IS THERE GEOGRAPHIC VARIATION IN DEVELOPMENT RATE OF AMERICAN LOBSTER (*HOMARUS AMERICANUS*) EMBRYOS?

by

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Abstract

American lobster fisheries in Canada are managed via Lobster Fishing Areas, which are divided based on sociopolitical considerations rather than biological stocks. Bio-physical models use physical and biological parameters to predict larval dispersal and contribute to understanding the identity of stocks, and the connectivity between management areas. Hatching time of lobster embryos is an important parameter of these models, as it impacts the survival and transport of larvae. This study aims to determine whether embryo development functions used to predict hatch need to be "location-specific". We sampled eggs from six locations in eastern Canada, reared them in the lab, and photographed them weekly to track embryo development based on changes in eye size. The results suggest that embryo development functions do not need to be developed for individual fishing ports, but that distinct development functions for larger marine systems may improve larval dispersal modelling and sustainable management of fisheries.

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List of Abbreviations

Locations

CAN – Canso, Nova Scotia

DIP – Dipper Harbour, New Brunswick

DIN – Dingwall, Nova Scotia

MAL – Malpeque, Prince Edward Island

MAR – St. Martins, New Brunswick

TRA – Tracadie, Prince Edward Island

Provinces

N.B. – New Brunswick

N.S. – Nova Scotia

P.E.I. – Prince Edward Island

Regions

BoF – Bay of Fundy

GoM – Gulf of Maine

GSL – Gulf of St. Lawrence

Other

PEI – Perkins Eye Index

LFA – Lobster Fishing Area

Introduction

The American lobster supports one of the most economically important fisheries on the east coast of Canada (Department of Fisheries and Oceans [DFO], 2015). In 2015 alone, the landed value of lobster was over one billion Canadian dollars (DFO, 2017). Currently, the American lobster fishery in Canada is divided into 45 Lobster Fishing Areas (LFAs; DFO, 2008), each managed separately with its own set of rules and regulations such as fishing season opening and closing dates, trap limit per license, minimum legal size, and gear design (DFO, 2008). It is important to note that these LFAs do not represent separate biological stocks, but rather are based on social, political, and economic considerations (Miller, 1995). This presents a risk to sustainable management, as management without consideration of biological data can lead to unsustainable resource use and population collapse (National Research Council and National Academy of Sciences, 2004).

That LFAs are not more closely linked to biological stocks is related to our limited understanding of what these stocks are (Ennis, 1986). Previous research into the identity and location of American lobster stocks has included analysis of landings data (Campbell and Mohn, 1983; Harding et al., 1983), genetics (Kenchington et al., 2009; Benestan et al., 2015), and dispersal models (Quinn et al., 2017). All three of these methods suggest a stock in the Gulf of St. Lawrence and a stock in the Gulf of Maine, which are separated somewhere midway along the Scotian Shelf (Campbell and Mohn, 1983; Harding et al., 1983; Kenchington et al., 2009; Benestan et al., 2015; Quinn et al.,

2017). However, these different approaches also suggest additional, and different, stock structure at smaller scales (Campbell and Mohn, 1983; Harding et al., 1983; Kenchington et al., 2009; Benestan et al., 2015; Quinn et al., 2017). Ultimately, lobster stocks remain ill-defined due to a poor understanding of the scale at which demography (e.g., density and size structure) is more greatly affected by intrinsic (i.e., natality, growth, and mortality) than by extrinsic (i.e., immigration and emigration) processes.

Connectivity between lobster management areas and true sub-populations occurs through two mechanisms: the benthic movement of adult lobsters, and the pelagic movement of their planktonic larvae. The importance of adult benthic movement to connectivity and stock structure in American lobster has been debated. Adult lobsters are highly mobile and have been shown to move tens to hundreds of kilometers over the course of a year (Campbell, 1989; den Heyer et al., 2009; Morse et al., 2017). Nevertheless, it is generally assumed (but see Morse et al., 2017) that benthic dispersal is less consequential to connectivity than is dispersal of larvae in the water column. Lobster have four pelagic larval stages, each separated by a molt (Factor, 1995). The direction and distance travelled by larvae can vary considerably due to circulation and wind patterns (Ennis, 1986; Harding and Trites, 1988; Xue et al., 2008). Larval dispersal and survival are also greatly affected by water temperature, which affects the rate at which the larva develops and hence the amount of time it spends drifting in the water column exposed to pelagic predators (MacKenzie, 1988; Quinn, 2017). Given that water temperature and currents vary considerably over the period of larval development, the actual hatch date of larvae will have a substantial effect on their dispersal and survival (Templeman, 1935; Ennis, 1986; MacKenzie, 1988; Incze et al., 2010). Therefore, the

