SEASONAL MIGRATIONS OF AMERICAN LOBSTER (*HOMARUS AMERICANUS*) IN THE BAY OF FUNDY: TEMPERATURE AND DEPTH PROFILES QUANTIFIED USING ARCHIVAL SATELLITE TAGS, AND FUNCTIONAL INFERENCES TESTED USING AN INDIVIDUAL-BASED MODEL

by

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ABSTRACT

Ovigerous American lobsters, *Homarus americanus*, undertake seasonal migrations thought to maximize temperature experienced by their embryos. Using satellite tags, we tracked two ovigerous females from Grand Manan between September 2013 and July 2014. The tags surfaced near Beaver Harbour, NB and Port George, NS, 33 and 123 km from the tagging location, respectively. Recorded depth and temperature for both lobsters were remarkably similar, reflecting shallow-to-deep and deep-to-shallow migrations in the fall and spring, respectively. A change in water temperature appeared to trigger fall movements, but probably not spring movements. An individual-based model indicated that our lobsters experienced higher temperatures than virtual lobsters moving randomly or not at all, but lower than the maximum possible. This study provides novel insights into the nature and function of these seasonal migrations, which represents an essential first step in our ability to predict lobster movements and hatch location in a rapidly changing ocean.

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1.0 Introduction

American lobsters, *Homarus americanus*, are cold-blooded animals that are dependent on external sources of heat to perform physiological functions (Factor, 1995). They are found in the coastal waters of the Northwest Atlantic Ocean, from the Strait of Belle Isle, NL in Canada to Cape Hatteras, NC in the United States (Lawton and Lavalli, 1995). Their distribution is affected by water temperature, as they avoid temperatures below 5 °C and above 25 °C (Aiken, 1977) and display particular movement patterns as a mechanism to thermoregulate (Reynolds and Casterlin, 1979; Crossin *et al.*, 1998; Jury and Watson, 2000; Jury and Watson, 2013). In certain parts of the species' range, adult American lobsters have been observed making seasonal migrations that are believed to be related to the thermal requirements of molting, growth, gonadal development, and egg development (Wilder and Murray, 1958; Cooper and Uzmann, 1971; Uzmann *et al*., 1977; Campbell, 1986; Campbell and Stasko, 1986; Cowan *et al*., 2007; Goldstein and Watson, 2015a).

Reproduction by female American lobster typically follows a two-year cycle (Herrick, 1909). The first summer following her sexual maturation, a female chooses a male that will guard her, and within 48 hours of molting the male will inseminate her while her carapace is still soft to facilitate copulation (Templeman, 1940). The following summer, the female spawns, which consists of the extrusion and fertilization of eggs using stored sperm (Templeman, 1940; Waddy and Aiken, 1986). More infrequently, molting and spawning can occur in the same summer, particularly in warmer waters

such as the Northumberland Strait in the Southern Gulf of St. Lawrence (Ennis, 1984; Waddy and Aiken, 1986). Furthermore, females greater than 120 mm carapace length may spawn in two successive years before molting again (Waddy and Aiken, 1986), making their relative fecundity greater than generally assumed (Factor, 1995). Females typically spawn between June and September, and they then carry their eggs externally on their abdomen until they are fully developed. The time required for embryonic development from spawning to hatch is 36 to 48 weeks (Factor, 1995). Hatching occurs in May and June in the southern part of the lobster's range, and from June to August in the northern part of the range (Factor, 1995). The hatching period of a single brood can last from a few days (Hughes and Matthiessen, 1962) to more than 4 weeks (Ennis, 1975).

Water temperature has marked effects on several of the different steps of the female reproductive cycle (Factor, 1995). For instance, spawning occurs earlier in the warm waters of the Gulf of St. Lawrence than in the cooler waters of the Gulf of Maine (Waddy and Aiken, 1990). Also, water temperature has been shown to have a strong effect on the rate of embryonic development, with embryos developing much faster in warm water (Templeman, 1940; Perkins, 1972; Aiken and Waddy, 1980). Perkins (1972) demonstrated that in constant controlled temperature, embryo development takes as few as 12 weeks at 25 °C and as many as 160 weeks at 5 °C. There is, however, evidence that embryo development is not always the same at a given temperature. For instance, a recent laboratory study on lobsters captured off the Magdalen Islands, in the Gulf of St. Lawrence, found differences in embryo development in early and late-

spawners (Gendron and Ouellet, 2009). In particular, embryos of "early-spawners" which achieved ca. 80% of their development in the fall, experienced a ca. 6-months "rest" period from November to May. In contrast, embryos of "late-spawners" which reached only ca. 50% development by late fall, continued development (albeit at a very slow rate) during the winter, even at temperatures of 1 - 1.5 °C. This study demonstrates that temperature not only affects the rate of embryo development, but that the effect depends on the stage of embryos when they experience said temperature.

Growing degree-days (GDD) is a metric that has been used to quantify the influence of water temperature on the growth and development of ectotherms (Neuheimer and Taggart, 2007), such as lobsters. GDD is the time integral of daily temperature measured above a certain temperature threshold of growth, or development (Neuheimer and Taggart, 2007). Different studies suggest different GDD requirements for embryo development in lobster, but it is unclear whether this reflects true biological differences given that these studies have made different assumptions concerning a temperature threshold for development, and because they are based on embryos originating from different parts of the species' range. Campbell (1986) proposed a temperature threshold of 3.4°C, and estimated that lobster embryos require 1832 GDD to complete development in the Bay of Fundy, Canada. Other estimates include 952-983 GDD for lobster in mid-coast Maine, U.S. (Cowan *et al*., 2007), 807-1490 GDD for lobster in Massachusetts Bay, U.S. (Tlusty *et al*., 2008), 1300-1440 GDD in Magdalen Islands, Canada (Gendron and Ouellet, 2009), and 905-938 GDD off the southern coast of Maine, U.S. (Goldstein and Watson, 2015b), based on temperature thresholds varying

from 0 to 6 °C (Perkins, 1972; Campbell, 1986; Cowan *et al*, 2007; Goldstein and Watson, 2015b). It is in fact likely that there does not exist a single temperature threshold for development of lobster embryos, considering evidence that this threshold varies depending on the embryos' development stage and the time of year when they experience lower temperatures (Gendron and Ouellet, 2009). Despite these uncertainties regarding thermal thresholds for embryo development and GDD required for complete development, GDD were used in this study to compare the thermal histories of real and simulated females in our study.

