlarvae search for suitable habitat for settlement once competent to do so (settlement). Settled postlarvae and early juveniles remain largely hidden in the substrate (cryptic). Larger juveniles gradually increase movement and foraging outside of their shelters (emergent) until reaching maturity (adult).*

Maintaining female productivity is an important aspect of the management of the lobster fishery. The fishery is effort-controlled (*i.e.*, without quotas) through license, season and gear restrictions, coupled with a minimum legal size (MLS) (Miller 1995). Efforts to introduce regulations to conserve the resource, including region-specific MLSs, were initiated as early as the 1870s. A ban on landing ovigerous females has been a key part of the management strategy since this time (DeWolf 1974). The protection of ovigerous females ensures greater egg production, and in some areas fishermen increase this protection by v-notching the tails of ovigerous females so that they can be recognised as reproductive and spared by the fishery even after hatching their clutches (until the mark is lost through moulting) (DeAngelis *et al.* 2010). However, through most of the history of the fishery, MLS was generally set well below the SM, resulting in high mortality of immature females (DFO 2012). In the 1990s-2000s, however, MLS was increased with the specific objective of allowing 50% of females to reach maturity and spawn at least once prior to recruiting to the fishery (*i.e.,* moulting to a size beyond the MLS) (DFO 2012). This objective has now been reached in several LFAs, although areas do remain with high mortality of immature females where the MLS is still set below the female SM (Tremblay *et al.* 2011; Rondeau *et al.* 2015). Female SM is currently the primary consideration when setting MLS regulations (Fisheries Resource Conservation Council 2007).

0.3 The importance of early life history to fisheries recruitment

Stock–recruitment processes are generally poorly understood in lobster and crab fisheries, and this is also the case for American lobster (Wahle 2003). Prior to the rapid escalation in landings starting in the 1980s, benthic recruitment (successful settlement of postlarvae) had largely been believed to be independent of spawning stock biomass and larval supply, unless spawning stocks were to decline drastically below some critical level (Fogarty an Idoine 1986; Wahle

2003). Benthic recruitment was believed to be limited largely by the relative scarcity of suitable, structurally complex cobble nursery habitats, creating a bottleneck effect (Fogarty and Idoine 1986; Wahle 2003). Fogarty and Idoine (1986) reported an asymptotic relationship between postlarval supply and subsequent recruitment to the fishery in the southern Gulf of St. Lawrence in the 1950s and 60s. Years with very low postlarval supply were followed by reduced stock size, but years with particularly high postlarval production did not result in subsequent increases to fisheries recruitment (Fogarty and Idoine 1986). This observation is consistent with the idea of limited carrying capacity for juveniles due to scarcity of nursery habitats.

The above notion was challenged, however, when landings began to steadily and drastically increase in the 1980s, suggesting instead that environmental forcing may have a greater bearing on stock-recruitment relationships than had been previously thought (Wahle 2003). Since then, several studies have reported positive relationships between postlarval supply and young-of-the-year abundance on the benthos in the Gulf of Maine (Wahle and Incze 1997; Incze *et al*. 1997, 2000) and the Magdalen Islands (Ouellet and Sainte-Marie 1998). Fogarty and Idoine (1986) also reported positive relationships between successive larval stages, such that very low production of stage I larvae would result in very low production of postlarvae. Correspondingly, low landings in the eastern Northumberland Strait are thought to be linked to low larval survival (Miller *et al.* 2006). The weak stock-recruitment relationships reported prior may have, at least partially, been a function of the spatial scales investigated. Chang *et al.* (2016) demonstrated that estimates of spawner-recruit relationships in the Gulf of Maine were highly dependent on the spatial scale over which they were investigated, and that the range of spatial scales revealing a relationship varied between the eastern and western Gulf.

The variable impacts of spatial scale on perceived spawner-recruit relationships likely reflect, in part, patterns of larval dispersal and connectivity. Biophysical modeling of larval drift suggests considerable variation in source-sinks dynamics and the degree to which lobster fishing areas are self-seeding or dependent on larval production elsewhere (Quinn *et al.* 2017). It has, for example, been suggested that postlarval supply in inshore areas of the Gulf of Maine is subsidised by larval production in less exploited populations further offshore (Wahle 2003). Such dynamics are not conducive to establishing spawner-recruit relationships, but modeling of larval drift nevertheless clearly implies that the level of egg production in an area can have significant impact on postlarval supply (and later fisheries recruitment) downstream.

There are cases where positive relationships between spawning stock and postlarval supply, and between benthic recruitment and subsequent fisheries recruitment, are clearly lacking, but these appear to reflect specific environmental disruptions. Benthic recruitment has been declining in the Gulf of Maine and Bay of Fundy the past approximately five years despite record high abundance of ovigerous females, and this discord has been hypothesised to be linked to a decline in the intermediate larval stages' copepod prey (Wahle and Carloni 2016). In southern New England, the intensity of benthic recruitment 1990-1996 accounted for >80% of variation in pre-recruit (*i.e.*, one size class/moult below the minimum legal size) abundance three years later (Wahle *et al.* 2009). However, there was no relationship between benthic recruitment and subsequent pre-recruit abundance 1997-2003 following an outbreak of epizootic shell disease in the late 1990s (Wahle *et al.* 2009).

In summary, the impact upon the fishery of variation in egg- and postlarval supply is not straightforward to predict, but it is clear that spatial and temporal variability of both may impact future fishery yields.

0.4 Life-history traits in a dynamic environment

The phenotype of organisms can change in response to natural and anthropogenically-mediated changes to the environment, resulting in temporal trends in life-history traits (Reznick and Ghalambor 2001). Progressive changes in reproductive parameters and life history attributes such as growth rates, size and age at maturation, fecundity and phenology (the timing of biological events) over time are important to fisheries management, as these changes may impact the accuracy of assumptions underlying management decisions. Yet while most stock assessment methods do incorporate some degree of stochasticity in variables such as growth, larval supply and benthic recruitment, they generally do not consider that these may be undergoing progressive and deterministic changes (Caputi *et al*. 2010). It is, however, important to recognize and consider possible changes in life history for sustainable and adaptive fisheries management, to better forecast recruitment patterns. Two key potential drivers of temporal change in life-history parameters of harvested species/populations are exploitation itself and climate change.

Altered mortality and selection patterns in the face of intense exploitation can result in phenotypic changes in a variety of traits. In agriculture, humans increase the frequency of individuals with desirable phenotypic traits through selective breeding to maximise crop and livestock yields. In contrast, when wild animal populations are exploited, individuals with desirable traits (*e.g.,* large body size) tend to be preferentially removed from the breeding population, which can cause a decline in the frequency of desirable traits over time, provided there is a genetic basis to this trait variation (Allendorf and Hard, 2009). In the context of most fisheries, where large body size is prized, individuals that reproduce at smaller sizes and younger ages are expected to have greater fitness than conspecifics that reproduce at larger

sizes and older ages, because of an increased probability of reproducing before being harvested. Reductions in growth rates and size- and age-at-maturity have been documented in numerous finfish fisheries during the past 50-60 years and attributed to high exploitation of larger, fast-growing, but late-reproducing individuals (Zhao and McGovern 1997; Sánchez Lizaso *et al.* 2000; Barot *et al.* 2004; Olsen *et al.* 2004; Kuparinen and Merilä 2007; Swain *et al.* 2007). Exploitation-induced changes in life-history traits remain poorly studied for invertebrate fisheries, but clearly merit further attention given documented impacts on finfish fisheries.

On average globally, ocean upper water (<75 m) temperatures have been increasing by approximately 0.1°C per decade since 1970 (Rhein *et al*. 2013). This increase has been greater in the northwest Atlantic, at approximately 1°C per decade (Knudsen et al. 2011; Loder et al. 2013). Along with increasing temperatures, oceans are also experiencing changes to circulation patterns, the frequency and intensity of storms, pH levels, salinity, stratification of the upper water layers, and sea levels (Doney *et al.* 2012; Rhein *et al*. 2013). Our oceans and their ecosystems are therefore experiencing considerable changes, which can have significant ramifications for marine life. Changes in temperature alone may directly impact species' survival, physiological processes and behaviour, and lead to changes in productivity, phenology, distribution and population structure (Doney *et al.* 2012). Climate change may also alter the processes regulating connectivity among marine populations (Gerber *et al.* 2014), and thus impact metapopulation dynamics, conservation efforts and fisheries stock structure. Over 70% of marine organisms have pelagic larval phases (Gerber *et al.* 2014). Alterations in ocean circulation patterns, wind-driven surface currents and stratification of the water column are likely to affect the dispersal patterns of these larvae given that these are largely driven by oceanographic conditions during the time spent adrift (Xue *et al.* 2008; Cowen and Sponaugle 2009). Altered environmental conditions may also affect the timing of reproductive events (*i.e.*,

phenology) (Doney *et al.* 2012; Gerber *et al.* 2014). Hundreds of terrestrial and aquatic species have been found to have altered reproductive phenology by 2-5 days per decade over the past 20-100 years, and most show advancements as predicted under climate change (Parmesan and Yohe 2003; Root *et al*. 2003). Altered phenology may further impact connectivity and recruitment by dictating the environmental conditions experienced during the pelagic phase. It thus seems clear that adaptive fisheries management practices should consider potential impacts of climate change on recruitment patterns.

An effective approach to fisheries management and conservation needs to consider not only temporal changes, but also spatial variation in life-history traits. Fisheries management units are often considerably larger than the scale at which there is trait variation in the exploited species. Marine spawning species, both fishes and invertebrates, are frequently managed as single-unit stocks (McBride 2014), even though life-history traits generally vary spatially within these single stocks. Demographic characteristics such as growth rates, longevity and mortality are routinely derived from age- and length-based data as a basis for many fisheries stock assessments (Gray 2015). Yet, as length-at-age in both fishes and invertebrates varies spatially and temporally (*e.g.*, Blanchette *et al.* 2007; Gray 2015; Kuparinen *et al.* 2016; Munroe *et al.* 2016), so do the estimates of demographic characteristics derived from them (Gray 2015; Kuparinen *et al.* 2016). This variability can occur over quite fine spatial scales; for example, cod (*Gadus morhua*) have wide-dispersing pelagic eggs and larvae, yet can display significantly different growth rates across scales of only a few km (Kuparinen *et al.* 2016). Even fisheries with management units smaller than likely stock sizes do not necessarily recognise spatial trait variation. In the Canadian lobster fishery, for example, minimum legal size regulations are uniform at 82.5 mm CL across 9 LFAs in the Bay of Fundy and along the Scotian Shelf (LFAs 30-38) despite female SM varying from 75 to 90 mm CL (Tremblay *et al.* 2011). Failing to

adequately address spatial variation in traits relevant to management can render conservation measures ineffective. For example, in the Tasmanian southern rock lobster (*Jasus edwardsii*) fishery, simulations show that uniform minimum legal size regulations that do not adequately address geographic variation in female size-at-maturity will reduce both egg production and the profitability of the fishery (Gardner *et al.* 2015). An investigation of spatial variation in traits relied upon in stock assessments should therefore be a given in all fisheries, as should an assessment of the implications of any variation on the scale of management units.

Spatial and temporal variability in at least some reproductive traits of the American lobster is expected because this species experiences a wide range of environmental conditions across its range (summer temperatures in the Canadian portion of its range alone vary from over 20°C to less than 12°C [Larouche and Galbraith 2016]) and is subject to potential pressures from climate change and intense exploitation. Given that reproduction, development and growth are primarily temperature regulated in the American lobster (Perkins 1972; MacKenzie 1988; Waddy and Aiken 1995; Tlusty *et al.* 2008), impacts of differing local thermal regimes and climate change on reproductive biology and phenology are highly likely, and there is evidence of this.

Female fecundity-at-size is believed to vary positively with latitude (Currie and Schneider 2011), and female size-at-maturity and the timing of hatching is broadly assumed to vary inversely with temperature (Templeman 1936; Waddy *et al.* 1995). Further, thermal stress caused by rising ocean temperature appears to be contributing to declines and habitat shifts in the southern portion of the species´ range (Caputi *et al*. 2010; Jury and Watson 2013; Wahle *et al.* 2015), while abundance increases have been reported in the northernmost part of the species' range (Bernard Sainte-Marie, DFO, pers. comm.). In the Bay of Fundy, size-specific female

lobster fecundity is believed to have declined by approximately 30% from 2008 to 2013 (Koopman *et al.* 2015). Increasing water temperature during winter months was hypothesised as a possible cause as females are believed to require periods of less than 5-8°C to properly initiate gonad development and this requirement was not necessarily met in deeper water in later years of this survey (Koopman *et al.* 2015).

In addition, the species has been exploited heavily for over a century, which has likely impacted at least some aspects of its life history, but not necessarily to the same extent in different areas given spatial variation in the intensity of exploitation (Fisheries Resource Conservation Council 2007). There is some evidence of temporal changes in American lobster female size-at-maturity over the past two decades, with both climate change and exploitation speculated as possible drivers (Landers *et al.* 2001; Gaudette *et al.* 2014; LeBris *et al.* 2017), yet the full extent of variation and its causes remain poorly understood and it is also unknown whether there are temporal changes in other reproductive traits such as the timing of larval release.

The American lobster fishery has experienced extensive anthropic and environmental pressures during the past century among intense exploitation, climate change, and record increases in abundance. Potential temporal changes in life-history traits should therefore be further investigated for this important fishery. Similarly, given the extensive range of the species, which spans ten degrees of latitude and thus a considerable range in environmental conditions, spatial trait variation should be given further attention. Including in reproductive traits other than female size-at-maturity (which is partially documented; *e.g.*, Watson *et al.* 2013; Waddy *et al.* 1995) relevant to fisheries management and benthic recruitment patterns.

0.5 Objectives of the thesis

The overarching objective of this thesis was to investigate spatial and temporal variability in egg production and larval supply in American lobster in eastern Canada; in particular (1) whether there is evidence of declines in size-at-maturity (SM) in since the early 1900s and if so, what has caused them, (2) which physical factors drive spatial variation and the optimal timing of egg hatching, and (3) whether contemporary increases in ocean temperature have advanced the timing of larval release. Each of these questions is addressed in a separate research chapter. The first and second chapters consider locations across eastern Canada, while the third chapter focuses specifically on the southern Gulf of St. Lawrence. In the second chapter I also address inter-individual variation in hatching characteristics.

In Chapter 1, I utilise a unique combination of published historical data, time series of fisheries monitoring data, and new data collected through the CFRN "Lobster Node" to investigate changes and patterns of female SM over the past 10-80 years in approximately half of Canada's 45 Lobster Fishing Areas (LFAs). I also investigate evidence for three potential drivers of such change: increasing water temperature, increasing abundance (and presumably density), and size-based selection through harvesting of large immature individuals. While local changes in SM have been noted in several locations over the past two to three decades (Landers *et al.* 2001; Gaudette *et al.* 2014; LeBris *et al.* 2017), this is the first study to address large-scale geographic patterns over a long historical perspective, and quantitatively investigate drivers behind the change. A secondary objective was to explore the effect of combinations of change in female SM and exploitation rate on population egg production through simulations with an egg-per-recruit (E/R) model. Male SM was not addressed, as scarce maturity data precludes similar analyses.

In Chapter 2, I compare hatching times to modeled optimal timing of hatching at 22 sites spread throughout the Bay of Fundy, the Scotian Shelf, and the Gulf of St. Lawrence based on (1) minimising the duration of the larval phase, (2) minimising the dispersal distance, and (3) maximising the proportion of larvae predicted to drift to locations potentially suitable for settlement (based on bottom temperature) by the time they are competent to do so. The hatching period and predicted optimal hatching times were compared to both determine what drives optimal hatching time (*i.e.*, which of the three metrics) and to attempt to explain spatial variation in hatching time. Hatching times were estimated by collecting embryo samples during the spring fishery, measuring their degree of development (indicated by eye size, known as the Perkins Eye Index [PEI]), and predicting when they would have hatched based on water temperature and temperature-dependent embryonic development functions (as in Miller *et al.* 2016). Optimal hatching times based on the three metrics above were predicted using a biophysical model of larval drift and simulating larval releases at weekly time steps throughout the year at each study site. I also investigated the full extent of variability in embryonic size at hatching and its sources (spatial, among females and within clutches) using a variety of field and lab samples (totalling ˜2,500 newly hatched embryos) from a total of 18 sampling sites across eastern Canada.

In Chapter 3, I utilised fisheries monitoring data from 1989 to 2014 from the southern Gulf of St. Lawrence comprising a total of 2,930 sampling days by harvesters from 90 fishing ports to assess interannual variation in hatching time. These data were not collected with this objective in mind and did not allow a full assessment of the hatching period; nevertheless, I was able to use data on visual categorisation of clutch maturation during the spring fishery to estimate the onset of the hatching period, and the population-level rate of clutch maturation through the spring. Bottom temperature data were obtained through a coupled ice-ocean hydrodynamic

model. I compared interannual variation in the onset-of-hatching and the rate of clutch maturation each spring to seasonal (fall-winter and spring-summer) cumulative degree days up to two years prior to hatch to determine (1) whether temperature increases have advanced the timing of hatch, and (2) during which portion of the reproductive cycle, incorporating both gonadal and embryonic development, temperature is most influential.

Combined, these three research chapters provide insight into potential sources of temporal and spatial variation in egg production and larval release dynamics, parameters important to benthic recruitment, of Canada´s largest fishery. Female SM has declined across the region by one to three moults over the past 10-80 years, with the magnitude of declines correlating spatially to the extent to which fishery regulations have allowed harvesting of immature females, suggesting SM declines have occurred in response to size-selective harvesting; there is no evidence that either increased abundance or temperature have driven SM changes. The general timing of hatching and release of larvae appears phased to minimise the duration of the pelagic phase, although local variation in the optimal timing of hatching does not appear to explain spatial variation in peak hatching time. Embryos may hatch over the staggering range of 40% to 120% of eye development when PEI-at-hatching is compared to previous work detailing the embryonic moult cycle (Helluy and Beltz 1991), with considerable variation spatially, among females and within clutches, possibly serving a bet-hedging function. The onset-of-hatching in the southern Gulf of St. Lawrence has advanced by 5 weeks on average and the population-level spring-time rate of clutch development increased by 40% over 25 years in response to more degree days available in the fall for first gonadal and then embryonic development. I thus show, for the first time in American lobster, fisheries-induced phenotypic changes, evidence of optimisation of hatching time, and phenological advancement in response to climate change.

The implications of the variability documented and its different sources to fisheries management and future research are discussed in the final chapter (General Discussion).

0.6 Statement of authorship

The three data chapters of this thesis represent independent research articles intended for publication. Chapter 1 has been published in the Canadian Journal of Fisheries and Aquatic Sciences; it was accepted April 2017 and is currently available online (dx.doi.org/10.1139/cjfas-2016-0434). Chapter 3 is currently being prepared for submission to Global Change Biology. Chapter 2 remains to be submitted for publication, but this will be achieved within 2018. The work itself culminates from a collaborative effort between myself (Marthe Larsen Haarr) and various co-authors. Co-authors of each article are listed on the corresponding title pages of each chapter. I am the principle author of all three articles (chapters). I assumed the leading role in identifying and designing each of the research proposals, and played a key role in the practical aspects of the research. Both Chapters 1 and 3 include large amounts of historical data I did not contribute to collect, but I was responsible for taking the necessary steps to access and organize the relevant data from various sources. All new data obtained during the course of my thesis and included in Chapters 1 to 3 were either collected by myself or I took a lead role in organising their collection by fishermen and at-sea-sampling technicians; the latter was a critical step in data collection, given the extensive geographic coverage and number of samplers involved. I also assumed the lead role in analysing data and preparing the manuscripts. I am the corresponding author on the manuscript resulting from Chapter 1, and will also be the corresponding author on the manuscripts resulting from Chapters 2 and 3.

0.7 Literature cited

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CHAPTER 1: Female American lobster (*Homarus americanus*) size-at-maturity has declined in Canada during the 20th and 21st century

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1.0 Abstract

Changes in the environment and fishing have been shown to affect life-history characteristics, such as size or age of maturation, in several finfish and invertebrates. The American lobster, *Homarus americanus*, supports Canada's most valuable fishery and has faced increased exploitation and warming temperatures over the last several decades. Female size-at-maturity (SM) is an important life-history parameter in management of this species, as it is used in establishing minimum-legal-size regulations. In this study, we show with historic and recent data, that SM of female American lobsters has declined over the past 10-80 years across most of Canada, in some areas by as much as 30%. The spatial patterns of these declines are inconsistent with patterns of rising ocean temperature and lobster abundance (density). They are, however, strongly correlated to the strength of size-based fishery selection, and egg-per-recruit modeling indicates a gain in lifetime egg production associated with observed SM declines under a range of realistic harvesting scenarios. These findings suggest that the marked decrease we document in SM of female American lobsters in Canada over the past century represents an evolutionary response to intense exploitation.

1.1 Introduction

The American lobster (*Homarus americanus*) currently supports Canada's most valuable fishery (DFO 2016*a,* Rochette *et al*. 2018). The commercial lobster fishery began in Canada in the 1800s, and landings increased rapidly to peak in the late 1880s, after which landings and average size of lobsters declined considerably before stabilising in early 1920s (Rutherford *et al.* 1967). Landings began rising again in the 1970s, reaching record highs in recent years (DFO 2016*b*). This last upsurge was partly related to increased fleet efficiency and effort, at least initially (Gendron and Archambault 1997; Boudreau and Worm 2010), yet rising landings also reflected increases in abundance (Boudreau *et al.* 2015). This increased abundance has been confirmed where fisheries-independent data exist, such as the southern Gulf of St. Lawrence (DFO 2016*c*). The reason for this upturn in abundance is unclear, but it is likely linked to a combination of increased productivity and catchability with warming oceans (Campbell *et al.* 1991; Drinkwater *et al*. 1996), reduced predation on juveniles due to the collapse of groundfish stocks (Boudreau *et al.* 2015) and the implementation or strengthening of various conservation measures to increase egg production (Gendron and Gagnon 2001). Effort-based regulations to conserve the resource were initiated as early as the 1870s (DeWolf 1974), but it was not until the 1990s-2000s that minimum legal size (MLS) regulations were set explicitly with the objective of allowing 50% of females to reach maturity and spawn at least once prior to being recruited into the fishery; before that time MLS had generally been well below the size-at-maturity (SM) (DFO 2012). Still, exploitation rates of legal-sized lobsters remain high, exceeding 75% in many regions and 90% in some (Fisheries Resource Conservation Council 2007).

Life history traits such as growth rates, size and age at maturity, fecundity and phenology can vary across space and time (*e.g.*, Campbell and Robinson 1983; Wanless *et al.* 2008; Mollet *et*

al. 2013; Pershing *et al.* 2015), and this variation is important to recognize and consider for sustainable and adaptive fisheries management. For example, there is evidence for American lobster in the Bay of Fundy of a decrease in fecundity and contribution of larger females to egg production (DFO 2013a; Koopman *et al.* 2015). A decline in female size at maturity (SM) has been observed over the past 15-30 years in most areas of the southern part of the species´ range, from Long Island Sound (US) to the Bay of Fundy (Landers *et al.* 2001; Pugh *et al.* 2013; Gaudette *et al.* 2014; LeBris *et al.* 2017). Why female SM has declined is uncertain; fishing pressure and rising water temperatures were proposed as potential mechanisms, but were not thoroughly investigated (Landers *et al.* 2001; Pugh *et al.* 2013; Gaudette *et al.* 2014) or unequivocally demonstrated (LeBris *et al.* 2017). These previous studies were also temporally limited relative to the time period over which potential mechanisms may have operated (*e.g.*, exploitation has been ongoing since the late 1800s and ocean temperatures rising since the 1970s). Thus, while there is some evidence that female SM may be decreasing in response to warming and/or exploitation, more work is needed to document the spatial and temporal extent of these declines and to elucidate their causes.

It has long been thought that geographical patterns of SM of female American lobster reflect an inverse relationship with regional temperature (*e.g.*, Templeman 1936; Waddy *et al.* 1995; LeBris *et al.* 2017). An inverse relationship between female SM and temperature at different locations has also been reported for the western rock lobster (*Panulirus cygnus*), and SM declines in this species since the 1970s were attributed largely to thermal increases (Melville-Smith and de Lestang 2006). Since the 1970s, climate change and decadal variability have resulted in an increase in mean annual surface temperature of approximately 1°C in the northwest Atlantic, with most of the warming occurring after the early 1990s (Knudsen *et al*. 2011; Galbraith *et al*. 2012, 2015; Loder *et al*. 2013). LeBris *et al.* (2017) suggested the declines

in American lobster female SM in the Gulf of Maine and Bay of Fundy were largely attributable to warming given the spatial relationship between SM and temperature, but they did not find a consistent relationship between temporal changes in SM and temperature within individual fishery statistical areas. Thus, further research on different temporal or spatial scales would help clarify the role of temperature in female SM declines.

An evolutionary response of American lobster populations to intense harvesting is also possible (LeBris *et al*. 2017). When wild animal populations are exploited, individuals with desirable traits are preferentially removed, which can cause a decline in the frequency of these traits over time (Allendorf and Hard 2009). In the context of fisheries, where large body size is usually prized, individuals that reproduce at smaller sizes and younger ages are expected to have greater fitness, and assuming some degree of heritability of maturation schedules, these may evolve (Kuparinen and Merilä 2007; Allendorf and Hard 2009). Reductions in growth rates and size- and age-at-maturity have been documented in numerous finfish fisheries during the past 50-60 years and frequently attributed to high exploitation of larger, fast-growing but late-reproducing individuals (*e.g.*, Olsen *et al.* 2004; Kuparinen and Merilä 2007; Swain *et al.* 2007). Although declines in SM have been documented for some crustaceans (*e.g.*, Charnov 1981; Melville Smith and de Lestang 2006), there is, to our knowledge, no empirical evidence of exploitation-induced phenotypic change in invertebrate fisheries.

Additionally, changing population density is also thought to affect SM in several lobster species (*e.g.*, Beyers and Goosen 1987; Tuck *et al.* 2000; Linnane *et al.* 2009), and may be a factor for American lobster as well. Given recent decades' increases in abundance, it is possible that declining SM reflects a negative density-dependent response. Increases in population density may reduce per capita food availability, which in turn causes reduced growth rates and

decreases in SM when the latter is age-specific (Tuck *et al.* 2000; Linnane *et al.* 2009), as in the rock lobsters *Jasus lalandii* and *J. edwardsii* (Beyers and Goosen 1987; Gardner *et al.* 2006). It is not known whether SM is age-specific in American lobster.

The "Lobster Node" of the NSERC Canadian Fisheries Research Network (Rochette *et al.,* 2018) provided a unique opportunity to study changes in female lobster SM on a hitherto unprecedented scale. Our primary objective was to determine whether the SM of female American lobster in Canada has declined over the past century and, if so, to investigate evidence for three potential drivers of such change: increasing water temperature, increasing abundance, and size-based selection through harvesting of large immature individuals. A secondary objective was to explore the effect of combinations of changes in female SM and exploitation rate on population egg production through simulations with an egg-per-recruit (E/R) model. Male SM was not addressed in this paper as maturity data for males are too scarce to complete similar analyses as for females.

1.2 Methods

1.2.1 Temporal changes in size-at-maturity

We assessed size-at-maturity (SM) in terms of the carapace length (CL) at which the smallest females mature (CL_{min}) and at which 50% of females mature (CL_{50}). We did not consider a more conservative metric of CL_{min}, such as the 5^{th} percentile, because the minimum size was often the only metric reported; note, however, that CL_{min} correlates well with the 5^{th} percentile in cases where both are available (Appendix A). For CL_{50} and CL_{min} we used values from the primary literature and government technical reports (Table 1.1). In addition, we derived values for CL_{min} from unpublished sources: (1) monitoring by the Department of Fisheries and Oceans

Canada (DFO) of Lobster Fishing Areas (LFAs) around Nova Scotia and the Bay of Fundy over the past approximately 20-40 years (Crustacean Research Information System [CRIS], M.J. Tremblay and A. Cook, DFO Science Branch, Bedford Institute of Oceanography, pers. comm. 2014), (2) monitoring by DFO and the Prince Edward Island Department Agriculture and Fisheries (PEIDAF) of LFAs in the southern Gulf of St. Lawrence (M. Comeau, DFO Acting Section, Gulf Fisheries Centre, and R. MacMillan, PEIDAF, pers. comm. 2014), (3) the "Lobster Node" of the Canadian Fisheries Research Network from 2011 to 2013 (http://www.cfrn-rcrp.ca, see project 1.2; Rochette *et al.* 2018), and (4) a DFO trawl survey in LFA 22 since 1995 (L. Gendron, DFO, pers. comm. 2015) (Appendix B). These sources contained information on ovigerous females collected from traps during commercial fishing operations and, in the case of the DFO, from some trawl surveys as well. Ovigerous females were measured by DFO to the nearest mm and by harvesters participating in the "Lobster Node" using gauges with 5 mm bins (midpoints used in analyses). To increase the SM data available for temporal comparisons, all data were pooled at the LFA (Fig. 1.1) level, as opposed to study site or port, and the smallest reported CL_{min} and CL_{50} values were used for each LFA. The earliest SM estimates used (generally 1930-1940) were typically expressed in terms of total length, which we converted to CL using regional equations for Newfoundland (LFAs 4-14B) (Ennis 1980), the southern Gulf of St. Lawrence (LFAs 23-26B) and the Scotian Shelf (LFAs 27-33) (Wilder 1953), and the Bay of Fundy (LFAs 34-38) (Estrella and Cadrin 1995). To avoid bias related to sample size in cases where CL_{min} estimates were derived from ovigerous female size frequency distributions (93% of CL_{min} data), for each LFA we discarded years with fewer than 20 ovigerous females, and we made sample size uniform across years by randomly subsampling to match the lowest annual n of the series.

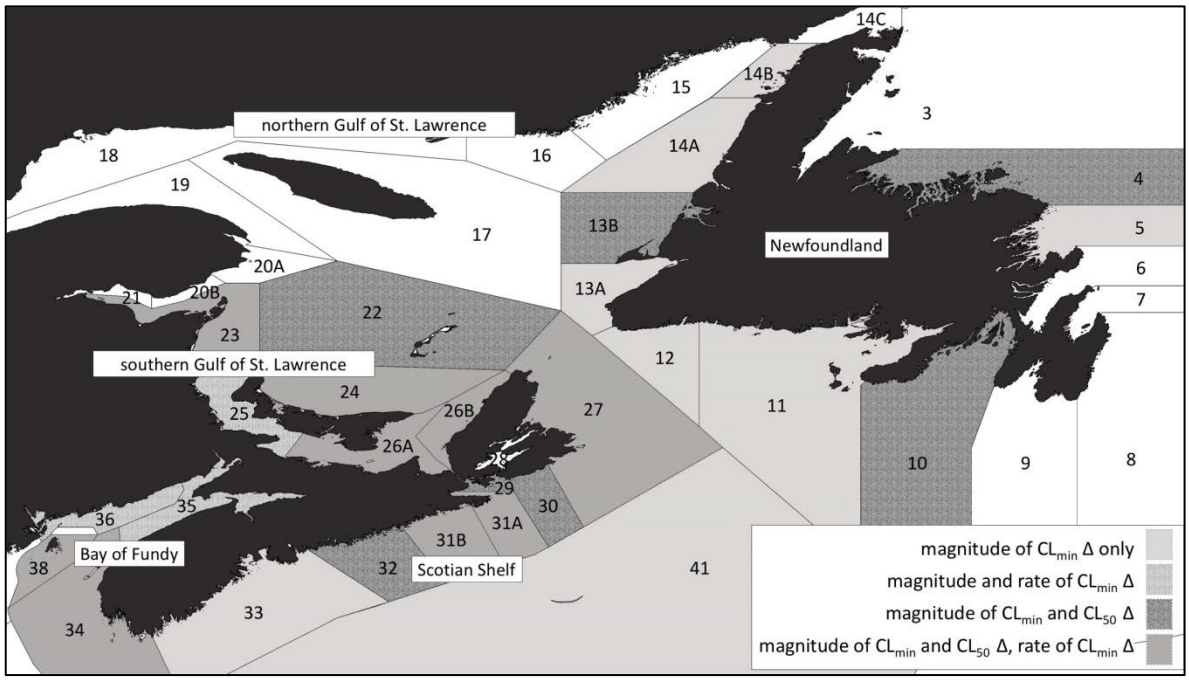

Figure 1.1: *Map of Canadian Lobster Fishing Areas (LFAs). Shaded areas indicate LFAs from which we were able to obtain size-at-maturity (SM) data, and the intensity of the shading indicates the nature of the SM data that was available in each LFA to construct Figures 1.3, 1.5 and 1.6.*

Female SM is mainly assessed using one of four methods: (1) presence/absence of eggs on the abdomen, (2) ovarian development, (3) cement gland development, and (4) ratio between abdomen width (AW) and CL (Aiken and Waddy 1980; Comeau and Savoie 2002*a*). Estimates of SM obtained through these different methods are comparable at the spatiotemporal resolution of our study (see Appendix C) and were thus all used in our analyses. However, the AW:CL ratio is not necessarily a reliable indicator of functional maturity and may underestimate CL_{min} and CL_{50} (Aiken and Waddy 1980; Ennis 1980; Émond *et al*. 2010), so it is now rarely used for that purpose. Because some of the earliest SM data used in our analyses were obtained by the AW:CL method, we repeated all analyses with these data excluded.

For each LFA where SM data $\geq$10 years apart was available, we estimated an overall change in SM based on the difference between the earliest and latest CL_{min} and CL_{50} estimates available.

In total, we could calculate such changes in CL_{min} and CL_{50} for 25 and 15 LFAs, respectively. Additionally, in LFAs where a time series of SM data was available ($\geq$3 annual observations over a period $\geq$10 years), linear regressions were carried out to assess temporal trends and rates of change in SM; assumptions of normality were not violated more often than expected by chance at an alpha of 0.05. We could assess temporal trends in CL_{min} for 19 LFAs, and CL_{50} for one. LeBris *et al.* (2017) showed that SM estimates based on the capture of ovigerous females are significantly higher when using vented compared to ventless traps; a phenomenon likely related to decreased catch rates of small individuals when escape vents are present. When minimum legal size (MLS) was increased in several LFAs starting around the 1990s, there was a concomitant increase in the size of escape vents. Thus, CL_{min} estimates based on commercial catches of ovigerous females are likely to have increased as MLS rose. We therefore censored the ovigerous CL_{min} data from the first year of MLS increase in LFAs where cumulative increases in MLS exceeded 5 mm. CL_{50} estimates were not censored because they were never based on fisheries-dependent data on ovigerous female size.

1.2.2 Elucidating the mechanism(s) behind changes in size-at-maturity

We used sea surface temperature (SST) to assess temporal changes in water temperature because available bottom temperature data do not cover the spatial and temporal extent of our SM data. SST is an acceptable proxy for bottom temperature in our study given that (1) in the Canadian portion of their range, the vast majority of lobsters are captured in relatively shallow, well-mixed water (*e.g.* Ennis 1984*a*; Campbell and Stasko 1986; Comeau and Savoie 2002*b*) where bottom and surface temperature anomalies are highly correlated (Hebert *et al.* 2014; Galbraith *et al.* 2015; Richaud et al. 2016), and (2) LeBris *et al.* (2017) showed that the relationships between SM and temperature from New England to the Bay of Fundy are similar

Table 1.1: *Source list for size-at-maturity (SM) data.*

	CL_{50}		CL_{min}	
LFA	*data source*	*method(s)*[†]	*data source*	*method(s)*[†]
4	Templeman and Tibbo 1945	3	Templeman and Tibbo 1945	4
	Ennis 1980	1	Ennis 1984*b*	2
	Ennis 1984*b*	1, 2	CFRN "Lobster Node"	6
5			Ennis 1971	1
			CFRN "Lobster Node"	4
10	Templeman and Tibbo 1945	3	Templeman and Tibbo 1945	4
	Ennis 1980	1	Ennis 1984*b*	2
	Ennis 1984*b*	1, 2	CFRN "Lobster Node"	4
11			Templeman and Tibbo 1945	4
			CFRN "Lobster Node"	4
12			Templeman 1939	3
			CFRN "Lobster Node"	4
13A			Templeman 1939	3
			CFRN "Lobster Node"	4
13B	Templeman and Tibbo 1945	3	Templeman 1939	3
	Ennis 1980	1, 3	Squires 1970	1
			CFRN "Lobster Node"	4
14A			Templeman 1939	3
			CFRN "Lobster Node"	4
14B			Templeman 1939	3
			CFRN "Lobster Node"	4
22	Dubé and Grondin 1985	1, 2	Templeman 1936	6
	Gendron 2003	2	CFRN "Lobster Node"	6
			Fisheries and Oceans Canada	6
23	Templeman 1944	3	Templeman 1944	3
	Comeau and Savoie 2002*a*	1, 2	Fisheries and Oceans Canada	4
24	Templeman 1944	3	Templeman 1936	4
	Comeau and Savoie 2002*a*	1, 2	Templeman 1944	3
			Fisheries and Oceans Canada	4
25			Templeman 1936	4
			Templeman 1944	3, 4
			Fisheries and Oceans Canada	4
26A	Templeman 1944	3	Templeman 1936	4
	Campbell and Robinson 1983	2	Templeman 1944	3
			Campbell and Robinson 1983	2
			Fisheries and Oceans Canada	4
26B	Templeman 1944	3	Templeman 1944	3
	Comeau 2003	1, 2	Fisheries and Oceans Canada	4
27	Templeman 1944	3	Templeman 1936	4
	Comeau 2003	2	Templeman 1944	3
	Reeves *et al*. 2011	2	CFRN "Lobster Node"	4
	Watson *et al*. 2013	2	Fisheries and Oceans Canada	4
29	Reeves *et al*. 2011	2	CFRN "Lobster Node"	4
	Watson *et al*. 2013	2	Fisheries and Oceans Canada	4
30	Campbell and Robinson 1983	2	Campbell and Robinson 1983	2
	Watson *et al*. 2013	2	CFRN "Lobster Node"	4
			Fisheries and Oceans Canada	4

31A+B	Templeman 1944	3	Templeman 1944	3
	Campbell and Robinson 1983	2	Campbell and Robinson 1983	2
	Watson *et al*. 2013	2	Silva *et al*. 2012	2
			CFRN "Lobster Node"	4
			Fisheries and Oceans Canada	4
32	Templeman 1944	3	Templeman 1944	3
	Watson *et al*. 2013	2	Silva *et al*. 2012	2
			CFRN "Lobster Node"	4
			Fisheries and Oceans Canada	4
33			Silva *et al*. 2012	2
			CFRN "Lobster Node"	4
			Fisheries and Oceans Canada	4
34	Templeman 1944	3	Templeman 1944	3
	DFO 2013a	2	Silva *et al*. 2012	2
			CFRN "Lobster Node"	4
			Fisheries and Oceans Canada	4
35			Templeman 1936	4
			Lawton *et al*. 1999	4
			CFRN "Lobster Node"	4
			Fisheries and Oceans Canada	4
36			CFRN "Lobster Node"	4
			Fisheries and Oceans Canada	4
38	Templeman 1944	3	Templeman 1944	3
	Campbell and Robinson 1983	2	Campbell and Robinson 1983	2
	Gaudette *et al*. 2014	2	CFRN "Lobster Node"	4
			Fisheries and Oceans Canada	4
41			Fisheries and Oceans Canada	4

† Maturity estimates are based on the following methods: (1) ovarian staging, (2) pleopods staging, (3) AW:CL ratio, and (4) ovigerous female size.

whether using bottom temperature or SST. To ensure full coverage of the spatial and temporal records of SM, we used NOAA's Extended Reconstructed Sea Surface Temperature (ERSST) dataset version 3b (https://www.ncdc.noaa.gov/data-access/marineocean-data/extended-reconstructed-sea-surface-temperature-ersst-v3b [accessed 24 March 2017]), which produces monthly SST averages from 1854 to current for 5° grid cells. These modeled temperatures are based on measurements of SST and land-near-surface temperature from the International Comprehensive Ocean–Atmosphere Dataset (http://icoads.noaa.gov/products.html), and anomalies between modeled and measured monthly temperatures from 1971 to 2000. We used monthly ERSST temperature values to estimate the mean annual temperature for each LFA, from 1930 to 2016, based on the proportional overlap between each LFA and the different model grid cells. In addition, SST data were extracted at the LFA level from DFO´s Sea Surface

Temperature Database using Pathfinder 5, which produces 16 km^2 weekly averages from 1985 to 2009 (available from http://www.bio.gc.ca/science/data-donnees/base/data-donnees/sst-en.php).