ability to accurately predict the time of larval hatch should improve our ability to accurately predict larval dispersal and connectivity between lobster management areas and sub-populations.

Biophysical models are arguably the most useful tool to understand how larval dispersal is likely to connect different regions. The principal physical parameters of these models are currents, tides, water temperature, salinity, atmospheric temperature, wind patterns, and river runoffs (Chassé and Miller, 2010; Incze and Naimie, 2000; Quinn et al., 2017). Biological parameters that have been included are: estimates of female egg production, hatch time and quantity of larvae released, as well as various parameters related to the larvae such as temperature-dependent development functions, swimming behavior, mortality, and settlement decision rules (Chassé and Miller, 2010; Incze and Naimie, 2000; Quinn et al., 2017). These models have provided considerable information regarding potential patterns of connectivity caused by larval dispersal, although their predictions have been infrequently validated and the quantity and quality of their biological underpinnings is generally very limited.

Although hatch time has been incorporated in drift predictions for biophysical models of larval dispersal, hatch functions are underdeveloped due to a lack of biological information surrounding embryonic development and hatch. To date, dispersal models have used a variety of approaches to parameterizing hatch time, including selecting a few values based on an educated guess (Incze and Naimie, 2000), using a hatch function derived from a single location over a much broader area (Quinn et al., 2017), or not including a hatch function at all for areas where there is none available (Chassé and Miller, 2010). There is research underway that is aiming to improve our ability to predict

embryo development and hatch time based on embryo samples, eye size, and temperature. Perkins (1972) proposed the Perkins Eye Index (PEI), which is the average of the maximum length and width of the embryo eye, as a way to track development of American lobster embryos. From this method, two different temperature-based embryo development functions have been proposed (see Perkins, 1972; Gendron and Ouellet, 2009). Given that these were based on embryos from different geographic origins, they both quantified development of lobster embryos in the lab (using PEI as an index of development) and have proposed different temperature-based development functions for embryos from Booth Bay, Maine, USA (Perkins, 1972) and the Magdalen Islands, Quebec, Canada (Gendron and Ouellet, 2009), which provides some evidence of geographic variation in lobster embryo development rate. However, this conclusion cannot be considered definitive given that the performance of the two development functions on the two "populations" of embryos, raised in a common environment, has not been compared. Miller et al. (2016) present evidence that these two temperature-based development functions from the literature are useful in predicting hatch time of wild-caught eggs. Given the importance of hatch time to larval survival and connectivity, this begs the question as to whether the development rate of lobster embryonic varies geographically.

The overarching goal of this study is to contribute to ongoing research that aims to improve our ability to predict dispersal of American lobster larvae through exploration of embryonic development functions in relation to geography. This is done by testing the hypothesis that there exists geographic variation in development rate of American lobster

embryos, and by attempting to obtain some initial understanding of the spatial scale at which such variability exists.

Methods

Eggs were sampled from ovigerous female American lobster caught in commercial lobster traps in six locations in Atlantic Canada from June 8th to 20th, 2017 (Figure 1). Eggs from one of these locations were collected by the author, and the rest were collected by various members of the Rochette Lab and other personnel attached to the Lobster Node, which is a large tri-partite research collaboration between industry, government and academia on lobster stock structure and connectivity in eastern Canada (Rochette et al., 2017). From each location, five clusters of approximately five to six eggs were removed haphazardly from the abdomen of 25 females; previous work has found no consistent variation in development status of embryos taken from different locations of a female's brood (R. Rochette, personal communication). All eggs from individual females were placed in seawater in small glass vials and kept cool for transport to the University of New Brunswick Saint John.