Poikilotherms can thermoregulate in the marine environment by moving to different depths at different times of the year, but this potential may vary geographically based on atmospheric conditions, oceanic features and bathymetry. In general, the influence of atmospheric weather on water temperature decreases with depth, resulting in thermal conditions being more variable over the course of a year in shallower than in deeper waters (Department of Fisheries and Oceans Canada, 1997; Richaud *et al*, 2016). In certain parts of the lobsters range, this seasonal variability in bottom temperature gives lobsters the opportunity to thermoregulate behaviorally by moving to different depths at different times of the year. Whereas lobsters have been documented to make seasonal movements in many parts of their range (Wilder, 1963; Morrisey, 1971; Fogarty and Borden, 1980; Krouse, 1981; Munro and Theriault, 1983; Campbell, 1986; Campbell and Stasko, 1986; Wahle and Steneck, 1992; Haakonsen and Anoruo, 1994; Lavalli and Lawton, 1996; Comeau and Savoie, 2002), the use of deep-shallow

migrations in lobster for thermal benefit varies geographically based on seasonal variation in bottom temperature and local bathymetry.

In the Gulf of St. Lawrence (GSL), the hydrographic conditions offer little opportunity for behavioural thermoregulation, due to the presence of a "cold intermediate layer" (CIL). The CIL is a large volume of water, between the coastal water (<40 m) and the deeper water (>150 m) located in the Laurentian Channel, that stays cold year round (-1 to 2.5 °C) (Gilbert and Pettigrew, 1996; Drinkwater and Gilbert, 2004). From January to March the CIL is from the surface down to ~150 m deep, with warmer saltier water below. As spring progresses into summer, the top layer warms much more rapidly than the waters underneath, and the water column becomes a three-layer system, with a warm and relatively fresh surface layer, a CIL, and a warmer and saltier bottom layer (Gilbert and Pettigrew, 1996; Drinkwater and Gilbert, 2004). The distribution of bottom temperature results in shallow (<40 m) water being warmer in the summer but colder in the winter compared to deep (>150 m) water, but the intermediate depths stay cold year round due to the CIL (Han *et al*., 1999; Richaud *et al.*, 2016; Chassé *et al*., 2014; Richaud *et al.*, 2016). This CIL is thought to prevent lobsters from thermoregulating, as lobsters do not pass through this zone of cold water, which is required in order for them to reach the warmer deep water in the winter. Moreover, the bathymetry in the southern GSL is mostly flat, gradual sloping bottom, requiring a lobster to travel between 50 and 200 km from most coastal areas to deep water (> 150 m), with some exceptions being the shallows of Chaleur Bay, Magdalen Islands, and Cape Breton that are closer to deep water. Most tagging studies in the GSL

were done in the southern GSL, and they do not allow inferences on whether lobsters undertake deep-shallow movements in these waters because movements were not tracked throughout the year (Comeau and Savoie, 2002). Nevertheless, a few studies have documented lobsters moving from the shallows (< 20 m) of Magdalen Island, Bonavista Bay in Newfoundland, and in the Chaleur Bay to slightly deeper water (20 - 40 m) for the winter (see Review by Comeau and Savoie, 2002). Although the thermal histories of these lobsters were not recorded, it is unlikely that these movements exposed lobsters to warmer waters, because of the CIL, and instead it is thought that lobsters undertake these movements to obtain protection from storm surges and sea ice (Ennis, 1984; Comeau and Savoie, 2002). GSL lobsters are therefore constrained almost exclusively to shallow coastal regions (Chasse *et al*., 2014), and they are unlikely to undertake movements to deeper (>150 m) and warmer waters of the Laurentian Channel because of the large travel distances involved and the thermal barrier to movements offered by the CIL (Stasko, 1980; Comeau and Savoie, 2002).

In the Gulf of Maine (GoM), the hydrographic climate and bathymetry offer the opportunity for lobsters to make deep-shallow migrations to increase the temperature they experience in the winter. In general, mean bottom temperature on the shelf (0 - 150 m) ranges from 6.5 to 10.4 °C from winter to summer, with ~8 °C year round in deep (150 - 200 m) basins (Richaud *et al*., 2016). The distance for a lobster to travel from inshore to a deep basin varies from 25 km in the Bay of Fundy to approximately 125 km in mid- to southern GoM (Mountain and Holzwarth, 1989). Lobsters have been observed making long-distance and deep-shallow movements in the GoM (Morrisey, 1971;

Cooper *et al*., 1975; Fogarty and Borden, 1980; Krouse, 1981; Campbell, 1986; Campbell and Stasko, 1986; Haakonsen and Anoruo, 1994; Goldstein and Watson, 2015a), but the thermal benefit will vary geographically depending on the extent of vertical displacement that lobsters are able to accomplish. The first study to record thermal histories of ovigerous lobster in nature was done in mid-GoM, in Muscongus Bay (Cowan *et al*., 2007). The temperatures recorded suggested that small (< 95 mm CL) ovigerous lobster tended to stay inshore year round, while large (> 95 mm CL) individuals tended to move into deeper water for the winter. Overall both groups accumulated similar GDD, but the temperatures experienced varied less for the large lobsters; larger lobsters experienced warmer water in the winter, and colder water in the spring, compared to smaller females. Depth was not recorded in this study, thus the extent of movements to deep water by large ovigerous lobsters is unclear. Nevertheless, given the hydrographic climate of this area it is understood that the larger lobsters would have had to be in deep water during the winter compared to the smaller females. The authors of this study hypothesized that large females moving away from shore avoid exposing their embryos to a rapid increase in water temperature in the spring, which could cause hatching to occur before optimal conditions. Moreover, they argue that the smaller lobster cannot afford this advantage because their risk of predation during migration may be high (Cowan *et al*., 2007). In another study further south in the GoM, off New Hampshire, movements and thermal histories of six ovigerous lobster were tracked using ultrasonic telemetry and attached temperature loggers (Goldstein and Watson, 2015a). These lobsters were caught and tagged at ≈9 m depth in fall 2006, and monitored till spring 2007. Of these lobsters, four moved “offshore” to somewhat deeper

water (~ 30 m) and stayed until after their eggs hatched, which resulted in an estimated hatch period that was markedly later (Aug 1st to Aug 20th) than that estimated for the two lobsters that stayed inshore (July 10 to July 27th). It was hypothesized that the ovigerous females that moved offshore did so to release their larvae offshore, to facilitate dispersal, rather than to gain GDD. Even though the hydrographic and topographic conditions in some areas of the GoM could allow seasonal deep-shallow migrations to increase temperatures, there is no evidence yet that this occurs. To fully address the potential of thermoregulation in lobster we need to investigate thermal histories of migrating lobsters, especially in northern regions of the GoM, where the distance to deeper (200 m) and warmer water is considerably shorter.