We used lobster landings as a proxy for population abundance. Annual landings by LFA were obtained by request through Regional DFO Strategic Services Branches (Statistic Divisions). The time series over which landings data were available at the LFA level varied somewhat among regions, starting 1965-1974 and going to 2012 in Newfoundland (LFAs 3-14C), from 1968 to 2013 in the southern Gulf of St. Lawrence (LFAs 23-26A), and from 1947 to 2013 in Cape Breton and Scotia-Fundy (LFAs 26B-38). In all cases the time series went back to before the start of the region-wide landings increase in the early-mid 1980s into a long period of time (1920-1975) of low, moderately variable and trendless landings for Canada as a whole (DFO 2016b). We correlated changes in maturity in each LFA to changes in landings over the same period. To estimate landings coinciding with early SM estimates that preceded available landings data, we calculated the average proportion of total Canadian landings (obtained from Williamson 1992) associated with each LFA over a 10-year period (1974-1983) that preceded the marked upswing in landings, and for which landings data were available in all LFAs, and used this proportion in conjunction with total landings to estimate missing data for a particular year and LFA; testing these estimates against cases where LFA-level landings data were available earlier than 1974 shows a good fit between actual and estimated annual landings ($p<0.0001$, $R^2=0.95$).

We derived a proxy for selection pressure due to size-selective harvesting as the difference between the MLS and female SM (MLS minus both CL_{50} and CL_{min}). The more negative the resulting value is, the stronger is the selection for smaller maturing females. This metric is not the selection differential (S) of quantitative genetics, which cannot be estimated with the data

at hand, but it does nonetheless reflect the strength of selection for smaller-maturing females; we will thus refer to this metric as selection henceforth. We determined MLS for each LFA as the average of all MLS values implemented over the period for which changes in SM were estimated, weighted by the number of years each different MLS was in effect and excluding the relatively small number of years where no MLS was in place (see Appendix D for MLS reference list). The SM value subtracted from the weighted average MLS to create our selection metric was the earliest estimate available.

We took two approaches to assessing the relationship between change over time in female SM and each independent variable (temperature, abundance and selection): one that maximized the spatial and temporal scope of the analysis, but used modeled SST and estimated landings data, when measured data were lacking (as explained above), and a second that constrained the spatiotemporal scope of the data to obtain a perfect temporal match between female SM and only measured values of the independent variables SST and landings. If increasing ocean temperature, negative density dependence or intense harvesting of immature individuals has caused declines of female lobster SM, we predict that SM changes would be negatively related to increases in the first two and positively related to the last across LFAs.

In the first approach, we estimated the temporal change in female SM (both CL_{50} and CL_{min}), mean annual SST and annual landings as the difference between the most recent available data and the oldest. For SM, where data are more limited, each of these points in time was represented by a single annual value, while for SST and landings, the start and end points were estimated based on the mean of the 5 years leading up to and including the year of measurement of SM. Averaging was done because SM is likely determined by conditions encountered by lobsters during their early benthic life stages (Aiken and Waddy 1980; LeBris *et*

al. 2017). Selection in each LFA was not calculated in terms of change over time, but rather as the magnitude of the MLS-SM discrepancy over the period for which a particular change in SM was estimated (see above). The change in female SM in each LFA was then regressed separately against the corresponding LFA's (1) change in mean annual SST, (2) change in landings, and (3) strength of selection over the same time period.

In the second approach, we focused on the years 1985-2009 only, when annual measured data were available for all independent variables and CL_{min} (there were insufficient data to repeat with CL_{50}). Over this shorter time period data were available for many years, allowing an estimated rate of change based on many data points, rather than only between the earliest and latest available data. This rate of change in CL_{min} in different LFAs was regressed against the (1) rate of change in annual mean SST, (2) rate of change in annual landings, as well as (3) selection (weighted mean MLS 1985-2009 minus 5-year mean CL_{min} 1983-1987) over the same time period. The CL_{min} estimates used in these analyses were based on annual monitoring of ovigerous females by DFO along the Scotian Shelf and in the Bay of Fundy; sufficient data were not available from the southern Gulf of St. Lawrence, Québec and Newfoundland regions.

1.2.3 Estimating the effect of changing size-at-maturity on egg production

We used a simplified version of the egg-per-recruit (E/R) model of Gendron and Gagnon (2001) to investigate potential population-level effects of SM changes on egg production by female lobsters. The model was used only to draw broad inferences regarding the relative impacts of changing SM under different harvesting scenarios, and not to assess absolute changes in egg production for any given LFA. Our version incorporated somewhat less stochasticity than the original, primarily by using fixed moult increments rather than a range (Fig. 1.2). Each model run began with a cohort of 1,000 immature females of 40-50 mm CL with 100 individuals in

each 1 mm size bin, and was run until all females were presumed dead. The initial cohort size range (40-50 mm CL) was chosen to allow a wide range of scenarios without incorporating the higher moult frequency and mortality of juveniles (Lawton and Lavalli 1995; Comeau and Savoie 2001; Gendron and Sainte-Marie 2006). Egg production by all spawning females in all years was summed and divided by the initial cohort size (1,000) to generate estimates of average lifetime egg production per individual (*i.e.*, eggs-per-recruit, E/R).

Each year in the model begins with natural and fishing mortality, assuming a spring fishing season prior to moulting and spawning. Natural mortality was set to a base rate of 5% with an additional 10% associated with moulting (Gendron and Gagnon 2001), and exploitation rate (*i.e.*, fishing mortality) varied from 0% to 90% in different simulations. MLS was set to reflect selection strengths of -30, 0 and +30 mm CL (*i.e.*, difference between SM and MLS). Surviving females were assumed to either moult or spawn during the summer (Waddy *et al.* 1995), with probability based on size as determined by the SM. Moult increments were assumed to be 15% of CL (Comeau and Savoie 2001). We used a maturity ogive (a logistic regression of probability of being mature vs. female size) derived for the southern Magdalen Islands (QC, Canada) by Dubé and Grondin (1985; used by Gendron and Gagnon 2001) to represent the probability of maturation by size, and then slid this ogive along the x-axis to reflect a range of CL_{50} scenarios. Fecundity-at-size was estimated based on Campbell and Robinson (1983). We did not incorporate in our simulations any temporal or spatial variability of maturity ogive or size-fecundity relationship, which is known to occur (*e.g.*, Currie and Schneider 2011; Koopman *et al.* 2015; LeBris *et al*. 2017), as this was irrelevant to our goal. Such variability would only attenuate or exacerbate trends identified through our simulations.

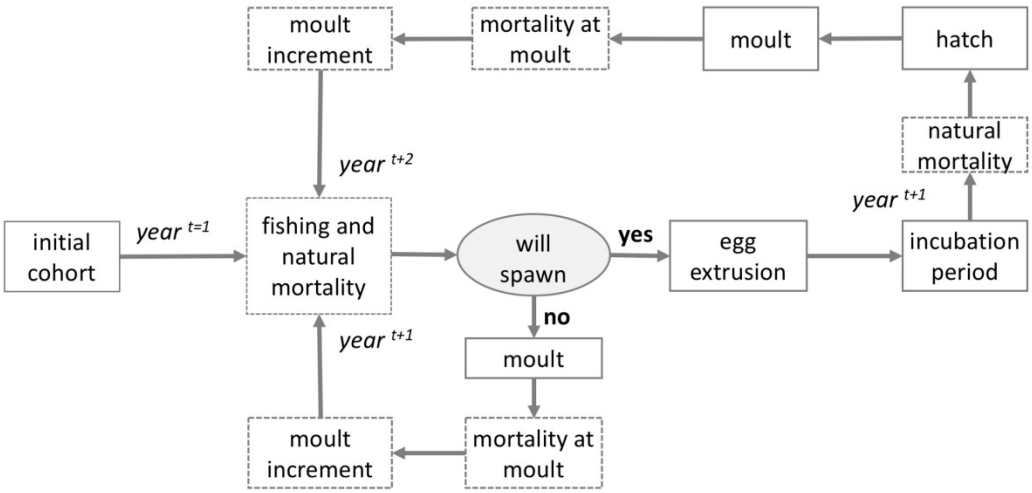

Figure 1.2: *Egg-per-recruit model (E/R) conceptual diagram. Squares with solid outline symbolise an event. Squares with stippled outline symbolise a fixed probability (i.e., deterministic). The shaded circle symbolises a size-based probability function.*

We ran simulations of pairs of "before" and "after" change in SM, under different scenarios of exploitation rate and selection, and plotted an index of change in predicted lifetime egg production per female against SM change for each scenario (*i.e.*, SM "after" minus SM "before" vs. E/R "after" minus E/R "before"). Scenarios investigated included exploitation rates of 0% (no fishing), 25%, 50%, 75% and 90%. For scenarios with exploitation, selection was fixed at -30, 0 or +30 mm for the initial simulation ("before" SM change) within each scenario; MLS remained unchanged for the final ("after" SM change) simulation. Within each scenario, initial CL_{50} values were tested in 5 mm increments across the range documented in this study (70-135 mm CL). Final CL_{50} values were chosen to equate to SM changes ranging from -45 mm CL (the greatest decline we documented) to +20 mm CL, also in 5 mm increments, while remaining within the range of 50-150 mm CL. We chose to create scenarios where CL_{50} increased, despite not documenting this, to better show the costs and benefits of SM change on E/R. In total, we ran the model for 1,150 scenarios. Within each simulation pair, the change in predicted E/R

(E/R_{Δ}) was calculated as an index of percent change from before (E/R_{before}) to after (E/R_{after}) the SM change, using the following equation:

$$E/R_{\Delta} = [E/R_{after} / (E/R_{before} +1000)] \times 100$$

A constant was added to the E/R_{before} term to avoid denominator values of 0, and 1000 was chosen because it enabled showing the outcome of different modeling scenarios on a common scale.

1.3 Results

1.3.1 Temporal changes in size-at-maturity

There has been an overall decline in SM of female lobsters in eastern Canada over the past 10-80 years. Time series were available for CL_{min} in 20 LFAs, covering parts of Newfoundland, the Gulf of St. Lawrence, the Scotian Shelf and the Bay of Fundy (Fig. 1.3), and for CL_{50} only in LFA 27. The start of the CL_{min} time series ranged from 1931 to 1999 (mean=1943), with the end in 2012 or 2013. Excluding annual data likely biased by a change in catchability of small females, related to substantial increases in MLS and the size of escape vents, limited the time series for the LFAs in the southern Gulf of St. Lawrence and excluded LFA 22 altogether; the apparent increase in SM with increasing MLS and resulting bias was obvious in LFAs 23-27 (Fig. 1.3). Of the remaining 19 LFAs, 15 showed a negative slope of CL_{min} over time (8 statistically significant), and 4 had a positive slope (none significant) (Fig. 1.3). The average slope across all LFAs was significantly negative (t_{18}=-3.58, p=0.001). LFAs in the Bay of Fundy and Canadian Gulf of Maine (LFAs 34, 35, 36, 38 and 41) have had steep rates of decline in CL_{min}, whereas the rate of decline was less (or nil) in parts of eastern Nova Scotia and the southern Gulf of St. Lawrence. These general trends hold if annual CL_{min} data based on the AW:CL ratio were excluded (relevant for

12 LFAs): 13 LFAs showed negative slopes (7 significant), 5 showed positive slopes (none significant), and one had insufficient data to estimate slope; on average across all LFAs slopes remained significantly negative (t_{17}=-1.90, p=0.04). CL_{50} has shown a significant rate of decline in LFA 27 from 1935 to 2007 ($F_{1,4}$=47.43, p=0.001), but not from 1987 to 2007 when the early datum inferred using the AW:CL ratio was removed ($F_{1,4}$=2.30, p=0.20).

There has been a similarly significant overall decline in female CL_{min} over the past 14-81 years (mean=62) when considering only the difference between the earliest and most recent SM estimate in each LFA (paired t-test: T_{26}=3.0, p=0.006) (Fig. 1.4), after data were censored for large MLS increases. Declines were observed in 20 of 25 LFAs, from northern Newfoundland to southwestern New Brunswick, and changes in the 25 LFAs ranged from +13 mm (+21%) to -30 mm (-29%) with an average of -7 mm CL (-8%). Large declines were again observed in the Bay of Fundy and Canadian Gulf of Maine (LFAs 34, 35, 36 and 38), except for LFA 41; this exception was likely related to the "coarseness" of the metric, as the very earliest maturity estimate in LFA 41 was markedly lower than the three estimates obtained over the following six years. The earliest CL_{min} estimates date back to 1931-1999 (mean=1947) and the latest were from 1986 to 2014 (mean=2007) (Table 1.2). The greatest declines in CL_{min} were documented in the LFAs with the longest time period between SM estimates ($F_{1,24}$=5.54, p=0.03). Temporally constraining the analysis to the 14 LFAs with a time series comprising pre-1950 to post-2000 data (temporal range 65-81 years) had little effect on the results, with changes remaining significantly negative overall (mean = -11 mm or -12%; T_{13}=-3.92, p<0.001) and ranging from +5 mm (+8%) to -30 mm (-29%). Similarly, excluding the earliest data where CL_{min} was inferred using the AW:CL ratio had little effect on results; changes in CL_{min} among the 17 remaining LFAs were still significantly negative on average (mean = -7 mm or -5%; T_{16}=-3.04, p=0.004) and ranged from +11 mm (+19%) to -26 mm (-26%) over a 12-81-year period (mean=45 years).

There has also been a highly significant decline in female CL_{50} (paired t-test: T_{14}=6.0, p<0.001) over the past 12-76 years (mean=49) (Fig. 1.4). This decline has been widespread, with reductions observed in all 15 LFAs with available data, from the Bay of Fundy to Newfoundland, and varying between -6 and -44 mm CL (mean = -18 mm) or -8% to -33% (mean = -18%) of initial CL_{50}. The earliest and latest CL_{50} estimates ranged from 1935 to 1987 and 1965 to 2011, respectively, for different LFAs (Table 1.3). There was a negative relationship between the amount of change in CL_{50} and the length of the time period over which change was documented ($F_{1,13}$=10.28, p=0.007). If the analysis was limited to the 5 LFAs with a time series comprising pre-1950 to post-2000 data (temporal range 67-76 years), declines remained significant (T_4=-5.69, p=0.002) and ranged from -14 to -44 mm CL (mean = -28 mm) or -16% to -33% (mean = -25%). Although this temporal constraint did reduce the spatial coverage of the maturity data, the latter still extended from the southern Gulf of St. Lawrence to the Bay of Fundy. If the analyses were limited to exclude the earliest data where SM was inferred using the AW:CL ratio, there was also a marked decrease in number of LFAs (n=8) and temporal coverage (12-32 years, mean=19 years; first year 1965-1987, mean=1977; final year 1982-2011, mean=1997), but CL_{50} changes remained significantly negative on average (T_7=-2.54, p=0.02) and ranged from +2 mm (+3%) to -18 mm (-19%) with a mean of -7 mm (-8%). The greatest decreases in CL_{50} have also occurred in and around the Bay of Fundy (LFAs 34 and 38), although a comparable reduction was also observed in north-eastern Cape Breton (LFA 27) (Fig. 1.4).

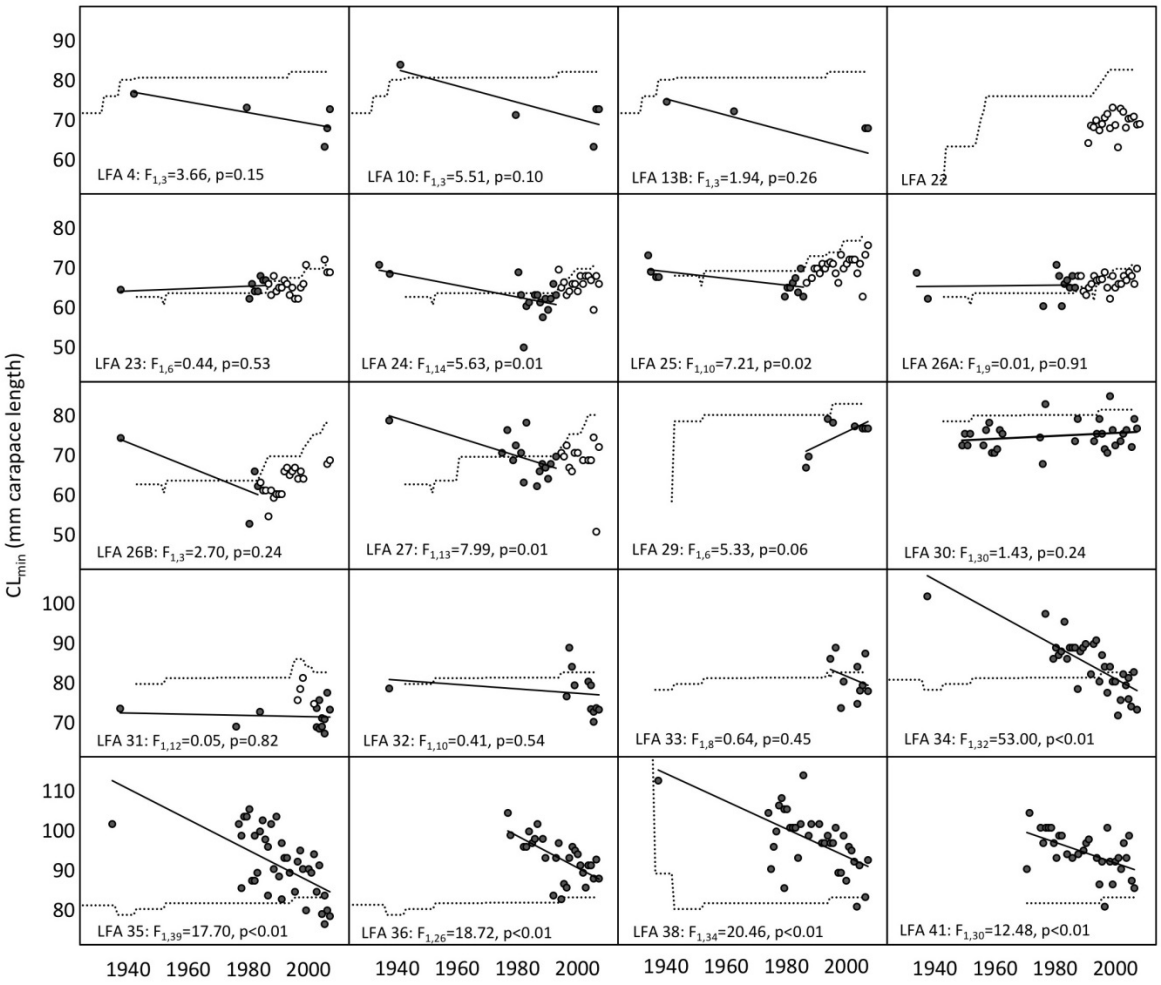

Figure 1.3: *Temporal trends in CL_{min} (the smallest carapace length at which females reach maturity) for LFAs with >3 years of data >10 years apart. Values are given as mm carapace length (CL). Closed circles show years used in the regressions; open circles indicate data points censored due to rapid MLS increases (see methods section 1.2.1 for explanation). The stippled lines represent minimum legal size (MLS) in mm CL. See Fig. 1.1 for map showing LFAs in eastern Canada.*

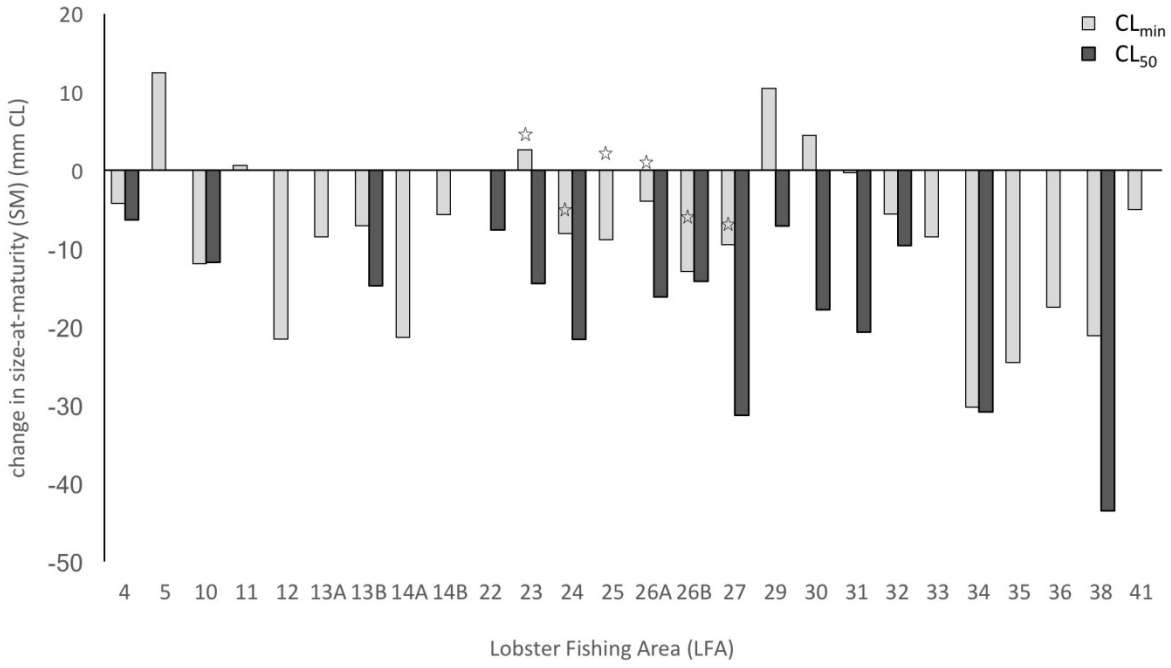

Figure 1.4: *Documented changes in female lobster size-at-maturity (SM) for first to last year of available data (first and last year min 10 years apart) by Lobster Fishing Area (LFA) in eastern Canada. CL_{min} is the smallest size at which females in an LFA reach maturity, and CL_{50} is the size at which half of females in an LFA reach maturity. All values are given in mm carapace length (CL). Stars indicate estimated CL_{min} change without censoring data likely affected by changes in catchability of small females following substantial MLS increases (see methods section 1.2.1).*

1.3.2 Mechanisms behind changes in size-at-maturity

Our modeled and measured temperature datasets showed expected patterns of increasing SST in eastern Canada, but we found no compelling evidence that temporal changes in female lobster SM in eastern Canada over the past approximately 80 years can be attributed to these increases. NOAA's ERSST modeled dataset showed increases in SST since the 1970's (Rhein *et al*. 2013), more pronounced increases since the early 1990's (Knudsen *et al*. 2011; Galbraith *et al*. 2012, 2015; Loder *et al*. 2013), and a certain amount of spatial coherence of temperature anomalies over our study domain (Richaud et al. 2016). However, the relationship between magnitude of SST increase and SM decrease across LFAs over the past 10-80 years was flat in

the case of both CL_{min} ($F_{1,22}$<0.01, p=0.96, R^2<0.01) and CL_{50} ($F_{1,13}$=1.03, p=0.33, R^2=0.07) (Fig. 1.5a-b); we obtained virtually the same results when we based these analyses on mean temperatures during the "growing season" (May-October, results not shown), rather than the entire year. Similarly, measured annual SST increased 1985-2009 ($F_{1,586}$=43.92, p<0.0001) at a similar rate in all LFAs (year*LFA: $F_{26,586}$=0.99, p=0.48), and there is no significant negative relationship between rates of change in SST and CL_{min} in different LFAs ($F_{1,4}$=1.05, p=0.36, R^2=0.21) (Fig. 1.6a). It is also worthy to note that no clear relation between SM and SST was apparent at the regional scale, *i.e.* for LFAs only within Newfoundland, Gulf of St. Lawrence, Scotian Shelf or Bay of Fundy (Figs. 1.5a-b and 1.6a).

We similarly found little evidence that increasing lobster abundance has contributed to declines in female lobster SM in eastern Canada over the past approximately 80 years. There was a significant negative relationship between the magnitude of overall changes in CL_{min} and landings in different LFAs over the past 10-80 years ($F_{1,22}$=6.25, p=0.02, R^2=0.22) (Fig. 1.5c), but this significant relationship was driven exclusively by the very large landings increase in LFA 34, and the relationship with this extreme value excluded was non-significant ($F_{1,21}$=0.933, p=0.35, R^2=0.04). There was also a negative relationship between CL_{50} and landings, but this was not significant ($F_{1,12}$=2.26, p=0.16, R^2=0.16) (Fig. 1.5d). Furthermore, there was no significant negative relationship between the rates of change in CL_{min} and landings from 1985 to 2009 in the more limited set of LFAs where measured data could be obtained for all three independent variables ($F_{1,4}$=0.61, p=0.48, R^2=0.13) (Fig. 1.6b).

Table 1.2: *Data on CL_{min} for each Lobster Fishing Area (LFA) used to generate Figures 1.4 and 1.5.*

LFA	first year (t=0)	last year (t=0+n)	# years btwn est.	$CL_{min}^{t=0}$	$CL_{min}^{t=0+n}$	CL_{min} Δ (mm) †	MLS (mm CL) ‡	selection §
4	1940	2013	73	73.9	72.5	-1.4	81.27	7.4
5	1967	2013	46	60.0	72.5	12.5	81.47	21.5
10	1939	2013	74	81.3	72.5	-8.8	81.26	-0.1
11	1939	2013	74	64.4	67.5	3.1	81.26	16.9
12	1938	2013	75	81.0	62.5	-18.5	81.25	0.2
13A	1938	2013	75	73.2	67.5	-5.7	81.25	8.0
13B	1938	2013	75	71.8	67.5	-4.3	81.25	9.4
14A	1938	2013	75	75.9	57.5	-18.4	81.25	5.3
14B	1938	2013	75	70.5	67.5	-3.0	81.25	10.8
23	1935	1989	54	63.7	67.0	2.6	63.24	-1.4
24	1931	1997	66	70.3	63.0	-8.1	63.28	-7.8
25	1931	1989	58	66.1	58.0	-8.9	63.24	-3.6
26A	1931	1990	59	68.2	65.0	-4.0	63.25	-5.7
26B	1935	1986	51	74.1	62.0	-13.0	63.23	-11.7
27	1935	1997	62	80.8	70.0	-9.5	67.45	-12.1
29	1990	2013	23	67.0	77.5	10.5	82.70	15.7
30	1948	2013	65	73.0	77.5	4.5	81.21	8.2
31	1935	2013	78	74.0	72.5	-1.5	81.31	7.3
32	1935	2013	78	79.4	72.5	-6.9	81.03	1.7
33	1999	2013	14	86.0	77.5	-8.5	82.39	-3.6
34	1935	2013	78	102.7	72.5	-30.2	80.76	-22.0
35	1932	2013	81	102.0	77.5	-24.5	80.73	-21.3
36	1979	2013	34	105.0	87.5	-17.5	81.60	-23.4
38	1935	2013	78	113.6	92.5	-21.1	81.64	-32.0
41	1972	2012	40	90.0	85	-5.0	81.48	-8.5

† CL_{min} Δ represents the change from the first to the last year of available data; a positive value indicates in increase in CL_{min} and a negative value a decline.

‡ Weighted mean minimum legal size (MLS) calculated based on the number of years an MLS was in effect during the applicable time period; years with no MLS were removed from calculations.

§ Strength of size-based selection calculated as weighted mean MLS – $CL_{min}^{t=0}$.

Table 1.3: *Data on CL_{50} for each Lobster Fishing Area (LFA) used to generate Figures 1.4 and 1.5.*

LFA	first year (t=0)	last year (t=0+n)	# years btwn est.	$CL_{50}^{t=0}$	$CL_{50}^{t=0+n}$	CL_{50} Δ (mm)†	MLS (mm CL)‡	selection§
4	1940	1982	42	85.5	76.0	-9.5	80.9	-4.6
10	1940	1982	42	89.0	74.0	-15.0	80.9	-8.1
13B	1940	1965	25	89.0	71.0	-18.0	80.9	-8.1
22	1983	2007	24	77.6	77.7	0.1	78.2	0.6
23	1935	1997	62	85.5	70.1	-15.4	63.7	-21.8
24	1935	2002	67	94.6	72.0	-22.6	63.5	-31.1
26A	1935	1978	43	95.7	78.5	-17.2	63.2	-32.5
26B	1935	2002	67	91.1	76.0	-15.1	64.8	-26.3
27	1935	2007	72	102.0	72.4	-29.6	68.5	-33.5
29	1987	2008	21	81.9	74.8	-7.1	82.2	0.3
30	1978	1990	12	92.5	74.7	-17.8	81.0	-11.5
31	1935	1990	55	94.6	75.5	-20.7	80.6	-14.0
32	1935	1990	55	102.7	94.8	-9.6	80.6	-22.1
34	1935	2011	76	127.4	96.5	-30.9	80.7	-46.7
38	1935	2011	76	133.7	90.2	-43.5	81.6	-52.1

† Represents the change from the first to the last year of available data; a positive value indicates an increase in CL_{50} and a negative value a decline.
‡ Weighted mean minimum legal size (MLS) calculated based on the number of years an MLS was in effect during the applicable time period; years with no MLS were removed from calculations.
§Strength of size-based selection calculated as weighted mean MLS - $CL_{50}^{t=0}$.

Size-selective harvesting has, in contrast to SST and lobster abundance, apparently contributed to the declines in female lobster SM in eastern Canada within the past approximately 80 years. There was a highly significant positive relationship between the overall reduction in both CL_{min} ($F_{1,23}$=36.63, p<0.001, R^2=0.61) (Fig. 1.5e) and CL_{50} ($F_{1,13}$=33.6, p<0.001, R^2=0.72) (Fig. 1.5f) and the strength of selection (discrepancy between MLS and SM) over the past 10-80 years. Although the metric we used as a proxy for selection strength was based on a time-weighted average MLS and excluded years during which no MLS was in place, these strong relationships remain virtually unchanged if the minimum or median MLS values are used or if MLS is considered 0 (or various arbitrary small values) in years without a MLS (results not shown).

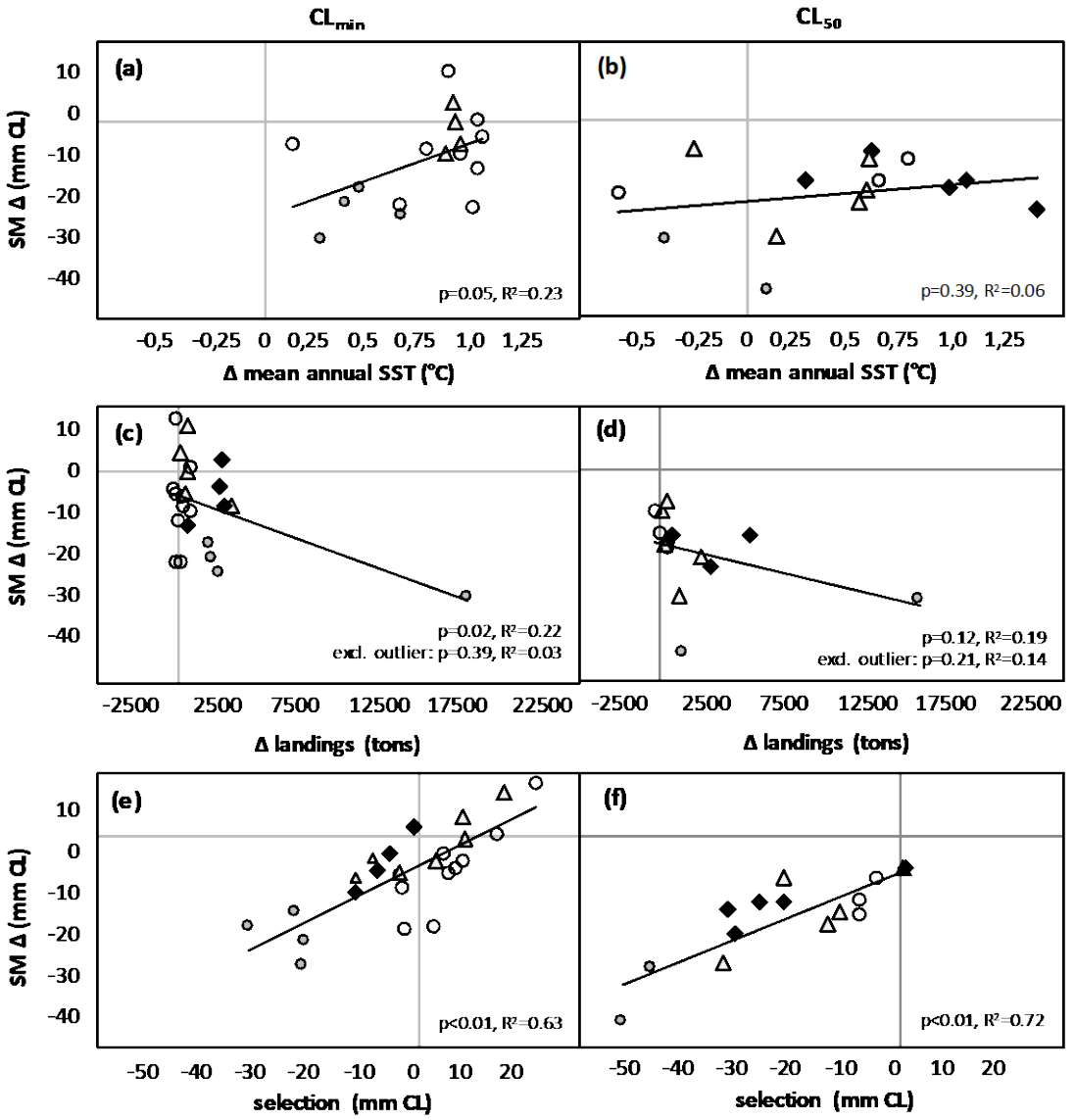

Figure 1.5: *Estimated change in SM (CLmin and CL50) over the past 10-80 years vs. change in mean annual SST and annual landings, as well as selection strength, in different LFAs. Selection strength was calculated as the weighted mean minimum legal size (MLS) over the time period of SM change minus the initial SM; negative values indicate that MLS was set below SM, presumably resulting in size- based selection for smaller maturation. CLmin is the smallest size at which females reach maturity, and L50 is the size at which half of females reach maturity. Different shape and color symbols represent LFAs in different regions of eastern Canada.*

There was also a significant positive relationship between the degree to which the MLS from 1985 to 2009 was set below CL_{min} at the beginning of this time series (1983-1987) and the rate of change in CL_{min} over the same period in the more limited set of LFAs where measured data could be obtained for all three independent variables ($F_{1,4}$=14.23, p=0.02, R^2=0.78) (Fig. 1.6c).

Elucidating the driver(s) implicated in female lobster SM declines was complicated by the variation in "initial SM" that existed among LFAs, which may have affected the potential scope for SM change in different LFAs and hence the correlation observed between external drivers and SM change in these LFAs. There was no significant relationship between initial CL_{min} and changes in landings ($F_{1,4}$=0.02, p=0.89, R^2<0.01) or SST ($F_{1,4}$=4.04, p=0.11, R^2=0.50) in different LFAs during the 1985-2009 period of complete overlap in independent variables, nor during the longer 10-80 years of imperfect overlap (landings: $F_{1,21}$=1.16, p=0.29, R^2=0.05; SST: $F_{1,22}$=1.54, p=0.23, R^2=0.06); these results are mirrored for initial CL_{50} (results not shown). There was, however, a significant relationship between initial CL_{min} and selection ($F_{1,4}$=4888.95, p<0.001, R^2=0.99) 1985-2009, as well as between initial SM and selection in CL_{min} ($F_{1,24}$=39.99, p<0.001, R^2=0.62) and CL_{50} ($F_{1,13}$=39.35, p<0.001, R^2=0.75) over the past 10-80 years. This relationship between initial SM and selection arose because there was an approximately 55 mm CL range in initial SM, but only an approximately 20 mm CL range in MLS, meaning selection was driven more by initial SM than by MLS regulations. There was no significant relationship between selection and MLS (CL_{min}: $F_{1,23}$=0.97, p=0.33, R^2=0.04; CL_{50}: $F_{1,13}$=1.64, p=0.22, R^2=0.11). There was also a significant negative relationship between initial SM and subsequent changes in SM in different LFAs (*i.e.*, greater rate of SM declines where initial SM was the largest) for CL_{min} from 1985 to 2009 ($F_{1,4}$=14.24, p=0.02, R^2=0.78), and for CL_{min} ($F_{1,23}$=35.47, p<0.001, R^2=0.61) and CL_{50} ($F_{1,13}$=40.68, p<0.001, R^2=0.76) over the past 10-80 years.

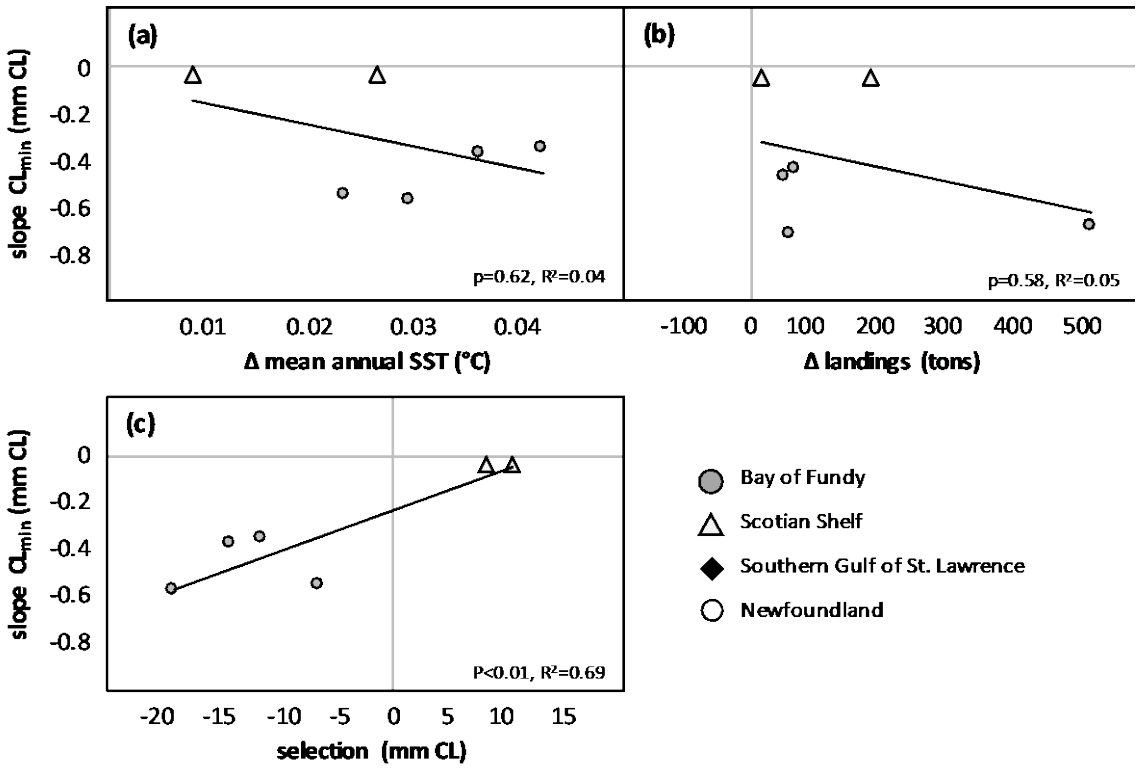

Figure 1.6: *Rate of change in CL_{min} (smallest size at which females mature) vs. rates of change in mean (a) annual SST and (b) landings, as well as (c) selection strength, in LFAs from the Scotian Shelf to the Bay of Fundy 1985-2009. Selection strength was calculated as the weighted mean minimum legal size (MLS) over the time period of SM change minus the initial SM; negative values indicate that MLS was set below SM, presumably resulting in size-based selection for smaller maturation.*

1.3.4 Estimated effect of changing size-at-maturity on egg production

Simulations using the egg-per-recruit (E/R) model revealed three main findings. First, they clearly indicated a cost, in terms of reduced lifetime egg production, of reducing SM in a population that is not exploited, and that the cost increases with the magnitude of the decrease in SM ($F_{1,495}$=639.03, p<0.001, R^2=0.56) (Fig. 1.7). Second, and most importantly, an increase in lifetime egg production will result from a reduced SM in populations that are exploited; and third, the magnitude of this increase depends on both the exploitation rate and the strength of size-based selection (Fig. 1.7). On average, there is a gain of female egg production with reduced SM under any level of exploitation, although this gain is quite small

with low exploitation rates (average estimated gain 7% and 2% for -30 and +30 mm selection, respectively; Fig. 1.7). The gain in female egg production by reducing SM is greater with stronger selection, and this effect of selection strength increases as exploitation rate increases (Fig. 1.7). However, even under strong selection and high exploitation rates large declines in SM are necessary for major increases in mean lifetime egg production, as seen by the exponential relationships between changes in SM and egg production (Fig. 1.7). However, with minimal and moderate selection, small reductions in SM (*i.e.* <10 mm) result in greater increases in egg production than at high selection. This difference in the relationship between changes in SM and egg production at the different levels of selection becomes more pronounced as exploitation rate increases (Fig. 1.7).