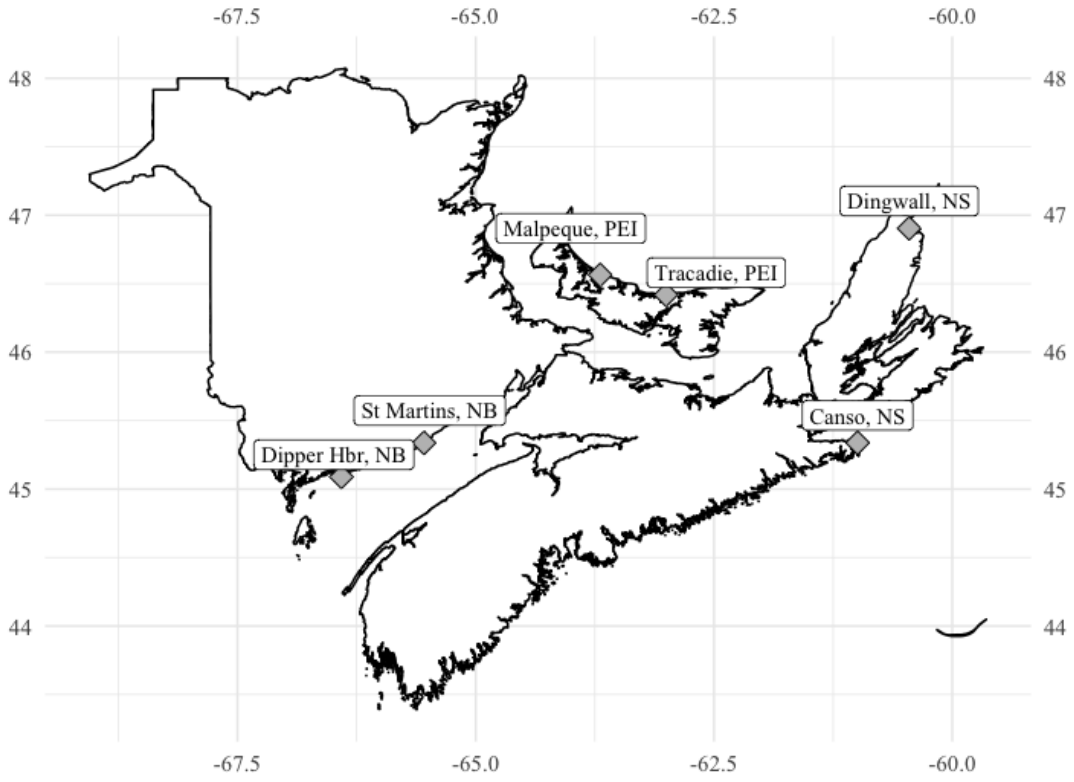

Figure 1. Six locations in eastern Canada from which American lobster egg samples were collected between June 8th and 20th, 2017: Dipper Harbour and St. Martins in New Brunswick (LFA 36); Malpeque and Tracadie in Prince Edward Island (LFA 24); Dingwall (LFA 27) and Canso (LFA 31A) in Nova Scotia.

Twelve females from each location, and eight eggs from each female, were haphazardly selected to take part in the study, for a total of 576 eggs. A larger number of females and eggs were initially sampled to allow for subsampling in the lab, to ensure similar stages of embryo development among females and locations at the beginning of the experiment. Eggs were selected based on embryo eye size (Perkins Eye Index [PEI]) between 350 and 400 μm, so as to start the experiment with embryos of similar index of developmental status (Perkins, 1972). The target PEI ranged from 350 to 400 μm, but there were not enough embryos within this range, so embryos with PEIs up to 524 μm were included. Trays were built to hold the eggs so that they would remain separate and could be tracked individually throughout the course of the experiment; each tray had 24 wells divided in two by a piece of mesh, for a total of 48 eggs per tray. Trays contained two eggs from each of four females per location, and a total of 12 trays were used. The position of eggs from each sampling location was rotated in every tray, so that in total each location had the same number of eggs in every well position. Trays were equally divided between four 30-L tanks with recirculated seawater kept at approximately 8°C until July 24th and at approximately 9°C thereafter (Table 1). The temperature was raised at four weeks (July 24th) to accelerate embryonic development, due to time constraints. A constant temperature was maintained by cooling the room temperature to 9°C and using a dual heating-cooling unit in each tank. The temperature was monitored throughout the duration of the experiment using a HOBO Pro V2 Data logger (U22-00). The experimental setup provided an effective control of temperature (Table 1). The tanks