The Bay of Fundy offers considerable potential for lobster seasonal thermoregulation, because the depth at which warmer water occurs changes over the course of the year, and the bathymetry is sufficiently steep that lobsters can readily access different depth-based thermal environments. Waters of the Bay of Fundy are generally well mixed from the surface to the bottom (≈ 150 m) due to tidal-currents, and fluctuate mostly between 1 to 12 °C annually (Department of Fisheries and Oceans Canada, 1997). However, near the mouth of the Bay there is a deep basin (Grand Manan Basin) of approximately 150 to 200 m, where bottom temperature varies little seasonally, ranging from 5 to 7 °C over the course of a year (Department of Fisheries and Oceans Canada, 1997; Richaud *et al.*, 2016). Interestingly, the interplay of temporal and spatial variation in temperature results in shallow-water temperature of the Bay of Fundy being markedly higher in the summer, and lower in the winter, compared to the

temperature in deeper waters (Campbell, 1986; Department of Fisheries and Oceans Canada, 1997). Moreover, the steeply sloping bottom in regions of the Bay of Fundy that are in proximity to the Grand Manan Basin allows lobsters to access this deep water over a relatively short horizontal distance. For example, a lobster off the coast of Grand Manan can make a vertical displacement of 100 m in just 10 km in horizontal space (Mountain, 2003). In the first large tagging study in the Bay of Fundy in 1982 to 1983, out of 2139 ovigerous lobster tagged in the summer and fall off Grand Manan, 1046 were recaptured, including 457 recaptured between 2 and 10 times (Campbell, 1986). Analyses of single and multiple recapture depths suggest that ovigerous lobsters in this area move to deep water in the fall, stay deep during the winter, and then move back to shallow water in the spring (Campbell, 1986). It was hypothesized, based on seasonal bottom temperature distribution, that these deep-shallow migrations position the lobster in the maximum temperature available to them year-round to ensure timely development of embryos (Campbell, 1986). However, to date no study has documented the depth and thermal history of migrating ovigerous lobsters in the Bay of Fundy (or any lobster in any part of the species' range for that matter). In addition, no study has contrasted temperatures experienced by such migrating lobsters to those that would have been experienced in the absence of such migrations, or under alternate movement scenarios. Therefore, the particular details of theses migrations (e.g. depth and temperature), as well as their actual thermal benefits, remain unclear.

The overarching goal of this study was to increase our understanding of seasonal migrations of ovigerous American lobster in the Bay of Fundy, including how these

affect the thermal histories of their developing embryos. The specific objectives were as follows:

i) Document in greater detail the depth and thermal histories of ovigerous American lobsters undertaking shallow-to-deep (fall) and deep-to-shallow (spring) migrations using pop-up satellite archival tag (PSAT) technology.

ii) Develop an individual-based model to investigate the role of temperature in observed deep-shallow migrations, and to contrast the thermal history of real lobsters to that of virtual lobsters under different movement scenarios, including “no movement”, “random walk”, or “maximized temperature”.

The hypothesis explored in this study is that seasonal movements by ovigerous lobsters in the Bay of Fundy-Canadian Gulf of Maine accelerate embryo development by increasing the temperature they experience. We predict that our tagged ovigerous lobsters will achieve a greater number of GDD than virtual lobsters that do not move or move randomly with respect to depth. Moreover, we attempted to determine whether movements appeared to be made to maximize temperature experienced by embryos, by comparing GDD experienced by tagged lobster to those experienced by virtual lobsters moving to the depth of maximum temperature each day.

2.0 Methods

2.1 Satellite Tagging of American Lobster

2.1.1 Seasonal Movements

We used pop-up satellite archival tags (PSATs) to document a complete seasonal migration of ovigerous lobsters. The PSATs that were used are called SeaTag-MOD (total length: 230 mm; mass: 145 g), and are built by Desert Star Systems (Fig. 1 left). They are equipped with sensors to detect the magnetic field, light, temperature (-20 to 50 °C, 0.0001 °C resolution), and pressure (to estimate depth down to 2000 m: 0.05 m resolution), along with a 2GB FLASH memory card for data storage. For this study, the tags were programmed to record temperature and pressure every 15 minutes. The depth recorded allowed us to confirm vertical movements and the temperature recorded allowed us to determine the temperature experienced by developing embryos. The tag is powered by solar energy and by a ½ AA battery in the absence of sunlight. At a pre-set date, an electric current passes through the metal lead that connects the tag to the anchor, creating a spark that causes a microburst of a flammable Potassium Chlorate compound, which causes fast and definite release. The detached tag then floats to the surface and starts communicating daily means of depth and temperature to satellites, assuming no obstructions of signal, until it is turned off, it loses power, or is damaged.

On October 1st 2013, two ovigerous lobsters were captured in Flagg Cove (44°.7623N, 66°.7804W), Grand Manan, by hand using SCUBA, brought back to a research vessel at the surface, equipped with a PSAT, and released by SCUBA (Fig. 2).

Both lobsters were 160 mm CL, as measured from the back of the eye stock to the end of the carapace on a line parallel to the longitudinal axis of the body. Large lobsters were chosen for this study to minimize effects the relatively large tags might have on movements, and also because they have been shown to display more extensive seasonal vertical migrations than smaller ovigerous females in the Gulf of Maine (Cowan *et al*., 2007). The lobsters chosen were carrying recently-spawned eggs, which are dark green/brown and have no visible eye spots; these embryos were to hatch the following summer (Factor, 1995). Prior to tagging, a lobster's carapace was first cleaned using sand paper, to scrape off biofilm or fouling organisms, and then patted down with an ethanol-soaked paper towel for quick drying. Custom Plexiglas attachments (Fig. 1, right) were made to hold the tags firmly and securely in place; one attachment secured the release section end cap, and the other secured the detachable SeaTag-MOD with battery. Pieces of commercial sponge cut out just larger than the base of the Plexiglas attachments were soaked with Home Bond® superglue from Home Hardware and stuck between the lobsters' carapace and attachments. The glue was allowed to dry for 2 hours, during which time the lobsters were placed in seawater to reduce stress, up to below where attachments were drying. The tags were then secured onto the attachments using a metal pin connecting the release section end cap of the tag to the anterior attachment, and the detachable portion of the tag (including float) was loosely held by the posterior attachment (Fig. 1, right). After tagging, lobsters were released by hand using SCUBA in the same area and depth of capture, within approximately three hours of capture. SCUBA diver observations of tagged lobsters after release suggested that the tags had minimal effects on movement or escape (tail flicking) ability. Tags were