1.4 Discussion

1.4.1 Size-at-maturity of female American lobsters has declined in eastern Canada

Female American lobster size-at-maturity (SM) has in general significantly decreased over the past 10-80 years in eastern Canada, particularly in and around the Bay of Fundy. More specifically, the CL_{50} (size by which 50% of females have reached maturity) and CL_{min} (smallest size at which females mature) have decreased in 15/15 LFAs and 20/25 LFAs examined, respectively. On average, CL_{50} has declined by 18 mm (18%) and CL_{min} by 8 mm (9%). The observed declines suggest that female American lobster are maturing one to three moults smaller or one to three years earlier than they were 10-80 years ago, assuming a 10-20% moult increment and a single annual moult (Comeau and Savoie 2001; Gendron and Sainte-Marie 2006). The evidence for these declines is particularly compelling considering the sources of

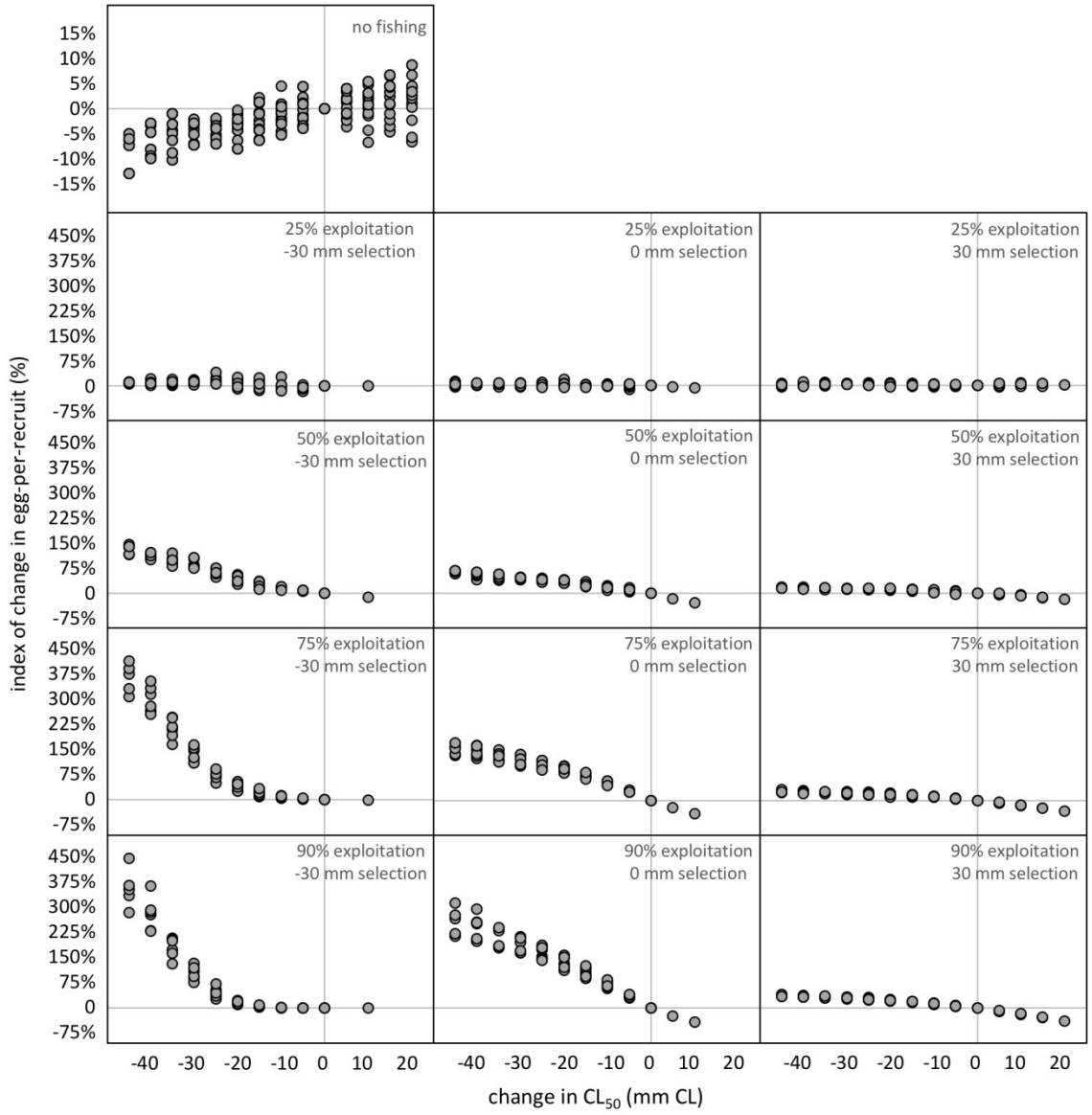

Figure 1.7: Egg-per-recruit model output and impacts of changing female size-at-maturity (SM) under different scenarios of harvesting intensity and size-based selection. X-axes show change in CL_{50} from the "before" to the "after" SM change scenario, and the y-axes show the subsequent predicted changes in mean lifetime fecundity in per cent (1000 added to E/R change in "before" scenario to create an index of change [see Methods]). Each data point at a given magnitude of change in CL_{50} represents different starting points (*i.e.*, initial CL_{50}).

error inherent to our broad meta-analyses, such as limitations concerning temporal and spatial coverage of some of the data, spatial variability in SM at finer scales than the LFA, and stochastic interannual variability in SM (*e.g.*, Watson *et al.* 2013). Furthermore, these mean declines probably represent a conservative assessment of true declines in SM given that many of the earliest SM values were derived using the AW:CL ratio, which may underestimate SM (Aiken and Waddy 1980; Émond *et al.* 2010). Early estimates of maturity were also missing from several LFAs, as were recent estimates from some, likely resulting in further underestimation.

We could investigate changes in SM for approximately half of Canada's LFAs across all regions, except the northern Gulf of St. Lawrence (LFAs 15-20B), indicating that the observed declines in female SM have been extensive. This statement can further be generalized to the southern part of the American lobster's range, where LeBris *et al*. (2017) demonstrated convincingly that female CL_{50} had declined significantly from 1989 to 2013 or 2000 to 2013 in 4 out of 7 US statistical areas considered from northern Maine to southern New England. The CL_{50} declined by up to 7.4 mm over 24 years and 4.9 mm over 13 years (LeBris *et al.* 2017). The only Canadian LFA (35) considered by LeBris *et al*. (2017) saw no change in CL_{50} over the period 2000-2013, but we found a large decline in CL_{min} in LFA 35 over a much longer period from 1932 to 2013.

While female lobster SM has declined in most of eastern Canada, the exact pattern of these declines remains unclear because maturity data are very limited and SM was likely underestimated until the last third of the 20th century. For example, it is difficult to conclude whether SM has declined steadily since the 1930s or whether changes occurred more rapidly over a shorter time period, and if so when they began. The available data do clearly suggest, however, that SM changes are not just a recent phenomenon and that large declines occurred

in some LFAs in the first three quarters of the 20th century. The lack of a clear relationship between time and magnitude of SM changes also likely reflects the geographic diversity of the fishery in terms of socioeconomic factors, environmental conditions, and management regulations. In fact, there is no reason to expect a common population response across all LFAs with respect to rate of SM change over time given that the driver(s) behind these changes probably operated at varying intensities during different times in different LFAs.

Given most lobster SM data were obtained through commercial trap catches, there are potential biases related to the catchability of lobsters that may alter perceived SM, although we think it improbable that these have significant bearing on our finding of female lobster SM declines. During the development of a fishery, one may erroneously conclude that CL_{min} is decreasing if the likelihood of capturing smaller ovigerous females increases for a given sampling effort as larger individuals are progressively depleted by removals. However, such a bias is not responsible for the declines shown in this study, given our earliest CL_{min} estimates (1935-1987) came well after the initial expansion (late 1800s) and collapse (ca. 1900-1920) of the fishery (Rutherford *et al.* 1967). However, the substantial increases in MLS and escape vent size that occurred in some LFAs in the 1990s clearly caused CL_{min} estimates to rise, but this catchability bias was dealt with by censoring SM values obtained after the MLS was escalated. This was done only in LFAs where the MLS increase exceeded 5 mm; there may still be some biases in CL_{min} estimates in LFAs where MLS increases were more modest, but such biases would only cause us to underestimate the decline in SM over time. Although CL_{50} estimates are not impervious to such biases (LeBris *et al*. 2017), they are less subject to them and likely the more reliable indicator of SM, yet CL_{min} data are more readily available and still provide invaluable information.

1.4.2 What has caused the declines in female American lobster size-at-maturity?

Three possible and non-exclusive drivers of declines in female lobster SM in eastern Canada were investigated: (1) rising ocean temperatures, (2) increased lobster abundance and density, and (3) size-based fishery selection. Our results suggest it is unlikely that increasing ocean temperature over the past 10-80 years has been a major contributing factor to female lobster SM declines. Mean annual SST has increased in eastern Canada since the 1970s (Rhein *et al*. 2013), but there is no evidence of greater SM declines where temperature increases have been highest. Hence, these results suggest that increasing water temperature is not pervasively responsible for the decline in female lobster SM in eastern Canada. LeBris *et al.* (2017) also found inconsistent evidence for a temporal temperature effect on SM at the scale of statistical fishing areas. Our data furthermore suggest that SM declines began prior to the onset of the most intense period of warming in the early 1990s (Knudsen *et al*. 2011; Galbraith *et al*. 2012, 2015; Loder *et al*. 2013). Thus, while the negative spatial relationship between SM and temperature (*e.g.*, LeBris *et al.* 2017) suggests that SM should decline in the face of warming arising through climate change and inter-decadal variability, this study and that by LeBris *et al.* (2017) suggest that any such impact to date has been over-shadowed by another mechanism driving SM changes.

Our results also suggest it is unlikely that increased abundance, proxied herein by landings, and the resulting potential for reduced growth rates from an increased competition for food, have been the major driver of female lobster SM declines in eastern Canada. Firstly, while the magnitudes of temporal changes in female SM in different LFAs did correlate negatively with changes in landings in these LFAs over the same time period, this correlation was relatively weak and became non-significant by removing a single datum (LFA 34). Secondly, there have

been well-documented cases of increased lobster abundance/density, for example in Chaleur Bay (LFA 23) and the Northumberland Strait (LFA 25) (DFO 2016*c*), with no or little accompanying SM change. Lastly, and importantly, landings have only been increasing over the past approximately 30-40 years (Fisheries Resource Conservation Council 2007), and our results suggest SM declines began long before this. We therefore conclude that it is highly unlikely that the declines in SM documented in this study are a density-dependent response to population growth.

Available evidence is most consistent with intense, size-selective harvesting being the primary driver behind the declines in female lobster SM. There was a strong positive relationship across LFAs between selection strength and both the magnitude of SM declines over the past 10-80 years and the rate of CL_{min} change over the past 30 years. This provides compelling evidence that selection for earlier maturation during exploitation of the fishery has been an important driver of declines in female lobster SM in eastern Canada. LeBris *et al*. (2017) suggested that the significant year effects in linear regression models for CL_{50} might reflect an evolutionary response to intense fishing. However, we are unable to say whether the observed changes are the result of evolution or phenotypic plasticity. An evolutionary response to exploitation might be expected, given the American lobster's life history. As a relatively slow-growing and late-maturing species, the lobster is more likely to be poorly adapted to high adult mortality, and hence more susceptible to fisheries-induced selection, compared to fast-growing and early-maturing species with high natural adult mortality (Kuparinen and Merilä 2007). High exploitation rates in the lobster fishery mean that adults are far more likely to die from fishing than from natural mortality, in which case fisheries-induced evolutionary responses are expected to be rapid, occurring up to 300% faster than "naturally-induced" changes (Kuparinen and Merilä 2007; Darimont *et al.* 2009).

It is currently believed that American lobsters take 6-10 years from hatching to recruit into the fishery, depending on water temperature and MLS (Elner and Campbell 1991; Gendron and Sainte-Marie 2006). The observed changes in SM thus likely occurred over up to about 10-15 generations, which is largely sufficient for genetically based evolutionary responses in other species. For example, studies have shown contemporary evolutionary changes in traits such as tolerance to environmental extremes, feeding behaviour, body size, size-at-age, and frequency of colour morphs in fish and molluscs over as few as 2-6 generations (*e.g.*, Michaud *et al.* 2008; Ozgo 2011; Bell and Aguirre 2013). Although there is no information on heritability of SM in American lobsters, it seems likely that this trait is at least partly heritable as 20%-30% of variation in SM and other life history traits are typically heritable in fishes (Kuparinen and Merilä 2007), and moderate to high heritability of body size and reproductive traits has been demonstrated in several shrimp species (*e.g.*, Acros *et al*. 2004; Luan *et al.* 2012; Sui *et al.* 2016).

The interpretation of selection as the main driver behind SM declines is somewhat confounded, as the regions with the strongest selection strength, coupled with the largest SM declines, are also those with the historically largest SM (*i.e.*, southwest Nova Scotia and Bay of Fundy). Under intense exploitation, SM declines may have been beneficial regardless of the size classes of females affected. The greatest SM declines may have occurred simply where the scope for change was greatest, assuming there is a physiological lower limit to SM. The latter likely does exist. However, fisheries monitoring conducted through the CFRN "Lobster Node" (see section 2.1 and Appendix B; Rochette *et al.* 2018) in areas of Nova Scotia and Newfoundland over the past five years (not included in this study due to lack of comparative historical data) has routinely reported berried females 48-60 mm CL. This shows maturation is possible at sizes smaller than reported in this study (minimum CL_{min} 58 mm CL). Ultimately, we believe

harvesting to have been the key driver of SM changes in female lobsters in eastern Canada over the past 10-80 years, whether or not physiological scope for change has played a role in the magnitude of these declines.

1.4.3 Effects of declining size-at-maturity on egg production

In an unfished population, declining SM is clearly predicted to have a negative effect on lifetime fecundity of female lobsters, as was evident in our E/R model simulations. This reduction in egg production is a result of the exponential relationship between female CL and clutch fecundity (*e.g.*, Ennis 1981; Campbell and Robinson 1983), combined with the slowing of somatic growth upon maturation because moult frequency is reduced from annual to biennial (Aiken and Waddy 1980). Our E/R simulations indicated declining SM would generally result in a gain in mean lifetime egg production in fished populations, although the amount of gain is dependent on both the intensity of harvesting and the strength of size-based selection (*i.e.,* MLS regulations relative to SM). This gain occurs because maturation at a smaller size increases the probability and number of spawning events prior to harvesting, despite the fact that the average number of eggs produced during each spawning will be lower. The gain in lifetime egg production is smaller and less certain under low (25%) exploitation rates, but quite consistent under moderate to high (50%-90%) exploitation rates. The results of our E/R model simulations also suggest that gains in lifetime egg production occur following reductions in SM under intense exploitation, even when size-based selection is reduced; *i.e.,* when the MLS is set at or above CL_{50}. The higher the mortality of immature females, the greater the decline of SM needed to obtain a comparable increase in egg production. This observation is important, as it provides a mechanistic underpinning for the causal relationship we argue exists between the magnitude of size-based selection and the magnitude of female SM decreases that have

occurred in different LFAs in eastern Canada over the past century. However, gains in egg production through reductions in SM when MLS is set at or above CL_{50} (*i.e.* little or no increased mortality of immature females), do suggest that increased mortality *per se* under exploitation may also constitute a driver of SM changes.

There is likely some degree of spatial variation in egg production gains through reduced SM. In some areas, particularly near the thermal extremes of the range, such as in parts of Newfoundland and the southern Gulf of St. Lawrence, there is a relatively high incidence (approximately 20%, and up to approximately 40%) of females moulting and spawning in the same season (Ennis 1980; Comeau and Savoie 2002*a*). A higher incidence of one-year reproductive cycles could result in greater gain from reduced SM. There is also spatial and temporal (Currie and Schneider 2011; Koopman *et al.* 2015) variation in size-specific fecundity of female American lobster. Gaudette *et al.* (2014) noted that the reduction in female lobster SM in the Bay of Fundy from approximately 1980 to 2010 had not appeared to result in the expected gain in egg production. This is likely owing to a high incidence of sperm limitation due to limited mate availability, suboptimal sperm allocation by available males and/or male preference for larger females in a context of high fishing mortality rates on males (Gaudette *et al.* 2014). Importantly, while these different sources of variation almost certainly affect the egg-production benefits afforded by SM changes to lobsters in different parts of the species' range, they do not change the broad conclusions drawn in the previous paragraph.

1.4.4 Declines in size-at-maturity and the lobster fishery

Given that our findings point to size-selective harvesting being responsible for declines in SM of female American lobster in eastern Canada, we have almost certainly (and potentially markedly) underestimated these declines, due to limited temporal coverage of the available

maturity data. In particular, none of our SM estimates (earliest 1930-1940) go back to the emergence of the fishery in the 1800s, and all were made well after it had collapsed in the 1920s (Rutherford *et al.* 1967). Consequently, fishery-induced changes in SM may already have occurred prior to the earliest available maturity data. Declines are likely also underestimated in areas where the most recent SM estimates are 30-50 years old (*e.g.*, CL_{50} around Newfoundland).

Fishing is likely having a lesser effect on SM of female lobster today than was the case historically as size-based selection is much reduced owing to improved MLS regulations. However, the adequacy of MLS regulations and potential for ongoing selection for reduced SM certainly differs among LFAs. In LFAs in southwest Nova Scotia and the Bay of Fundy, MLS is still considerably smaller than CL_{50} (DFO 2013*a*, *b*), so selection pressure there for smaller maturing females is likely still strong. It is important to also note that reduced size-based selection through MLS increases does not necessarily remove selection pressure for earlier maturing females given that E/R modeling clearly suggests SM declines will have rapid positive effects on egg production under heavy exploitation even in the absence of harvesting of immature individuals.

The implications of reduced SM to the lobster fishery are not entirely clear. Given high fishing mortality (Fisheries Resource Conservation Council 2007), reduced SM relative to the MLS is likely adaptive at the level of the individual and indirectly provides stocks some degree of resiliency to offset strong fishing pressure. However, depending on the mechanism behind reduced SM, declines could also reduce stock yield. If SM has declined because the fishery is selecting for slower-growing individuals (*i.e.,* SM is age-specific), this could negatively affect yield by increasing the time from settlement and juvenile life stages to recruitment into the

fishery (although ocean warming may offset this). Further research into the mechanism(s) behind SM declines, and the relative contributions of phenotypic plasticity and evolutionary change, are therefore necessary to fully understand the effects of harvesting on stock egg production and yield of American lobster and determine whether it is desirable (and possible) for management to halt or reverse declines in female SM.

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CHAPTER 2: Optimisation of hatching time by American lobster (*Homarus americanus*) in Atlantic Canada

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2.0 Abstract

The timing of release of marine pelagic larvae will affect the biotic and abiotic conditions these larvae experience and hence their subsequent survival and dispersal. Therefore, optimisation of hatching time is an important component of reproductive success. However, the proximate and ultimate factors that govern the release of marine pelagic larvae are known for only a few species. We used a biophysical model of larval drift to investigate three potential drivers of hatching time in the American lobster, *Homarus americanus*: (1) duration of the pelagic phase, (2) dispersal distance, and (3) suitability of settlement location (*i.e.*, temperature >10°C) reached upon competency. Hatching times were estimated for 22 locations in eastern Canada using embryo samples collected during the spring fishery in 2014 combined with temperature data, temperature-dependent embryonic development functions, and estimates of embryonic size at hatching. The larval drift model was used to estimate weekly values of each potential driver should hatching occur then. These were then compared to the estimated hatching times. Most hatching occurred from July to September, corresponding closely to the time that minimised drift duration in comparison to hatching occurring at any other time of the year. The hatching period did not correspond as well with times that would minimise dispersal distance and maximise potential settlement success. We also documented embryos hatching over a surprising range of eye sizes, corresponding to approximately 40%-120% of previously assumed complete eye development. Our results suggest that minimising drift time is an important aspect of optimising hatching time in lobster, and likely increases larval survival given high mortality during the pelagic phase.

2.1. Introduction

The timing of reproductive events is an important factor in their success. Over 70% of marine organisms produce pelagic embryos and/or larvae (Gerber *et al.* 2014), and the timing of release of these into the water column can have profound impacts on fitness. Pelagic eggs and larvae have likely evolved because they increase offspring survival (Strathmann 2007), as while mortality of eggs and larvae in in surface waters is high (typically >10% day^{-1}, up to 50% day^{-1} [Pepin 1991; Strathmann 2007]), for larvae with indirect development it is expected to be even greater on the bottom (Strathmann 2007; Bueno *et al.* 2010). For benthic organisms with a lengthy (weeks to months) feeding pelagic larval stage, the most adaptive strategy is likely to grow as rapidly as possible to reach the size or developmental stage at which the ontogenetic shift to benthic habitat occurs (Strathmann 2007). Since it is likely adaptive for organisms to minimise the duration of the pelagic phase, it is probable that dispersal distance of larvae with water currents is a consequence of the duration of pelagic development, rather than its cause (Strathmann 2007). Survival and growth of pelagic larvae is dependent on a variety of biotic and abiotic factors that vary seasonally, such as food availability, predator density, temperature, and water currents (*e.g.*, Pepin 1991; Knickle and Rose 2010), which highlights the importance of hatching during the ideal window to be able to minimise larval duration and maximise survival. For example, densities and quality of phyto- and zooplankton vary with season (*e.g.*, Runge and Jones 2012), and the timing of larval hatching relative to peak prey abundance impacts food availability and larval survival (Durant *et al.* 2007). Abiotic factors are also critical, as food availability is of little importance if physical conditions are not also favourable for successful development, or if larvae are transported to unfavourable environments. Given the likely importance of the timing of larval release to recruitment, understanding when larvae hatch and the mechanisms behind this timing is pertinent to

understanding recruitment patterns and population dynamics of marine organisms with pelagic larvae.

Temperature is likely a key abiotic determinant of optimal hatching time in marine fishes and invertebrates. As poikilotherms, these organisms and their larvae are highly dependent on ambient temperature for the completion of physiological processes (*e.g.*, Hoegh-Guldberg and Pearce 1995). Temperature positively impacts development rates of pelagic marine larvae (Hoegh-Guldberg and Pearce 1995) within tolerance limits (Quinn 2017). Temperature experienced during development may also result in changes to larval morphology and swimming speeds, which can impact the probability of survival (*e.g.*, Green and Fisher 2004; Lotterhos and Markel 2012; Moyano *et al.* 2016). As the timing of hatching will impact temperatures experienced, it will also impact the duration of the larval phase. Given generally high mortality rates during the pelagic larval phase (Strathmann 2007), more rapid development is presumably favourable in most species and circumstances, suggesting that hatching (and spawning for species with pelagic eggs) should ideally occur during, or shortly prior to, peak summer temperatures. This has been shown in Atlantic cod (*Gadus morhua*) off Newfoundland, Canada, where summer spawning results in greater hatching success, more rapid embryonic and larval development, and greater local retention than does spring spawning (Bradbury *et al.* 2000; Knickle and Rose 2010). Among reef fishes, the degree of seasonality in spawning decreases towards the equator. This is likely due to decreased seasonality in weather patterns and environmental conditions in equatorial regions resulting in less impact of hatching time on larval development time (Abesamis *et al*. 2015). However, not all larvae are released during summer months in temperate and polar regions. Bowden *et al.* (2009), for example, found that while abundance of larvae for most marine invertebrate

species in Antarctica do peak in summer, many also peak in winter or other times of the year, have multiple seasonal maxima, or are present year-round.

The timing of hatching not only influences the duration of the pelagic phase, but also the dispersal of larvae. Ocean currents, particularly wind-driven surface currents, vary seasonally (*e.g.*, Hadfield and Strathmann 1996; Churchill *et al.* 2011). As such, the timing of larval release will influence population dynamics such as the degree of local retention, connectivity patterns, and whether larvae are transported to unsuitable sites (*e.g.*, Bradbury *et al.* 2000; Cowen and Sponaugle 2009). Temporal variation in recruitment of cod in the Gulf of Maine, USA has been attributed to temporal variation in wind-driven dispersal patterns of pelagic eggs and early-stage larvae (Churchill *et al.* 2011). Broad dispersal may increase the risk of offspring arriving at unsuitable habitats, and there is increasing evidence that some species utilise nearshore circulation patterns to increase local retention (Bueno *et al.* 2010). For example, the barnacle *Chthamalus bisinuatus* releases larvae in rhythmic patterns coinciding with neap tides, when tidal currents are the weakest, and the periwinkle *Nodilittorina lineolate* releases eggs in a highly irregular pattern coinciding with rough seas when directions of surface currents and wave action are expected to be primarily shoreward (Bueno *et al.* 2010). Similarly, peak reproduction of reef fishes often coincides with periods of reduced winds, which presumably increases chances of larval survival by limiting dispersal to potentially unfavourable environments (Abesamis *et al.* 2015).

Nonetheless, some species appear to release larvae to induce offshore dispersal. Supralittoral and littoral decapod crustaceans often release their larvae during high tides at night, presumably for the ebbing tide to remove them from high predation pressure and stranding risk in nearshore areas (Forward 1987). This apparent strategy for increased dispersal may be

related to the relatively lengthy larval phase combined with the mobility of adult decapods, where the increased risk of disadvantageous dispersal associated with offshore movements is outweighed by the risk of nearshore predation (Bueno *et al.* 2010). These contrasting examples of synchronisation of hatching indicate different strategies for the optimisation of larval release among species possessing different life histories and habitats. Presumably, though, these species still have "optimal" release periods that are related to water temperature, current conditions, and other abiotic/biotic factors they experience in their ranges.

American lobster (*Homarus americanus*) constitutes the most valuable fishery on the North American east coast, employing over 10,000 licenced harvesters and generating approximately a billion dollars annually in export revenue in Canada alone (DFO 2015). Female lobsters typically have a two-year reproductive cycle where a female moults and mates in one summer, stores the sperm in her seminal receptacle until the following summer when spawning occurs, and then carries eggs on her abdomen for 9-12 months before releasing her larvae during the third summer (Aiken and Waddy 1980). Embryonic development is temperature-dependent (Perkins 1972), and embryos undergo rapid development after spawning in the fall, reaching 50-80% of development before going into diapause in the winter (Gendron and Ouellet 2009). Development resumes in the spring, and hatching occurs sometime between May and September (Ennis 1995; Gendron and Ouellet 2009). During the hatching process, embryos break free of the egg membrane, at which stage they are referred to as a prezoeae, but they are not released from the clutch and hatching completed until a final moult to stage I larvae and mechanical stimulation by the female through pleopod fanning (Davis 1964; Ennis 1975). The pelagic larvae then go through three moults in the water column over a period of 2-8 weeks or more, depending on temperature, before becoming competent to settle onto the benthos (Ennis 1995). Relatively little is known about the progression of hatching in nature, but

in captivity females release larvae in batches of less than ten to a few thousand larvae over a period lasting from several days to up to a month (Ennis 1975; Talbot and Helluy 1995). Laboratory studies suggest these batches are most often released shortly after the onset of darkness, which is likely a strategy to reduce predation (Ennis 1975). Larvae are mainly released in shallow coastal areas in nature (Ennis 1995).

The geographic range of lobsters is extensive, spanning from North Carolina, USA, in the south to Newfoundland, Canada, in the north (DFO 2015). As a result, lobsters experience considerable environmental variation throughout their range, inhabiting waters with summer temperatures from >20°C to <12°C (Larouche and Galbraith 2016). There is thus reason to expect some degree of phenotypic plasticity and local adaptation in reproductive traits. Variability, albeit not necessarily the mechanism behind it, has been confirmed, for example, for size-at-maturity (*e.g.*, Watson *et al.* 2013; LeBris *et al.* 2017; Chapter 1) and fecundity (*e.g.*, Currie and Schneider 2011). Anecdotal evidence from sporadic at-sea-sampling of ovigerous females, and from the presence of larvae in lobster hatcheries, suggests temperature-related spatial variation in the timing of hatching in different parts of Eastern Canada (Templeman 1936). The timing of hatching is also affected by spawning time, with embryos spawned later in the summer hatching later the following summer (Perkins 1972; Gendron and Ouellet 2009).

Tagging studies suggest that ovigerous females exert some control over the rate of egg development and the timing and site of larval release through seasonal movements (*i.e.,* exhibit behavioural thermoregulation) (Campbell 1986; Goldstein and Watson 2015). For example, ovigerous females off New Hampshire, USA move offshore for the winter, and females who remain in the cooler waters offshore until their clutch has hatched likely hatch their larvae in mid-August, while those returning to warmer inshore waters to release larvae

likely do so a month earlier (Goldstein and Watson 2015). Harding *et al.* (2005) found that the body condition of late-stage American lobster larvae around Georges Bank was greater in areas with higher temperatures and more rapid development. Similarly, Jaini *et al.* (2010) found settlement around Rhode Island (USA) to be higher in years when water temperature over the larval release grounds on George's Bank was warmer during the summer. However, despite these different lines of evidence suggesting that temperature is an important factor in both the timing of hatching and larval fitness, spatial and temporal variation in the timing of hatching in American lobster has not been rigorously demonstrated or quantified, and there exists little evidence of when the optimal time(s) for hatching may be, and what factors affect it.

The lack of detailed knowledge regarding hatching times in American lobster is due, in part, to the logistical challenges of field sampling to acquire the necessary data. Regular field sampling of ovigerous females can be used to determine, non-destructively, the hatching period of female lobster in an area, as ovigerous females in the process of hatching can be readily identified (Miller *et al.* 2016). However, the cost of repeated at-sea-sampling necessary to gather this information is typically prohibitive, especially over large areas. Sampling in collaboration with fishing activities provides a potential solution, but in Canada most Lobster Fishing Areas (LFAs) have spring fishing seasons that end prior to the hatching period, partially to reduce capture and handling of ovigerous females, which is believed to cause egg loss and reduce fecundity (Tang 2016; M. Comeau, DFO, pers. comm. 2017). Miller *et al*. (2016) recently tested, with success, an alternative method to quantify lobster hatching times in the field based on measurements of embryonic development from egg samples taken at a single point in time during the spring fishing season. Miller *et al.* (2016) then made predictions of hatching time from these measurements using temperature data and temperature-dependent embryonic development functions (Perkins 1972; Gendron and Ouellet 2009). The average of

the longest and shortest axes of the pigmented area of an eye of each embryo, also known as the Perkins Eye Index (PEI), was used as an indicator of the degree of embryonic development (Perkins 1972; Helluy and Beltz 1991).

PEI-at-hatching is an important parameter in estimating hatching time as it provides the endpoint of embryonic development at which hatching occurs. Miller *et al*. (2016) showed that PEI-at-hatching is not a fixed parameter as it was believed to be, and that using a frequency distribution of PEI-at-hatching significantly improved the accuracy of hatching predictions. Previous research had not truly considered variability in developmental status at hatching in lobster. Perkins (1972) estimated hatching in southeast New England to occur when an embryo's eye reaches approximately 560 µm in diameter, Helluy and Beltz (1991) estimated 570 µm in Massachusetts, and Gendron and Ouellet (2009) reported a mean PEI-at-hatching of 550 µm in the Magdalen Islands. Perkins (1972) did not report the observed variability in this endpoint, Helluy and Beltz (1991) gave a range of $\pm$20 µm, and while Figure 1b in Gendron and Ouellet (2009) does suggest variability in this endpoint, it was not quantified. In contrast, Miller *et al*. (2016) reported a range in PEI-at-hatching from 460 to 611 µm (mean = 520 µm) based on a total of only 60 prezoeae from 7 females sampled from Cheticamp, Nova Scotia, clearly suggesting that variability in developmental status at hatching merits further investigation. Approximately two thirds of the variability in PEI-at-hatching reported by Miller *et al.* (2016) was within clutches (*i.e.*, variability among eggs in a clutch carried by the same female), which may explain the observation that females hatch their larvae over the span of several days to weeks. Potential spatial variation in PEI-at-hatching may similarly contribute to spatial variation in the timing of hatching.

Our overarching goals in this study were to quantify variability in hatching time of American lobster in eastern Canada, and to identify the factors that make the timing of hatching adaptive. We had three specific objectives. First, because variability in developmental status at hatching impacts predicted hatching time, we set out to partition variability in PEI-at-hatching among sites, females and embryos of a same clutch using samples from 18 sampling sites spread throughout the Bay of Fundy, the Scotian Shelf, the Gulf of St. Lawrence, and Newfoundland. Second, we quantified spatial variation in the timing of hatching based on samples from 22 sites spread throughout the Bay of Fundy, the Scotian Shelf, and the southern Gulf of St. Lawrence. Third and finally, we investigated the degree to which hatching at these sites occurs at the time of year that is predicted, based on spatiotemporal patterns in temperature and water currents, to (1) minimise time spent drifting in the water column, (2) minimise dispersal distance of larvae, or (3) maximise the proportion of larvae that reach the postlarval stage in a location potentially suitable for settlement (*i.e.*, not too cold/deep, substrate suitability not considered).

2.2. Methods

2.2.1 Amount and sources of variability in PEI-at-hatching

To quantify and partition variability in PEI-at-hatching of American lobster in Eastern Canada we obtained samples from a total of 18 sites from three sources: (1) prezoeae in egg samples obtained *in situ* in 2012 and 2013 through field sampling at various localities by the "*Lobster Node*" of the NSERC Canadian Fisheries Research Network (Rochette *et al*. 2018), (2) prezoeae collected from ovigerous females from one site in the Bay of Fundy and four sites in the southern Gulf of St. Lawrence and held in the laboratory in 2013 and 2014, and (3) PEI-at-

hatching data for prezoea sampled *in situ* in Cheticamp, NS from the recent study by Miller *et al.* (2016) (Fig. 2.1).

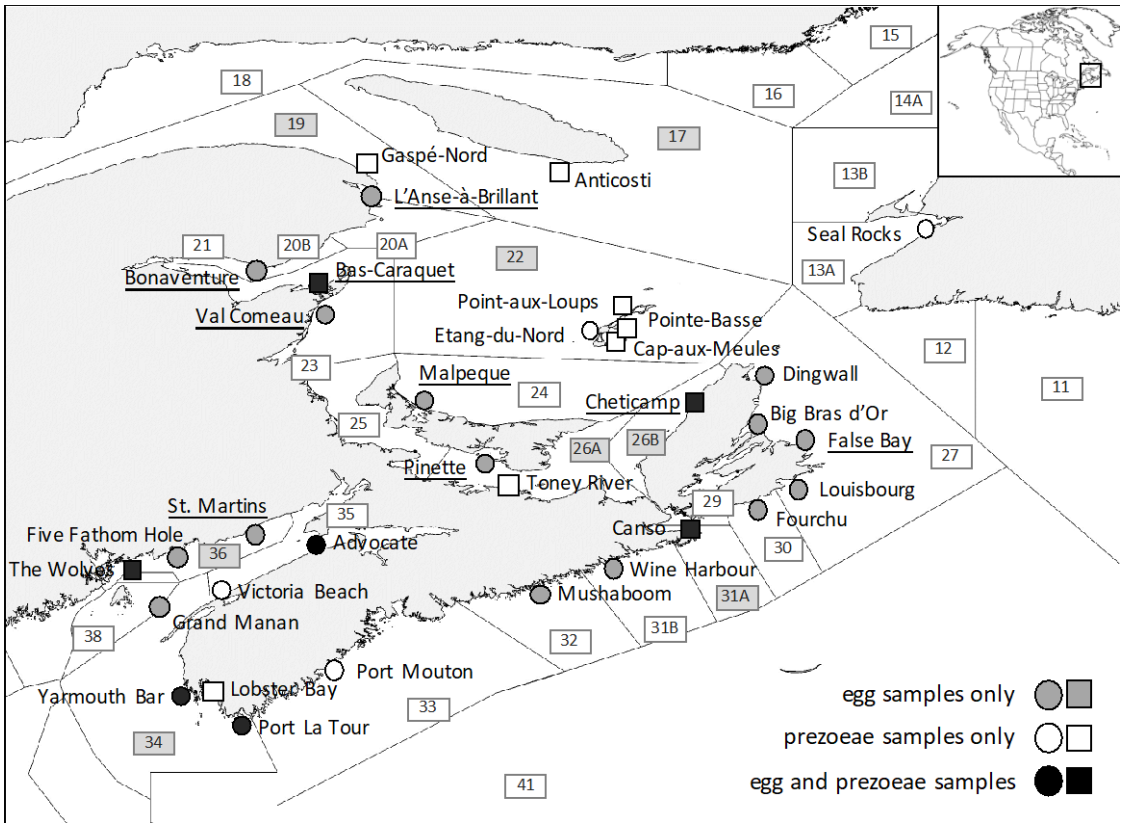

Figure 2.1: *Map of sampling sites in eastern Canada. White symbols indicate sites from which we obtained prezoeae to estimate PEI-at-hatching (see Table 2.1 for details) (only), grey symbols indicate sites from which we obtained egg samples to determine timing of hatching (only), and black symbols indicate sites from which we obtained samples to estimate both PEI-at-hatch and the timing of hatching. Square symbols identify the sites with sufficient sample size (see Methods) to be included in variance components analyses (VCA) of PEI-at-hatch (Fig. 2.2c1), whereas circles identify sites that were not included in VCA. Numbered boxes identify Lobster Fishing Areas (LFAs), and those that are shaded were used to generate Fig. 2.2c. Temperature loggers were deployed at underlined sites.*

In 2012, ovigerous females from 17 sites across eastern Canada, from the Bay of Fundy to northern Newfoundland, were sampled for genetic analyses (see Benestan *et al.* 2015), and eggs from these females were also collected and preserved in a 65:35 mixture of ethanol and glycerin. As the study by Benestan *et al.* (2015) targeted ovigerous females that would be

hatching larvae locally in the same season they were sampled, some sites were sampled sufficiently late for hatching to have already begun, and we were able to obtain prezoeae from 5 sites: four across Nova Scotia, and one in Newfoundland (Fig. 2.1, Table 2.1). In 2013, an additional 4 sites around the Magdalen Islands, QC, and 3 sites off southwest Nova Scotia were similarly sampled and prezoeae obtained (Fig. 2.1, Table 2.1). Given the prezoeae from both sources were obtained opportunistically rather than through targeted sampling, sample sizes varied considerably. Specifically, prezoeae were obtained from a total of 2-38 females (mean = 10) from each site, and as few as a single prezoea to as many as 20 from each clutch (site-level mean = 5-11 per clutch per site) (Table 2.1).