were also kept at a constant salinity of approximately 33ppt and monitored manually daily with a YSI.

Table 1. Target tank temperature, average, standard deviation (SD), and range (in ˚C) for the four 30-L tanks that were used in this study; tanks were held at approximately 8˚C for four weeks and then at approximately 9˚C for eight weeks.

Tank	Target	Average	SD	Range
1	8	7.90	0.01	7.87, 8.10
2	8	8.09	0.01	8.07, 8.12
3	8	8.12	0.02	8.10, 8.25
4	8	7.97	0.02	7.95, 8.05
1	9	8.99	0.32	8.84, 10.74
2	9	9.09	0.09	8.92, 9.81
3	9	9.17	0.37	8.94, 11.13
4	9	9.09	0.39	8.79, 10.98

Embryo development was recorded on a weekly basis using photographs taken from the left-side sagittal orientation using an AMSCOPE MD 1900 camera attached to a Lecia M212 5 microscope. When eggs were close to hatch (determined by a relatively larger size, and a low amount of yolk), they were monitored on a daily basis so hatch date could be recorded more accurately.

The ImageJ software was used to trace the perimeter of the eye and yolk on the weekly egg photos (Schneider et al., 2012). The eye outline was used to determine the Perkins Eye Index (PEI), which is calculated by taking the sum of the maximum length and width of the eye and dividing by two (Perkins, 1972). Only PEI was used in analyses presented in this thesis due to time constraints. Development rates were calculated from PEI measurements by subtracting the first week's measurement from the final week's measurement and dividing by the number of days between those two values.

Linear mixed-effects models using various combinations of location, female (as a random effect, nested within location), and initial PEI were used to explain variation in PEI development rate. All possible combinations of the three parameters were compared, and the usefulness of the top eight models was compared using Akaike Information Criterion (AIC); a null intercept-only model was included in these comparisons. The best-fitted model was then analyzed with a mixed-model ANOVA to assess statistical significance. A Tukey HSD post-hoc test was used to compare development rates between locations. Similarity of development rates among broader geographic areas was also investigated using AIC, first by dividing the six sampling locations into the three provinces from which they came (P.E.I., N.B. and N.S.), and secondly by dividing them into three distinct regions based on similar environmental conditions such as temperature,

salinity, and currents (Hunt et al., 2017): Gulf of St. Lawrence (Malpeque, Tracadie, and Dingwall), Bay of Fundy (Dipper Harbour and St. Martins), and Scotian Shelf (Canso). All statistical analyses were carried out using the statistical package R (R Core Team, 2013).

Results

Based on the AIC approach to model selection, the best-fitted model includes a location term, a term accounting for females nested within their location of origin, and a term accounting for the PEI at the beginning of the experiment (Table 2, model 4). This model explained 39% of the variation in embryo development rate. Of the variation in embryo development rate that is not explained by the ANOVA model, 14.38% is associated with the random term female (nested in location) and 85.63% to individual embryos belonging to a same female. The mixed-effects ANOVA of this best-fitted model also revealed significant variation in the development rate of American lobster embryos in relation to their initial PEI, with significant variation among females of a same location and among the six locations sampled in eastern Canada (Figure 2, Table 3). Post-hoc Tukey-type comparisons indicated that the development rate of embryos from the two New Brunswick (N.B.) locations (MAR and DIP) were significantly greater than those from the two Prince Edward Island (P.E.I.) locations (TRA and MAL), whereas that of embryos from the two Nova Scotia (N.S.) locations did not consistently differ from these; embryos from Dingwall in N.S. developed at a rate similar to those from N.B., and greater than those from P.E.I., while embryos from Canso had an "intermediate" rate of development that did not differ significantly from N.B. or N.S. embryos.