programmed to detach on July 31st, 2014, which coincides with the earlier part of the hatching period (July - September) of ovigerous lobster in the Bay of Fundy (Campbell, 1986). The Plexiglas attachments and release end cap were expected to stay on the lobster until molt. One of the PSATs was recovered, which gave us access to a nearly complete record of the temperature and depth data for every 15 minutes of the tagging period. For analyses, daily summaries of temperature and depth records obtained by transmission from the ARGOS Satellite System were used. The data that were not received within our purchased satellite access time were interpolated by taking the average depth and temperature of the day before and after, resulting in 55 and 58 days out of 305 being estimated for each tag. Note that differences in mean daily depth recorded by the tags that would be owed to changes in average daily tidal height, and hence would be unrelated to movement, is negligible compared to the extensive movements expected in this study. Specifically, using 100 days of hourly tidal height estimates from the Canadian Hydrographic Services (http://www.waterlevels.gc.ca/eng) for North Head (close to our lobster release location off Grand Manan) in 2017 (starting in September), we estimated that the change in mean tidal height over two consecutive days was on average 2 cm and at maximum 7 cm. Importantly, this small bias does not get progressively bigger or smaller over the course of the study, but rather cycles between increasingly negative and increasingly positive values over periods of about 28 days. The maximum difference in mean tidal height observed between any two days over the course of the ≈100 days examined was 30 cm. Considering that large lobsters can move large horizontal distances, changing depth by 100s of meters over the course

of a year, these small biases due to changes in tidal height are not consequential to any of our inferences.

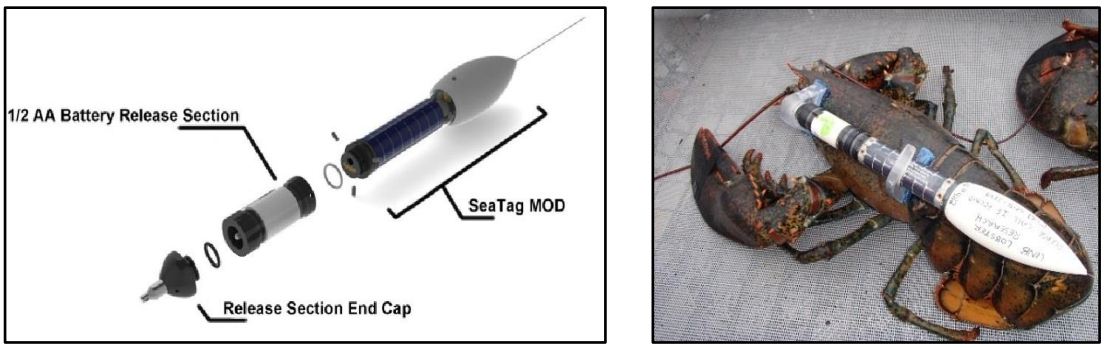

Figure 1. (Left) Desert Star Systems' pop-up satellite archival tag (SeaTag-MOD) with 1/2 AA battery and release section (http://desertstar.com/), and (right) one of the two 160 mm CL ovigerous lobsters tagged during this study; the two tagged lobsters were captured and released in Flagg Cove, Grand Manan, New Brunswick, in October 2013.

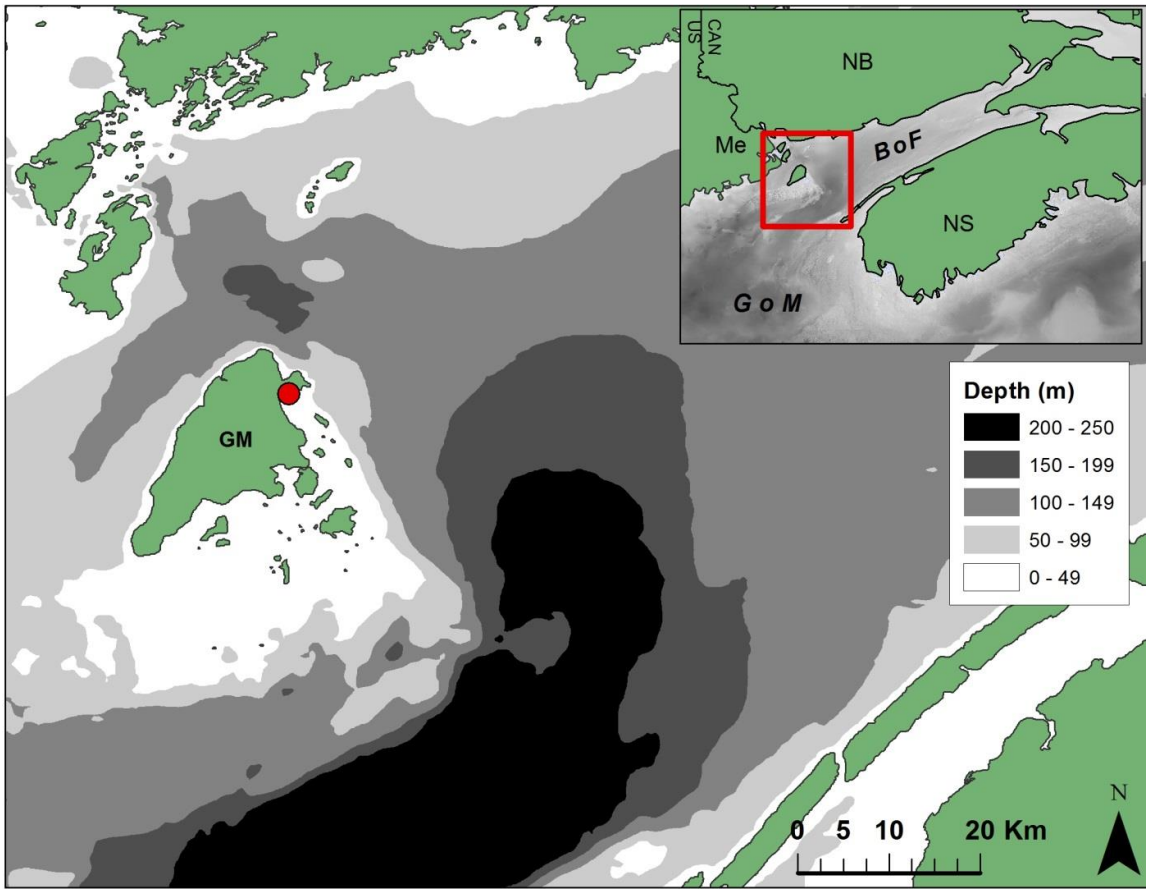

Figure 2. Map of southern Bay of Fundy showing the location (red circle: Flagg Cove, Grand Manan) where two 160 mm CL ovigerous American lobsters were captured, equipped with satellite tags, and released, in October 2013. Me: Maine, NB: New Brunswick, NS: Nova Scotia; GM: Grand Manan; BoF: Bay of Fundy, GoM: Gulf of Maine.