In addition to the above field samples of prezoeae from 12 sites, we also obtained prezoeae through systematic sampling of ovigerous females from 5 sites held in the laboratory. Prezoeae were collected from 11-22 ovigerous females from 4 sites in the Gulf of St. Lawrence (two in Québec, one in New Brunswick and one in Nova Scotia) (Fig. 2.1, Table 2.1) held at the Maurice Lamontagne Institute, Mont-Joli, QC (DFO) for a larval rearing experiment during the summer of 2013. These females all spawned in the field the previous year, and were already ovigerous when captured and brought to the lab in the spring of 2013, after which they were housed under seasonal temperature until hatching occurred. When the females were brought to the lab in June, temperatures were kept at approximately 6°C to match field-recorded temperatures at the time of collection; temperature was then increased gradually to 13-15°C over the course of a month to mimic average conditions the females would have experienced during the spring warming at their sites of origin. An additional 8 pre-spawn females from the outer Bay of Fundy (New Brunswick) (Fig. 2.1, Fig. 2.1), were brought back to the St. Andrews Biological Station, St. Andrews, NB (DFO) in late summer 2013, spawned in the lab, and held under ambient local temperature (bottom temperature at 10 m depth below mean low water,

intake approximately 100 m from shore in Brody's Cove, Passamaquoddy Bay) until they hatched their larvae in the summer of 2014 (Chapter 3), at which time prezoeae were collected. Sample size per clutch was greater for these females held in the lab (site-level mean number prezoeae per clutch ranged from 15-40) than for those sampled *in situ* because each laboratory female was sampled multiple times during the hatching period (Table 2.1).

Table 2.1: *Summary of prezoeae sampling effort to determine amounts and sources of variation in PEI-at-hatching.*

origin (site)*	LFA†	sampling year	source	n females	n prezoa (n_p)	min n_p per brood	max n_p per brood	mean n_p per brood
Seal Rocks	13A	2012	field	4	42	6	17	11
Anticosti	17	2013	lab	22	539	10	44	25
Gaspé-Nord	19	2013	lab	11	177	4	24	16
Pointe-aux-Loups	22	2013	field	12	75	1	10	6
Etang-du -Nord	22	2013	field	5	27	3	9	5
Pointe-Basse	22	2013	field	38	396	1	20	10
Cap-aux-Meules	22	2013	field	8	46	1	10	6
Caraquet	23	2013	lab	18	270	1	40	15
Toney River	26A	2013	lab	17	310	4	40	19
Cheticamp	26B	2012	field	7	60	4	16	9
Canso	31A	2012	field	12	75	2	12	6
Port Mouton	33	2012	field	2	13	3	10	7
Lobster Bay	34	2013	field	9	61	4	13	7
Port La Tour	34	2013	field	3	20	6	7	7
Yarmouth	34	2013	field	2	20	10	10	10
Advocate	35	2012	field	4	29	3	10	7
Victoria Beach	35	2012	field	6	18	2	6	5
The Wolves	36	2014	lab	8	321	2	79	40

* Locations where the sample size was sufficient for inclusion in the location-level variance components analyses (VCA) (see Methods and Fig. $2c_1$) are underlined.
† LFAs where the sample size was sufficient for inclusion in the Lobster Fishing Area (LFA) level VCA are underlined (see Methods and Fig. $2c_2$).

PEI measurements were made under a microscope. Technicians taking measurements practiced in advance until they could reliably replicate measurements with ≤2.5% precision

(*i.e.*, CV of 5 measurements $\leq$2.5%). This applied to both measurements of the eye's longest and shortest axes once placed under the microscope, and to how the embryos were placed under it as the orientation of the eye on the sphere will impact measurements if not reliably placed with the centre of the eye facing directly up.

We used a nested ANOVA to assess whether there was significant variation in PEI-at-hatching among the 18 sampling sites, with females nested within sampling sites, and individual prezoeae nested within females. We also used variance components analyses to assess the relative contributions of spatial (among sites), inter-clutch (among females of a same site), and intra-clutch (among embryos of a same female) to variability in PEI-at-hatching. Given the markedly uneven sample sizes, both in terms of the number of females sampled per site and the number of prezoeae sampled per clutch, we utilised random sub-samples of the data with *n* of 5 for all levels (intra-clutch, inter-clutch, and site of origin), and estimated the mean variance components based on 20 such random sub-samples. Because some sites were quite close together, such as around the Magdalen Islands (Fig. 2.1), we also pooled females by Lobster Fishing Area (LFA) and repeated the randomised subsampling with n of 5 for all levels, with sites being replaced by LFAs in this analysis. All sampled prezoeae were considered in these analyses, including those obtained from the laboratory. To exclude potential variation associated with the year and nature of the sampling (field versus lab), the randomisation procedure was also done separately with the females held in the laboratory at IML (four sites), *n* of 4; data were insufficient to conduct a similar analysis for prezoeae samples obtained in the field given variability in sample size and year of sampling. We also converted the PEI of each sampled prezoeae to percent development based on a linear regression of Table 1 in Helluy and Beltz (1991) to quantify variability in developmental status at hatching relative to expected 100% development based on the authors´ study of the embryonic moult cycle.

2.2.2 Spatial variation in the timing of hatching

We assessed the timing of hatching of lobster larvae at 22 sites throughout eastern Canada in 2014 (Fig. 2.1), using temperature data and PEI as an index of embryonic development status (Perkins 1972; Gendron and Ouellet 2009) during the spring fishery at each site. Egg samples were collected from all 22 sites within a one-month period from May 26th to June 24th, 2014; these samples were independent of the PEI-at-hatching samples. Four haphazardly chosen clumps of 10-20 eggs were removed from within the clutches of 25-30 ovigerous females from each site. Repeated randomised sub-sampling of Miller *et al.*'s (2016) dataset showed that variability in predicted hatching period stabilized when 25 or more females were sampled (Appendix E). Only ovigerous females that would hatch their clutches that season were sampled; thus, newly-spawned clutches were not sampled (see Chapter 3 for description, Fig. 3.3). Eggs were preserved in a 65:35 mixture of ethanol and glycerin, and brought to the laboratory for further processing. Five haphazardly selected embryos were processed from each clutch sampled. The average of the shortest and longest axis of an embryo's oblong eye (*i.e.*, the Perkins Eye index [PEI]) was used as an indicator of embryonic development (Perkins 1972; Helluy and Beltz 1991). PEI of each sample was converted to percent development (based on Helluy and Beltz [1991]) as described above (section 2.2.1).

To estimate hatching time from egg samples, temperature data are needed from the time of sampling until the end of the hatching period. We utilised an oceanographic model (see section 2.2.3) to generate bottom temperature data for all sites from April to December 2014. Modeled bottom temperature was extracted as daily averages from the cluster of grid cells comprising a site (Table 2.2; see section 2.2.3). In addition, HOBO or Vemco temperature loggers were weighted and deployed on fishing grounds (exact location chosen by individual

fishermen) from spring to fall at 9 of the 22 sampling sites (Fig. 2.1) to assess the accuracy of modeled temperature data during the period of embryo development. We then used the linear temperature-dependent embryonic development function developed by Perkins (1972) and the logarithmic function developed by Gendron and Ouellet (2009) to project how rapidly the sampled embryos would have progressed to hatching, and subsequently their predicted hatching dates (see Miller *et al.* 2016 for further details). We made these projections based on both modeled temperature data (22 sites) and measured temperature (9 sites).

Given that data on the value of the PEI at which embryos hatched (*i.e.*, PEI-at-hatching) were unavailable for most sites, we generated a PEI-at-hatching frequency distribution based on all 2,499 prezoeae sampled from 188 females from 18 sites as the endpoint to estimate when hatching occurred at the 22 sites from which egg samples were obtained. We also estimated hatching time using "local PEI-at-hatching" frequency distributions for a total of 7 sites where these data were either directly available or available from a site in close proximity, to compare hatching times based on local versus pooled PEI-at-hatching distributions. There were 4 sites (Bas-Caraquet, NB; Cheticamp, NS; Canso, NS; and the Wolves, NB) from which PEI-at-hatching data were available in sufficient quantity to assess a local PEI-at-hatching frequency distribution (>5 females and >20 prezoea). In addition, we used PEI-at-hatching data from Gaspé-Nord and Toney River as local frequency distributions for L'Anse-à-Brillant and Pinette, respectively, due to their close proximities (see Fig. 2.1). Similarly, we pooled PEI-at-hatching data from Yarmouth and Lobster Bay to generate a local frequency distribution for Yarmouth (see Fig. 2.1).

All the PEI-at-hatching distributions were generated based on the proportion of each female´s prezoeae with a particular PEI to avoid excessive weighting by a small number of heavily

sampled females (see Miller *et al.* 2016), fitted with a normal distribution. The best-fit model to describe the overall pooled distribution of PEI-at-hatching was a normal mixture with a combination of 3 normal curves fitted. A single normal distribution was chosen for the purpose of the hatching prediction method because (1) the distribution of PEI-at-hatching deviated relatively little from a single normal upon visual inspection (see Fig. 2.2a in Results), (2) it is unknown if the slightly higher frequency of very small PEI-at-hatching values than what is expected from a single normal distribution (Fig. 2.2a) persists in reality given the still limited PEI-at-hatching data available, and (3) its inclusion in the form of a normal mixture distribution would significantly complicate modeling while having negligible impact on the outcome of hatching predictions. The latter because (a) the low frequencies of very small values and the fact that a single normal distribution does still encompass these values to an extent, and (b) that the primary goal of incorporating natural variability in PEI-at-hatching during hatching predictions was obtained with a single normal distribution. PEI-at-hatching was assigned randomly for each sampled embryo based on the normal probability distributions.

To assess the robustness of our hatching predictions using different approaches to parameter estimation, we compared, for each site, the predicted hatching period generated using the linear versus the logarithmic development functions, modeled versus recorded (where available) temperature, and pooled versus local (where available) PEI-at-hatching frequency distributions. These different methods and data sources used to estimate hatching at each site will henceforth be referred to as "scenarios". We compared scenarios visually, and by calculating the percentage of calendar weeks during which hatching was predicted to occur that overlapped between approaches used. We then estimated the peak hatching time for each site, and based on these different approaches to parameter estimation, using (1) a moving average based on time steps equivalent to $1/5^{th}$ of the total hatching period at each site, and

(2) the peak of Gaussian models fitted to the weekly hatching frequency throughout the year. Time steps equivalent to 1/5th of the total hatching period were chosen to match the 10-week moving average used for estimating the optimal timing of hatching (see section 2.2.3), which is equivalent to approximately 1/5th of the number of weeks in a year. For the remainder of the document "peak hatch" refers to estimated peaks generated using both methods, unless otherwise specified.

2.2.3 Modeled optimal timing of hatching

The optimal timing of hatching for each sample site was estimated with the aid of computer simulations using a biophysical model of larval drift to project (1) potential settlement success based on the final drift destinations (defined below), (2) drift duration, and (3) drift distance of larvae released at weekly time steps throughout the entire year of 2014. The physical portion of the drift model was based on the regional shelf model of eastern North America developed by Brickman and Drozdowski (2012). The physical oceanographic model output was used to drive a semi-Lagrangian individual-based bio-physical model for lobster larvae, developed by J. Chassé (Maurice Lamontagne Institute, DFO) and based partially on the code used by Chassé and Miller (2010), but with modifications (see Quinn *et al.* 2017 for details). The model domain (longitude 71.5°-54.9°W, latitude 38.6°-52.0°N) extends from Cape Cod, Massachusetts, USA in the south to the Strait of Bell Isle, Newfoundland and Labrador, Canada in the north and covers most of the American lobster's range and all its major fisheries (Pezzack 1992; Fogarty 1995). The spatial resolution of the model is 1/12th of a degree, resulting in approximately 6 x 9 km grid cells (Quinn *et al.* 2017). The physical model has been well validated (Brickman and Drozdowski 2012; Lavoie *et al.* 2015; Daigle *et al.* 2016), and physical data include bathymetry, temperature, salinity, currents, and wind. To simulate physical processes occurring at scales

Table 2.2: *Summary of characteristics of the 22 study sites, as derived from the biophysical model that was used to predict hatching of embryos and dispersal of larvae.*

Location	# of model grid cells	Depth (m) *Mean*	Depth (m) *Range*	Distance from shore* (km) *Mean*	Distance from shore* (km) *Range*
Advocate	8	43.9	33 – 50	21.2	12 – 30
Bas-Caraquet	7	33.1	5 – 75	16.1	11 – 22
Big Bras d´Or	3	30.1	18 – 43	13.2	11 – 18
Bonaventure	3	26.4	15 – 33	15.7	12 – 20
Canso	5	40.8	10 – 69	15.2	12 – 19
Cheticamp	1	49.4		10.8	
Deer Island	7	91.2	59 – 118	14.5	6 – 20
Dingwall	5	36.4	5 – 67	10.6	6 – 15
False Bay	2	23.0	5 – 41	18.3	15 – 22
Five Fathom Hole	3	52.6	41 – 66	10.0	6 – 12
Fourchu	2	22.4	11 – 34	11.4	11 – 12
Grand Manan	2	147.3	105 – 189	53.1	51 – 55
L´Anse-à-Brillant	4	34.0	13 – 55	16.7	11 - 19
Louisbourg	3	21.8	5 – 50	12.2	11 – 15
Malpeque	9	20.9	5 – 35	24.1	11 – 36
Pinette	4	13.5	5 – 19	11.3	6 – 15
Port La Tour	7	21.0	5 – 37	14.9	11 – 22
St. Martins	3	64.9	58 – 69	12.6	11 – 15
Mushaboom	7	24.4	5 – 61	10.4	6 – 15
Val Comeau	2	7.1	5 – 9	14.4	11 – 18
Wine Harbour	4	24.1	5 – 48	14.9	11 – 22
Yarmouth Bar	12	51.4	27 – 74	18.6	9 – 28

* Approximate distances calculated as the linear distance between the centre of each "wet" model cell making up a location to the centre of the nearest "dry" model cell. Wet and dry model cells refers to each cell's designation as sea or land in the model domain.

smaller than the grid resolution, a random walk algorithm (*e.g.*, Visser 1997; Xue et al. 2008) was used, with small-scale diffusivity set to 2.0 $m^2 \cdot s^{-1}$ and random numbers obtained from the function RANLUX (James 1994); this random walk was applied after movements by currents. Physical data to run the model are available from 2005-2016, although we only utilised 2014-2015 data to study settlement and drift of larvae released each week of 2014 (see Quinn *et al.* 2017 for source of physical data and details of model forcing). Each of our 22 study sites were defined within the model as the sum of all model grid cells within which eggs had been sampled for hatching predictions, which varied between one and twelve (mean = 5) among

sites (Table 2.2); samples from each site were obtained onboard a single fishing vessel, yet individual fishermen may cover substantial fishing grounds.

In our simulations, we released clusters of 1000 larvae per grid cell included in each site in weekly time steps from January 1st to December 31st 2014, and we replicated each release event (*i.e.,* hatching date and grid cell) ten times to incorporate stochastic variability among model runs. The model was forced in 5-minute time steps and larvae kept at a depth of 1 m (Hudon et al. 1986; Harding et al. 1987; Ennis 1995) as they drifted. Time spent drifting by larvae was controlled based on water temperature experienced during development and temperature-based development equations derived from previous laboratory studies. Given possible local adaptation in temperature-dependent larval development rates (Quinn *et al.* 2013), we used the development functions derived by Quinn *et al.* (2013) for larvae from the relatively cold northern Gulf of St. Lawrence for L´Anse-à-Brillant, and the functions derived by MacKenzie (1988) for larvae from the warmer waters of the southern Gulf of St. Lawrence and the Gulf of Maine for the remaining sites (see Quinn *et al.* 2017).

Postlarvae were presumed competent to settle beginning halfway through stage IV (the postlarval stage), peaking approximately 2/3 through this stage (Cobb *et al.* 1989a). It was assumed that settlement could not occur in temperatures below 10°C (Chiasson *et al.* 2015), which effectively regulates the depth and distance offshore where successful settlement was predicted to occur should larvae drift there. Note, however, that substrate was not an available parameter in the model, and suitable settlement substrate could therefore not be considered. No larval mortality was included in simulations, other than failure to settle when larvae reached the end of stage IV (*i.e.*, when predicted to moult to stage V) in a site that was too cold. In the modeled domain this typically meant the site was also too deep for settlement.

Larval stages I-III are relatively weak swimmers and are assumed to disperse with currents; stage IV larvae (known as postlarvae) are stronger swimmers and actively seek suitable settlement habitat (Cobb *et al.* 1989b; Factor 1995; Stanley *et al.* 2016). If the latter is found, settlement occurs approximately halfway through stage IV and the benthic phase begins (Cobb 1989b; Factor 1995). Data on suitable settlement habitat were not available in the model as these data simply do not exist over much of the model domain, and also varies over scales much smaller than that of the model grid cells. However, if postlarvae in the model were predicted to be in waters with bottom temperature below 10°C during this settlement period, then settlement was presumed impossible, wherein the larvae "died".

We used three indices of the optimal timing of hatching: (1) percentage of the larvae released from each site predicted to be above bottom with suitable temperature for settlement (minimum 10°C; Quinn *et al.* 2017) upon reaching the postlarval stage and competency to settle (hereafter referred to as settlement success), (2) average duration (in days) of the pelagic larval phase (hereafter referred to as drift time), and (3) average Euclidean distance (in km) between the site of hatching and the predicted site of settlement (hereafter referred to as drift distance). The first index was calculated as the percentage of the 1000 larvae in a “cohort”, and the latter two independently as the average value for the larvae predicted to achieve settlement success (*i.e.,* if the latter was 65%, then drift distance and time for this simulation would be the average of 650 larvae). For each weekly time step of larval release in the model, each of the three metrics was calculated as the average of the 10 replicate simulations from each grid cell and averaged across all cells of each site. The three indices were calculated and analysed separately. We considered the optimal hatching time to be the calendar week of larval release that resulted in (1) settlement success being the highest, (2) drift time being the lowest and (3) drift distance being the lowest. We used two metrics to estimate when these

maxima (settlement success) and minima (drift time and distance) occurred at each site: (1) The 10-week moving average, and (2) the best-fit polynomial as determined through AICc model selection of polynomials of order 2-5. We chose a 10-week moving average to comfortably encompass the approximately 7-week hatching window reported by Miller *et al.* (2016).

2.2.4 Comparison between peak hatching optimal timing of hatching

We first assessed how the optimal hatching time based on each of the three indices coincided with the estimated hatching period for each site individually. We then compared hatching time versus the optimal timing of hatching across sites to determine whether spatial variation in the former can be explained by corresponding variation in the latter.

We assessed within-site temporal matches between hatching and the optimal timing of hatching through independent one-tailed *t*-tests to determine whether the settlement success resulting from weekly releases was predicted to be higher, and drift time and distance lower, during the weeks with hatching compared to the rest of year. Next, we compared the match between the peak hatching and the optimal timing of hatching among sites using paired two-tailed *t*-tests with a null hypothesis of 0. This determined whether, across sites, the average difference was equal to zero, or whether there was a systematic bias in peak hatching versus the optimal timing of hatching. To determine whether spatial variation across sites in hatching time is related to spatial variation in the optimal timing of hatching, we regressed the weeks of estimated peak hatching against the weeks predicted as the optimal timing of hatching. All analyses were done using peaks and optima estimated through both fitted models and moving averages, and for each scenario used to estimate hatching time (combinations of temperature

source, development function, and PEI-at-hatching distribution). All statistical analyses were carried out in JMP 13.

2.3. Results

2.3.1 Amount and sources of variation in PEI-at-hatching

Our results confirm the recent findings by Miller *et al.* (2016) that PEI-at-hatching is considerably more variable than previously considered in the literature. Moreover we provide an extensive analysis of this variation among geographic sites, among females at a site, and among eggs of a clutch (Fig. 2.2). We measured the Perkins Eye Index (PEI, Perkins 1972) of a total of 2,499 prezoeae from 188 females and 18 sites between the Bay of Fundy and Newfoundland. Of these prezoeae, 79% had a smaller PEI than the average 560 µm PEI-at-hatching reported in the literature prior to Miller *et al.* (2016) (Perkins 1972 [560 µm]; Helluy and Beltz 1991 [570 µm]; Gendron and Ouellet 2009 [550 µm]) (Fig. 2.2a-b). The range in prezoeae PEI was 260-706 µm, with a mean (±95% confidence intervals) of 515 (± 2.2) µm. Despite large amounts of variance in PEI-at-hatching occurring within clutches, there were highly significant differences among clutches (females of a same site) ($F_{161,2204}$ = 13.13, $p < 0.0001$) and among sites ($F_{17,144.7}$ = 8.75, $p < 0.0001$) (Fig. 2.2b). The largest PEI-at-hatching values were observed among samples from the southern part of the range studied, in the Bay of Fundy and southwest Nova Scotia, while the smallest were among samples from the southern Gulf of St. Lawrence, including around the Magdalen Islands (Fig. 2.2b).

Variation in PEI-at-hatching was divided roughly evenly among eggs of a same clutch, among clutches, and among sampling sites. If considering all available data, 23% of variance is

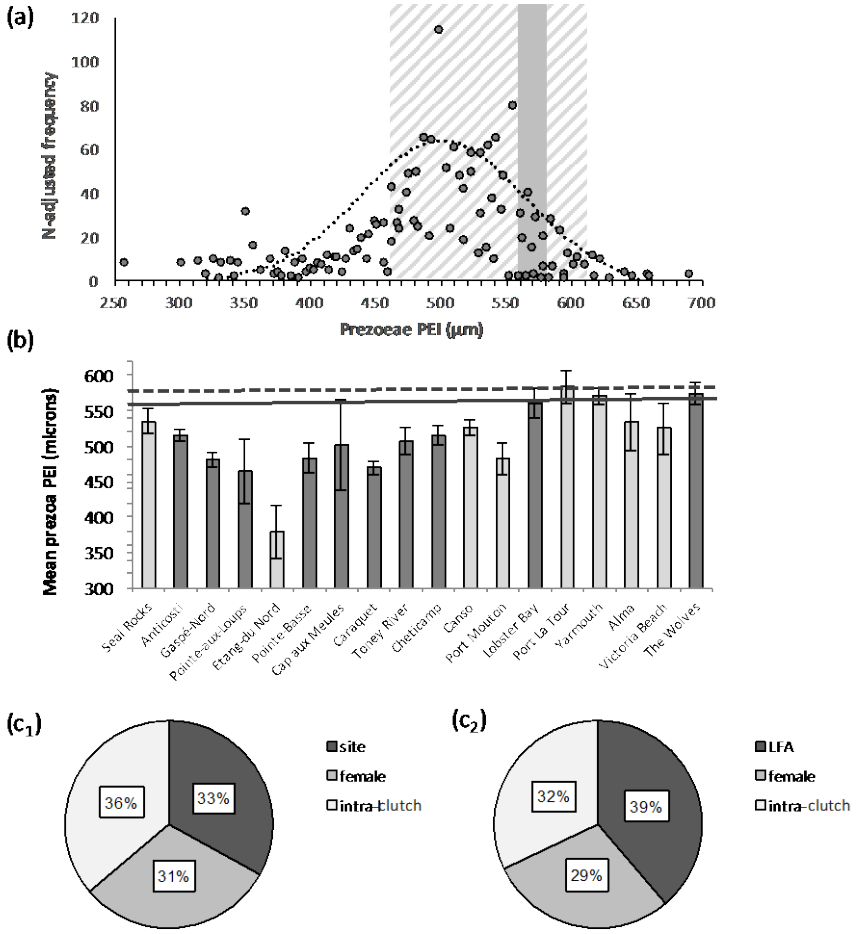

Figure 2.2: *Prezoeae eye size (i.e., PEI) at hatching, representing embryonic size at hatching. (a) The n-adjusted frequency distribution (i.e., adjusted to give the same weight to each female) of prezoeae sampled from all locations. The stippled curve shows the normal distribution fitted to these data to generate a PEI-at-hatch probability curve for the hatching prediction calculations. The shaded and hatched areas represent the range of PEI-at-hatch values reported in the literature prior to, and by, Miller et al. (2016), respectively. (b) Mean (± 95% confidence intervals) PEI-at-hatch of females sampled from each study location. The stippled and solid lines indicate the mean PEI-at-hatch reported in the literature prior to, and by, Miller et al. (2016), respectively. The dark gray bars indicate the sites used to generate c1 and c2 (light grey bars show sites with insufficient sample size). (c) Results of variance component analyses showing the mean portion of variance in PEI-at-hatch among eggs of a same clutch (within-clutch), among clutches of females from a same location (female), and among females in different locations (c1: locations; c2: LFAs). The mean estimates are the result of 20 random subsamples of prezoeae taken to obtain a consistent n of 5 for all sources of variance (i.e. 5 prezoeae from each of 5 females from each of 5 locations (sites or LFAs). These prezoeae were randomly sampled from 10 locations (dark grey bars in (b)) and 8 LFAs (same sites pooled by LFA) (see Methods for rationale, and Fig 2.1 for map of locations and LFAs).*

attributable to variation within a clutch, 34% to variation among clutches, and 44% to spatial variation; although these estimates are likely affected by the very uneven sample sizes among the three sources of variance. If sample sizes are standardised across these levels of variance by randomly sub-sampling 5 prezoeae from each of 5 females from each of 5 locations (sites or LFAs), on average, approximately one third of variance in PEI-at-hatching is attributable to each of within-clutch variation, among-clutch variation and spatial variation (Fig. 2.2c). If the comparison is limited to the four sites (Anticosti, Gaspé, Caraquet, Toney River) from which ovigerous females were sampled routinely in the laboratory in 2013, randomised sub-sampling with an equal n of four showed an average of 43% of variance attributable to eggs within a clutch, 38% to clutches from a same site, and 19% to clutches from different sites.

2.3.2 Timing of hatching

2.3.2.1 General patterns

The mean predicted hatching date of all 3,140 embryos we obtained from the 22 sample sites was August 16th, with 30%-40% of hatching predicted to occur during August irrespective of the scenario; *i.e.*, source of temperature data (modeled versus recorded), or temperature-dependent embryonic development function used (linear [Perkins 1972] or logarithmic [Gendron and Ouellet 2009]). Overall, 85%-90% of hatching was predicted to occur from July to September. A small percentage of hatching was predicted as early as June (6%) and as late as December (1%). For individual sites, the average hatching date ranged from July 12th to September 9th. The earliest peak hatching across sites was predicted to occur in early to mid-July (weeks 27-30) regardless of the scenario. The latest predicted peak hatching varied more in relation to the scenario, ranging from early September (week 37) to late October (week 44). The earliest peak hatching was consistently predicted to occur in the Northumberland Strait

(Pinette), and the latest in the Bay of Fundy and southwest Nova Scotia (Grand Manan to Port La Tour) (see Fig. 2.1 for map).

At sampling in mid-May to mid-June, mean clutch development at a site (averaged among eggs of a female and then averaged among females) ranged from PEI 239-428 µm, which is equivalent to 42%-74% development according to the scale developed by Helluy and Beltz (1991). When standardised for the first week of June, mean clutch development ranged from 46% to 68%. There was a significant difference in mean clutch development among sites ($F_{21,601}$ = 7.39, $p < 0.0001$), but no consistent effect of sampling date among sites ($F_{1,601}$ = 0.04, p = 0.84). Among individual females, mean clutch development ranged from 15% to 95%, with the within-clutch range in embryonic development (*i.e.,* difference between most and least developed embryos in a clutch) varying between 1% and 40% (mean = 7%). There was some evidence of a weak relation between mean clutch development at time of sampling and within-clutch variation in embryonic development. There was a marginally non-significant positive relationship between mean PEI (µm) of embryos of individual females and within-clutch standard deviation in development (µm PEI) ($F_{1,622}$ = 3.64, p = 0.057, $R^2 < 0.01$), and a marginally significant positive relationship with within-clutch range in development (%) ($F_{1,622}$ = 3.94, p = 0.048, $R^2 < 0.01$). Both relationships are, however, very weak. Mean development explains little of the within-clutch variability in development ($R^2 < 0.01$), and predicts an average increase in within-clutch standard deviation and range of development of only 3.3 µm and 1.5%, respectively, over the range in mean clutch development observed.

2.3.2.2 Effect of PEI-at-hatching frequency distribution on estimated hatching time

In general, the hatching period did not differ markedly whether PEI-at-hatching frequency distributions used to make estimate it were derived locally or based on samples from all

available sites pooled. For six of the seven sites where local PEI-at-hatching data were available there was a close overlap (64%-96%; mean = 79%) in the weeks during which hatching was predicted to occur using only local versus all-sites-pooled PEI-at-hatching frequency distributions (Fig. 2.3). The site with the least overlap (45%), was the Wolves, which was among the sites with highest average PEI-at-hatching.

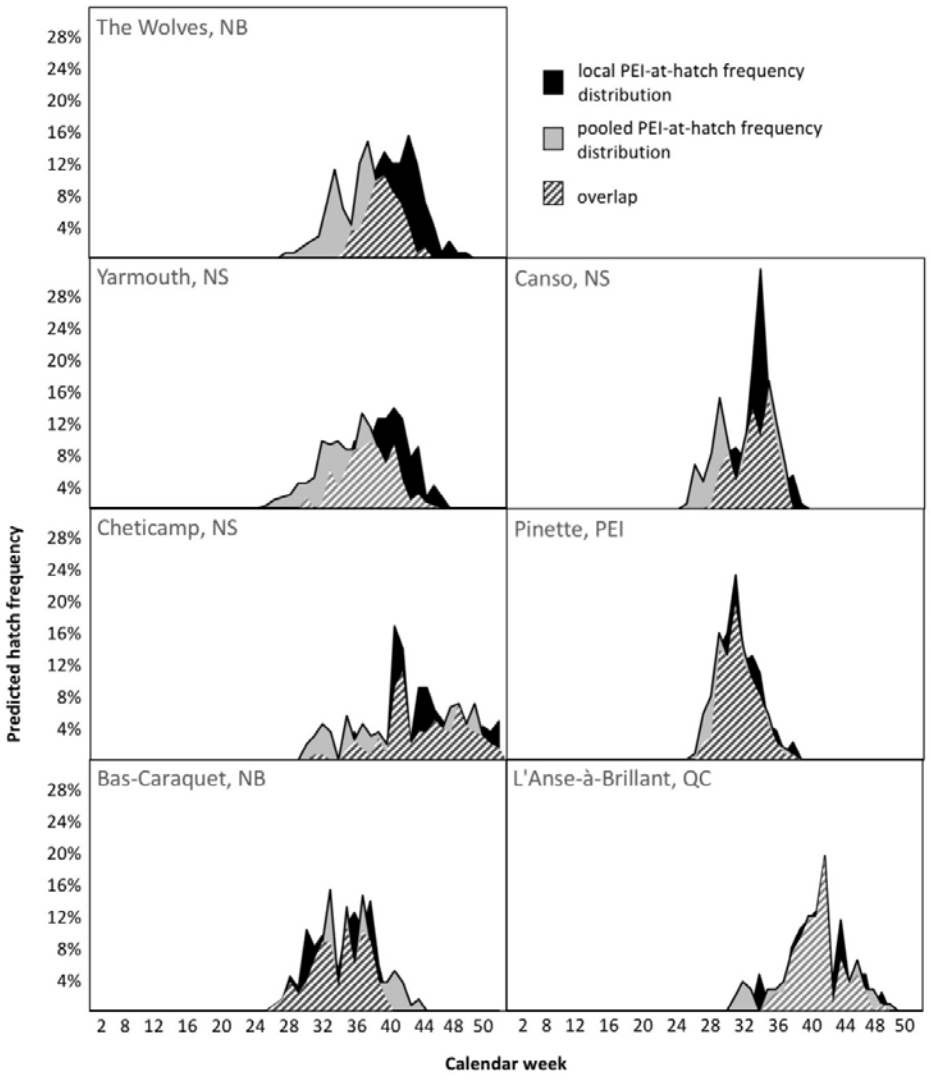

Figure 2.3: *Comparison of hatching periods estimated using local vs. pooled PEI-at-hatch as endpoints. All predictions shown are based on modeled temperature data and the linear temperature dependent embryonic development function (Perkins 1972). Contrast between these two estimates is very similar when using recorded temperature (where available) and/or the logarithmic development function (Gendron and Ouellet 2009) (results not shown). See Fig. 2.1 for site locations.*

2.3.2.3 Effect of source of temperature data on estimated hatching time

Recorded temperature data were available for nine of the 22 sampling sites, and modeled bottom temperature frequently corresponded rather poorly with recorded temperature, although the degree of discrepancy between modeled and recorded temperature was not consistent across time or thermal range (Fig. 2.4). From June through September (the time between sampling and the end of the main hatching period) the mean difference between daily averaged modeled and recorded temperature ranged from -7°C to +2.5°C among sites, with an overall average of -1.8°C (*i.e.*, modeled temperature generally underestimated measured temperature) (Fig. 2.4). This bias is clear when hatching times predicted with both sources of temperature were pooled, as approximately 60% of all hatching predicted in June and July were generated using logger temperature data, while the proportion generated based on modeled temperature increased progressively through the fall from about 60% in September to 100% in December.

Despite the relatively poor match between modeled and recorded temperature, predicted hatching dates generally did not vary considerably when generated using the two temperature sources relative to the range of the hatching period (see Figs. 2.5-7). The discrepancy was greater when using the logarithmic temperature-dependent development function (results not shown) compared to the linear (Figs. 2.5-7). When using the linear development function, the mean (among sites) overlap in the weeks with predicted hatching generated using recorded or modeled temperature data, was 70% of the total number of weeks predicted to have hatching using either temperature source. The degree of this overlap varied among sites, with 6 of the 9 sites showing a 71%-94% overlap, and 3 showing overlaps of 56% (Bonaventure), 39% (L´Anse-à-Brillant) and 34% (Cheticamp). The degree of overlap was lesser when hatching predictions

were based on the logarithmic (mean = 61%; range 25%-100%) temperature-based development function.

At the 3 sites where hatching predictions made using modeled temperature deviated considerably from those made using recorded temperature (Cheticamp, Bonaventure and L'Anse-à-Brillant; see Fig. 2.5-7), modeled temperature underestimated recorded temperature by 5.1-7.1°C from June to September (mean model deviations for the remaining 6 sites ranged from +2.5°C to -2.1°C) (Fig. 2.4). Modeled temperature at these 3 sites resulted in hatching predictions into November and December, which did not occur at any of the remaining 6 sites where recorded temperature was available. Of the 11 sites where recorded temperature data were not available, there were an additional 4 where hatching was predicted to occur into November and December: Grand Manan, Mushaboom, Wine Harbour and Fourchu (Fig. 2.5-7), suggesting that the biophysical model may have underestimated true bottom temperatures sufficiently enough to markedly impact the accuracy of hatching predictions at these sites as well. The physical model is expected to be somewhat less accurate in shallow nearshore waters given the relatively coarse spatial resolution of the model grid (approximately 6x9 km) (Quinn *et al.* 2017), yet in these sites where modeled temperature deviated considerably from real conditions model cells were not significantly shallower or closer to shore than sites where the temperature model performed well (one-tailed t-tests: $t_{7.3} = -0.56$, $p = 0.70$ and $t_{6.4} = -0.66$, $p = 0.73$, respectively); however, the poor performance sites were characterised by generally being smaller (*i.e.*, consisting of fewer grid cells) than other sites ($t_{16.9} = 1.93$, $p = 0.035$) (Table 2.2) and the mean depths and distances from shore of the grid cells in the model may be overestimated relative to reality.