AIC model selection indicated that of the three combinations tested, the grouping of the six study locations that explained the greatest amount of variation in embryo development rate was the provincial grouping, where the locations were grouped by their

province of origin (N.B., P.E.I., or N.S.; Table 4). Grouping the locations according to broader region or individually resulted in less useful models (Table 4).

Table 2. Comparison of nine models to explain variation in the rate of PEI increase in American lobster embryos, which is used as a proxy for embryo development. Eight of these models include different combinations of geographic location (Dipper Harbour and St. Martins, N.B., Canso and Dingwall, N.S., and Tracadie and Malpeque, P.E.I.), female (as a random effect nested within location), and PEI at the beginning of the experiment. These models are the best eight, out of all possible models. The ninth model is a null intercept-only model. AICc is an estimate of the relative quality of a model in relation to the other models (for models with a large number of levels in relation to data points), and delta indicates the difference in AICc between that model and the best fitted model.

	Model	AICc	Δ
1	Location + Initial PEI + Location*Initial PEI + Female(Location)	2210.46	25.22
2	Location + Location*Initial PEI + Female(Location)	2210.46	25.22
3	Initial PEI + Location*Initial PEI + Female(Location)	2245.06	59.82
4	Location + Initial PEI + Female(Location)	2185.24	0.00
5	Location + Female(Location)	2224.20	38.96
6	Initial PEI + Female(Location)	2201.41	16.22
7	Location*Initial PEI + Female(Location)	2245.01	59.77
8	Female(Location)	2229.45	44.21
9	NULL	2214.61	29.37