2.1.2 Environmental Conditions at Migration Onset

To investigate whether a change in bottom temperature may have been associated with the onset of seasonal migrations of the tagged lobsters, we examined the temperatures recorded by the satellite tags 20 days prior to the lobsters initiating shallow-to-deep and deep-to-shallow movements in the fall and spring, respectively. Over most of our study domain, a lobster can change depth by 15 m in only 2 to 6 km (0.13 - 0.41 km/m). The bathymetry where the lobsters were released in the fall is steep sloping, with depth changing from 0 to 40 m in less than 5 km (~ 0.13 km/m). The bathymetry is considerably flatter in deeper water, where lobsters were in the spring, with depth changing from 150 m to 200 m over approximately 25 km (~ 0.5 km/m). Given these depth profiles, the precision of our lobster depth estimates (0.05 m), and the fact that migrating lobsters in our study region can move several kilometers in a day (Campbell, 1986), we expect to notice a change in the depth of our lobsters when they initiate fall/spring migrations. We used a one-day change in depth ≥ 5 m, followed by continued movements in the same direction as the day that lobsters initiated fall and spring vertical migrations. Given that this 5-m criterion is somewhat arbitrary, we also estimated the day migrations were initiated by using 2-m and 8-m thresholds.

2.2 Individual-Based Modelling

2.2.1 FVCOM-GOM bottom temperature validation

The Finite-Volume Community Ocean Model (FVCOM) was used to produce bottom temperature estimates by depth, time, and location in the Bay of Fundy from

1978 to 2014 (Chen *et al.*, 2006). This ocean circulation model is based on a non-overlapping, unstructured triangular grid, which allows the model to resolve highly irregular coastlines and bathymetry, such as in the Gulf of Maine. The grid provides horizontal resolution ranging from as fine as 10 m inshore to as coarse as 10 km at the open boundary off the continental shelf (Li *et al.*, 2017). The model can hindcast, nowcast, and forecast key ocean features such as bottom temperature, sea surface height and total water depth, which were used here to create a depth-based model of bottom temperature our tagged lobsters could have experienced (see below).

In order to assess the accuracy and precision of daily average bottom temperatures modeled by FVCOM-GOM, model predictions were compared to spatially- and temporally-matched observations from the July 2013 and July 2014 groundfish surveys conducted by the Canadian Department of Fisheries and Oceans (Fig. 3). Bottom water temperatures were measured using a CTD instrument, and each measure was paired with temperature reported for the nearest corresponding FVCOM grid cell for the same date. A total of 25 and 22 FVCOM-CTD data pairs were identified using this approach in 2013 and 2014, respectively, at depths ranging from 42 to 218 m.

Linear regression analysis was used to compare observed (CTD) and modeled (FVCOM) bottom temperatures, by way of coefficient of determination, intercept, and slope obtained by minimizing the sum of squared errors. In particular, a potential bias in modeled temperature predictions was assessed by comparing the intercept of these regressions to a value of 0, and the slope to a value of 1. The coefficient of

determination was used to assess the “goodness-of-fit”, or more specifically the amount of variance in the observed data that is explained by the linear model (Fitzpatrick, 2009). The linear regression package available in R was used to run tests and estimate linear regression parameters. We also performed t-tests to compare the mean difference between observed and modeled bottom temperatures to zero (i.e., no bias), and linear regressions to determine whether the differences between observed and modeled temperatures were related to depth (i.e., potential depth-based bias).

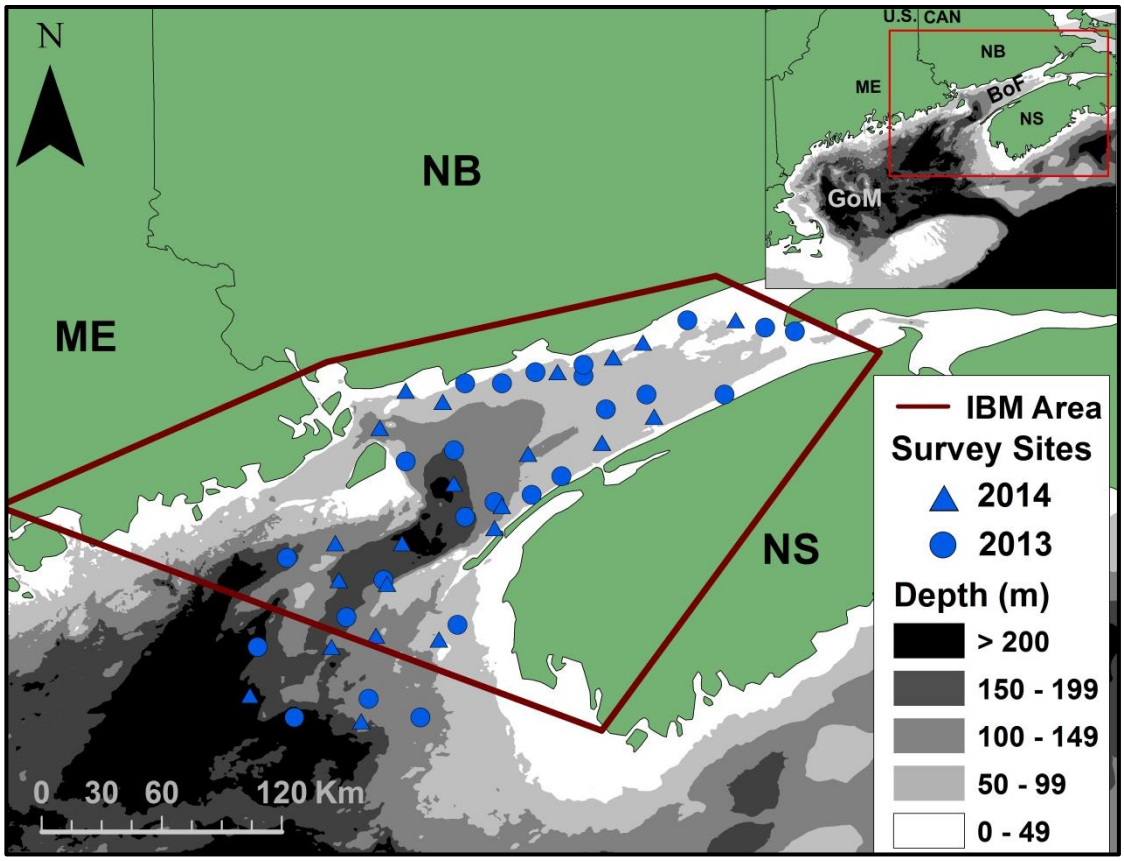

Figure 3. Map of the Bay of Fundy and Canadian Gulf of Maine showing the area used to study the movement of our two tagged lobsters (red polygon: 45°.20N, 64°.50W; 43°.50N, 65°.75W; 44°.50N, 68°.47W; 45°.15N, 67°.00W; 45°.54N, 65°.24W), and the location where CTD profiles were taken during the July 2013 (blue circles) and July 2014 (blue triangles) groundfish surveys of the Canadian Department of Fisheries and Oceans. Bottom temperature values obtained during these surveys were used to validate bottom temperatures predicted by the Finite Volume Community Ocean Model (FVCOM) (Chen et al., 2007). GoM: Gulf of Maine; CAN: Canada; US: United States; NB: New Brunswick, NS: Nova Scotia; ME: Maine; GM: Grand Manan.