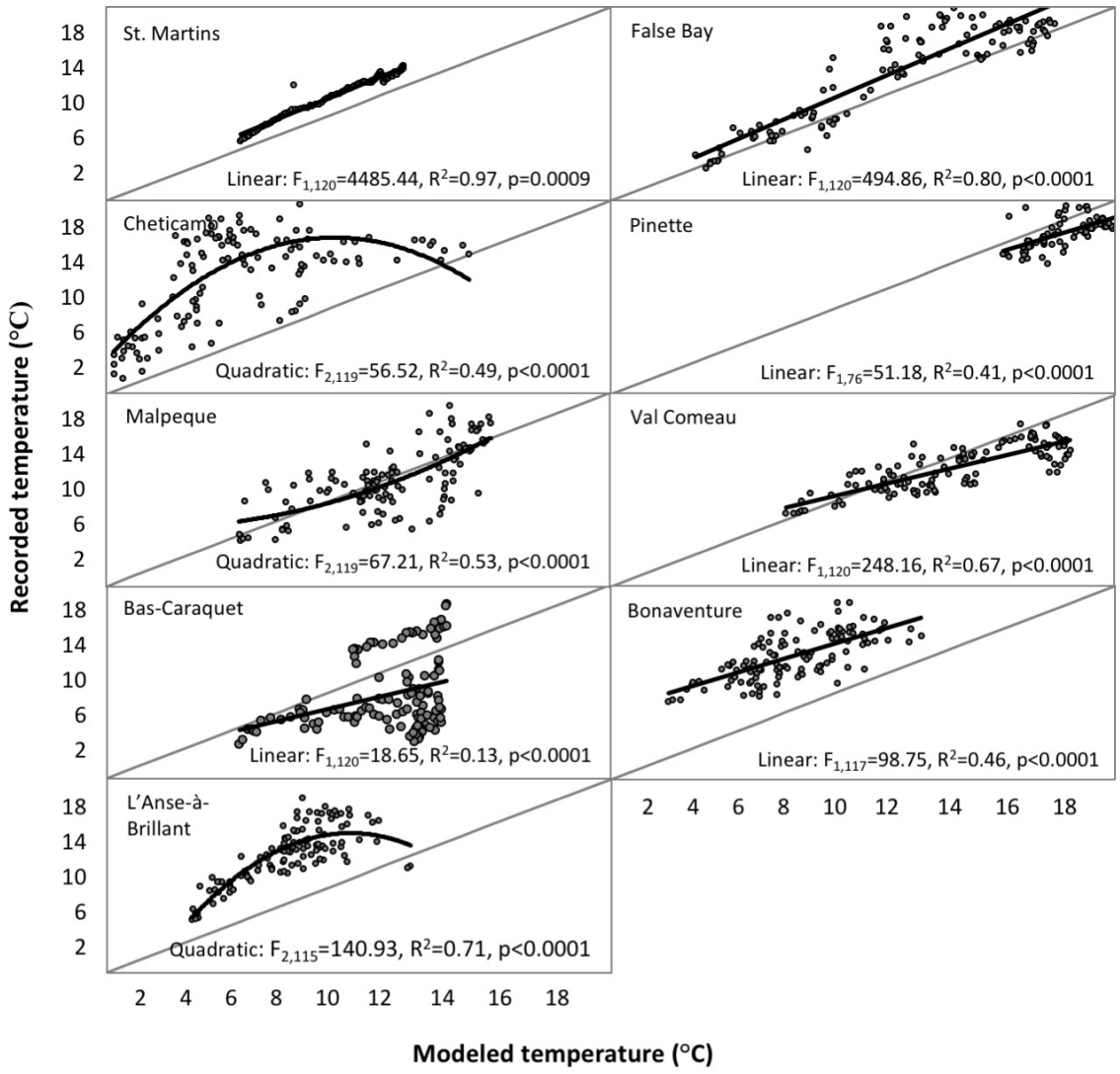

Figure 2.4: *Comparisons between model-derived (see Methods) and recorded temperature between June and September 2014 for the 9 study locations where recorded temperature was available. The diagonal lines indicate the 1:1 relation. Linear and polynomial regressions were fitted to the data from each location, and the best fit model (shown here) was chosen based on minimising AICc. See Fig. 2.1 for site locations.*

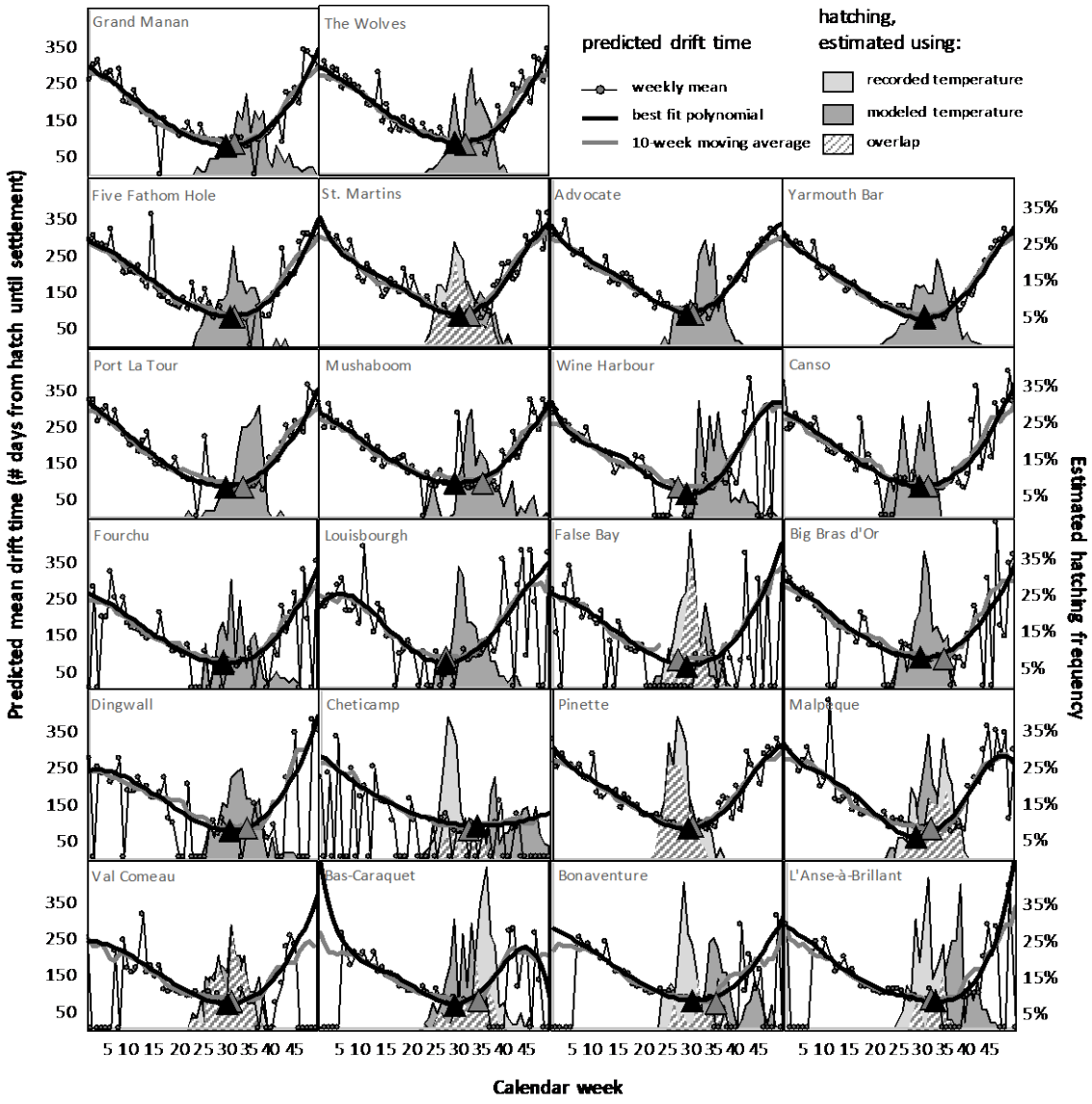

Figure 2.5: *Predicted mean drift time of larvae released on different weeks of the year (lines) from 22 study sites in eastern Canada, and the estimated hatching period (shaded areas) of lobster embryos sampled from these same sites. The predicted drift time (in days) is shown as the average of 10 cohorts released per site grid cell on the Wednesday of each week (grey circles), as well as a polynomial fit (black line), and 10-week running average (grey line) of these weekly values over an entire calendar year, with optima identified by a triangle. The hatching period is shown as the weekly hatching frequency predicted using model-derived temperature (dark grey), as well as recorded temperature (light grey) where this was available. The hatching periods were all estimated using the linear temperature-dependent embryonic development function. See Methods for computations details, and Fig. 2.1 for site map.*

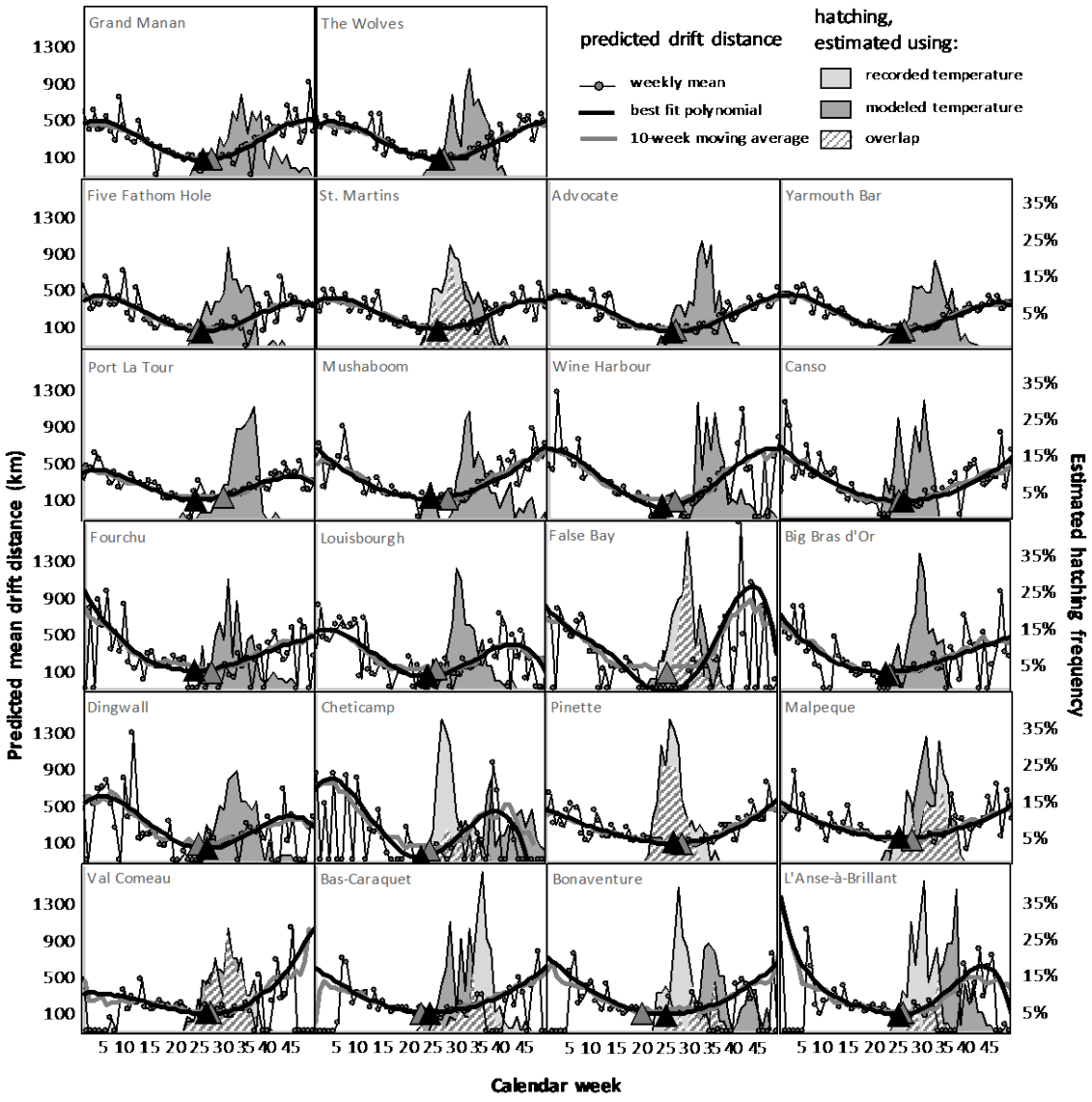

Figure 2.6: *Predicted mean drift distance of larvae released on different weeks of the year (lines) from 22 study sites in eastern Canada, and the estimated hatching period (shaded areas) of lobster embryos sampled from these same sites. The predicted drift distance (in km) is shown as the average of 10 cohorts released per site grid cell on the Wednesday of each week (grey circles), as well as a polynomial fit (black line), and 10-week running average (grey line) of these weekly values over an entire calendar year, with optima identified by a triangle. The hatching period is shown as the weekly hatching frequency predicted using model-derived temperature (dark grey), as well as recorded temperature (light grey) where this was available. The hatching periods were all estimated using the linear temperature-dependent embryonic development function. See Methods for computations details, and Fig. 2.1 for site map.*

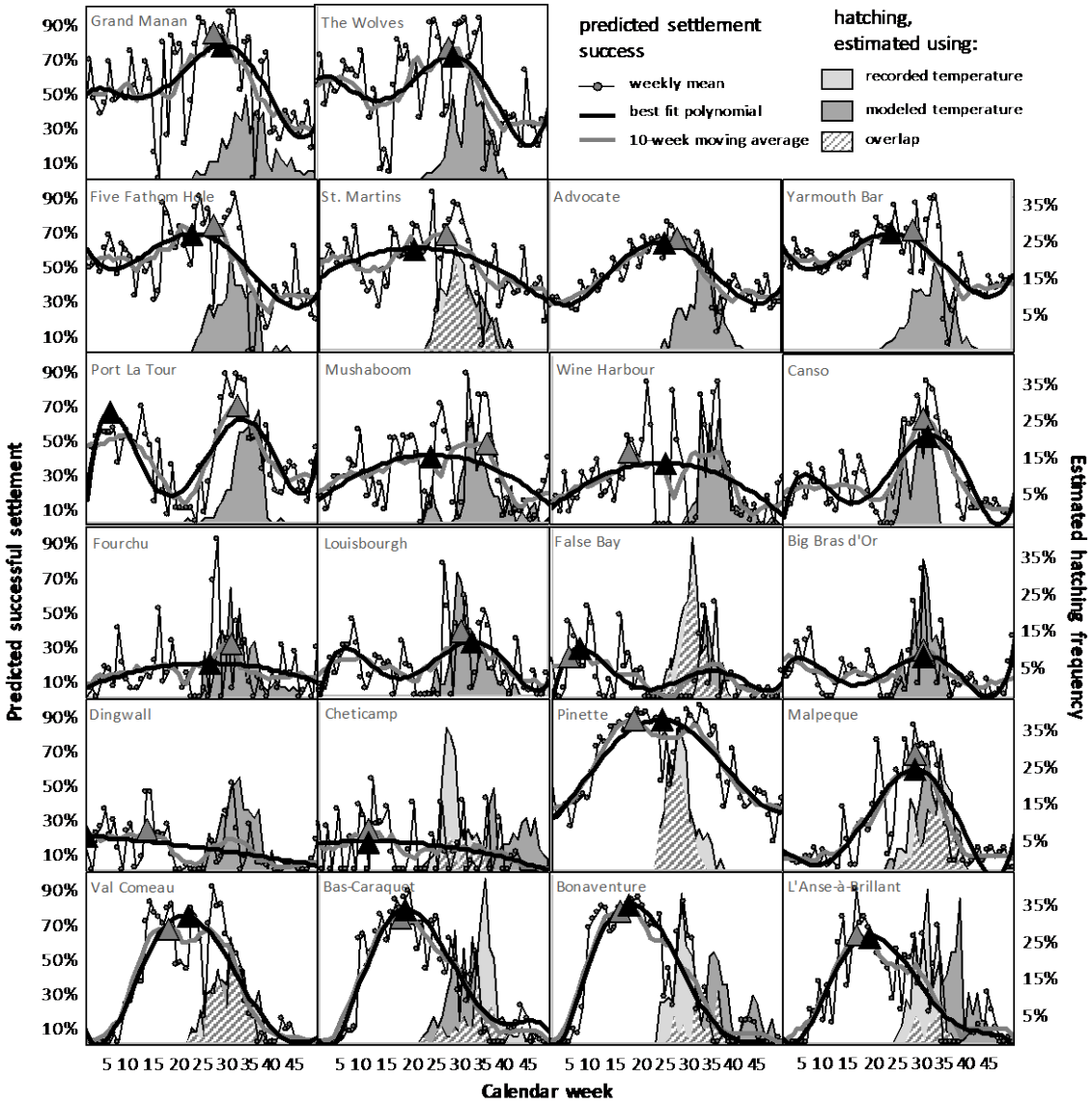

Figure 2.7: *Predicted mean settlement success of larvae released on different weeks of the year (lines) from 22 study sites in eastern Canada, and the estimated hatching period (shaded areas) of lobster embryos sampled from the same sites. The predicted settlement success (in per cent) is shown as the average of 10 cohorts released per site grid cell on the Wednesday of each week (grey circles), as well as a polynomial fit (black line), and 10-week running average (grey line) of these weekly values over an entire calendar year, with optima identified by triangles. The hatching period is shown as the weekly hatching frequency predicted using model-derived temperature (dark grey), and recorded temperature (light grey) where this was available. The hatching periods were all estimated using the linear temperature-dependent embryonic development function. See Methods for computations details, and Fig. 2.1 for site map.*

2.3.2.4 Effect of embryonic development function on estimated hatching time

Predicted hatching dates were generally earlier when made using the logarithmic development function compared to the linear one. Most hatching dates predicted in June and July (approximately 60%) were predicted using the logarithmic function. Of the hatching dates predicted from September to December, a progressively greater proportion were made using the linear function (58%-74%). At the site-level, the logarithmic embryonic development function generally predicted peak hatching 1.5 to 2 weeks earlier than the linear function (moving average peak: $t_{29} = -4.54$, $p < 0.0001$; Gaussian fit peak: $t_{29} = -8.41$, $p < 0.0001$). However, both did result in a similar overall predicted hatching period, as the difference in peak hatching of up to two weeks is relatively small compared to the breadth of the hatching period. The percentage of weeks during which hatching predictions overlapped between the linear and logarithmic functions of development was 57%-92% (mean = 73%) and 30% - 76% (mean = 56%), when calculations were based on modeled (22 sites) and recorded (9 sites) temperature, respectively.

2.3.3 Modeled optimal timing of hatching

Potential settlement success of lobster larvae, the duration of the pelagic phase, and dispersal distance were all predicted to vary markedly according to the timing of hatching. Relatively clear and consistent (polynomial fit and moving average) optimal hatching times were predicted for the different sites on the basis of reduced dispersal distance and duration, and to a lesser extent on the basis of settlement success (Figs. 2.5-7). Predicted larval drift time, or the duration of the larval phase from hatching until presumed settlement, showed a very distinct u-shaped pattern over the course of the year at almost all 22 study sites, with shortest drift time predicted to result from larval releases in week 29 (mid-July) to week 37 (early September)

(mean = 33 [mid-August]) in different sites (Fig. 2.5). Dispersal distance was generally predicted to vary intra-annually in a similar concave/u-shaped pattern as drift time, with the shortest dispersal distance predicted to result from larval releases ranging from week 22 (late May) to week 29 (early August) (mean = 28 [early July]) (Fig. 2.6). The proportion of a cohort (*i.e.*, larvae released from the same site and date) predicted to successfully settle also tended to show an optimum hatching time for most sites, when settlement success was maximised. However, this relationship was not as clear as for dispersal distance and drift time, due to high variability in predicted settlement success between consecutive weeks (including 0 settlement from some weeks), often distributed intermittently throughout the year (Fig. 2.7). Hatching dates resulting in peak settlement success also varied more among sites than did the hatching dates that led to predicted optimum dispersal distance and drift time, ranging from week 5 (late January) to week 38 (mid-September) (overall mean = 25 [mid-June]). There was no agreement between weeks resulting in maximum settlement success and minimum drift time ($F_{1,20} = 0.81$, $R^2 = 0.04$, $p = 0.38$) or distance ($F_{1,20} = 1.18$, $R^2 < 0.01$, $p = 0.67$), or between drift time and distance ($F_{1,20} = 0.03$, $R^2 < 0.01$, $p = 0.86$) (based on fitted polynomials). Predictions of optimal hatching time thus differed somewhat between the three metrics, but all suggested late spring through summer as the optimal time of year for female lobsters to hatch larvae, with dispersal time and distance generating more distinct minima and predicted optima than peak settlement success.

2.3.4 Relationship between peak hatching and optimal timing of hatching

Results provide strong evidence that lobster larvae hatch during a time of year that decreases dispersal distance and time, and increases settlement success (Fig. 2.5-7). Hatching times resulting in predicted drift time minima generally coincided with the main hatching period (Fig. 2.5) and the former fell in the 5^{th}-95^{th} and 25^{th}-75^{th} percentile hatching dates in an average 85%

and 54% of cases, respectively. Predicted drift time was significantly ($p < 0.05$) lower for the period of hatching compared to hatch occurring during other weeks of the year in 89%-100% of the 22 study sites depending on the scenario used to predict hatching. Furthermore, there was no significant difference between the optimal timing of hatching and hatching time across sites for three of the four development function - temperature source scenarios using fitted peaks (Fig. 2.8), and two of four using moving averages.

Similarly, hatching resulting in predicted drift distance minima also generally coincided with the start of the estimated hatching period, and to a lesser extent with peak hatching times (Fig. 2.6). The hatching week minimising drift distance fell during the 5^{th}-95^{th} and 25^{th}-75^{th} percentile hatching dates in an average 67% and 19% of cases, respectively. The predicted drift distance was significantly ($p < 0.05$) lower during the hatching period than at other times of the year in 68%-89% of sites depending on the scenario. Nevertheless, the optimal timing of hatching based on minimising dispersal distance generally occurred slightly before the peak hatching period, as indicated by significant positive differences (4-9 weeks) between it and the optimal timing of hatching across sites (Fig. 2.8).

Settlement success was not well correlated with the estimated hatching period (Fig. 2.7). For most sites, the 5^{th}-95^{th} and 25^{th}-75^{th} percentile hatching dates occurred after the time predicted to result in the highest settlement success, and the predicted peak settlement success only fell within these periods in 36% and 18% of cases, respectively. Nonetheless, settlement success was predicted to be significantly higher ($p < 0.05$) during the hatching period than during other times of the year in approximately half the study sites (41%-62% depending on scenario). The highest settlement success was frequently predicted to occur

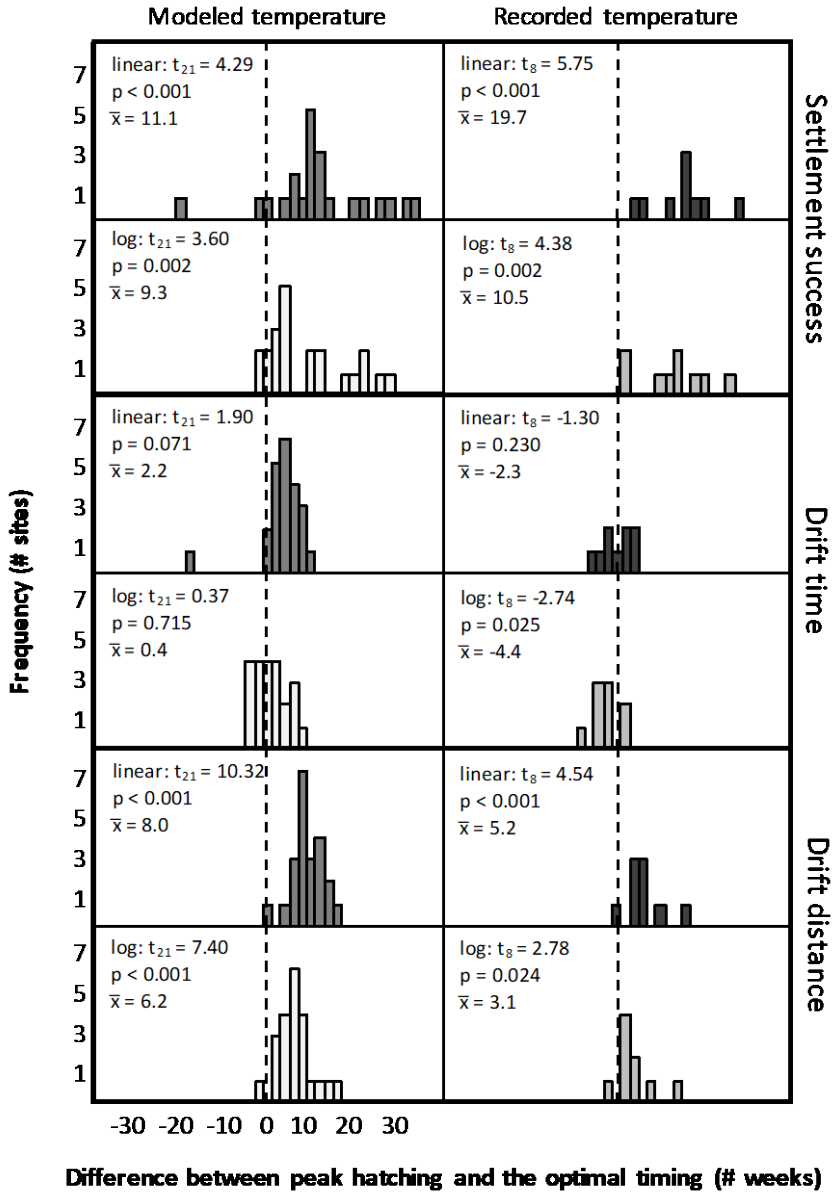

Figure 2.8: *Difference between the peak hatching and the predicted the optimal timing of hatching, with optima according to settlement success, drift time and drift distance. Peaks were estimated from fitted model: Gaussian peaks for the hatching peak, and best-fit polynomials for the optimal timing of hatching. Results are similar when using moving averages rather than fitted models to estimate peaks (not shown). Results are shown for hatching estimated using both linear and logarithmic temperature-dependent embryonic development functions, and using modeled and recorded temperature. Statistics given are results of two-tailed paired t-tests with the hypothesised difference equal to zero.*

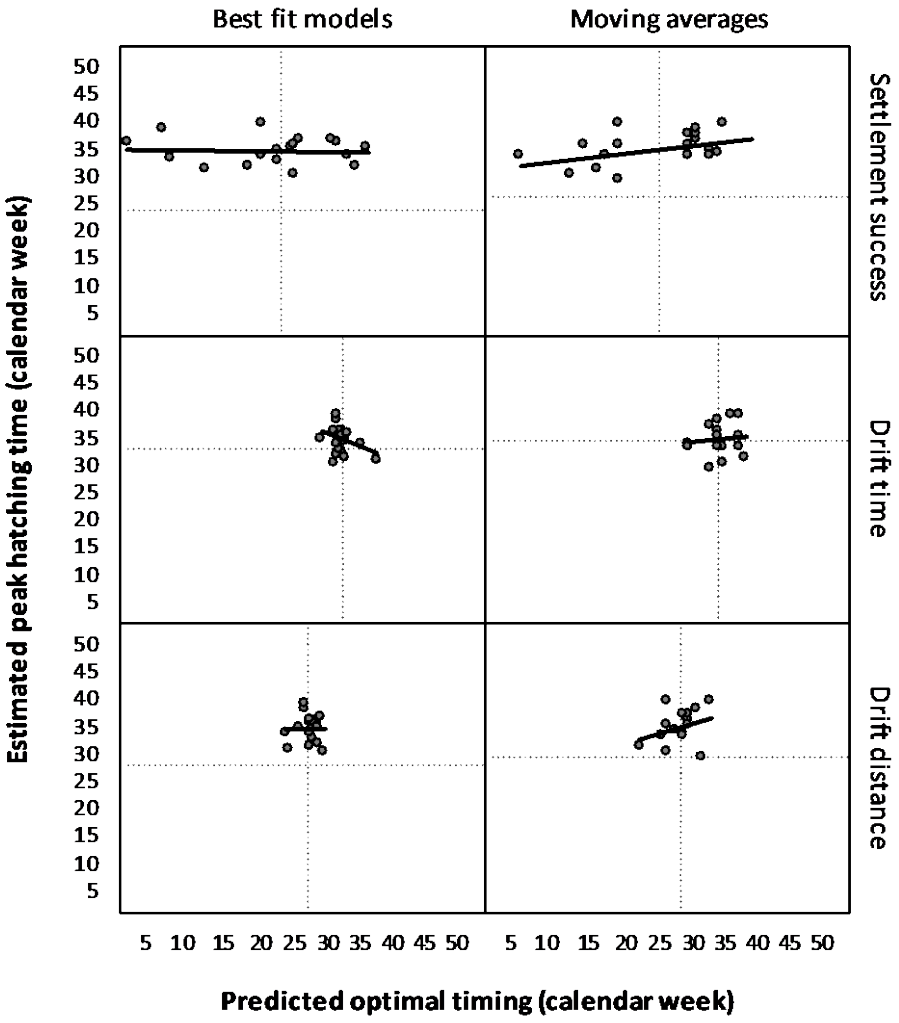

Figure 2.9: *Relationship between estimated peak hatching and the predicted optimal timing of hatching across 22 sampling locations in eastern Canada. The optimal timing of hatching was estimated based on maximising predicted settlement success (a-b), and minimising drift time (c-d) and distance (e-f). Peak hatching was estimated using recorded temperature data when available and modeled temperature data when not (see Fig. 2.1), and the linear (Perkins 1972) temperature dependent embryonic development function. Panels (a), (c) and (e) show results when peak hatching and the optimal timing of hatching were based on fitted models (Gaussian peak models and best-fit polynomials, respectively), while panels (b), (d) and (f) show results based on moving averages. We obtain similar non-significant relationships when estimating hatching using the logarithmic development function (Gendron and Ouellet 2009), and when using only modeled temperature (results not shown). The vertical stippled lines indicate the mean optimal timing of hatching across the 22 sampling locations, and the horizontal stippled lines show the same mean transposed onto the y-axis; thus, the intersect of the two lines indicate when peak hatching would match the predicted optimal timing of hatching.*

before the hatching period at a site, as indicated by significant positive differences between peak hatching and the optimal timing of hatching across sites (Fig. 2.8).

While hatching does occur during a time of year predicted to be optimal for subsequent survival and development of larvae, particularly in terms of minimising the amount of time spent drifting in the water column, there was no evidence of a relationship between spatial variation in peak hatching and the predicted optimum hatching time with respect to drift time, distance or settlement success, whether peaks and troughs were assessed using fitted polynomials or moving averages (Fig. 2.9).

2.4. Discussion

2.4.1 The timing of release of lobster larvae appears to minimise time adrift

Minimising drift time appears to be an important driver of hatching time of American lobster larvae in Eastern Canada. Egg hatching was estimated to occur at a time of the year that results in significantly shorter drift times than other times of the year, and for 85% sampling sites the hatching period included the calendar week expected to result in the shortest drift time. Moreover, the peak hatching week across different sites did not differ significantly from the one that would minimise drift time. On average across sites, the shortest drift time was predicted to result from hatching in mid-August, and nearly half of all estimated hatching dates fell during this month. As water temperature peaked from mid-August to September in over 80% of the study sites, this agrees with the expectation observed in other species that release of pelagic eggs or larvae should correspond to or just precede the warmest part of the year to minimise development and drift time (*e.g.*, cod; Bradbury *et al.* 2000; Knickle and Rose 2010). Relative to the optimal timing of hatching based on minimising drift time, optima based on

minimising drift distance or maximising settlement success were not as tightly linked to the hatching period.

The hatching time predicted to minimise dispersal distance generally occurred somewhat earlier in the summer than that which minimised drift time (early to late July), and almost always preceded the estimated peak hatching period. The hatching time predicted to result in the greatest settlement success was much more variable among sites, while predicted on average to occur in mid-June, and often well before the estimated hatching period. Importantly, these different conclusions stand irrespective of the scenario used to estimate hatching time; whether we used recorded or model derived temperature, whether we used a linear (Perkins 1972) or a logarithmic (Gendron and Ouellet 2009) temperature-dependent embryonic development function, and whether the PEI-at-hatching distribution used as the development endpoint to indicate hatching was local (site specific) or a generalised pooled distribution.

This provides persuasive evidence that hatching time of lobster larvae has evolved to reduce the amount of time, and perhaps to a lesser extent the distance, spent adrift in the water column. This finding is consistent with the hypothesis that for benthic organisms with a feeding larval phase lasting weeks to months, the most adaptive strategy is to grow rapidly and reach as quickly as possible the developmental stage at which the ontogenetic shift to benthic habitats occurs (Strathmann 2007). It should be noted, however, that biotic factors not investigated, such as the timing of peak larval food supply, may also play a prominent role and/or occur at a similar time as that minimising drift time.

Minimising drift time likely increases the number of larvae surviving to the post-larval stage by reducing mortality rates during the planktonic phase. Mortality of small pelagic larvae is high,

often exceeding 10% per day (Strathmann 2007), and while lobster larvae are larger than many other pelagic larvae occurring in the northwest Atlantic (Squires *et al.* 1997), they still experience high mortality with only 1% to 2.5% estimated to survive until settlement and up to 40% estimated to die daily (Harding *et al*. 1982; Incze *et al.* 2003; Chassé and Miller 2010). After settling on the benthos, juvenile lobsters are thought to spend most of their time in shelter (Lawton and Lavalli 1995). Even during the first few years of life they behave as central place foragers, using a home shelter as base for foraging excursions (Morse and Rochette 2016). The ability to remain hidden reduces predation post-settlement, and survival in cobble nurseries is believed to be considerably higher than during the pelagic phase. For example, Wahle and Steneck (1992) observed mean daily survival rates of 90% during field tethering experiments with recent settlers (settlement occurs during latter half of instar IV, the postlarval stage) in cobble substrate, and Wahle and Incze (1997) estimated 50% survival rate of free ranging post-larval lobsters (instar V, first juvenile stage, at start of study) over the course of 10 months following the initial 24 hours after seeding on cobble substrate.

Intuitively, one may expect our settlement success metric to reflect survival, and thus its lack of correlation with predicted hatching time to contradict the above conclusion. However, settlement success in this study reflects the likelihood that larvae hatched from a given site and at a particular time will not have drifted to colder (*i.e.,* below 10°C) offshore waters definitively unsuitable for settlement by the time they reach competency to do so, rather than the probability of surviving until competency to settle, which is a critical distinction. Our larval drift model simulations did not include daily mortality rates of larvae, which will obviously affect the true settlement success, as well as drift time and distances. We decided not to include larval mortality in our model simulations in hopes of being better able to assess the separate effects of drift time, drift distance, and drift "destination" (*i.e.,* what we coined settlement success for

simplicity – whether competency to settle was reached in a location with suitable bottom temperatures for settlement; suitable substrate was unable to be considered due to insufficient data) on hatching time. Drift time is primarily a function of sea surface temperature, and drift distance and settlement success a function of both ocean currents and temperature; thus, the hatching times resulting in their minima and maxima reflect the timing of optimal conditions in these and which optima are independent of other biotic and abiotic factors causing larval mortality.

Daily mortality of larvae is impacted by a host of additional environmental and biological factors, such as predation and food availability, and likely varies markedly in space and time. However, we do not have sufficient knowledge of this spatiotemporal variability in larval mortality to accurately model it over our large study domain. As such, excluding larval mortality from the model allowed us to investigate the optimal timing of hatching of hatching according to the variables under study: essentially sea surface temperature and currents and their impacts on larval drift time, distance, and destination. Furthermore, while undoubtedly a source of error, the exclusion of daily mortality is unlikely to have caused significant bias in our estimated optimal hatching times. Previous work with this model found that while the average drift distance (and time) of larvae is shorter overall when daily mortality is included, its inclusion changes the overall predicted drift patterns produced by the model relatively little (Quinn *et al.* 2017). There is similarly little reason to believe that the hatching time at which drift time and distance will be the shortest and settlement success highest were altered by exclusion of daily mortality estimates, unless we are able to integrate spatially and temporally realistic patterns of larval mortality.

Strathmann (2007) hypothesised that, from a macro-evolutionary perspective, dispersal is a consequence of larvae needing several weeks to develop and grow until competent to settle, rather than being a trait that is selected for *per se*, which is consistent with our conclusion that the timing of hatching of lobster larvae appears to be primarily timed to minimise drift time. Minimising the time spent adrift in the water column is likely to also reduce the distance over which larvae are dispersed, other things being equal. Dispersal distance is not only a function of drift time, however, but also of current and wind conditions, which vary seasonally and geographically (Strathmann 2007). This spatiotemporal variation in circulation patterns is why there was not a perfect correlation between the hatching times that were predicted to minimise drift time and distance, with the former generally predicted to occur somewhat later than the latter across our study area.

Another factor that can further increase the independence between drift time and distance is larval behaviour. The observed larval dispersal distance of various marine species is often less than predicted by ocean circulation models, suggesting that larvae often engage in behaviours that reduce their dispersal (Strathmann 2007). We did not include any larval behaviour in the drift model given insufficient knowledge of how to model this. It seems unlikely that larvae engaging in behaviours to reduce dispersion would drastically change the timing of hatching that would result in minimal dispersal as they would still be affected by current conditions, especially during stages I-III when swimming abilities are relatively poor (Stanley *et al.* 2016). Yet it is possible that larval behaviours could result in a disconnect between realised drift distances versus those larvae would drift passively. Hatching was rarely estimated to occur at the time that would result in the lowest dispersal, yet dispersal distance was nevertheless generally predicted to be lower during the hatching period compared to other times of the year. This was likely due to a spurious correlation arising from the relationship between drift

time and distance, although given the nature of our data we cannot entirely exclude the possibility that minimising drift distance also plays a role in driving hatching time.

Given that hatching appears timed to minimise drift time, we expected to see a relationship between spatial variation in peak hatching and the predicted optimal timing of hatching, although was not the case. While the peak hatching period varied by 10 to 12 weeks across study sites, the optimal timing of hatching based on minimising drift time varied by only 8 weeks among sites, and did so independently of spatial variation in estimated hatching times. We postulate that there are three broad categories of reasons for this absence of match across study sites: (1) a biological limit to the ability of lobster to perfectly match hatching to the optimum time in a particular year, given unpredictable environmental factors such as interannual variation in temperature during the brooding period, (2) other factors also driving hatching time, such as food availability and a temporal match with prey, and (3) prediction errors preventing us from detecting a match.

Firstly, finer-scale variation in hatching time may be influenced by environmental factors unrelated to the conditions into which larvae will be released. There is, for example, evidence that the onset of hatching has advanced in some parts of the southern Gulf of St. Lawrence over the past 25-30 years in response to increased temperatures early in embryonic development (Chapter 3). Such a relationship suggests that at least some variation in hatching time is driven by environmental conditions several months before it occurs, making a perfect match between optimal and actual hatching time less likely given there is certainly inter-annual variability in the timing of peak summer temperatures (*i.e.*, when drift time will be minimised).

Secondly, there are other potential evolutionary drivers of hatching time not considered in this paper, notably biotic factors such as the timing of the spring plankton bloom and prey

availability. American lobster larvae are active predators, feeding on a variety of other zooplankton, such as copepods, diatoms, cladocerans and other decapod larvae, and at times phytoplankton (Ennis 1995). Wild-caught larvae are typically in better condition than laboratory- or hatchery-reared larvae, presumably because of the higher nutritional value of natural plankton assemblages compared to artificial feeds, suggesting that food limitation is generally not an important factor in larval mortality in nature (Ennis 1995). One reason for this could be that larval release is generally well timed to match peak prey abundance, and this could well be another central driver of hatching time that we were unable to investigate in this study. Lastly, uncertainty in estimates of hatching time and the optimal timing of hatching likely limited our ability to detect a spatial correlation between these two parameters does it exist.

Thirdly, the method used to estimate the hatching period is subject to error related to the temperature-dependent embryonic development function used, the accuracy of temperature data, and variability in the stage of embryonic development at which hatching occurs (PEI-at-hatching). For example, estimated hatching dates differ somewhat depending on the development function used, and while Miller *et al.* (2016) found the linear function (Perkins 1972) to be more accurate in Cheticamp, NS in 2012, it remains unknown whether this is consistently the case across years and geographic areas. The fact that two fundamentally different (linear versus logarithmic) development functions have been derived for American lobster (Perkins 1972; Gendron and Ouellet 2009), combined with within-clutch variation in embryonic development, and the observation that some clutches continue development, albeit slowly, during cold winter months while others remain dormant (Gendron and Ouellet 2009), indicate that we do not fully understand the effect of temperature on embryonic development and that the relationship is not constant. The modeled temperature used to estimate hatching similarly appears to comprise considerable error, and on average a slight bias towards

underestimating measured temperature. Nonetheless, there was little evidence that the average bias just shy of -2°C was sufficient to also result in a substantial bias in estimated hatching time as the hatching period estimated using both recorded and modeled temperature were generally very similar at a site. Cases where the model-derived temperatures performed particularly badly were evident by resulting in hatching predicted right to the end of the year and in some cases failing to predict hatching (*i.e.*, embryos did not hatch by December 31st), and were thus able to be identified and excluded from further analyses.

Similarly, PEI-at-hatching is highly variable, which we accounted for by using frequency distributions reflecting variation we documented within and among clutches. However, we also found evidence of spatial variation in PEI-at-hatching, but were unable to run all hatching predictions with local PEI-at-hatching distributions given insufficient data for most sites, which contributed error to local hatching estimates. Nevertheless, using a local PEI-at-hatching distribution rarely resulted in a notable shift of the predicted hatching period compared to using the pooled distribution, suggesting that the latter adequately reflects variability in PEI-at-hatching in most cases. The exception to this was where the local PEI-at-hatching was considerably above average, in which case using the pooled PEI-at-hatching distribution did result in bias. One potential explanation for this discrepancy is that PEI-at hatching may vary with female size. Of the seven sites for which we were able to compare hatching estimates made using local and pooled PEI-at-hatching distributions, 2 showed a bias when using the pooled distribution (the Wolves and to a lesser extent Yarmouth Bar), and both are locations where ovigerous females reach considerably larger sizes than in other areas (see Chapter 1). Future research should investigate whether PEI-at hatching varies in relation to female size, and potentially adjust hatch predictions according to this relation. For example, the 95% point estimate confidence interval of the linear regression of PEI-at-hatching vs. female size could be

used to generate size-specific probability distributions of varying PEI-at-hatching values that would account for both variability related to female size and that existing among embryos of a same female.

Our estimates of the optimal timing of hatching are subject to errors associated with the dispersal model. The spatial and temporal scale of physical oceanographic data used to force the model (54 km^2 cells, 6-m deep surface layer, and daily inputs; Brickman and Drozdowski 2012) is relatively coarse. This influences its ability to account for the effects of tidal cycles, nearshore circulation, small-scale eddy diffusivity, or winds on larval dispersal in nature (*e.g.*, Katz et al. 1994; Incze and Naimie 2000; Largier 2003). Additionally, the coarse model resolution may exclude water along the coast (*e.g.*, embayments) or miss islands in or around which retention and settlement occur (Quinn *et al.* 2017). Lastly, if larval development times differ in nature relative to the lab-based rates used in the model (Annis et al. 2007) and/or geographically across the model domain (Quinn *et al.* 2013), larval dispersal times and distances could have been over or underestimated in simulations. Nonetheless, it is important to note that overall, the differences between the estimated peak hatching and the predicted optimal timing of hatching, in terms of minimising drift time, are not consistently (among study sites) in the same direction, indicating error rather than bias. While bias would suggest that drift time is not the correct driver, error suggests either additional biological controls of hatching or simply prediction errors for hatching and optimal timing of hatching estimates.

2.4.2 High variability in hatching time may be a bet-hedging strategy

The hatching period in American lobster is quite long. In our study, estimated hatching was spread, on average, over approximately three months at each site, with half of the estimated hatching dates concentrated within a four-week period. This finding is consistent with other

field studies, in which hatching has been reported to occur over periods of two to four months (Ennis 1995; Miller *et al.* 2016). While most hatching was estimated to occur in August, the timing of the hatching period varied among sites by up to two months. Hatching was estimated to peak as early as the first week of July in the Northumberland Strait, and as late as mid-September in the Bay of Fundy and around the Gaspé Peninsula.

The hatching period is also known to be protracted for individual clutches, as females have been found to release their larvae over a period of a few days to several weeks during laboratory and field caging experiments (Ennis 1975; Talbot and Helluy 1995). Frequent observations of "mossy" females in the process of hatching their clutches (clutch stage 4) over several weeks is consistent with free-ranging females also hatching their clutches over a protracted period in nature. Lab studies show hatched larvae are released from the female in batches, typically at night (Ennis 1975; Talbot and Helluy 1995), with the number and size of batches dictating how long a female will take to release her entire clutch. The number of larvae released in each event can range from only a few to ≈2000 (Ennis 1975; Talbot and Helluy 1995).

Yet the trigger(s) for eclosion, and the underlying mechanism(s) behind embryos emerging over such an extended period, both at the population and individual clutch levels, are poorly understood. Our study highlights two potential proximate mechanisms by which hatching may vary; variable rates of embryonic development, and variable PEI-at-hatching. The sheer amount of variability documented in these parameters should also be noted for future research as it clearly highlights the need to consider multiple sources of variability when conducting life-history research – a fact pointed out by Hadfield and Strathmann (1996) two decades ago when they stated that life-histories of marine invertebrates are typically too rigidly defined, due

partly to a prevalence of low sample sizes in research; yet single-site and low sample size studies remain common.