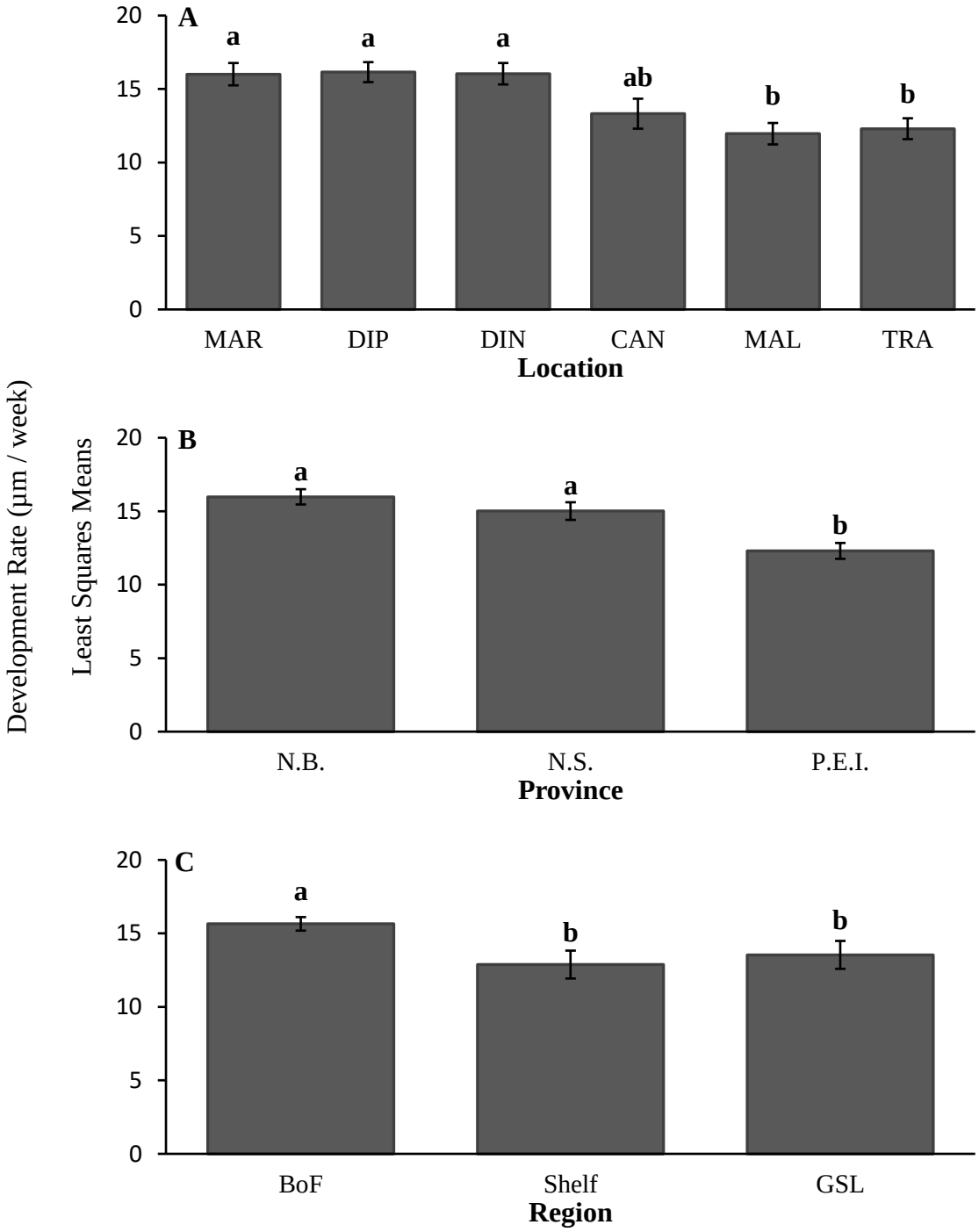

Figure 2. Least squares means development rate of American lobster embryos from (**A**) six locations in eastern Canada: St. Martins (MAR) and Dipper Harbour (DIP) in N.B., Tracadie (TRA) and Malpeque (MAL) in P.E.I., and Dingwall (DIN) and Canso (CAN)

in N.S.; (**B**) these locations divided by provinces: New Brunswick (N.B.), Nova Scotia (N.S.), and Prince Edward Island (P.E.I.); and (**C**) these locations divided into regions: the Bay of Fundy (BoF), the Scotian Shelf (Shelf), and the Gulf of St. Lawrence (GSL). Embryo development rate was estimated on the basis of changes in PEI over the course of the study. Different letters represent significant differences based on a Tukey HSD post-hoc test. Error bars represent a 95% confidence interval.

Table 3. Mixed-model ANOVA for the best-fitted model (model 4, Table 1) to explain the rate of PEI development in American lobster embryos based on six geographic locations (Dipper Harbour and St. Martins in N.B., Canso and Dingwall in N.S., and Tracadie and Malpeque in P.E.I.), female (as a random effect nested within location), and PEI at the beginning of the experiment. The significance of the initial PEI and female term is assessed using the mean square model error term, and that for location using a female-model error composite error term (0.83 x female + 0.17 x model error).

	Sum of Squares	df	Mean Square	F	Sig.
Initial PEI	750.94	1	750.94	46.18	<0.0001
Location	803.50	5	160.70	5.63	0.0002
Female(Location)	1922.20	62	31.00	1.91	0.0002
Error	4959.52	305	16.26		

Table 4. AIC-based comparison of three variants of model 4 separating the sampling locations by individual location (Dipper Harbour and St. Martins in N.B., Canso and Dingwall in N.S., Tracadie and Malpeque in P.E.I.), province of origin (N.B., P.E.I., or N.S.), or broader regions based on similar environmental conditions (Gulf of St. Lawrence: Malpeque, Tracadie, and Dingwall; Scotian Shelf: Canso; Bay of Fundy: St. Martins and Dipper Harbour) to explain variation in the rate of development of embryos; the three models also include female (as a random effect nested within location) and PEI at the beginning of the experiment. AIC is an estimate of the relative quality of a model in relation to the other models; delta indicates the difference in AIC between a potential model and the best-fitted model, and omega represents the relative likelihood of each model given the data.