2.2.2 Spatial Domain

We built a simple individual-based model (IBM) in R programming that simulates lobster movement in a one-dimensional depth-based environment. In daily time steps, virtual lobsters "chose" a depth to move to every day based on the temperature at different depths as well as individual properties related to their response to temperature and movement capacity (described below). To create this model domain, we extracted mean daily bottom temperature from FVCOM-GOM model grid cells within an area that was expected to encompass the movements our tagged lobsters could make during this study (Fig. 3). Using modelled temperature, we calculated the daily mean temperature-at-depth for every 1 m increment in depth, for the period of September 2013 to August 2014, which spans the period during which our tagged lobsters were at large (Fig. 4 left). In other words, all FVCOM bottom temperatures that exists within our study domain at a given depth and time were averaged. This smoothing method eliminates differences in bottom temperature in different areas of the same depth, however, it also reduces the error associated with FVCOM bottom temperature predictions. Model temperature was warmer in shallower water than in deeper water from late May to late November, but the opposite was true throughout winter (Fig. 4 left). The standard deviation of these mean daily temperatures is generally higher in shallow water (<50 m) compared to deep water, except during the winter and early spring when it is moderate to high across all depths (Fig. 4 right).

In order to assess the ability of our one-dimensional depth-based model to mimic the temperature experienced by our tagged lobsters, we compared mean daily bottom

temperature of the satellite tags attached to our two lobsters to the mean daily temperature of model grid cells that were at the same depth as the tag. Linear regression analyses were used to compare observed (tag) and average modeled (FVCOM) bottom temperatures, by way of coefficient of determination, intercept, and slope obtained by minimizing the sum of squared errors. The linear regression package available in R was used to run tests and estimate linear regression parameters.

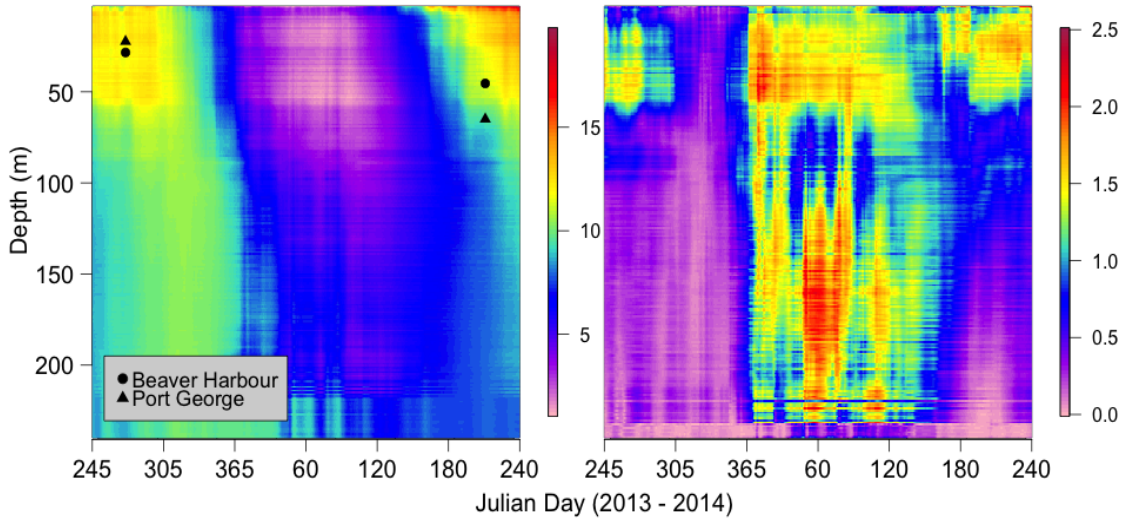

Figure 4. One-dimensional thematic map of (left) mean and (right) standard deviation of bottom temperature extracted from FVCOM for our study area (Fig. 3) in the Bay of Fundy, Canadian Gulf of Maine, in relation to depth and date, from September 2nd 2013 (Julian day 345) to August 28th 2014 (Julian day 240). The left panel also shows when (Julian Day 274, October 1st 2013) two lobsters were captured in Flagg's Cove, Grand Manan, equipped with a pop-up archival satellite tag and released at 28.4 and 22.4 m depth, as well as when (Julian Day 212, July 31st 2014) their tags released in Beaver Harbour, New Brunswick, and Port George, Nova Scotia, from depths of 45.4 and 65.0 m, respectively.

2.2.3 Movement Scenarios

The probability that a lobster will move to a given depth (d) based on its current depth (D_t) and the present bottom temperature profile may be expressed as:

$$\text{Eq 1.} \qquad Pr(D_{t+1} = d) \sim \begin{cases} 0, d > D_t + VMS \\ exp\{-TS\,|d_{maxT} - d|\}.\, d \in [D_t \pm VMS] \\ 0, d < D_t - VMS \end{cases}$$

for d ranging from 0 to the maximum depth in the domain (e.g., 220 m); where TS is the 'Temperature Sensitivity'; D_t is the virtual lobster's current depth; d_{maxT} is the depth of maximum temperature; VMS is the Vertical Movement Scope.

This equation is based on the following three elements of the rules assumed to govern movement in the virtual lobsters:

- Temperature Information Range (TIR) determines the range of depths over which temperature information is "known", with values explored ranging from zero (i.e., no information) to 220 m (i.e., information for all depths).
- Vertical Movement Scope (VMS) determines the maximum allowable depth change per day, with values explored ranging from zero m per day (i.e., no movement) to 220 m per day (i.e., access to all depths).
- Temperature Sensitivity (TS) is a coefficient used in the probability equation (Eq. 1) that determines how precisely the virtual lobster accesses the depth at which the maximum temperature possible occurs, for particular values of TIR

and VMS, with values explored ranging from zero (i.e., random walk) to one (i.e., maximizing temperature).