Spatial variation in the timing of the hatching period can undoubtedly be explained at least in part by differences in mean clutch development in spring, which (after being standardised for sampling date) varied from 240 to 395 µm PEI among sites in our study. This variation did not follow an easily discernable pattern, and ovigerous females at nearby sites did not necessarily have clutches in a similar stage of development. It is thus not obvious how these differences arose, whether through local differences in spawning time, varying temperature during embryonic development, behavioural thermoregulation, or different mixes of early- and late-spawners (*i.e.*, primiparous vs. multiparous females).

Some degree of spatial variation in hatching time can also likely be attributed to spatial patterns in PEI-at-hatching. Females in different sites do, on average, hatch their larvae at varying degrees of development, with approximately one third of the variability in PEI-at-hatching attributable to spatial variation. The mechanism(s) behind this phenomenon is unknown. The evolutionary driver behind spatial variation in hatching time (if there is one) is also unclear. There was little evidence from our study that minimising drift time at a local scale plays a role, even though this is likely a driver of the general time of year when larvae are released. Spatiotemporal variation in prey availability may be a driver of local variation in hatching time, but was not investigated in this study and merits further research. It is also worth noting that it remains unknown whether inter-clutch variation in both embryonic development and PEI-at-hatching are consistent among females across consecutive clutches, which in turn leaves some uncertainty regarding spatial patterns and their persistence over time.

Variability in hatching time among females, which contributes to the long period over which larvae are released within a given a site, is likely the result of clutches having reached varying degrees of embryonic development by spring. In the first week of June, we observed a range of mean embryonic development among clutches in a same location ranging from 110 to 370 µm PEI, which is likely due at least in part to variation in spawning time. It is well documented that females spawn over a wide time period; most spawn during July and August, but as many as 20%-25% may spawn during other months (Talbot and Helluy 1995). In particular, first-time spawners and those displaying a less typical one-year reproductive cycle (*i.e.,* moulting and spawning in the same year), spawn later than most multiparous females following the more common two-year reproductive cycle (Waddy *et al.* 1995; Gendron and Ouellet 2009). Varying degrees of behavioural thermoregulation may also contribute to different clutches having reached different degrees of development come spring. Many lobsters undergo seasonal migrations and in ovigerous females this may have considerable impacts on clutch development and hatching time by influencing the temperatures experienced by the embryos (Goldstein and Watson 2015). Cowan *et al.* (2007) showed that of ovigerous females captured in Muscongus Bay, Maine, USA, small, likely first-time spawners, and larger multiparous females displayed different seasonal movements that exposed their embryos to different temperatures.

Females hatching their clutches at varying stages of development undoubtedly further contribute to variability in hatching times among clutches. We documented mean PEI of newly hatched prezoeae ranging from 349 to 603 µm among clutches, and these differences among females of a same site were highly significant; approximately one third of variation in PEI-at-hatching appears attributable to differences among clutches of a same site. Thus, high inter-clutch variation in both the degree of embryonic development come spring, as a result of

variable spawning time and/or behavioural thermoregulation, and in PEI-at-hatching provide ready mechanisms by which females may hatch their larvae at different times, resulting in the overall lengthy hatching period in an area.

Similarly, within-clutch variation in embryonic development rates and PEI-at-hatching likely contribute to the protracted hatching period of individual females. The developmental stage of same-clutch embryos sampled in this study varied by 7% on average, and up to 40%, indicating non-uniform development rates among embryos in the same clutch given eggs are spawned during a single rapid event (Talbot and Helluy 1995). While embryonic development has been shown to be temperature-dependent (Perkins 1972; Gendron and Ouellet 2009), this variability clearly indicates that there exists some degree of variability in development rates among embryos exposed to the same temperature. Whereas no study has yet quantified the development rate of individual embryos within the same clutch, considerable plasticity in development rate is suggested by the fact that whereas most embryos develop little or not at all at temperatures below 3-4°C, those in less advanced clutches spawned late continue slow development at temperatures down to 1.5°C (Perkins 1972; Gendron and Ouellet 2009); the mechanism underlying this plasticity is unknown. It is worth noting that we found limited evidence of greater divergence in development among embryos in a clutch with increasing mean development of a clutch over the range of development sampled in the spring prior to hatching (80-550 µm PEI, clutch mean), indicating that this divergence may arise early during development in the first months following spawning. In brachyuran crabs, within-clutch heterogeneity is well documented and believed to be the result of variable oxygen provisioning to different parts of the clutch where embryos towards the centre of the egg mass develops slower than embryos towards the periphery (Fernández *et al.* 2003). However, a similar mechanism does not appear responsible for within-clutch heterogeneity in embryonic

development in American lobster as there is no significant difference in developmental stage of embryos from the periphery and/or surface of the egg mass compared to embryos from the centre and/or bottom of the egg mas (M.L. Haarr and E.H. Miller, unpublished data).

We also documented prezoeae with PEI ranging from 260 to 710 µm, which corresponds to embryos hatching at 45% to 120% of development according to Helluy and Beltz's (1991) scale; with an average range in development at hatching in a clutch of 110 µm PEI, and up to 280 µm PEI, providing another ready mechanism for the spread of hatching times within clutches. Variability in developmental status at hatching has been documented in other species as well. For example, tadpoles of the anuran *Pseudophryne australi* have been found to hatch at Gosner stages 24 to 36; at stage 24 the tadpole has no hind limbs and the gut and mouth are only starting to develop, while by stage 36 hind limbs are fully formed and the gut and teeth are functional (Thumm and Mahony 2005). Variability in developmental status at hatching in lobster (*i.e.*, PEI-at-hatching) likely reflects a less dramatic range in developmental stage at eclosion. Helluy and Beltz (1991) noted that by 50% development, digestive glands had formed and there were no further major changes in morphology prior to hatching, only an increase in size and the development of setae. Embryos were also noted to exhibit tail flips, an escape response, when removed from the egg at this stage (Helluy and Beltz 1991). It is therefore not improbable that embryos may hatch at any time from this point (PEI ≈ 290 µm) onwards, nor that they may grow larger than the size deemed to equate 100% of embryonic development (PEI ≈ 570 µm). However, it is worth keeping in mind that the study by Helluy and Beltz (1991) had limited replication, as did the initial study by Perkins (1972), and it may well be that PEI is not as good a proxy for embryonic development as thought, and that further research is merited here; variability in prezoeae PEI was well documented, but the estimated equivalent per cent development may be less accurate.

It should be noted that as the underlying driver(s) of variable embryonic development and PEI-at-hatching remain unknown, as is the nature of their interaction. Variable embryonic development and PEI-at-hatching could work in concert to drastically increase the range in hatching times (*i.e.*, rapidly developing embryos hatching at a small size and inversely), or counter one another and "equalise" it (*i.e*., rapidly developing embryos hatching at a large size and inversely). We currently lack the data to investigate whether variation in these two parameters occurs independently, or whether they interact according to a pattern. Further research is needed to improve our knowledge of the physiological processes that govern spawning, maternal provisioning, embryonic development, eclosion, and variation in these to fully understand the hatching process, accurately predict hatching time, and understand the drivers of hatching. One fruitful line of investigation is maternal provisioning of yolk reserves. Within- and among-clutch variability in fatty acid profiles has been documented in embryos of various clawed lobsters, and confirmed to be the result of variable maternal provisioning rather than variable yolk utilisation by embryos (Sibert *et al.* 2004; Pochelon *et al.* 2011; Leal *et al.* 2013). These observations provide a possible mechanism for variable larval size at hatching; embryos awarded less yolk reserves may be best served hatching at a smaller size, and thus commencing feeding earlier, compared to embryos with more ample yolk reserves.

Regardless of the mechanism(s) causing it to occur, the protracted hatching period of a clutch likely serves a bet-hedging function. Temporally spreading the release of larvae reduces the risks associated with variable environmental conditions (Poethke *et al.* 2016), and within-clutch variation in offspring size is a known mechanism by which to achieve this (Marshall *et al.* 2008). There are several reasons why adopting such a strategy may be favourable for American lobster. Firstly, lobsters reproduce relatively slowly, attaining maturity at a relatively late stage in life and typically adopting a two-year reproductive cycle (Waddy *et al.* 1995). They produce

relatively large eggs and larvae (Squires *et al.* 1997), which they protect on their abdomen for the better part of a year (Waddy *et al.* 1995). This slow maturation and high maternal investment means that survival of released larvae is paramount, given the relatively small number of offspring compared to species producing a greater number of smaller, less energetically expensive eggs (Marshall *et al.* 2008). Secondly, the frequency and unpredictability with which drift model predicted larval release to result in no (or very poor) possible settlement due to offshore transport suggest a risk of complete reproductive failure if a clutch is released in a single event. Particularly as such events were predicted to occur during the estimated hatching period in some sites. Thirdly, while synchrony may reduce predation on individual larvae through prey saturation, it may also increase competition among conspecifics (Poethke *et al.* 2016). The protracted hatching period may therefore also serve to reduce sibling rivalry, while potential negative predation effects are likely mitigated by releasing larvae predominantly at night (Ennis 1975). Lastly, temporal variation in prey availability is also likely, and the environmental factors impacting lobster hatching time likely differ from those controlling the availability of their zooplankton prey whose reproductive cycles are generally considerably shorter (*e.g.*, Fransz *et al.* 1991), providing further adaptive value to spreading the release of offspring and reducing the risk of a mismatch. The protracted hatching window in American lobster is thus likely an adaptive strategy to minimise the risk of catastrophic loss of larvae in the face of environmental uncertainty.

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CHAPTER 3: Onset of egg hatching by the American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence, Canada, is linked to rising temperature over a 25 year period (1989-2014)

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3.0 Abstract

Increasing ocean temperature may be impacting the life cycles of organisms whose biological processes are temperature-dependent. Our objective was to determine whether the timing of hatching of American lobster (*Homarus americanus*), which has a lengthy two-year reproductive cycle (12+ months gametogenesis and 9-12 months embryogenesis), has advanced in the southern Gulf of St. Lawrence in response to rising temperature. Using fisheries monitoring data we investigated temporal trends in the first week of the year when ovigerous females with ready-to-hatch or hatching clutches were observed (onset-of-hatching [OH]), and in the rate of change in the ratio of females with ready-to-hatch/hatching and immature clutches each spring fishing season (rate of clutch development [RCD]) from 1989 to 2014. Over this study period, OH advanced by 5 weeks and RCD increased by 40% on average among regions. Comparisons of OH and RCD to cumulative degree days (CDD) over four 6-month periods going back two years prior to hatching, suggested that the observed advancement of hatching is associated with higher fall temperatures potentially accelerating gametogenesis approximately 1.5 years pre-hatching as well as allowing more embryonic development in the fall prior to winter dormancy approximately 6-9 months pre-hatching. 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 whose life cycles are shorter.

3.1. Introduction

Our oceans and their ecosystems are experiencing considerable changes in the face of climate change, including increasing temperature, alterations in ocean circulation patterns, changes to the frequency and intensity of storms, ocean acidification, changes in salinity, increased stratification of the upper water layers, and sea-level rises (Doney *et al.* 2012; Rhein *et al*. 2013). Globally, upper water (<75 m) temperature has been increasing on average by approximately 0.1°C per decade since 1970; this warming trend is particularly pronounced in the northwest Atlantic where increases have been in the order of 1 °C per decade (Knudsen *et al*. 2011; Galbraith *et al*. 2012, 2015; Loder *et al*. 2013; Rhein *et al*. 2013). Changes in temperature are particularly consequential to marine life, as most marine organisms are ectothermic, *i.e*., physiological processes are directly regulated by ambient temperature.

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 and Aiken 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). Climate change driven phenological shifts in marine organisms remain relatively poorly studied. Nevertheless, shifts in seasonal peak abundances of various marine zooplankton and larval fishes have been documented (*e.g.*, Sullivan *et al.* 2007; Schlüter *et al.* 2010; Asch 2015), and 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).

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 (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 markedly affect their survival success, rate of development, and associated dispersal (Cowen and Sponaugle 2009; Gerber *et al.* 2014). This has not yet been shown empirically, but is suggested by modeling work. For example, the connectivity of the dusky grouper (*Epinephelus marginatus*) among Marine Protected Areas and commercial fishing grounds in the Mediterranean are expected to be altered, based on a model with predicted climate change over 130 years (between 1970-2099) (Andrello *et al.* 2015). Primarily because of predicted temperature-induced changes to the timing and frequency of spawning (Andrello *et al.* 2015). Long-distance connections, in particular, are predicted to be lost (Andrello *et al.* 2015). It has also been empirically shown that benthic recruitment of American lobster (*Homarus americanus*) around the Magdalen Islands (QC, Canada) has increased over a 19-year period. This has been partially attributed to later hatching of embryos resulting in shorter drift times and dispersal due to warmer water (L. Gendron, D., Lefaivre and B. Sainte-Marie, in review). Investigating how increasing water temperature will affect the timing of larval release is critical to understanding how climate change is, and will, affect 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, employing well over 15,000 licenced harvesters and earning over 1.5

billion dollars annually in exports (DFO 2015; NOAA 2017). 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, hypoxia and disease outbreak appears responsible for marked stock declines and collapses (Jury and Watson 2013; Wahle *et al.* 2015). In southern New England, shallow nearshore lobster nursery grounds are declining and receding (Jury and Watson 2013; Wahle *et al.* 2015). Summer water temperature there has increased above physiological limits for benthic lobster (above 20°C) (Wahle *et al.* 2015), and movement and distribution patterns of juveniles and adults are likely being modified by high-temperature stress, including a withdrawal to deeper cooler waters (Jury and Watson 2013). In contrast, increasing abundances have been observed in the northern part of the species' range (northern Gulf of St. Lawrence; Bernard Sainte-Marie, DFO, pers. comm. 2016). 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 approximately 30% from 2008 to 2013, with increasing water temperature hypothesised as a possible cause (Koopman *et al.* 2015). Further impacts 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 could be influenced by temperature observed during the female reproductive cycle. For small/young mature females, reproduction is typically considered a two-year process, where a female moults and mates in one summer, stores the sperm in its seminal receptacle until the following summer, when spawning occurs, and then carries the eggs under its abdomen for nine to twelve months before hatching and releasing larvae during the third summer (Aiken and Waddy 1982) (Fig. 3.1). A smaller proportion of mature females have what is considered a one-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 2002a) (Fig. 3.1). Also, larger/older females may skip moulting between spawnings and spawn in consecutive years (Waddy and Aiken 1986).

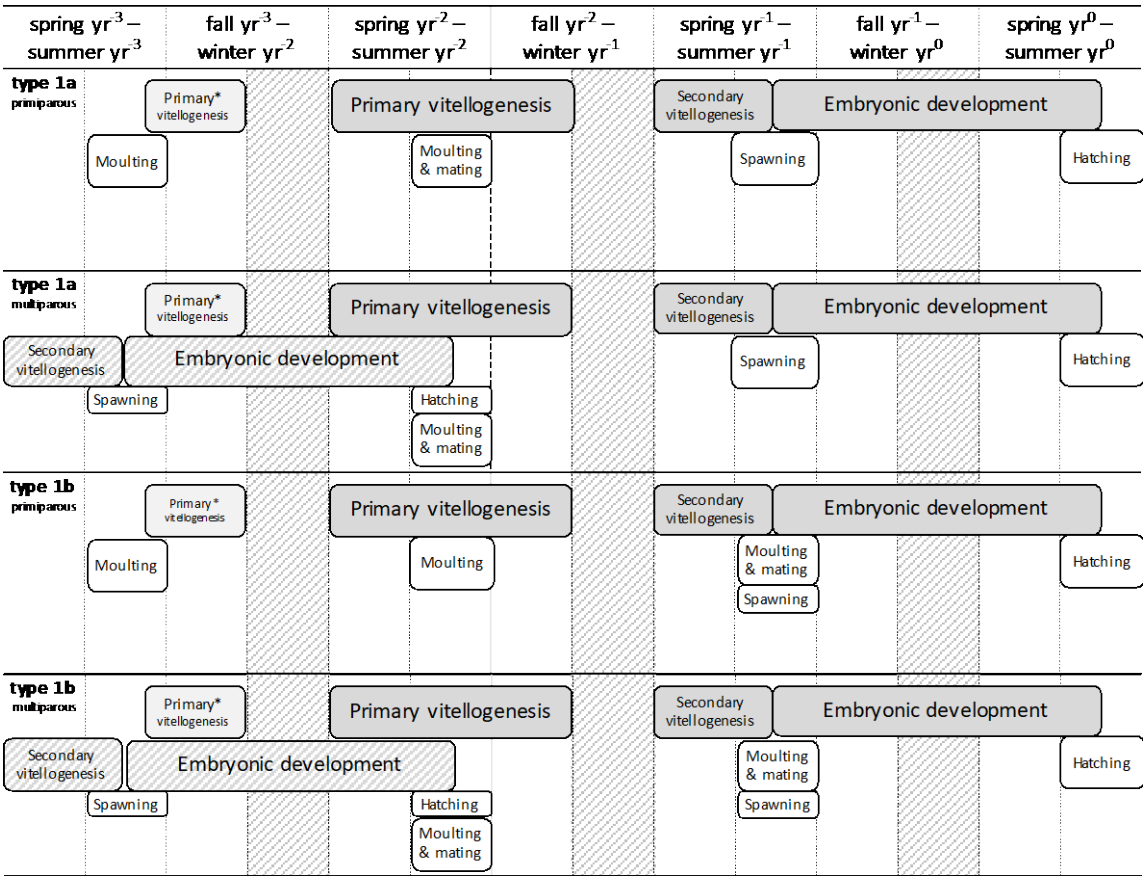

Figure 3.1: *Gantt chart showing a conceptual model of the female American lobster (Homarus americanus) typical 2-yr (type 1a) and less common 1-yr (type 1b) reproductive cycles between molting and egg hatching. Processes shaded in dark grey are those under consideration in this study; the dotted vertical line indicates the point after which energy reserves are used primarily 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 while the onset of primary vitellogenesis in yr-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°C in the southern Gulf of St. Lawrence).*

Primary vitellogenesis, during which yolk is synthesised within the oocytes and which results in a slow increase in ovarian size, begins as early as four summers prior to hatching, immediately following spawning of the prior cycle's clutch of eggs for multiparous females (*i.e.*, not first-time spawners) (Aiken and Waddy 1980; Ennis 1995; Waddy and Aiken 1995) (Fig. 3.1). However, it is only after moulting and mating that a female can direct energy primarily towards ovarian development, as prior to this she also allocates energy to somatic growth and moulting (Adiyodi 1985). Secondary vitellogenesis, during which yolk synthesis is exogenous and its deposition and oocyte growth occur rapidly, is shorter than primary vitellogenesis and generally begins in the spring prior to summer spawning and 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 a diapause in the winter (Gendron and Ouellet 2009). They resume development in the spring, followed by hatching, and immediately after larval release, sometime between May and September (Ennis 1995; Gendron and Ouellet 2009). In the laboratory, hatching can be induced as little as four to six months after spawning when females are held in water >10°C (Tlusty *et al.* 2008). The pelagic larvae go through three moults in the water column over a period of two to eight weeks, depending on temperature, before becoming competent to settle on the benthos (Ennis 1995). There is anecdotal evidence from sporadic at-sea sampling of ovigerous females that temperature can cause spatial variation in the timing of hatching in nature (Templeman 1936).

The objective of this study was to determine whether there is evidence that increases in ocean temperature have modified the timing of hatching (closely linked to larval release) of American lobster in the southern Gulf of St. Lawrence (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 the (1) onset of the hatching period and (2) the rate of clutch maturation through spring, at the population (*i.e.*, site) level rather than for individual females/clutches. We compared interannual variation in the onset of egg hatching and the rate of clutch maturation each spring to seasonal (fall-winter and spring-summer) cumulative degree-days (CDD) up to two years prior to hatching to determine (1) whether temperature has influenced hatching time, and (2) during which portion of the reproductive cycle, incorporating both ovarian and embryonic development, temperature is most influential.

3.2. Methods

3.2.1 Monitoring of ovigerous females in the southern Gulf of St. Lawrence

At-sea sampling has been carried out during the lobster fishing seasons along the coasts of New Brunswick and Prince Edward Island in the southern Gulf of St. Lawrence (sGSL) since 1989 as a fisheries monitoring program to inform management (Mallet *et al.* 2006). Data collected through the at-sea sampling program included gender, 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); all sampling was conducted by trained technicians. We utilised clutch stage data from the spring fisheries (May-June) in Lobster Fishing Areas 23, 24 and 26A (Fig. 3.2) to investigate temporal trends in the timing of hatching in the sGSL between 1989 and 2014.

Clutch stage is based on egg development and is categorized on a scale from 1 to 4 (Fig. 3.3). At stage 1, the clutch consists of newly spawned eggs that appear black or olive green in colour with no embryo visible to the naked eye (*i.e*., eggs consist primarily of yolk). At stage 2, eggs are further developed and the clutch lighter in colour, usually a shade of brown, with embryos'

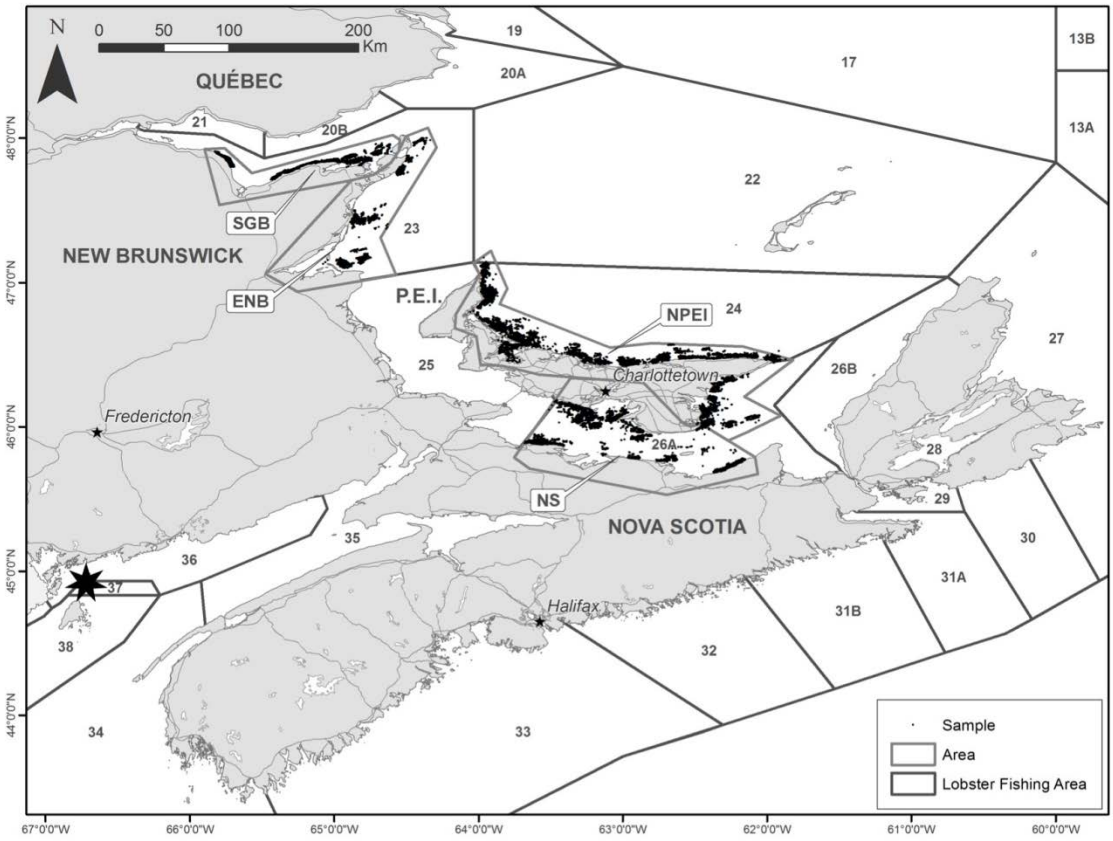

Figure 3.2*: Map of eastern Canada showing the four main study areas (grey polygons) in the southern Gulf of St. Lawrence, as well as the location (large black star) from which females were sampled in the Bay of Fundy for lab observations on clutch development. The four study areas were divided based on lobster sampling locations (small black circles) and mean summer temperatures (see Table 3.1). They are southern Chaleur Bay (SCB), eastern New Brunswick (ENB), the Northumberland Strait (NS), and northern Prince Edward Island (NPEI). The map also indicates in black the boundaries of different Lobster Fishing Areas.*

eye spots visible within the eggs; individual eggs are clearly two-toned, with one portion consisting of the embryo and the other of yolk. At stage 3, eggs are well-developed and close to hatching with the overall clutch appearing 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). At stage 4, eggs are in the process of hatching and are dark in colour without yolk, and clearly visible embryos, prezoeae larvae, and (later in the hatching period) empty egg casings and adhesive material are

found beneath the abdomen (*i.e.*, the clutch appears "mossy"). During stage 4, eggs will hatch over several days to weeks (Tlusty *et al.* 2008, chapter 2). From 1989 to 2003 stages 3 and 4 were not distinguished, but rather grouped together as clutches with well-developed eggs, whereas from 2004 to 2014 all four categories were distinguished and recorded.

Table 3.1: *Summary of sampling conditions in each of our 4 study areas, including the number of years with adequate data to estimate the two metrics of the timing of hatching (onset-of-hatching [OH] and rate of clutch development [RCD]), the timing of the sampling period, as well as temperature conditions in terms of cumulative degree-days (CDD) (3.4° threshold) in spring-summer (April-September) and fall-winter (October-March) months, showing both average conditions and temporal trends.*

area	# years adequate data OH*	# years adequate data RCD†	annual sampling intensity (# weeks)	start annual sampling period (week #)‡	end annual sampling period (week #)‡	cumulative degree days spring/ summer§	cumulative degree days fall/winter§
Southern Chaleur Bay **(SCB)**	14	13	$\bar{x}$ = 5.4 min = 2 max = 9	$\bar{x}$ = 19.0 min = 18 max = 20	$\bar{x}$ = 25.7 min = 24 max = 27	$\bar{x}$ = 690 slope = -0.68	$\bar{x}$ = 150 slope = 3.12
Eastern New Brunswick **(ENB)**	14	8	$\bar{x}$ = 4.2 min = 1 max = 9	$\bar{x}$ = 19.6 min = 18 max = 23	$\bar{x}$ = 25.3 min = 23 max = 27	$\bar{x}$ = 896 slope = -2.05	$\bar{x}$ = 234 slope = 3.53
The eastern Northumberland Strait **(NS)**	24	21	$\bar{x}$ = 5.2 min = 2 max = 10	$\bar{x}$ = 19.9 min = 18 max = 22	$\bar{x}$ = 26.6 min = 25 max = 28	$\bar{x}$ = 1,308 slope = -2.65	$\bar{x}$ = 329 slope = 3.69
The northern shore of Prince Edward Island **(NPEI)**	25	23	$\bar{x}$ = 6.9 min = 2 max = 9	$\bar{x}$ = 19.0 min = 18 max = 21	$\bar{x}$ = 26.3 min = 25 max = 28	$\bar{x}$ = 721 slope = -2.20	$\bar{x}$ = 257 slope = 3.40

*OH was the first calendar week when ovigerous females with mature and/or hatching clutches were observed.
† RCD was the rate of increase of females with mature and/or hatching clutches (stage 3-4) through the spring each year.
‡ The start and end of the sampling period are given in calendar weeks.
§ Slope shows the interannual trend in CDD.

In total, we acquired data from 1,126 sampling days from 58 fishing ports. Sampling was conducted with varying intensity at different ports and years in terms of number of vessels and size of fishing ground covered, depending on the key management concerns at the time (Mallet *et al.* 2006). The exact timing of the spring at-sea sampling season varied somewhat inter-

annually due to factors such as ice coverage and storm days (Mallet *et al.* 2006). There was a trend for sampling to extend slightly later (5 days) into the year as the study progressed from 1989 to 2014 ($F_{1,78.3}$=9.40, p=0.003), although the start of sampling did not change progressively during the study period ($F_{1,78.74}$=2.45, p=0.12; area set as random factor). 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 3.1).

3.2.2 Confirmation of the biological relevance of the clutch staging scheme

Given that ovigerous females with stage 3 and stage 4 clutches were not distinguished for the first 14 years of sampling, we conducted a laboratory study to determine the duration of stage 3, to help us better draw conclusions with respect to the onset of egg hatching. Pre-ovigerous female lobsters were collected during a trawl survey around Grand Manan and the Wolves in the southwest Bay of Fundy, Canada (Fig. 3.2) on July 5th, 2013 and brought to the Department of Fisheries and Oceans Canada St. Andrews Biological Station. In November, we selected 10 females that spawned in the lab in September; these females ranged between 96 and 145 mm CL and possessed embryos with a Perkins Eye Index (PEI; Perkins 1971) of 255 to 415 µm (44%-72% development per Helluy and Beltz 1991). Qualitatively all these clutches were in the transition from stage 1 to 2; *i.e.,* eye spots were not yet visible to the naked eye, but some yolk had been used, lightening the overall color of the eggs from dark green/black to dark brown. These 10 experimental females were housed in individual floating crates in large flow-through holding tanks with natural photoperiod and fed primarily herring twice a week. The water temperature dropped from 13°C (September) to 1°C in February and March, then increased to 10 to 14°C during the period of hatching in July and August.

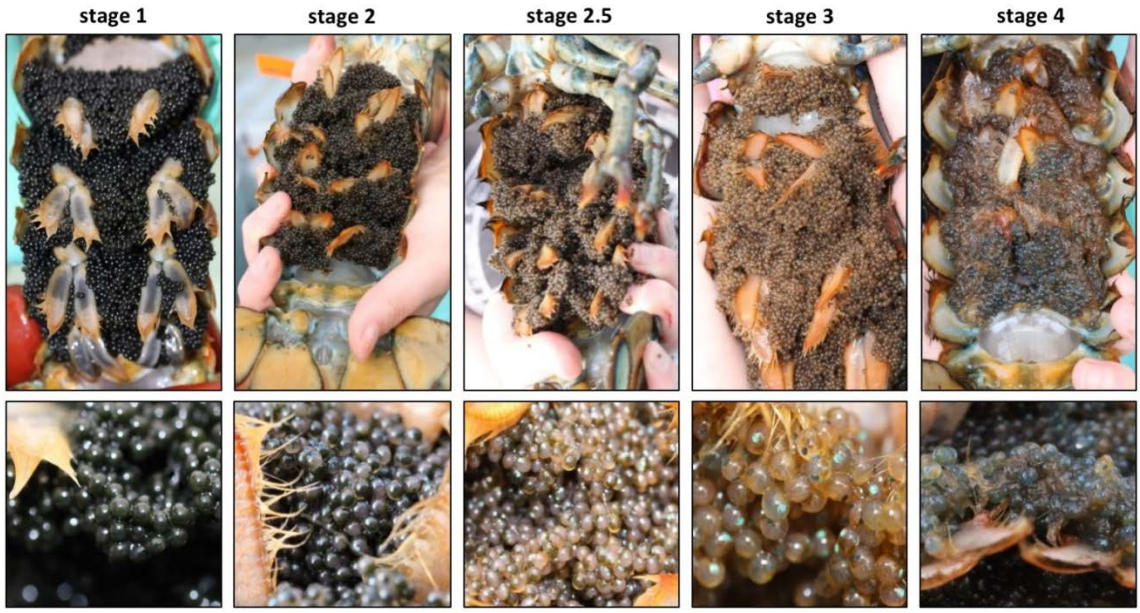

Figure 3.3: *Visual clutch staging scheme. Stages 1, 2, 3 and 4 were used during at-sea-sampling. Stage 2.5 was added during our laboratory study. A stage 1 clutch is newly spawned; clutch appears black or olive green, and no part of the embryo is visible (i.e. eggs consist primarily of yolk). A stage 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). Stage 2.5 is an intermediate between stages 2 and 3, as the clutch and eggs are clearly lighter in colour than in stage 2 but eggs clearly comprise more yolk than in stage 3. A stage 4 clutch is in the process of hatching and can be recognised by primarily dark eggs without yolk and clearly visible embryos, the presence of prezoeae (newly hatched pre-larvae), and (later in the hatching period) empty egg casings and adhesive material (the clutch appears "mossy").*

Embryonic development was assessed on a regular basis and with increasing frequency closer to hatching by (1) using the same clutch staging done during the at-sea sampling, but with the addition of a stage 2.5 (Fig. 3.3) to capture the transition between stages 2 and 3, and (2) taking and preserving (in 65:35 ethanol: glycerine) a small sub-sample of eggs (10-20 from 3-4 haphazard locations within the clutch) for measuring the PEI of five to ten embryos from each

female for each sampling date. To minimise handling of the animals and potential egg loss, females' clutches were only assessed once a month from November through March, and then the monitoring was increased to every other week in April, and weekly in May and June, when egg development is accelerating. In July and August visual clutch staging was increased to daily with egg samples taken every other day.

The duration of clutch stages 2-4 and the rate of embryonic development during each stage were compared using one-way ANOVAs. The duration of each stage was assessed as the most and least conservative estimates given that sampling was not continuous (*i.e.*, sampling did not occur daily, thus the precise date of the end and onset of a stage were not known). The most conservative duration estimates were based on the time between the first and last dates on which a given stage was observed for a female. The least conservative estimates were based on the time between the last date the previous stage was observed plus one day, and the first date the following stage was observed minus one day for each female. The rate of clutch development was calculated as the slope of mean clutch PEI (µm) over time during each stage, resulting in a metric of mean daily growth rates in embryonic eye diameter within each clutch stage. Stage 1 was excluded from the analyses as all females' clutches were in transition between stages 1 and 2 at the beginning of the study, and because stage 1 clutches are not relevant for investigating spring and summer embryonic development leading to hatching (*i.e.*, scope of this study).

3.2.3 Study areas and temperature data

For the purpose of this study the sGSL was divided into 4 sub-areas (Fig. 3.2) based on a combination of spatial variation in thermal regime (Table 3.1; J. Chassé, DFO, pers. comm. 2015) and ovigerous female sampling locations within the nine sub-regions in the sGSL

managed by DFO Gulf Region (Comeau *et al.* 2008). Spatial differences in seasonal CDD provided the primary means of dividing areas, while the distribution of ovigerous female sampling locations dictated the outer boundary (distance from shore) of each area once regions had been set based on temperature. The four areas were the south shore of Chaleur Bay (SCB), eastern New Brunswick between Miscou and Escuminac (ENB), the Northumberland Strait (NS), and the north shore of Prince Edward Island (NPEI), (Fig. 3.2). All data originating from a same area were pooled. In the two largest areas (NS and NPEI) between 4 and 13 ports were sampled annually, respectively, while in the two smaller areas (SCB, ENB) 2 to 3 ports were sampled annually. Between 600 and 1,100 traps were hauled weekly for an average of four to seven weeks annually in the different areas. For each area, years with fewer than three weeks sampled (*i.e.,* insufficient data for regression, see section 3.2.4) were excluded from analyses. An average of 250 ovigerous females were sampled each week with 1,300 ovigerous females sampled annually on average. While the range of years sampled in each area was 1989-2014, not every year was sampled in each area; the total number of years sampled ranged from 8 to 25 years in different areas (Table 3.1). In general, lobsters in the sGSL are believed to move relatively little, with average displacement of less than 10 km a year (Comeau and Savoie 2002b; Bowlby *et al.* 2007), thus significant movement of females between study areas was likely not a frequent occurrence.

The 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 (NEMO, Madec 2012) and the setup is described in Brickman and Drozdowski (2012). The ice model is LIM2 (Goosse and Fichefet 1999; Madec *et al.* 1998) and includes thermodynamic and rheology components. The coupled model domain covers the Gulf of St. Lawrence, the Scotian Shelf, and the Gulf of Maine at a horizontal resolution of 1/12° 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 runoff 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 NCEP 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 to 2015 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 two years prior to the biological data and cover different time periods potentially consequential to hatching time.

3.2.4 Indices for the timing of egg hatching

Given that sampling was restricted to the commercial fishing season, we are unable to directly assess temporal changes in the peak larval hatching period, as the fishing seasons end prior to the main summer hatching period of July and August (Ennis 1995; Waddy and Aiken 1995; Miller *et al.* 2016). As such, we assessed temporal changes in the timing of hatching through two indirect metrics: (1) the change in ratio of ovigerous females with stages 3+4 (mature) to stages 1+2 (immature) each spring, and (2) the first week in spring when females with mature 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 mature 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 relative occurrence of females with mature clutches during the spring fishing season is an indicator of the site-level (not individual clutches) "rate of clutch development" (RCD) in the spring following the winter diapause, and will henceforth be referred to as such. Based on the premise that a more rapid progression from immature to mature clutches in the spring should result in earlier hatching of larvae, we suggest that change in RCD across years likely reflects population-level changes in the hatching period. For each year we calculated the ratio of ovigerous females with mature to immature clutches for each sampling week in each area. For weeks when only mature clutches were observed, we substituted a value of 1 for the zero count of immature clutches to allow a ratio to be estimated. Similarly, for weeks when no mature clutches were observed we substituted the counts of 0 with 0.5 to ensure a ratio greater than zero; 0.5 was chosen rather than 1 as a single female with a mature clutch 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 immature (stages 1-2) through winter prior to embryo development in the spring. Week 15 was chosen as modeled bottom temperature then consistently averaged around 0°C (-1.7° to 0.9°), *i.e.,* no embryonic development would be occurring. We set the ratio of mature to immature clutches at this forced zero to 0.0010, to be just below the lowest observed ratio of 0.0011. We subsequently log transformed all ratios to linearize plots of ratios by sampling week and calculated the linear slope of change in ratios over time each spring for each year in each area; this slope is the RCD. We only calculated the

RCD for year–area combinations with a minimum of three sampling weeks and R^2 greater than 0.4; the latter excluded 6 of 70 data points.

3.2.5 Statistical analyses

Evidence of an earlier hatching period between 1989 and 2014 was investigated using linear regressions, where OH and RCD were the dependent variables regressed against year, with geographic area set as a random factor. The potential role of temperature in influencing these trends was investigated using linear regressions compared with AICc model selection. We used the latter to assess the time period(s) during the reproductive cycle in which temperature seemed most influential to the RCD and OH.

In attempting to determine how temperature might affect hatching, we considered temperature starting the fall following mating in a typical two-year reproductive cycle. We chose to consider temperature only from this time onwards, as it is after the final moult pre-spawn that females expend energy primarily on ovarian development rather than somatic growth. To reduce correlations among independent variables, we only estimated temperature over broad time periods that might be important to ovarian and embryonic development prior to hatching. Following mating, the biological processes and temperature periods considered were (1) primary vitellogenesis (fall-winter 1.5 yr. preceding hatching), (2) secondary vitellogenesis and spawning (spring-summer the year preceding hatching), (3) early embryonic development (fall-winter the year preceding hatching) and (4) late embryonic development (spring prior to hatching).

We built a total of 32 models, which were based on all combinations of the four temperature parameters and an area term, including their exclusion from models, and then compared these

with AIC. The CDD during the four seasons of the reproductive cycle and study area resulted in a total of 32 models fitted (including null models) for each of the two hatching metrics. Area was used as a random term in these models (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 the biotic and abiotic conditions in these areas. We used 3.4°C as the threshold for degree-days, given embryonic development 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 ($p<0.05$).

3.3. Results

3.3.1 Biological relevancy of visual clutch staging

Our laboratory study confirmed that clutch stage 3 can be used as a reliable indicator for imminent hatching. All clutches reached stage 2 by mid-December and remained in this stage throughout the winter. The duration of clutch stages 2, 2.5, 3 and 4 differed significantly ($F_{3,36}=559.85$, $p<0.0001$ and $F_{3,36}=899.02$, $p<0.0001$; most and least conservative estimates, respectively), as did the rate of embryonic development during each stage ($F_{3,29}=11.04$, $p<0.0001$). The mean duration of stage 2 was significantly longer than stages 2.5, 3 and 4 (Tukey HSD, all $p<0.05$), and embryonic development during clutch stage 2 was significantly slower than during stages 2.5 and 3 (Tukey HSD, all $p<0.05$). On average, embryos developed at a rate of only 0.4 µm day^{-1} during stage 2 (range 0-0.7 µm day^{-1}), for an average total growth in PEI of approximately 80 µm over 192 and 223 days for the most and least conservative estimate, respectively. Embryonic development during clutch stage 3 was markedly faster, with an average increase in PEI of 11.0 µm day^{-1} (6-24 µm day^{-1}), and only lasted between five and

nine days. Embryonic development was also rapid during the stage 2.5 transitional phase, with an average increase in PEI of 7.7 µm day^{-1} (3-15 µm day^{-1}) and duration of 5-13 days. Hatching itself (stage 4) lasted on average 16 days, with a slowing of embryonic development to an average of 3.0 µm day^{-1} (0-9 µm day^{-1}).