	Model	AIC	Δ	ω_i
4	Location + Initial PEI + Female(Location)	2200.89	28.61	6.13e-07
10	Province + Initial PEI + Female(Location)	2172.28	0.00	9.99e-01
11	Region + Initial PEI + Female(Location)	2194.56	6.33	1.45e-05

Discussion

There is spatial variation in the development rate of American lobster embryos when raised under constant environmental conditions. The AIC approach to model selection showed that the models that included location were better than all models that did not include location, providing strong evidence for the importance of location to the development rate of embryos used in this study. The ANOVA results confirm this, as the location term in the best model (model 4) is highly significant (Table 3). Spatial variation in embryonic development rate might be responsible, at least in part, for the fact that previous studies on American lobster of different geographic origin have proposed differing temperature based embryonic development functions (Gendron and Ouellet, 2009; Perkins, 1972). However, these functions cannot, and have not, been directly compared since the two studies differed in the conditions under which their embryos were raised (Gendron and Ouellet, 2009; Perkins, 1972). This is the first study to test development rates of embryos from different locations raised in a common environment, and the first to demonstrate spatial variation in those development rates.

The significant effect of location on variability in lobster embryo development rate was only seen when initial PEI was included in the model (results not shown). The inclusion of initial PEI in the models accounted for the fact that embryos that had a smaller PEI at the beginning of this study developed at a faster rate than those that began with a large PEI (results not shown). Adjustment in development rate has not been studied in American lobster, but it has been observed in the Blue King Crab *Paralithodes*

platypus (Stevens et al., 2008). In this species of crab, embryonic development has been observed to take 35 weeks at 4.3˚C and adjusts by increasing to 50 weeks at 6.1 ˚C (Stevens et al., 2008). The reason for the variation seen in the embryos of this study is uncertain. A large portion of embryonic development in American lobster occurs during the autumn following egg extrusion, up until late December where a lull in development occurs (Sibert et al., 2004; Gendron and Ouellet, 2009). In early April, development resumes and eventually leads to hatch (Sibert et al., 2004; Gendron and Ouellet, 2009). The results from the present study suggest that embryos that complete a larger amount of development before the winter have a slower development after the winter, whereas the embryos that did not complete as much of their development prior to winter diapause might develop more rapidly after the winter.

There are factors unaccounted for in this study that are contributing considerably to variability in development rate of individual lobster embryos. This can be seen first from the relatively low R^2 value for the best-fitted model (0.39). It is also seen from results of variance component analysis of this best model, which showed that only a small proportion of the random-term variation in PEI development rate is associated with the female term (14.38%), whereas the majority of this variation is attributed to individual embryos belonging to a same female (85.63%). We do not know the cause of this variation, but this result is consistent with the observation that individual female American lobsters hatch their embryos over a protracted period of time: night and day over the course of several weeks (Ennis, 1975). This is, however, not often seen in all lobster species. For example, the European lobster (*Homarus gammarus*) releases larvae

at night in one minute or less (Ennis, 1973), and the Red King Crab (*Paralithoides camtschaticus*) releases at night and over the course of approximately four hours (Stevens and Swiney, 2007). It is unclear why hatch is protracted in American lobster embryos. In a study on two species of tide pool shrimp (*Branchinecta sandiegonensis* and *Streptocephalus woottoni*), it was suggested that a protracted hatch period might be a bet-hedging strategy to increase the probability that the timing of occurrence of at least some offspring will align with favourable conditions in the face of an uncertain environment that has the potential to result in high mortality (Simovich and Hathaway, 1997). A common source of mortality for recently-hatched larvae is mismatch with food availability (Hjort, 1914; Cushing, 1990). It could be that hatch is protracted in American lobster in an attempt to match at least some of the offspring with the period of peak food availability, potentially explaining the variation in development rate between embryos from a single female in this study.