For particular values of Vertical Movement Scope (VMS) and Temperature Information Range (TIR), the model calculates the truncated probability (Eq.1) of selecting each depth within the TIR as an exponential decline from the depth of maximum temperature and is subsequently scaled so that total probability sums to one. This probability distribution is influenced by the Temperature sensitivity (TS), which basically reflects how precisely a virtual lobster is focused on moving towards the depth of maximum (known) temperature, with higher TS values resulting in the probability distribution becoming increasingly concentrated near the depth at which maximum (known) temperature occurs (Fig. 7). In the case of lobsters having information on temperatures (TIR) beyond their movement scope (VMS), this would lead to a virtual lobster moving to the limit of their VMS towards the depth of maximum temperature within their TIR (Fig. 7 right). Note that the model does not account for variability in temperature over the TIR, and depends solely on the depth at which maximum detected temperature occurs. In other words, a maximum temperature 10 m shallower than a lobster is equally attractive whether it is 4 °C or 0.04 °C warmer.

Based on the movement rule expressed in Eq. (1), the model proceeds in daily time steps by working through four steps for each virtual lobster to select a new depth (or stay at the current depth) every day (Fig. 5). (i) The first step is to determine the depth at

which the maximum temperature occurs within the range of depths over which the virtual lobster has information, which is based on its Temperature Information Range (TIR) (Fig. 6). (ii) Second, the model determines what depths are "physically accessible" by the virtual lobster, which is determined by its Vertical Movement Scope (VMS). (iii) Third, the probability of moving to a given depth within the accessible range is determined from Eq. (1) based on the lobsters Temperature Sensitivity (TS). (iv) The virtual lobster selects a new depth based on a random draw from the resulting probability distribution. The depth chosen on a given day becomes the starting depth the following day, where the lobster will be faced with new values of temperature at depth and will work through the four model steps again.

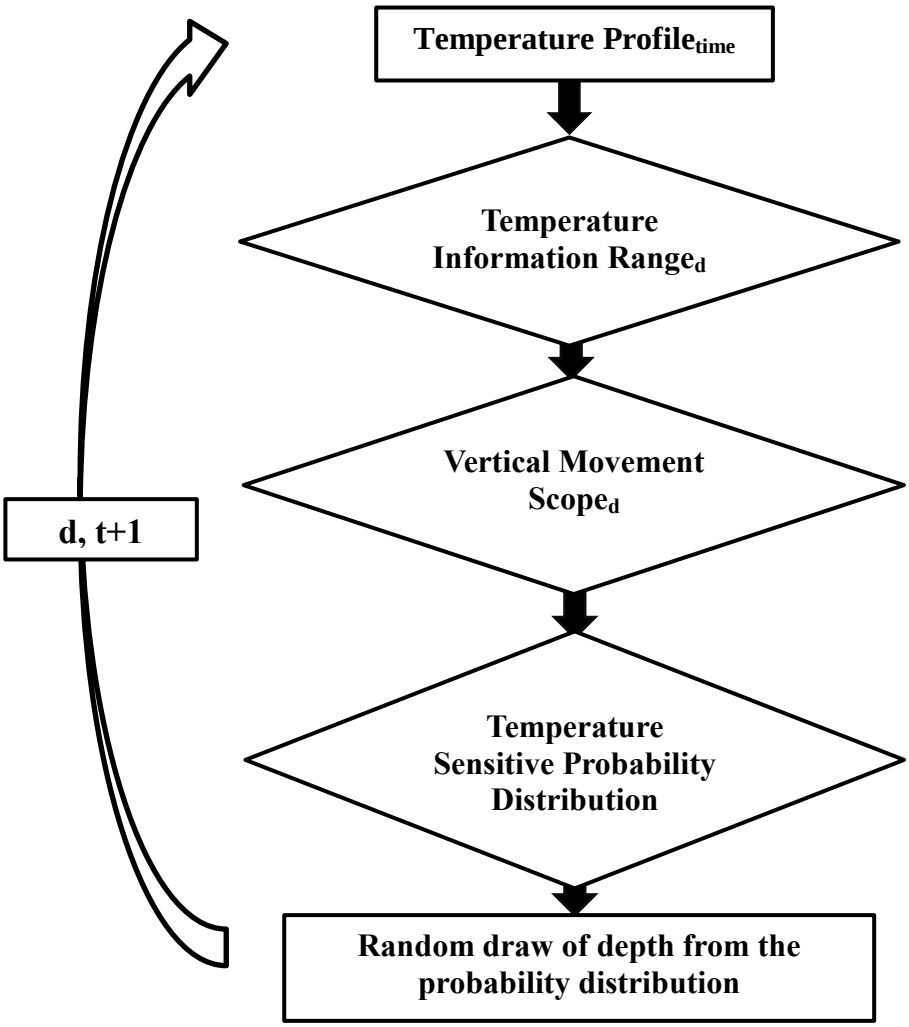

Figure 5. Flow diagram of the individual-based model, showing the four steps that are taken to determine depth change of each virtual lobster at each daily time step (t). At a given time (t), the model first obtains the mean value of temperature at all bottom depths (1 m increments) based on FVCOM, and it then goes through three "lobster decision rules" (diamonds) to generate a frequency distribution of depth choices that is randomly drawn upon to select the lobster's depth at time t + 1 (bottom rectangle). See Methods for details concerning these four steps. The virtual lobster then works through these four steps again the following day, based on its new depth.