3.3.2 Temporal trends in the rate of clutch development and onset-of-hatching

Our results suggest that female lobsters have been hatching their eggs progressively earlier in the season between 1989 and 2014 in the sGSL. There has been a significant increase in the spring rate of clutch development (RCD) over the study period ($F_{1,86.95}$=14.52; R^2=0.12, p=0.0003) (Fig. 3.4a). Based on the model slope, the RCD occurred 1.4 times more rapidly at the end compared to the start of the study period. The onset-of-hatching (OH) has also been occurring progressively and significantly earlier over the study period ($F_{1,79.32}$=35.16; R^2=0.34, p<0.0001) (Fig. 3.4b). Based on the model slope OH occurred on average 5 weeks earlier at the end relative to the start of the study period.

3.3.3 Relationship between temperature and timing of hatching

Modeled 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*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*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*Year: $F_{3,96}$=0.79, p=0.50) (Fig. 3.5; Table 3.1). The temperature increase during the fall has been pronounced, representing 20%-60% more CDD from 1989 to 2014, in contrast to a 5% to 15%

reduction in the summer. Temperature during winter did not surpass 3.4 degrees, resulting in zero CDD, negating any need for statistical analysis.

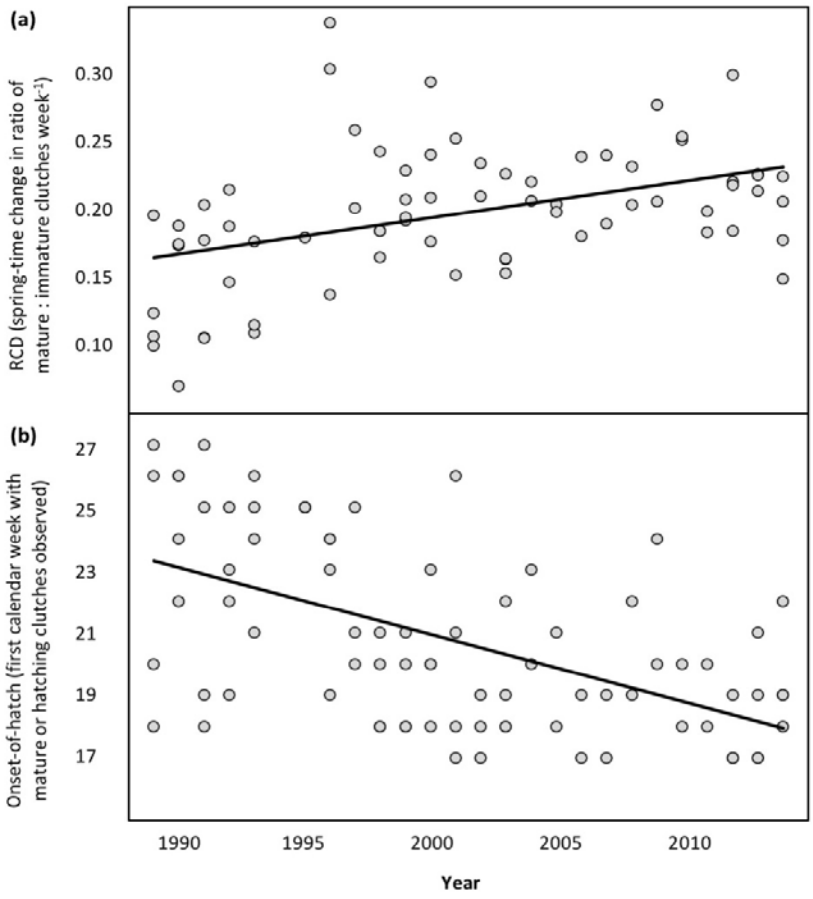

Figure 3.4: *Temporal trends in two indices of the timing of hatching 1989-2014 in 4 study areas in the southern Gulf of St. Lawrence: (a) rate of clutch development (RCD), indicated by the rate of change in ratios of ovigerous females with mature vs. immature clutches (stages 3-4 vs. 1-2) through the 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).*

The model that best explained inter-annual variation in the RCD in the spring included the parameters CDD during secondary vitellogenesis and spawning (*i.e.,* the spring-summer one year prior to hatching) and CDD during early embryogenesis (*i.e.,* fall-winter prior to hatching).

This model comprised 21% of the AICc weight of the 32 models compared (Table 3.2). Overall, the model was significant ($F_{2,68}$=3.86, p=0.026) and had R^2=0.10. The model showed a positive relationship between CDD during early embryogenesis and the 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 the RCD ($F_{1,68}$=-1.61, p=0.11), suggesting a warmer summer the year of spawning results in slower RCD, and presumably a later hatching, the following year (Table 3.2). CDD during early embryogenesis accounted for considerably more of the variation in the RCD explained by the model than did CDD during spawning (75% and 25%, respectively). The second best model, which had nearly as much AICc weight as the best model (17% versus 19%) and a Delta AIC <2, included only CDD during early embryogenesis (Table 3.2).

The model that best explained variation in OH included the parameters CDD during primary vitellogenesis (*i.e.,* the fall-winter prior to spawning, thus, approximately 1.5 years prior to OH) and CDD during secondary vitellogenesis and spawning (Table 3.3). This model comprised 50% of the AICc weight of the 32 models compared (Table 3.3). Overall, the model was highly significant ($F_{2,79}$=9.94, p<0.0001) and had R^2=0.20. The model showed a negative relationship between onset-of-hatching and CDD during primary vitellogenesis ($F_{1,79}$=-4.26, p<0.0001), indicating that higher temperature during this period results in earlier onset-of-hatching. 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 3.3). CDD during primary 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). OH was sensitive to the frequency of

sampling each year; there was a negative relationship between onset-of-hatching and the number of at-sea-sampling events in a year ($F_{1,80}$=14.88, p=0.0002, R^2=0.16), with OH more likely to be observed earlier in the spring in years and locations when sampling occurred more often during the fishing season. This is not unexpected given fewer sampling events limit the time when OH can be observed, and represents a source of error in this metric.

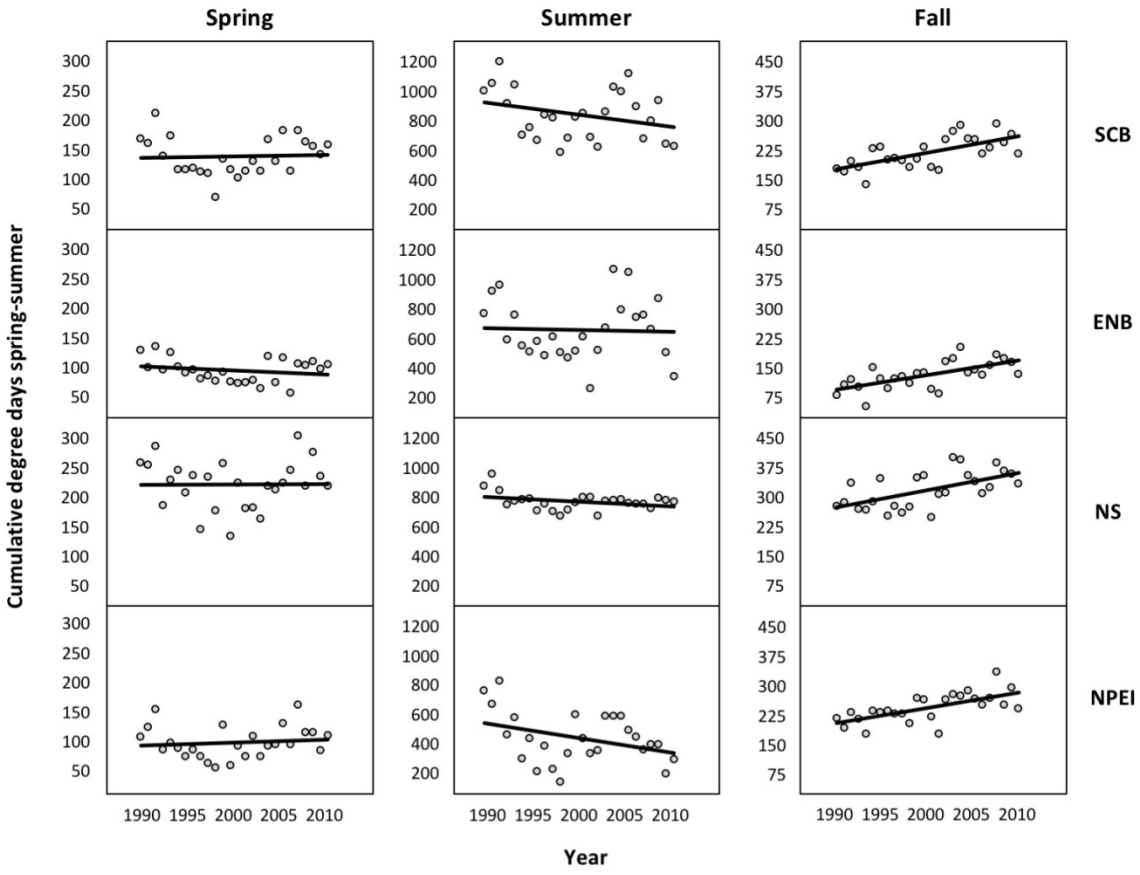

Figure 3.5: *Temporal trends (1989-2014) in cumulative degree-days (CDD) above 3.4°C in spring (April – June), summer (July– September) and fall (October – December); winter (January to March is not shown as CDD never exceeded zero. There are clear spatial differences in CDD in all three seasons (spring: $F_{5,144}$=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 show an increase over the study period ($F_{1,144}$=87.44, p<0.0001); spring CDD show no temporal trends ($F_{1,144}$=0.21, p=0.65) and summer CDD show 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*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).*

Table 3.2: *AIC model selection for spatial and temporal variation in the rate of clutch development (RCD) in relation to temperature during different phases of the reproductive cycle.*

model*	parameter estimate†	k‡	AICc	Δ§	AICc weight‖
CDD spawning CDD early embryogenesis	-4.646e-5 0.000283	3	-219.61	0.00	20.9%
CDD early embryogenesis	0.000017	2	-219.19	0.42	16.9%
CDD early embryogenesis CDD late embryogenesis	0.000242 -0.000121	3	-218.37	1.25	11.2%
CDD gametogenesis	0.000144	2	-217.52	2.10	7.3%
CDD spawning CDD early embryogenesis CDD late embryogenesis	-5.570e-5 0.000282 4.024e-5	4	-217.35	2.26	6.7%

* The rate of clutch development was indicated by the change in ratios of ovigerous females with mature vs. immature clutches (stage 3-4 vs. 1-2) through the spring each year. Temperature considered are cumulative degree days >3.4°C over six month periods (spring/summer [Apr-Sep] and fall/winter [Oct- Mar]) starting from the spring of sampling immediately prior to larvae hatching (summer months excl.) and going back to the spring/summer 3 years prior when the previous clutch was spawned and the onset of ovarian development for the current clutch occurred.

† Parameter estimates (coefficients) are given for temperature indices only; intercepts are not shown.

‡ K indicates the number of parameters in each model (number of variables plus intercept).

§ The best-fit model is indicated by the lowest AICc value (Δ=0).

‖ 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).

3.4. Discussion

3.4.1 Timing of egg hatching in the southern Gulf of St. Lawrence

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 mature (stages 3-4) to immature (stages 1-2) clutches through the spring fishing season, which we refer to as the "rate of clutch development" (RCD), occurs on average 40% faster across the study domain now than it did 25 years ago. Secondly, we showed that the first appearance of ovigerous females with mature or hatching clutches, which we refer to as the "onset-of-

hatching" (OH), was observed on average 5 weeks earlier. Thus, we believe our results provide a compelling case that hatching has been occurring progressively earlier between 1989 and 2014.

Both the RCD and the 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

Table 3.3: *AIC model selection for trends in onset-of-hatching (OH) in relation to temperature during different phases of the reproductive cycle.*

model*	parameter estimate†	k‡	AICc	Δ§	AICc weight‖
CDD gametogenesis CDD spawning	-0.022914 0.005620	3	401.43	0.00	49.7%
CDD gametogenesis CDD spawning CDD late embryogenesis	-0.023081 0.005012 0.002822	4	403.60	2.16	16.9%
CDD gametogenesis CDD spawning CDD early embryogenesis	-0.021342 0.005716 -0.002032	4	403.65	2.21	16.5%
CDD gametogenesis CDD late embryogenesis	-0.019378 0.017390	3	405.71	4.27	5.9%
CDD gametogenesis CDD spawning CDD early embryogenesis CDD late embryogenesis	-0.021637 0.005127 -0.001857 0.002695	5	405.88	4.45	5.4%

*Onset-of-hatching is indicated by the first calendar week with ovigerous females with mature or hatching (stages 3-4) clutches observed each year. Temperature considered are cumulative degree days >3.4°C over six month periods (spring/summer [Apr-Sep] and fall/winter [Oct- Mar]) starting from the spring of sampling immediately prior to larvae hatching (summer months excl.) and going back to the spring/summer 3 years prior when the previous clutch was spawned and the onset of ovarian development for the current clutch occurred.

† Parameter estimates (coefficients) are given for temperature indices only; intercepts are not shown.

‡ K indicates the number of parameters in each model (number of variables plus intercept).

§ The best-fit model is indicated by the lowest AICc value (Δ=0).

‖ 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).

in different areas, and in such instances, we likely over-estimated the OH, even though we partially corrected for this by setting OH as the week prior to the onset of sampling in these cases. The frequency with which this occurred increased later in the study period (33%, 46%, 67% of cases (year-area combination) in 1989-1997, 1998-2005, 2006-2014, respectively), which means that we likely under-estimated to some extent the true advancement in onset-of-hatching that occurred in the sGSL over our study period. Also, no females with mature clutches were reported during the fishing season in a particular area 5 times between 1989 and 1991, in which case we arbitrarily set onset-of-hatching as the week following the end of sampling. This was consistent with later hatching during the earlier part of our survey, and further suggests that our data likely under-report the true advancement of hatching.

Our laboratory study provided quantitative estimates for the duration of different stages used during the at-sea sampling visual clutch staging, which enhanced our ability to use these qualitative data to assess changes in the timing of the hatching period. In particular, it justified grouping stage 3 and 4 clutches as indicative of hatching, because the rate of embryo development in stage 3 clutches was fast and hatching was forthcoming (within one week on average). While this visual clutch staging has been in use in the field for many years, and in multiple sampling programs, this is the first study to quantify the relationship between visual stages and patterns of embryonic development. Without the confirmation that hatching is imminent when a clutch reaches stage 3, we would not have been able to use these fisheries data to investigate the timing of OH in American lobster, as stage 4 clutches were not distinguished from stage 3 clutches in the sampling protocol until 2004.

Our study also showed that there is a biologically relevant transition between visual clutch stages 2 and 3, which may be worth categorizing depending on research goals. This transitional

phase (identified as stage 2.5) clearly differs visually from stage 2, with eggs being more transparent and lighter in color, and from stage 3, in that fair amounts of yolk remain in the eggs. Egg clutches during the winter diapause are normally in stage 2 with virtually no embryonic development. In stage 2.5, however, embryonic development was rapid, suggesting that it reflects the end of the diapause (*i.e.*, winter period) when embryonic development resumes. Hence, ovigerous females with transitioning clutches (*i.e.*, stage 2.5) should generally also be classified as stage 3, rather than stage 2, as the embryonic development was more comparable to the former than the latter. However, to precisely identify the timing of hatching, it is advisable to classify stage 3 clutches as accurately as possible and categorize stage 2.5 as stage 2 (as done during this study), or ideally add stage 2.5 to the categorization of visual clutch stages.

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

We found strong evidence that temperature during parts of the female reproductive cycle influences the timing of hatching of American lobster larvae in the sGSL, which is not surprising given known thermal regulation of several aspects of lobster biology and reproduction (Waddy and Aiken 1995). The rate of embryonic development increases with temperature (Perkins 1972; Gendron and Ouellet 2009), and the number of degree-days available for embryonic development in the fall has increased over the past 25 years. It is therefore anticipated that the latter results in more embryonic development following spawning and prior to the winter diapause. Up to 80% of embryogenesis can be completed prior to the winter period (Gendron and Ouellet 2009). Higher temperature in the fall presumably allows more development to occur then, leaving less development necessary in the spring preceding egg hatching and leading to earlier larval release. This assumption is supported by our results suggesting that

temperature during early embryogenesis is the best predictor of the RCD at the site level. Given that winter temperature did not exceed the degree-days threshold, this effect of temperature during early embryogenesis is presumably due only to more development prior to the winter diapause, rather than a cessation of the diapause period.

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 hatch in nature based on spring temperature and temperature-based embryonic development functions (Miller *et al*. 2016), the lack of a relationship in our study between inter-annual variation in spring temperature and our two metrics of hatching time is somewhat surprising. This lack of relationship may be related to the imprecision of our hatch metrics (see above) and/or temperature data, as well as to an imperfect match between temperature data and sampling time each spring (*i.e.*, spring-time temperature considered April-June with at-sea-sampling occurring in May and June). 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). Modeled temperature in our study showed interannual variation of 30% around the mean CDD in spring, compared to only 10% in the fall. That embryos might be able to progress to hatch 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 (Chapter 2), increasing the likelihood that embryos may have the ability to deplete their yolk reserves and proceed to visual clutch staging categories 3 and 4 and hatch irrespective of the degree-days available for embryogenesis during spring.

We also found evidence that temperature during primary vitellogenesis plays an important role in regulating hatching time. Rising temperature in the fall may not only affect early embryonic development, but also ovarian development a year and a half prior to hatching, as suggested by the relationship between CDD during this time and onset-of-hatching. Like embryonic development, ovarian development and subsequent spawning is also temperature-dependent (Aiken and Waddy 1980). We propose that warmer water during primary vitellogenesis may lead to earlier spawning, amplifying the effects of more degree-days available for embryonic development in the fall a year later. Primary vitellogenesis occurs over several months in the spring, summer and fall the year before spawning, resulting in a slow increase in ovarian size (Aiken and Waddy 1980; Waddy and Aiken 1995) before the ovary enters a winter diapause period (Fig. 3.1). 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 the ovarian development cycle in the sGSL indicate that secondary vitellogenesis is well underway in the fall prior to the spawning season (M. Comeau, DFO pers. comm. 2017). As the rate of primary vitellogenesis is believed to increase positively with temperature (Waddy and Aiken 1995; Waddy *et al.* 1995), we propose that the mechanism behind the inverse relationship temperature during the fall-winter prior to spawning and OH approximately 1.5 years later is an increase in fall CDD over the past 25 years allowing the completion of primary vitellogenesis and the initiation of secondary vitellogenesis prior to the winter diapause. Given the ovary diapause during winter and the observation that winter months never contribute a single degree-day, it is likely that in the sGSL only fall temperature affects vitellogenesis.

We do not have a good explanation for the counterintuitive relationship observed where higher spring-summer temperature the year of secondary vitellogenesis and spawning results in slower RCD and later OH the following year compared to colder summers. This result is

counterintuitive, because we would expect colder summers to result in delayed secondary vitellogenesis and spawning (Aiken and Waddy 1980, 1982; Waddy and Aiken 1995), and hence potentially delayed hatching as well. The observation that hatching has advanced despite cooler summers may suggest that these cooler summers have little impact on spawning time, and the negative relation observed may be spurious. As the onset of secondary vitellogenesis has advanced to the previous fall (M. Comeau, personal observations), which may mean it is not delayed by colder spring/summer temperatures (*i.e.*, due to sufficient CDD as fall temperature has increased).

3.4.3 Impacts of an earlier timing of hatching

In eastern Canada, most lobster larvae hatch during summer months, with a peak in August (Chapter 2). There is potential for considerable ecological implications of the timing of larval release changing primarily 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 *et al*. 2000; Chassé and Miller 2010), and thus likely critical 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, the advancement of spring larval release we document in this study does not appear to be associated with an increase in spring-summer temperature (in fact, the latter has decreased over the study period), suggesting that larvae may now be released into colder water, and hence experience slower development, greater dispersal and greater mortality, than they did 25 years ago.

An earlier timing of hatching driven by past thermal conditions 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, and environmental changes during the initiation of reproduction (*i.e*., during ovarian development, spawning and embryonic development) do not predict or reflect similar environmental changes during the planktonic larval phase (Visser *et al*. 1998; Edwards and Richardson 2004; Durant *et al.* 2007). American lobster larvae are active predators, feeding on a variety of other zooplankton and at times phytoplankton (Ennis 1995). Early larval stages I and II feed on smaller zooplankton (approximately 200-600 µm) (Harding *et al*. 1983; Ennis 1995), while stage III larvae and postlarvae (stage IV) seem to prefer feeding on larger zooplankton (up to approximately 1,500 µm), including insects, fish eggs, gastropod larvae and other decapod larvae (Harding *et al*. 1983; Ennis 1995). Given lobster larvae appear to be hatching earlier in the summer mostly due to temperature affecting ovarian and (early) embryonic development up to 1.5 years prior to hatching, they may face a temporal mismatch with other zooplankton upon which they prey. It seems unlikely in fact that the prey of lobster have seen a similar advancement in their presence in the plankton, given the shorter life cycles of most zooplankton prey species (approximately one 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, such as the copepods and holozooplankton that dominate the diet of early larval stages (Ennis 1995), is therefore clearly possible, and similar scenarios have been documented in various zooplankton, crustaceans, fishes and birds (*e.g*.,

Gotceitas *et al.* 1996; Visser *et al*. 1998; Edwards and Richardson 2004; Durant *et al.* 2007; Asch 2015). Food limitation is generally not an important factor in larval mortality (Ennis 1995). However, if the timing of hatching is altered (*i.e.,* an earlier onset due to climate change) resulting in a decoupling between peak prey abundance and lobster larval release, starvation from food limitation could result in a mass larval mortality jeopardizing benthic lobster recruitment. This hypothesized decoupling causing massive larval mortality might already be detected in the Gulf of Maine (Joshua Corloni, New Hampshire Fish and Game Department, NH, USA, pers. comm. 2017) as the historically high level of spawning stock biomass (ASMFS 2015) has been associated with a significant increase in abundance of stage I larvae but a significant decrease in postlarvae and young-of-the-year since 2011 (http://umaine.edu/wahlelab/american-lobster-settlement-index-alsi/american-lobster-settlement-index/, accessed 15 August 2017).

An earlier onset-of-hatching also has the potential to affect larval drift trajectories and connectivity patterns, both through altering the duration of the pelagic phase, and thus the drift time, but also by exposing the larvae to different currents (Xue *et al.* 2008; Chassé and Miller 2010; Quinn 2014). Based on a biophysical model of larval drift in the Gulf of Maine (Xue *et al.* 2008), early egg hatching in lower water temperature observed in early spring-summer likely results in a prolonged larval phase. Similarly, a larval drift model in the sGSL predicts significantly lower survival for larvae released in locations where the peak hatching period occurred earlier in the 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 an earlier hatching period may expose larvae to different wind-driven surface currents not normally experienced during the pelagic phase, which has been shown to have great impacts on spatial and temporal patterns in postlarval supply and subsequent settlement

(Harding *et al* 1982; Wahle and Incze 1997; Incze *et al.* 2000; Pershing *et al.* 2012). Seasonal variation in temperature and currents is predicted to result in variation in drift time and distance in excess of one month and 100 km, respectively, of larvae released from various locations in the sGSL at different times in a four to five week window during the summer, and up to >2 months and >300 km over a 10 week window (B. Quinn, Biology Department, University of New Brunswick, Saint John, pers. comm. 2016). Thus, it seems clear that even relatively modest changes in the timing of hatching (especially an early onset-of-hatching) have the potential to alter connectivity and survival patterns of American lobster larvae.

The extent to which changes in OH and larval release would influence subsequent recruitment to the fishery depends on the degree to which recruitment is governed by pre- versus post-settlement processes. Stock–recruitment dynamics are generally poorly understood for lobster and crab fisheries, including the American lobster (Wahle 2003). Prior to the rapid increase of landings to record highs starting in the 1980s, fisheries recruitment had been believed to be largely independent of spawning stock biomass and larval supply, unless spawning stocks declined to below some critical level (Fogarty and Idoine 1986; Wahle 2003). Instead, recruitment was believed to be driven largely by habitat limitations and low carrying capacities of juvenile cobble nursery habitats, creating a bottleneck effect (Fogarty an Idoine 1986; Wahle 2003). This bottleneck may have been released with the collapse of groundfish and subsequent release from predation for juvenile lobster, which may have increased survival in alternate nursery habitats (Wahle 2003). However, other studies have reported no relationship between groundfish and lobster predation, particularly in the sGSL where our study took place (Hanson and Lanteigne 2000; Link and Garrison 2002; Smith *et al.* 2007; Hanson 2009; Boudreau and Worm 2010; Hanson *et al*. 2014), and significant positive relationships between postlarval supply, young-of-the-year abundance on the benthos, and pre-recruit sizes of lobster have

been documented (Wahle and Incze 1997; Incze *et al*. 1997, 2000; Ouellet and Sainte-Marie 1998; Burdett-Coutts *et al.* 2014; Rondeau *et al*. 2015; DFO 2016). This link between postlarval supply and recruitment to the fishery may vary spatially (*e.g*., Miller *et al.* 2006; Pershing *et al.* 2012), and be confounded by factors such as disease (Wahle *et al.* 2009). The effect on the fishery of potential reductions in larval survival are therefore not straightforward to predict, but will likely have ramifications in the sGSL.

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), based on clear signals provided by spring fisheries monitoring data. There is no evidence of a warming trend in the spring and summer over this time period, but there has been a clear warming trend in the fall. It is thus not surprising that the latter appears to be an important driver for the earlier hatching time. The relatively narrow annual window provided by the spring fishery to observe changes in the RCD and the OH may have caused an under-estimation of the true advancement of hatching that has occurred in the sGSL. The implications of the changes in phenology we document are not clear, but negative impacts for the fishery are possible. Hatching earlier in the season most likely results in larvae being exposed to colder water, causing prolonged development (MacKenzie 1988; Quinn *et al.* 2013). As mortality is believed to be considerably higher during the pelagic phase than after settlement onto the bottom (Lawton and Lavalli 1995), a prolonged drift time until settlement could negatively impact recruitment of settlers. Such an effect could also be amplified if larval survival is further reduced by changes in food availability following a possible loss of synchronicity with prey species. An earlier timing of hatching will also, as already observed, result in increased catch rates and handling of ovigerous females with mature clutches during the spring fishing seasons. Given that eggs are more readily lost from a female's abdomen in mature clutches than less developed ones (Talbot *et al.* 1984),

increased handling of females while their clutches are mature may result in increased egg loss and further negatively impact larval supply (Tang 2016). What is clear is that further research into effects of climate change on lobster phenology is merited.

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CHAPTER 4: General discussion

4.1 Life histories of marine invertebrates are too rigidly defined

Hadfield and Strathmann (1996) pointed out two decades ago that documented life-history traits of marine invertebrates have not captured the full range of variability because they have been based on studies using low sample sizes. Life-history traits such as growth rates, size- and age-at-maturity, fecundity and phenology of marine organisms can vary markedly across space and time (*e.g.*, Campbell and Robinson 1983; Wanless *et al.* 2008; Mollet *et al.* 2013; Pershing *et al.* 2015). The three data chapters of this thesis have documented considerable temporal, spatial and inter-individual variability in reproductive biology attributes of the American lobster *Homarus americanus*. Such variability in reproductive traits has been documented in a variety of marine invertebrates. For example, certain polychaete and mollusc species can produce both feeding (planktotrophic) and non-feeding (lecithotrophic) larvae, exhibit both pelagic and benthic larvae, and release both pre- and post-metamorphic larvae from a same clutch (Hadfield and Strathmann 1996). Yet most studies likely have not captured the full range of variability in life-history traits and the field as a whole has done too little to assess the repeatability and generalisability of research findings (Hadfield and Strathmann 1996).

Twenty years after Hadfield and Strathmann's review (1996), little appears to have changed in marine invertebrate research, and most studies still fail to adequately consider or report trait variability. For example, the search engine Scopus produces 24 publications in 2016 and 2017 on ecological studies (*i.e.*, not aquacultural or ecotoxicological) investigating "marine invertebrate reproduction", on taxa including crustaceans, echinoderms, molluscs and ascidians, and over half of these (14) studied individuals from a single location (Collin and

Ochoa 2016; Krampah *et al.* 2016; Leite-Castro *et al.* 2016; Mendo *et al.* 2016; Peck *et al.* 2016; Rey *et al.* 2016; Baskur *et al.* 2017; Collin *et al.* 2017; Kim *et al.* 2017; Kovalyova 2017; Phillippi and Yund 2017; Rey *et al.* 2017; Ru *et al.* 2017; Thyrring *et al.* 2017). An additional two studies sampled individuals from multiple sites within a narrow spatial range and pooled them (Herrera *et al.* 2017; Rangel *et al.* 2017), and five did not adequately disclose sampling locations (Eads *et al.* 2016; Xue *et al.* 2016; Burukovsky 2017; Mericer *et al.* 2017; Verkaik *et al.* 2017). As a result, 88% of the studies did not consider spatial variation in reproductive traits (the remaining 12% were: Denly and Metaxas 2017; Gaitán-Espitia *et al.* 2017: Triday-Portella *et al.* 2017). Inter-individual differences were generally better considered in the sense that tens (sometimes hundreds) of individuals were used in most studies, yet six studies used 10 or fewer individuals (Peck *et al.* 2016; Rey *et al.* 2016; Xue *et al.* 2016; Mericer *et al.* 2017; Phillippi and Yund 2017; Thyrring *et al.* 2017) and inter-individual differences were rarely explicitly reported; only one of the 24 studies disclosed variance components and visualised variability beyond reporting mean values with confidence intervals (Denly and Metaxas 2017).

Within-clutch (*i.e.,* sibling) variation was also rarely considered among the 24 studies reviewed. Rey *et al.* (2016) did specifically set out to investigate within-clutch variation in maternal provisioning and cumulative lipid metabolism of embryos by the end of the brooding period in the green crab (*Carcinus maenas*), and compared fatty acid composition of embryos from different parts of the clutch (left, right, peripheral and interior) in early and late development. They concluded that there is no within-clutch variation in lipid composition of green crab embryos at either point in development (Rey *et al.* 2016). However, it is important to note that the authors only considered "spatial" variation within the clutches and not stochastic variation among embryos within a clutch; embryos from the different areas within a clutch were pooled for lipid extractions (Rey *et al.* 2016). Consequently, the conclusion of homogeneous maternal

provisioning and embryonic lipid metabolism is based on the assumption that no systematic (*i.e.,* spatial) variability within the clutch implies homogeneity among all embryos. In the other 5 studies that assessed various aspects of development at the level of individual embryos, none considered this variability in analyses and inferences (Collin and Ochoa 2016; Peck *et al.* 2016; Bascur *et al.* 2017; Rey *et al.* 2017; Triday-Portella *et al.* 2017).

There exists a considerable body of research regarding the reproductive biology and life-history of clawed lobsters (*H. americanus, H. gammarus* and *Nephrops norvegicus*), to which one or several of the following applies: (1) inferences were based on a very limited number of females, (2) the authors failed to fully report variability in the parameters studied, and (3) the study failed to consider spatial variation. For example, in their study of spawning, egg attachment and retention, Talbot *et al.* (1984) based their classification scheme of clutch fullness on a single female. Whereas the latter is an extreme case of low sample size, studies investigating morphology, energetics and development of embryos have frequently been limited to 5 or fewer clutches per treatment (*e.g.*, Perkins 1972; Helluy and Beltz 1991; Pochelon *et al.* 2011; Leal *et al.* 2013), or failed to disclose the number of females and embryos tested (*e.g.,* Davis 1964; Perkins 1972). Sibert *et al.* (2004) documented considerable within- and among-clutch variation in egg dry weight, diameter, lipid and protein content, yet did so using only 7 females from a single site. Most laboratory studies investigating the influence of temperature on embryonic development have used fewer than 10 females per treatment and/or studied females from a single area (Perkins 1972; Gendron and Ouellet 2009; Goldstein and Watson 2015). Studies investigating thermal histories of ovigerous females and patterns of hatching in the field, while typically using tens of females, have predominantly been based on a single study site (*e.g.,* Ennis 1975; Cowan *et al.* 2007); the same applies to several studies concerning the role of environmental factors in the regulation of spawning (*e.g.,* Aiken and Waddy 1986;

1989). Barret *et al.* (2017) looked for evidence of local adaptation in temperature-dependent postlarval settlement behaviour and found no effect of maternal origin. However, only five to ten postlarvae from a pool comprised of larvae from ten to twelve females were used per treatment (Barret *et al.* 2017), which makes it entirely possible that unaccounted variation among and within clutches masked any effect of maternal origin.

Logistical challenges around investigating variability and its sources is an obvious reason for this prevalence of low sample sizes in life-history research, and the subsequent tendency to underestimate trait variability. This practical constraint is inevitable in many cases, making follow-up studies and further replication an important strategy to ensure our understanding of marine invertebrate (and presumably also vertebrate) life-history traits is accurate. Two key steps in improving future study design and data reporting habits are to (1) review what is known about variability in life-history traits and its sources, and (2) identify the implications of this variability to robust design of future research and fisheries management. For the remainder of this discussion I attempt to address these two points for American lobster.

4.2 There is considerable variability in life-history traits of American lobster

The three data chapters in this thesis utilised a unique combination of historical data, fisheries monitoring data, and modeling to quantify spatial, temporal and inter-individual variability in female size-at-maturity (SM), hatching time, and variability in developmental status at hatching at hitherto unprecedented scales. This was done with extensive datasets, rarely rivalled in lobster research, resulting from collaboration with government scientists and lobster fishermen in different regions of eastern Canada. The traits investigated were studied across nearly the entire species´ range in Canada, whereas most research to date has focused on individuals from a single location. To my knowledge, only two studies have been conducted to date at a

comparable spatial scale (Currie and Schneider 2011 [female fecundity]; Raper and Schneider 2013 [growth rates]), and both collected limited new data, relying instead primarily on historic data where spatial and temporal variation were confounded. In addition to the large geographic scope, I utilised a combination of new and historic data to investigate temporal variability in size-at-maturity and hatching time during the past 25 to 80 years. As a result, this thesis investigated aspects of lobster egg production at spatial and temporal scales seldom seen in ecological studies.

4.2.1 Female size-at-maturity

Female American lobster SM in Canadian waters is highly variable spatially and follows a geographic pattern. The smallest carapace length (CL) at which females reach maturity (CL_{min}) is currently approximately 60 mm CL in parts of the southern Gulf of St. Lawrence (sGSL) and around Newfoundland, and as much as 60% larger (approximately 90 mm CL) in the Bay of Fundy; SM is generally intermediate along the Scotian Shelf (Chapter 1). In addition to these broad geographic patterns (approximately 1,000 km scale), SM can also vary by up to 10 mm CL among neighbouring Lobster Fishing Areas (LFAs) (approximately 10s to 100s km scales) (Watson *et al.* 2013; Chapter 1), which can mean a difference as large as one moult (*i.e.,* one year) (Comeau and Savoie 2001; Gendron and Sainte-Marie 2006). In any given location, females reach maturity over a range of sizes; the interquartile range in SM can be up to 20 mm CL, or up to approximately 20% of the median SM ($CL_{50\%}$) (Watson *et al.* 2013; Gaudette *et al.* 2014).

Female SM varies not only in space and among individuals, but also over time. A decline in SM had already been documented over the past 15 to 30 years in several areas of the southern part of the species´ range, from Long Island Sound (US) to the Bay of Fundy (Landers *et al.*

2001; Pugh *et al.* 2013; Gaudette *et al.* 2014; LeBris *et al.* 2017). I demonstrated that these declines are more geographically widespread, having occurred across the species' Canadian (*i.e.,* northern) range, and that the magnitude of declines has varied spatially (Chapter 1). I was also able to document that SM declines have likely been ongoing since the early part of the 1900s, and not only over the past two to three decades (Chapter 1). Female lobsters in most of eastern Canada currently reach maturity one to three moults (*i.e.,* one to three years) earlier than during the first half of the 20th century (Chapter 1). Female SM also shows interannual variation. The estimated size by which 50% of females have reached maturity ($CL_{50\%}$) in a location can vary significantly from one year to the next by up to 10 mm CL or more (Watson *et al.* 2013). I similarly demonstrated interannual variability in SM by documenting variation in CL_{min} up to 10 to 20 mm over one- to two-year periods (Chapter 1); these results were obtained after standardising for sampling effort across locations and years, given that measures of CL_{min} are sensitive to sampling intensity and the probability of capturing the very smallest mature females.

4.2.2 Hatching time

Hatching time also varies spatially, although the large-scale geographic patterns are not as evident as for female SM. Previous research has concluded that hatching typically occurs earlier in the southern relative to the northern part of the species' range, and in warmer relative to colder areas (Templeman 1936; Factor 1995). I showed a similar yet weak trend in Canadian waters, where the latest peak hatching occurred in the cooler waters of the Bay of Fundy and the Gaspé Peninsula (QC), and the earliest in the warmer waters of the sGSL (Chapter 2). However, I also showed that the differences in peak hatching time within and among these regions were frequently of similar magnitudes (Chapter 2), suggesting a lack of true large-scale

spatial patterns. In addition to spatial variation in peak hatching time, there is considerable variation among females of a same location; hatching time varies among females by up to several weeks, and the range in clutch development at any point in time shows an average range of 50%, and up to 70%, of embryonic development among females (Chapter 2). This is to the best of my knowledge the first time such inter-individual variation in hatching time has been shown, even though it was largely implicit in the lengthy hatching seasons seen in nature. Goldstein and Watson (2015) showed that ovigerous females tagged and released in a same location may release larvae at different times through either remaining resident inshore or moving offshore in the fall and remaining to hatch their larvae there (resulting in different temperature exposure and development rate of embryos), but they did not disclose variation in hatching time within the two groups of females and small sample size (<5) did not truly enable quantification of such variability.

This thesis has also documented that the start of the hatching period has advanced in the sGSL by approximately five weeks over the past 25 to 30 years (Chapter 3), which represents the first evidence of phenological changes in American lobster. It also documented considerable unexplained variation in the timing of hatching in the sGSL (Chapter 3), which has previously been hinted at in the literature (Factor 1995), but not quantified. While there has been a significant advancement in the onset-of-hatching in this region over the past 25 years, this progressive negative trend only accounts for approximately 35% of the inter-annual variation in the onset-of-hatching (Chapter 3). Similarly, while the location-level rate of clutch development is significantly more rapid now than 25 years ago, the progressive temporal trend only accounts for approximately 20% of the inter-annual variation observed in this trait (Chapter 3); meriting further research into the causes of interannual variability hatching time.

4.2.3 Variability in development status at hatch

Variability in the developmental status at hatching is a recent discovery in American lobster (Miller *et al.* 2016), and had until now been given little attention. Earlier research has treated the developmental stage at which embryos hatch, indicated by the embryo's average eye diameter (Perkins eye index or PEI), as a relatively fixed parameter. Perkins (1972), who established that embryonic eye size (PEI) serves as a good indicator of embryonic size, concluded that embryos hatch when the PEI reaches 560 µm and reported no variability around this estimate. Helluy and Beltz (1991), who studied the embryonic moult cycle and related it to PEI, concluded that 570 µm (±20) equates 100% development and disclosed no further variability in PEI-at-hatching. A degree of variability in mean PEI-at-hatching among clutches is evident from Figure 1.1 in Gendron and Ouellet (2009), but was not discussed; the authors stating only that the mean PEI-at-hatching is 550 µm. Miller *et al.* (2016) was the first to acknowledge and consider variability in developmental status at hatching in American lobster. The authors documented a range in PEI-at-hatching of 460-611 µm, or from 80% to 105% of development according to the scale developed by Helluy and Beltz (1991), in only 60 prezoeae (embryos recently released from the egg envelope, but which have yet to moult to stage I larvae) from 7 females in a single location (Cheticamp, NS). I further investigated and documented the extent of this variability. By sampling 2,500 prezoeae I revealed considerable variability in developmental status at hatching, showing that embryos may hatch over the staggering range of 40% to 120% of development (PEI 260-706 µm). At 50% development (PEI of ≈ 290 µm) organ development is complete and growth becomes the dominant process at

moult (Helluy and Beltz 1991); my findings suggest that lobster embryos may hatch at any time after this point.