The model that grouped the sampling locations by their province of origin (N.B., N.S., P.E.I.) was even better than the model using single location in explaining embryonic development rates, and it was also better than a model using broader geographic regions (Gulf of St. Lawrence, Scotian Shelf, Bay of Fundy). When the six locations are compared in a same model, it is evident that there is a "provincial pattern", and embryos from the two locations in N.B. (St. Martins and Dipper Harbour) developed at a considerably faster rate than those from P.E.I. (Tracadie and Malpeque). The environmental conditions in these two locations are substantially different (Hunt et al., 2017). In particular, during the spring and summer when embryos are completing a large

portion of their development, water temperature on the north shore of P.E.I. is warmer than is seen in the Bay of Fundy (Hunt et al., 2017). Since embryonic development in American lobster has been shown to slow at colder temperatures (Templeman, 1940; Perkins, 1972), when embryos acclimated to the warmer P.E.I waters were placed in cooler water for this study it would be expected that their development would slow more than that of embryos from the N.B. waters, which are generally colder than the water temperature of this study. The spring and summer temperature at the N.S. locations are intermediary; they are more similar to, but slightly warmer than, the temperatures at N.B., and they do not reach the warm temperatures on the north shore of P.E.I. (Hunt et al., 2017). The development rates for the N.S. locations are also more similar to those from the N.B. locations, perhaps as a result of the similarity between the water temperature in those provinces. The regional grouping placed Dingwall, N.S. with the P.E.I. locations because all three lie along the Gulf of St. Lawrence, but the development rate for embryos from Dingwall is significantly different from the P.E.I. locations. For this reason, the regional grouping is inferior to the provincial grouping. It is unclear why the embryonic development rate from the Canso, N.S. location is not significantly different from that of the P.E.I. locations, so further sampling should be completed to determine the geographic scope of these differences. From these results, it can be concluded that a single embryonic development function for the entirety of Atlantic Canada would miss some meaningful spatial variation and would therefore be less effective at predicting timing of hatch, but it is not necessary to have development functions at the small scale of individual fishing ports. Further study is required to determine a more exact scale for which these development functions should be created.

It is possible that the groupings of locations that were suggested by the modeling exercise represent different stocks. Our results showed that embryonic development rates for P.E.I. are substantially lower than those for N.B., potentially suggesting that these two areas represent separate stocks. This is consistent with other studies that have found that lobsters from the Gulf of St. Lawrence, the Bay of Fundy and the Gulf of Maine likely belong to different stocks or sub-populations, based on differences in landings over time (Campbell and Mohn, 1983; Harding et al., 1983), genetics (Kenchington et al., 2009; Benestan et al., 2015), and dispersal models (Quinn et al., 2017). Previous stock divisions present ambiguous results as to where the N.S. sites should be grouped (Campbell and Mohn, 1983; Harding et al., 1983; Kenchington et al., 2009). Similar to the provincial groupings of this study, Campbell and Mohn (1983) identified the Scotian Shelf as being different from the BoF/GoM and the GSL based on landings data. From divisions proposed by Harding et al. (1983), based on trends in landings data, the two N.S. sites should be separated from each other as well as being separate from the BoF and GSL. However, Kenchington et al. (2009) grouped N.S. with the GSL, based on genetics. In general, the Scotian Shelf has been described as being a transitional area between the GSL and the BoF/GoM (Campbell and Mohn, 1983), so the mixed results from this study and the previous literature on stock divisions are not unexpected. The difference in results between the present study and these other studies might be caused by the aforementioned similarities to N.B. conditions with regards to spring and summer water temperature (Hunt et al., 2017).

The present research has shown that development rate of PEI increase, and thus embryonic development varies among provinces, so future research should continue to explore differences in embryonic development at this resolution to determine where divisions lie and whether they can be considered separate stocks. In particular, more locations should be sampled along the coast of Nova Scotia to attempt to verify whether development rates are more similar to either other province, or whether it should be considered on its own. It would also be useful to expand this work to the more northern and southern extremities of the American lobster's range (e.g. in Newfoundland and in the northeastern US), which are perhaps likely to show the most pronounced differences in embryonic development rates, given that it would represent the most drastic differences in environmental conditions (e.g. temperature) lobster embryos are likely to encounter. Once the areas with the most similar embryonic development rates are identified, they can then be integrated into management decisions alongside the other suggestions for potential stick divisions, since fisheries are more effectively sustained when they are managed based on up-to-date biological information (National Research Council and National Academy of Sciences, 2004).

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