Variability in developmental status at hatching occurs spatially, among females and within-clutches. Miller *et al.* (2016) found two-thirds of the variability documented within clutches (and one-third among, spatial variation not considered). Adding a spatial component, I found variability to be roughly equally distributed among the three sources (Chapter 2). I documented spatial variation in developmental status at hatching for the first time; PEI-at-hatching varied significantly among sampling locations by up to 35%, but without any obvious large-scale trends, varying primarily among locations (˜100 km scale) and not regions (˜1000 km scale; *e.g.,* Bay of Fundy vs. sGSL) (Chapter 2). There is also considerable variability in developmental status at hatching among different females' clutches. Miller *et al.* (2016) found that the mean clutch PEI-at-hatching varied by up to 49 µm among the seven females sampled. I found that the mean PEI-at-hatching among the clutches of 2 to 38 different females in a same location (mean = 10 per site, 188 total) varied by 100 µm (20%) on average, and up to 260 µm (45%) (Chapter 2). Miller *et al.* (2016) showed variation in PEI-at-hatching within a single clutch to be up to a 20% range in development, and I found it can be as high as 50% (Chapter 2). Such sibling variability is consistent with studies of other species; considerable variability in developmental status at hatching has been documented in for example echinoderms (Armstrong *et al.* 2013) and amphibians (Thumm and Mahony 2005). Sibling variation in American lobster exists in other traits as well, such as egg energetic content, egg size, and in size of newly released stage I larvae (Attard and Hudon 1987; Ouellet and Plante 2004; Sibert *et al.* 2004).

There was one scale of variability in life-history traits in American lobster that was not addressed in this thesis, and that has been relatively little addressed in the literature, which is that among clutches of a same female. Collin (2010) investigated such variability over three to seven consecutive clutches of two marine gastropods, *Crepidula atrasolea* and *C. ustulatulina*, and found that 55%-85% of variance in egg size was attributable to variability among eggs of a same female (spatial variation was not considered), which was split nearly equally between variability within and among a female´s clutches. This is an important observation as if a female´s clutches vary markedly through her lifetime it means the within-female component of variability in egg and larval attributes may be considerably higher than it appears in studies where only single clutches are considered (Collin 2010). This also means that much of the variability quantified among females at a given point in time may not represent true individual-level variability. The likelihood of variability among clutches of a same female makes variability among females and locations more difficult to interpret as their repeatability is unknown without comparing multiple clutches from each female, which is challenging with lobster given its long (typically 2-year) reproductive cycle. However, there is evidence that larger multiparous females produce larger eggs with higher energetic content than do smaller primiparous females (first time-spawners) (Ouellet and Plante 2004; Sibert *et al.* 2004), suggesting females may invest more energy in reproduction later in life when they have already spawned at least once before.

4.3 Causes and function of variability in life-history traits

The two broad mechanisms responsible for spatial, temporal and individual variability in life-history traits are local adaptation and phenotypic plasticity. Local adaptation is genetic variation among populations in different geographic areas (or over time), created by

environmental differences resulting in varying selection pressures (Sanford and Kelly 2011). Phenotypic plasticity is the ability of an individual with a particular genotype to display different phenotypes in response to environmental variation, allowing trait variation without a genetic basis (Padilla and Savedo 2013). The two mechanisms can be hard to distinguish, and both mechanisms can coexist if the environment fluctuates at varying scales simultaneously (*e.g.,* inter-annual stochasticity in temperature combined with a long-term warming trend) (Lampert 2001). A relatively predictable environment with clear selection pressures often favours local adaptation and relatively fixed life-history traits, while an unpredictable and heterogeneous environment (both in space and time) is hypothesised to favour phenotypic plasticity (Lampert 2001). Local adaptation typically occurs over scales of 100-1,000 km, and is more likely to occur when the scale over which a selection gradient occurs is smaller than the scale of dispersal (Sanford and Kelly 2011). At smaller spatial scales, phenotypic plasticity is more likely; nevertheless, selection may also vary over very small scales (*i.e.,* meters) (Lange *et al.* 2016).

Relatively little is known about population structure and the potential for local adaptation in the American lobster. Very recent work shows evidence of fine-scale genetic structuring (Benestan *et al*., 2015), along with evidence of temperature influences on putatively adaptive genetic variation (Benestan *et al*., 2016). At the same time, phenotypic plasticity is common among marine invertebrates and also highly likely in American lobster (Padilla and Savedo 2013), especially given the species' extensive dispersal through larval drift (Sanford and Kelly 2011; Quinn *et al.* 2017). Consequently, the variability in reproductive traits documented in this thesis could be the result of either mechanism. Conclusively deciphering which is not possible based on the available data. For the remainder of the discussion I will consider potential drivers

behind variability regardless of the underlying mechanism (*i.e.,* genetic adaptation versus phenotypic plasticity).

High variability, both in space and time, of reproductive traits is likely a function of a variable and unpredictable, changing environment. The American lobster´s range is extensive, from Newfoundland in the north to North Carolina in the south, spanning over 10 degrees of latitude (Pezzack 1992). Consequently, the species experiences a wide range of environmental conditions, spanning -1.5°C to 7°C during winter months and 10 to 24°C during summer months (Raper and Schneider 2013; DFO 2017). Thus, the American lobster experiences substantial spatial variability across its range and through its lifetime, given the considerable potential for both larval drift and adult migrations moving individuals geographically (*e.g.,* Campbell and Stasko 1986; Quinn *et al.* 2017). Environmental conditions do not vary only across space, but also across time. There can be considerable variation in thermal conditions from year to year. In the southern Gulf St. Lawrence, mean temperature during spring and summer months varies by 3-6°C, and the start and end of winter sea ice by 20 days or more from one year to the next (Chassé *et al.* 2014). Lobsters are also experiencing progressive changes in temperature as mean annual temperature in the northwest Atlantic has increased approximately 1°C since the 1970s (Knudsen *et al*. 2011; Loder *et al*. 2013). The amount and composition of zooplankton available as prey for pelagic larvae also varies widely from year to year (DFO 2017). Optimisation of phenology (*i.e.,* the timing of various biological events) may therefore vary considerably and unpredictably between years, in addition to being under the influence of more progressive changes linked to climate change. As such, combined with considerable spatial variation in environmental conditions and long-distance larval dispersal, extensive variability in life-history traits likely serves as a biological safeguard against reproductive failure following a mismatch between larval phenotype and the environment to which it is exposed.

The proximate drivers of variability in female SM are not fully understood, but it seems clear that temperature and size-selective harvesting play a role in spatial and temporal variation in this trait, respectively. Geographic patterns in female SM have typically been explained in terms of temperature. The observation that SM is quite large in the cooler waters of the Bay of Fundy and southwest Nova Scotia and much smaller in the warmer sGSL (Chapter 1), along with similar patterns elsewhere, has led to the general assumption that SM follows a negative relationship with temperature (Templeman 1936; Aiken and Waddy 1980; Estrella and McKiernan 1989; Waddy *et al.* 1995; LeBris *et al.* 2017). However, the regular presence of small mature females in the cool waters around Newfoundland, in the species´ northern-most range, which rivals SM in the very warm Northumberland Strait (Chapter 1), challenges this otherwise well-documented relationship and clearly highlights that there are aspects of SM regulation that we are currently unable to explain.

Increasing water temperatures also cannot explain temporal changes in female SM (Chapter 1), even if thermal regime in general explains some spatial variation in SM. Instead, I provide compelling evidence that a marked reduction in female SM has occurred in eastern Canada over the past 10 to 80 years, and that this decrease is most likely the result of size-selective harvesting, with high exploitation rates of immature individuals creating a strong selection gradient for smaller-maturing females (Chapter 1). In an unfished population, a reduction in female SM is expected to reduce egg production due to the exponential relationship between female size and fecundity and the slowing of somatic growth upon maturation because moult frequency is reduced from annual to biennial (Chapter 1). Under intense exploitation, however, reduced SM is expected to result in a gain in egg production because maturation at a smaller size increases the probability and number of spawning events prior to harvesting, despite fewer eggs produced during each spawning (Chapter 1). The greater this selection strength, or the

greater the discrepancy between the minimum legal size (MLS) and SM, the greater the resulting declines in SM (Chapter 1).

Progressive temporal variation in hatching time in the sGSL appears to be a response to changing temperature conditions during gametogenesis and early embryonic development (Chapter 3). Over the past 30 years in the sGSL, summer temperature has declined somewhat while fall temperature has increased. The latter appears to have initiated an advance in the timing of hatching through impacts on the reproductive cycle 6 to 18 months earlier (Chapter 3). Higher fall temperature during gonadal development seem to cause earlier hatching, presumably by advancing spawning. Similarly, higher fall temperatures during early embryonic development also appear to advance hatching, presumably by allowing longer and/or more rapid embryonic development before winter diapause, which results in less embryonic development necessary before hatching in the following spring (Chapter 3). I also explored variation in temperature as a possible cause of spatial variation in hatching time (Chapter 2), but the driver(s) of this variability remain elusive. Thermal regime and the resulting time needed to obtain sufficient degree days to complete embryonic development in the spring likely play a role, as hatching starts the earliest in some of the warmest areas of Atlantic Canada and the latest in some of the coldest (Chapter 2). Yet there is also small-scale spatial variation among neighbouring sites in the timing of hatching and in the degree of embryonic development reached by spring, indicating there is variability which cannot be explained by regional trends in temperature (Chapter 2).

One possible explanation for small-scale variation in hatching time seemingly independent of temperature is behavioural thermoregulation by females. Ovigerous females have long been known to undertake seasonal migrations that alter the cumulative degree days experienced by

their embryos (Campbell 1986; Cowan *et al.* 2007; Goldstein and Watson 2015), and different females engage in different seasonal migration strategies (Goldstein and Watson 2015). As such, depending on the depths and locations that individual females seek out, they can exert considerable control over the rate of embryonic development and may thus both generate variability in hatching time and resist spatial and seasonal thermal variability to a degree.

It is not clear what is driving variability in reproductive traits among females in a location. For hatching time and development status (*i.e.,* PEI) at hatching this is partially because it is unknown how much of this variability persists over time and how much variation there is among clutches of a same female. Yet maternal effects (*i.e.,* non-genetic effects of maternal phenotype or environment on offspring phenotype) are common in both marine vertebrates and invertebrates (Marshall *et al.* 2008a). For example, across taxa larger females generally produce larger eggs (Marshall *et al.* 2008a; Cameron *et al.* 2016). This relationship has been confirmed in the European lobster (*Homarus gammarus*) (Moland *et al.* 2010), and in the American lobster larger females have been shown to produce eggs with higher energy content (Attard and Hudon 1987). Around the Magdalen Islands, larger American lobster females spawn and hatch their eggs earlier than do smaller females (Attard and Hudon 1987; Gendron and Ouellet 2009). Yet larval size in American lobster is not affected by female size except that primiparous females (first-time spawners) hatch smaller larvae than do multiparous females (Ouellet and Plante 2004).

Variable egg size and maternal provisioning provides a potential mechanism behind variability in developmental status at hatching among females (Chapter 2), perhaps allowing that embryos may hatch at a smaller size if embryonic resources are limited. Maternal nutritional status also forms a basis for maternal effects (Marshall *et al.* 2008a), and may play a role in

individual differences in SM. In many species, increases in population density are believed to cause increased intraspecific competition and reduced food availability, which in turn causes reduced growth rates and decreases in SM if SM is age-specific (*e.g.* Trippel 1995; Sánchez Lizaso *et al.* 2000). It is unknown whether SM is age-specific in American lobster, but SM has been shown to be age-specific in the southern rock lobster (*Jasus edwardsii*) (Gardener *et al.* 2006), and links between density, growth rates and SM have been reported for other lobster species (Beyers and Goosen 1987; Tuck *et al.* 2000; Linnane *et al.* 2009). Consequently, while it seems unlikely that changes in stock size and population density has driven temporal changes in female SM in American lobster (Chapter 1), individual differences in maturation size among females may be related to food availability and growth rate.

Variability among siblings in a same clutch is ubiquitous across most taxa and likely represents a maternal bet-hedging strategy or resource partitioning among siblings (Cameron *et al.* 2017). Theory states that in an environment which is variable across both space and time, sibling variation represents a way to increase the probability that at least a portion of offspring have the phenotype of maximal fitness, subsequently increasing mean maternal fitness while reducing fitness variation among generations (Marshall *et al.* 2008b; Scheiner 2014). For example, in marine sticklebacks (*Gasterosteus aculeatus*), females held under more variable environmental conditions (temperature) produce clutches with more variable egg sizes than females held under stable temperature conditions (Shama 2015). Alternatively, sibling variation may be a strategy to promote resource partitioning and allow siblings to occupy slightly different niches, thus reducing competition and increasing maternal fitness irrespective of the degree of unpredictability in environmental conditions (Cameron *et al.* 2017).

Variability in developmental status at hatching in American lobster, where embryos hatch over a wide range in development (Chapter 2), presumably results in variably-sized larvae upon hatching given the strong correlation between embryonic eye diameter (the indicator of development) and embryonic size (Perkins 1972). Whether this variability represents diversifying bet-hedging to increase maternal fitness by increasing the likelihood of some larvae having the phenotype of maximum fitness, or a resource partitioning strategy to reduce sibling competition, is likely dependent on the amount of environmental unpredictability experienced by lobsters (Marshall *et al.* 2008b; Cameron *et al.* 2017), and there is no clear answer to this question at this stage given attempts to empirically tease these strategies apart are still very recent (Cameron *et al.* 2017). The observation that female lobsters release their larvae in small batches over many consecutive days, and even weeks (Ennis 1975; Talbot and Helluy 1995), may be indicative of either strategy as well – it could represent bet-hedging by spreading larvae in time and over small-scale variations in environmental conditions (*e.g.*, variable wind-driven currents, Chapter 3), or it could be a method to dilute larvae in space and time to reduce sibling competition.

4.4 Implications of variable life-history traits to fisheries management

Failing to capture the true variability in life-history traits can have consequences to fisheries management. Fisheries management units are variable in size depending on the species and location. In the USA, for example, marine spawning species, both fishes and invertebrates, are frequently managed as single-unit stocks, while estuarine and anadromous spawning species are managed over finer spatial scales (McBride 2014). However, species spawning in the open marine environment frequently exhibit variation in life-history traits at scales smaller than their management units. Demographic characteristics, such as growth rates, longevity and mortality

are routinely derived from age- and length-based data as a basis for fisheries stock assessments (Gray 2015). Yet, as length-at-age in both fishes and invertebrates varies spatially and temporally (*e.g.,* Blanchette *et al.* 2007; Gray 2015; Kuparinen *et al.* 2016; Munroe *et al.* 2016), so do the estimates of demographic characteristics derived from them (Gray 2015; Kuparinen *et al.* 2016). This variability can occur over quite fine spatial scales. For example, cod (*Gadus morhua*) have wide-dispersing pelagic eggs and larvae, yet can display significantly different growth rates across scales of only a few km; cod aged one to five years show differences in size-at-age up to 50% between individuals living in the inner and outer area of a Norwegian fjord (Kuparinen *et al.* 2016). In American lobster, female SM can vary over scales of 10s of km (Watson *et al.* 2013; Chapter 1). Such examples of fine-scale variation clearly show that life-history traits can vary over much smaller spatial scales than most management units, even for species managed as multiple stocks (*e.g.,* lobster), and generalisation across these areas can result in stock assessments that are unrepresentative of large parts of the stock (Gray 2015; Kuparinen *et al.* 2016). Failing to adequately quantify spatial variation in life-history and demographic traits poses the risk of a mismatch between variation in management measures and demography. An increased awareness of life-history variation and its potential implications is therefore necessary to ensure effective harvesting and conservation strategies for marine species.

Minimum legal size (MLS) regulations are an important tool in the management of the Canadian lobster fishery, controlling the proportion of females likely to reproduce prior to recruiting to the fishery and thus egg production levels (Fisheries Resource Conservation Council 2007). The current primary determinant of MLS regulations is female lobster SM (Fisheries Resource Conservation Council 2007), which varies considerably across Canadian waters (Chapter 1). MLS varies from as low as 72 mm CL in large parts of the sGSL to as high as

84 mm CL in some areas of Cape Breton, with a MLS of 82.5 mm CL in most LFAs (Tremblay *et al.* 2013; Rondeau *et al.* 2015; Chapter 1). These regional, and in some instances relatively local, differences in MLS regulations reflect differences in female SM to a certain extent. The low MLS in the sGSL, for example, reflects the small female SM in the area (*e.g.,* 50% of females are mature at 72 mm CL in most areas; Rondeau *et al.* 2015). The western shore of Cape Breton (LFA 26B) is an exception with slighter larger SM (75 mm CL) and relatively higher MLS (79-81 mm CL) (Rondeau *et al.* 2015). The entire sGSL reached its target of MLS set at or above the size by which 50% of females reach maturity in 2013 (Rondeau *et al.* 2015). Along the Scotian Shelf and in the Bay of Fundy, however, MLS regulations are not as consistently linked to variation in SM. Along the eastern shore of Nova Scotia to the Bay of Fundy (LFAs 31A-38), the MLS is 82.5 mm CL throughout (Tremblay *et al.* 2013), even though female SM varies from 75-90 mm CL (Chapter 1). Thus, this region represents an area of uniform management measures (in terms of MLS), but with considerable heterogeneity in the biological parameter underpinning the said management measure. In the Bay of Fundy, this means that females may recruit to the fishery a full moult and one year before maturation, assuming a 10% to 20% moult increment and a single annual moult (Comeau and Savoie 2001; Gendron and Sainte-Marie 2006), which significantly reduces the potential egg production given the exploitation rate is estimated to 53% to 70% (Fisheries Resource Conservation Council 2007).

The southern rock lobster (*Jasus edwardsii*) provides a cautionary example concerning the potential impact of generalised management measures regarding MLS regulations (Gardner *et al.* 2015). On the northwest coast of Tasmania, individuals grow rapidly (14 mm yr^{-1} for a 100 mm CL lobster) and females reach maturity at approximately 112 mm CL, whereas individuals along the southwest coast grow much more slowly (1 mm yr^{-1} for a 100 mm CL lobster) and females mature as small as 59 mm CL (Gardner *et al.* 2015). In 1966, the MLS was reduced in

the southern part of the fishery to increase yield of slow-growing individuals in this area, yet remained considerably above female SM (Gardner *et al.* 2015). At the same time, the industry in the northern part of the fishery lobbied extensively to obtain the same reduction in MLS, and succeeded, which resulted in the MLS being now set well below the SM (Gardner *et al.* 2015). Looking ahead to the future of the fishery, this spatially uniform management scheme is expected to considerably reduce egg production in the northern part of the fishery and to result in only a 1% to 2% chance of meeting egg production targets over a 10-year period (Gardner *et al.* 2015). Uniformly raising the MLS across the fishery to approximately the size of female SM in the northern region would increase egg production, but still fail to meet egg production targets while also resulting in a substantial reduction in catch and profitability of the fishery to the south where female SM is much smaller (Gardner *et al.* 2015). A scenario where MLS is kept low in the south and at approximately the female SM in the north improves yield in the south, but does little to improve the low egg production in the north. The management scenario that would maximise egg production and result in an acceptable probability of meeting targets is a spatially targeted MLS, remaining at the current low MLS in the south, being at intermediate levels in central areas, and raised to well above current female MLS in the north (Gardner *et al.* 2015).

It is thus recommended that MLS regulations be set according to up-to-date local female SM data in each LFA across the Canadian lobster fishery, which is currently done in a limited way. In general, increasing MLS will also lead to higher egg production (Chapter 1; Gardner *et al.* 2015). Consideration should also be given to the effects of size-selective harvesting on female SM. As MLS regulations that allow harvesting of immature females appears to drive down SM (Chapter 1), it should be carefully considered whether this is acceptable and whether attempts at reversals are desirable. The implications of decreased female SM on egg production are not

fully understood. Given high fishing mortality (Fisheries Resource Conservation Council 2007), reduced SM relative to the MLS likely increases egg production (Chapter 1). However, depending on the mechanism behind reduced SM, declines could also reduce stock yield. If SM has declined because the fishery is selecting for slower-growing individuals (*i.e.,* SM is age-specific as in southern rock lobster [*Jasus edwardsii*] [Gardener *et al.,* 2006]), this could negatively affect yield by increasing the time from settlement and juvenile life stages to recruitment into the fishery. In Atlantic cod (*Gadus morhua*) SM declines more than double the probability of negative population growth every generation, highlighting the potential for fishing-induced changes to life-history traits to negatively impact recovery of heavily exploited stocks (Hutchings 2005).

In addition to declining SM, females also appear to be releasing their larvae earlier in the year, at least in the parts of the sGSL where the onset-of-hatching has advanced on average five weeks over the past 25 years, which may also have consequences for fisheries recruitment and dynamics. One direct impact of a greater proportion of ovigerous females having mature clutches during the spring fishing seasons is increased egg loss due to increased catch rates and handling of ovigerous females during this late stage of embryonic development. Given eggs are more readily lost from a female's abdomen in mature clutches than less developed ones (Talbot *et al.* 1984; Tang 2016), increased handling of females while their clutches are mature may result in increased egg loss and negatively impact larval supply. The degree to which decreased larval production may impact subsequent fisheries recruitment is unclear, given uncertainty regarding spawner-recruit relationships in lobster (see Chapter 3), but drastic declines in larval production would likely have ramifications for recruitment.

An advancement in hatching time may also alter dispersal patterns for larvae, which can contribute to a disconnect between larval supply and benthic recruitment, resulting in a possible decline in the latter even if the former stays high. Based on a biophysical model of larval drift in the Gulf of Maine (Xue *et al.* 2008), early egg hatching in lower water temperatures observed in early spring-summer will likely result in a prolonged larval phase and subsequently potentially increased larval mortality through predation. Similarly, there is evidence, both empirical and from larval drift modeling, that earlier hatching results in reduced larval survival in the sGSL (Miller 1997; Chassé and Miller 2010). Wind and weather patterns also vary seasonally and an earlier hatching period may expose larvae to different wind-driven surface currents, which has been shown to have great impacts on spatial and temporal patterns in postlarval supply and subsequent settlement (Harding *et al.* 1982; Wahle and Incze 1997; Incze *et al.* 2000; Pershing *et al.* 2012). Based on modeling of larval drift (Chapter 2), there is on average a 15-day (max = 100 days) and 45-km (max = 300+ km) difference in mean drift time and distance, respectively, between larvae released from one week to the next throughout the hatching season (May to September) in the 22 locations studied. There is also predicted to be an average variation in the percentage of larvae transported to unsuitable settlement locations (*i.e.,* too cold and deep water; see Chapter 3) of 15% among larvae hatched in consecutive weeks, and hatching during some weeks was predicted to result in total loss of larvae (Chapter 2). It is thus not difficult to see how changes in hatching time have the potential to alter both dispersal and connectivity patterns.

An advancement of the timing of hatching driven by past thermal cues may also have ramifications for larval food supply. American lobster larvae are active predators, feeding on a variety of other zooplankton and at times phytoplankton (Ennis 1995). Given the advancement in hatching in the sGSL appears mostly due to temperature effects during gonadal and early

embryonic development 6 to 18 months, larvae released earlier may face a temporal mismatch with other zooplankton upon which they prey. It seems unlikely, indeed, that prey of lobster larvae have seen a similar advancement in their presence in the sGSL plankton, given the shorter life cycles of most zooplankton prey species (approximately one month generation time in copepods; Fransz *et al.* 1991) compared to lobster, and the lack of warming during spring. A loss of synchronicity between the timing of hatching of lobster larvae and their prey is therefore clearly possible, and such scenarios have been documented in various zooplankton, crustaceans, fishes and birds (*e.g.,* Gotceitas *et al.* 1996; Visser *et al*. 1998; Edwards and Richardson 2004; Durant *et al.* 2007; Asch 2015). If the timing of hatching is altered (*i.e.,* an earlier onset due to climate change) and results in a decoupling between peak prey abundance and lobster larval release, starvation from food limitation could result in a mass larval mortality jeopardizing benthic recruitment. This hypothesised decoupling causing massive larval mortality might be occurring in the Gulf of Maine (Joshua Carloni, pers. comm., New Hampshire Fish and Game Department, Durham, NH, USA), where a historically high level of spawning stock biomass (ASMFS 2015) has been associated with a significant increase in stage I larvae, but a significant decrease, and in some areas nil, young-of-the-year abundances since 2011, potentially as a result of declines in the copepod prey available to larvae (Wahle and Carloni 2016; http://umaine.edu/wahlelab/american-lobster-settlement-index-alsi/american-lobster-settlement-index/, accessed 15 August 2017).

The amount of variability in developmental status at hatching has significant implications for the accuracy of hatching time predictions in both ecological studies and hatchery settings. Miller *et al.* (2016) showed that one achieves considerably more accurate estimates when variability in PEI-at-hatching is considered when using temperature-dependent embryonic development functions to predict hatching time. Using the previous assumption of negligible

variability in developmental status at hatching (hatching occurs when PEI = 560-570 µm [Perkins 1972; Helluy and Beltz 1991]) is inadequate when embryos may in reality hatch with PEI ranging from 260 to 706 µm (Chapter 2). In fact, Goldstein (2012) concluded that the Perkins Eye Index and accompanying temperature-dependent embryonic development function is unreliable for predicting hatching times of embryos under naturally fluctuating temperatures; however, this conclusion was probably influenced by the fact that PEI-at-hatching was considered a fixed endpoint with 570 µm equating 100% development.

4.5 Recommendation for new monitoring and research

To fully understand and predict the impact of declining female SM on the fishery, the underlying control of maturation needs to be further investigated. The relationship between female SM and temperature is not as clear-cut as it has often been presented, and warrants further investigation. Females in the cold waters around Newfoundland, at the northern end of the species´ range, mature at sizes small enough to rival those in the warm Northumberland Straight (Chapter 1), an observation that is directly at odds with the general negative spatial relationship between SM and temperature (*e.g.,* Waddy *et al.* 1995; LeBris *et al.* 2017). It should also be determined whether maturation is age-specific and by what mechanism size-selective harvesting has driven down female SM (*e.g.,* is it by selecting for slower-growing individuals?). Most American lobster stocks in Canada are at record highs (DFO 2015a) and thus a potential negative impact on stock status is currently less relevant than for many fishes, but it should nevertheless be considered given there are areas of stock declines (DFO 2013a, b, 2015b; Rondeau *et al.* 2015) and drastic reductions in benthic recruitment elsewhere (Wahle and Carloni 2016). Consequently, research to better understand the control of maturation is clearly merited. The drivers behind and mechanisms of hatching time and variability in

developmental status at hatching also merit further research. The general time of year during which eggs are hatched seems timed to minimise the time larvae spend drifting in the water column to ensure rapid settlement onto the benthos, but the driver(s) of finer-scale spatial variation in the timing of hatching remain unclear (Chapter 2). It is also unknown what determines variability in developmental status at hatching (Chapter 2), how susceptible this is to environmental variation, and how it may compound or mitigate advancement of hatching (Chapter 3).

With respect to fisheries management, variable life-history traits can be made a more integral part of stock assessments than is currently the norm. Temporal variation in reproductive parameters is monitored relatively little for management of the Canadian lobster fishery. For example, changes in MLS over the past two to three decades have been made primarily to reach the objective of allowing approximately half of females to spawn prior to recruiting to the fishery and rectifying the historical state of allowing intense harvesting of immature females (Chapter 1), but the possibility of changing female SM has not been considered. Female SM was not considered in the 2013 or 2016 Newfoundland stock assessments (DFO 2014; 2016a), and the most recent estimates of the size at which 50% of females are mature (CL_{50}) in the region are from 1982 or 1965, depending on the location (Ennis 1980; 1984; Chapter 1). In comparison, female SM has been monitored with some regularity in the sGSL. For example, female SM was assessed between 1994 and 1997, and again in 2014 in eastern New Brunswick (LFA 23), along the north shore of Prince Edward Island (LFA 24) and along northwestern Nova Scotia (LFAs 26A and B) (DFO 2016b). While spatial variation, and temporal variation to a lesser degree, in female SM is considered in the management of the Canadian lobster fishery, variability in other life-history traits should be considered also. The timing of

hatching is relevant for fishing season regulations, and has been discussed during recent stock assessments in the sGSL (M. Comeau, DFO; pers. comm. 2017).

Overall, the spatial, temporal and individual variation in life-history traits documented in this thesis highlight the importance of considering these sources of variability when conducting new research, and suggests that some of our current "understanding" of life-history traits in marine organisms should be re-visited with this variability in mind. As stated by Jensen's Inequality, except in rare cases, the response of a system to average conditions is different from the same system's average response to variable conditions (Denny 2017). A complete understanding of life-history traits, including of their potential modulation by factors such as exploitation and climate change, thus requires a thorough investigation of their variability at multiple scales.

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APPENDIX

Appendix A: Relationship between the minimum ovigerous female size vs. 5th percentile ovigerous female size

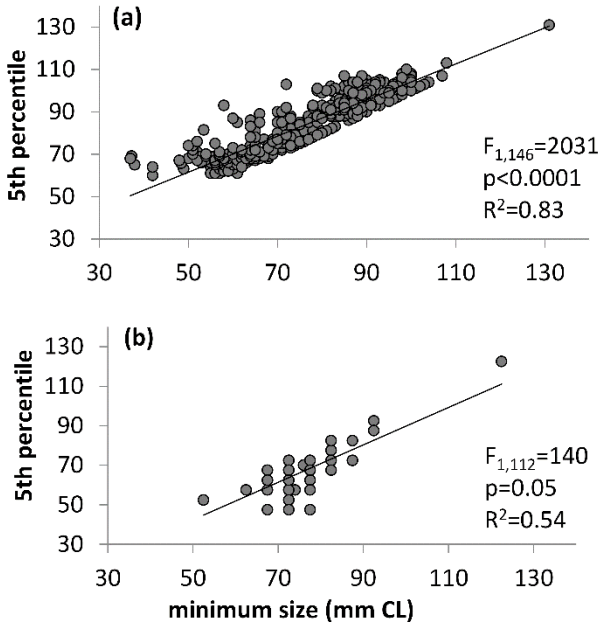

Figure A1: *Relationship between the minimum ovigerous female size vs. 5th percentile ovigerous female size for data taken from the (a) DFO Crustacean Research Information System (CRIS) database (carapace length measured to the nearest mm) and (b) Canadian Fisheries Research Network "Lobster Node" database (carapace length measured to the nearest 5 mm size bin). Each data point is one year and lobster fishing area (LFA) combination.*

Appendix B: Previously unpublished sources of CL_{min} data used to estimate declines

The majority of CL_{min} estimates were obtained from unpublished ovigerous female size data from two databases, the "Lobster Node" of the Canadian Fisheries Research Network (http://www.cfrn-rcrp.ca, see project 1.2 [Rochette *et al.* 2018]) and the Department of Fisheries and Oceans Canada (DFO) Crustacean Research Information System (CRIS) (M.J. Tremblay, A. Cook and M. Comeau, Department of Fisheries and Oceans Canada [DFO]). Data from both sources are based on information collected from traps during normal commercial fishing operations. Data collection through the "Lobster Node" began in 2011 with weekly sampling throughout the fishing season at 50-75 km intervals of coastline across eastern Canada with the exception of the northern Gulf of St. Lawrence. Approximately 90 fishermen participated in data collection in 2011 and approximately 130 in 2012 and 2013. Ovigerous female size was measured to the nearest 5 mm bin. Fishermen/technicians also recorded clutch fullness and development, as well as location, soak time and number of trap hauls. Data collected for CRIS included carapace length to the nearest millimetre, sex and egg presence. Other variables that have been recorded with varying degrees of consistency over time include egg stage, shell hardness, occurrence of culls and v-notches, and the number, location and depth of traps. Frequency and distribution of sampling has varied by LFA and year, reflecting changes in resources available and in assessment priorities (see *e.g.*, Mallet *et al.* 2006 [Can. Man. Rep. Fish. Aquat. Sci. no. 2769]). CL_{min} data from the Magdalen Islands, QC (LFA 22) originate from a trawl survey that has been carried out annually in the southern part of the archipelago since 1995 by DFO (see section 2.1.4 of Gendron and Savard 2012 [DFO Can. Sci. Advis. Sec. Res. Doc. 2012/010] for details).

Appendix C: Different methods of assessing size-at-maturity in American lobster

Size-at-maturity (SM) of female American lobsters (*Homarus americanus*) is assessed and reported in a number of different ways in the literature, the four most common being (a) presence/absence of eggs on the abdomen, (b) ovarian development, (c) cement gland development, and (d) ratio between abdominal width and carapace length (Aiken and Waddy 1980; Comeau and Savoie 2002). However, SM estimates derived by these four approaches are sufficiently comparable to be used interchangeably in our analyses, considering the spatial and temporal scales of our study. More specifically, when we regressed against each other estimates obtained from the same LFA and decade using two different methods, we consistently found strong 1:1 relations and intercepts that did not differ from zero (Fig. A2). We were unable to confirm these strong relations between all pairs of methods, due to insufficient comparative data ($n < 5$), but there is circumstantial evidence that all estimates are sufficiently comparable for the purpose of this study. For example, for CL_{50} (size at which 50% of females reach maturity) no direct comparison could be made between estimates based on cement gland development vs. abdominal width to carapace length ratio, but both estimates showed a significant 1:1 correlation with estimates based on ovarian development, suggesting that all three methods yield comparable estimates. No comparisons could be made involving CL_{50} estimates based on the size of ovigerous females, because this method is rarely used to assess CL_{50} and no such estimates were present in our dataset. Similarly, for CL_{min} (the smallest size at which females reach maturity) estimates based on cement gland development and abdominal width to carapace length ratio both showed a significant 1:1 relation with estimates based on ovigerous female size, suggesting that estimates based on these three methods are comparable. There was insufficient data to compare CL_{min} estimates based on ovarian

development to other methods, but < 3% of CL_{min} estimates in the dataset were based on ovarian development. Given these different results, all available SM estimates were used regardless of method used to obtain them, and no corrections were made.

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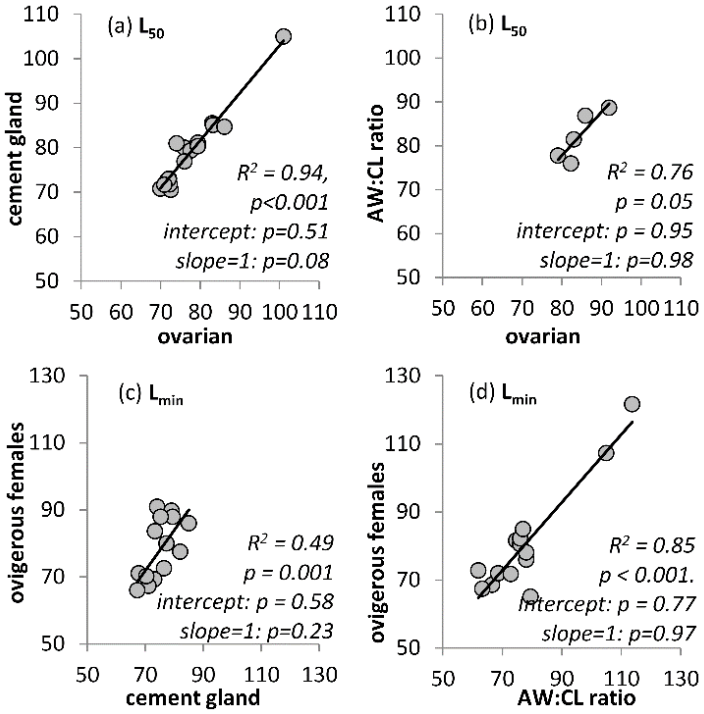

Figure A2: *Comparisons between size-at-maturity (SM) estimates (CL_{50} and CL_{min}) from different methods. Each data point represents SM estimates from the same lobster fishing area (LFA) and decade, and all values are carapace length in mm. (a) CL_{50} estimates based on ovarian development vs. cement gland development. (b) CL_{50} estimates based on ovarian development vs. abdominal width: carapace length ratio. (c) CL_{min} estimates based on cement gland development vs. size of ovigerous females. (d) CL_{min} estimates based on abdominal width: carapace length ratio vs. size of ovigerous females.*

Appendix D: References minimum legal size (MLS) data sources

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Appendix E: The relationship between sample size and length of predicted hatching window

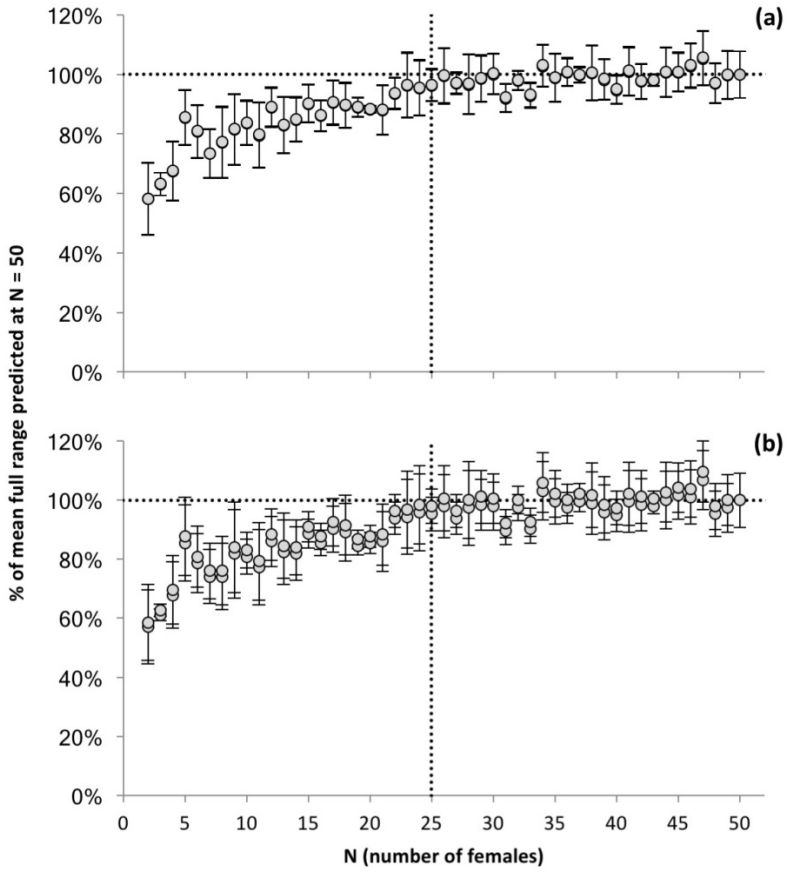

Figure A3: *Plots showing the relationship between sample size (i.e., number of females from which embryos were sampled) and the range of predicted hatching dates (i.e., full length of the hatching window from first to last date of predicted hatching), based on randomised sub-sampling of the data from Miller* et al. *(2016). A total of 50 females were sampled on each of two sampling dates (June 13th and 23rd 2013) in Cheticamp, NS. Sub-sets of females with n from 2 to 49 were randomly selected 10 times and hatching dates predicted for each selection of females; hatching dates were also predicted 5 times for the full n of 50. I used variable PEI-at-hatching as the endpoint, resulting in slightly different predictions each model run even if using the same females and embryo samples (see section 2.2.2 for method details). Hatching dates were predicted using both the* ***(a)*** *linear temperature-dependent embryonic development function (Perkins 1972) and* ***(b)*** *logarithmic temperature-dependent embryonic development function (Gendron and Ouellet 2009). Each data point shows the average range in hatching dates predicted for each sample of females. The stippled horizontal lines show the mean range of hatch dates predicted based on all 50 females each sampling date, represented as 100%. The stippled vertical*

lines show n = 25, which was selected as the minimum sample size for further embryo sampling to predict hatching times.

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