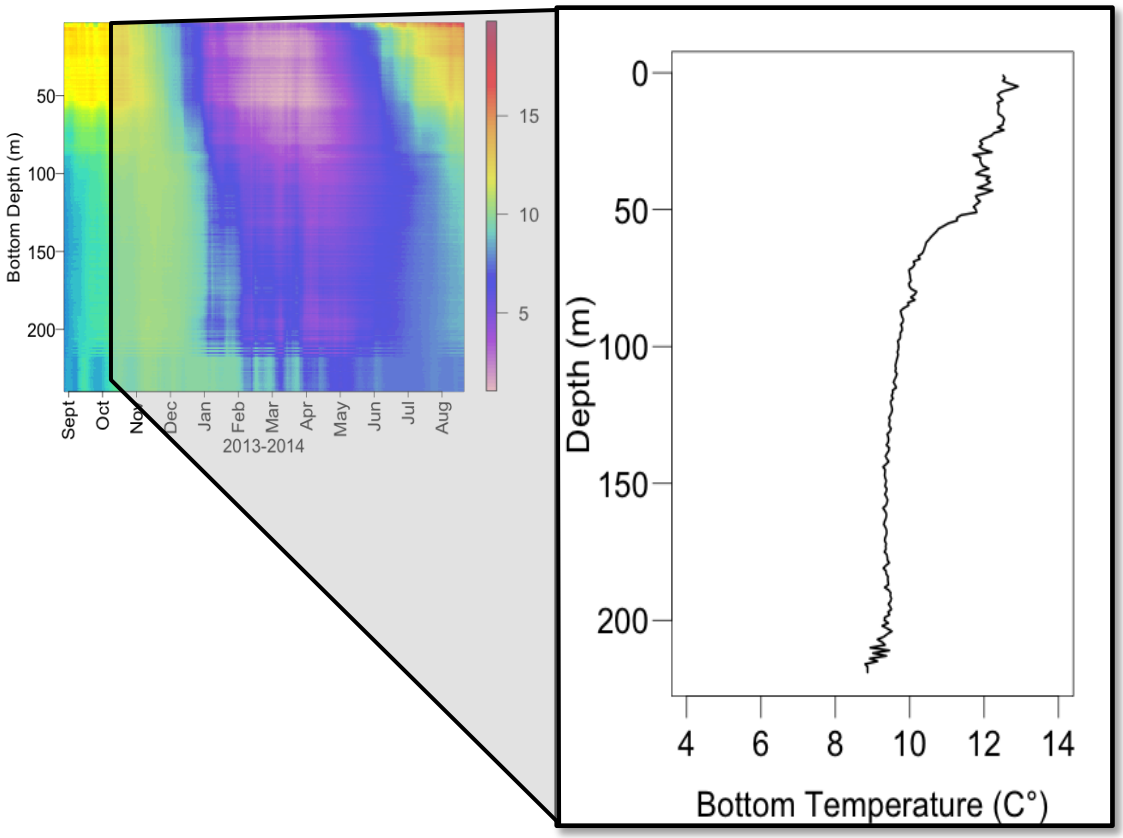

Figure 6. (Left) One-dimension individual-based model environmental domain, where mean temperature at depth varies over time. (Right) Figure illustrating, as an example, mean temperature at depth for a single day in the fall.

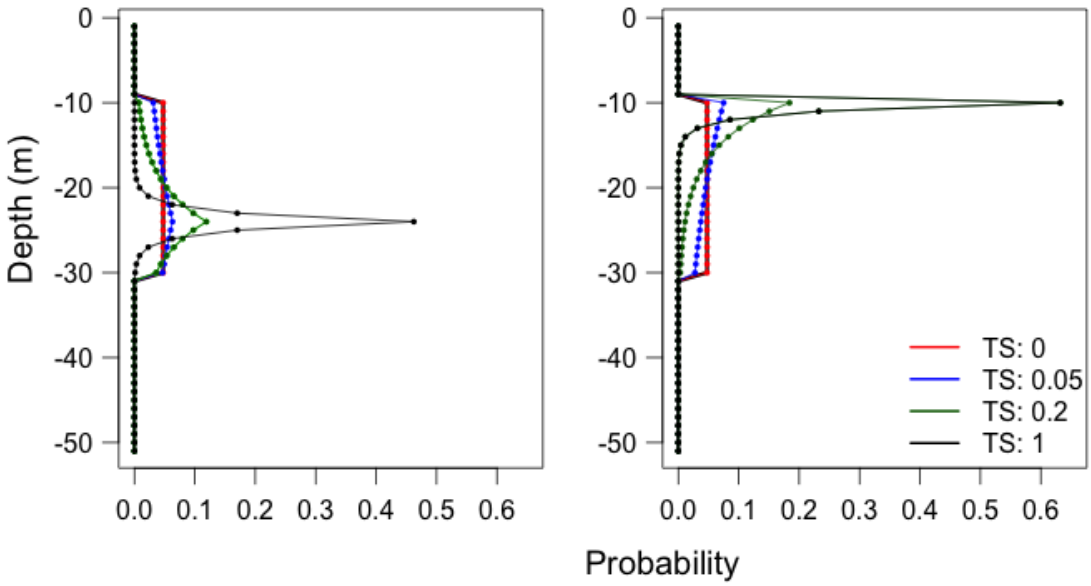

Figure 7. Plot depicting truncated probability distributions for a virtual lobster at 20 m having a Vertical Movement Scope (VMS) of ±10 m, Temperature Information Range (TIR) of ± 30 m, and Temperature Sensitivity (TS) of 0 (red lines), 0.05 (blues lines), 0.2 (green lines), and 1 (black lines) for the case where the depth of maximum temperature is located at 25 meters (left), hence within the lobsters VMS and at 0 m (right), hence outside the lobsters' VMS. Note that in the case where the depth of maximum temperature is deeper than the lobster's VMS the probability distribution will be the reflection of the right plot.

For a given set of movement rules the individual-based model was run for 100 virtual lobsters over the period of October 1st (Julian Day 274) to July 31st (Julian Day 212), the same period that our tagged lobsters were at large. The simulations produced a depth trajectory and thermal history for each virtual lobster. From these data we calculated the cumulative growing degree-days (GDD) for embryos attached to each virtual lobster by summing mean daily temperatures (in °C) corrected for an arbitrary thermal threshold of embryo development of 0 °C, to compare the outcome of different combinations of movement rules on GDD experienced by embryos of virtual lobsters as well as GDD experienced by embryos of our tagged lobsters.

We considered many combinations of movement rules with varying temperature directedness to investigate how it affected virtual lobster movements (VMS: 0 to 220 m; TIR: 0 to 220 m; TS: 0 to 1) and to determine which combination of rules generated depth trajectories and thermal profiles that best matched those recorded by the satellite tags on our tagged lobster . We present 18 such combinations here, which illustrate the step-wise method we used to determine which movement rules and parameter values are important to our ability to simulate the observed vertical migrations. We first investigated the TS rule at 0, 0.025, 0.05, 0.075, and 0.1, where TIR and VMS were set to ± 15 m per day (i.e., the virtual lobster was able to perceive differences in temperature up to 15 m shallower or deeper than its current depth, and had the ability to move within this range of depths in a single time step, or day). We used TIR and VMS of ± 15 m for these tests because these values reduced variability in simulated depth trajectories, and hence facilitated assessment of the influence of TS on these. We then

investigated the TIR rule at ± 15, 30, 50, 100, and 220 m per day, where VMS was set to ± 15 per day and TS to 0.05, and finally investigated the VMS rule at ± 5, 10, 15, 30, and 45 m per day, where the TIR was set to ± 15 m and the TS to 0.05. We used TS of 0.05 for these tests because it allowed virtual lobster to move to depths of warmer waters accurately, and hence facilitated assessment of the influence of VMS and TIR on these, but not so accurate as to have each virtual lobster do the exact same thing for particular values of TIR and VMS. We also simulated "no-movement" (TIR, VMS, TS = 0), "randomly walking" (TIR, VMS = ± 15 m per day, TS = 0) and "maximized temperature" (TIR and VMS = ± 220 m per day, TS = 1) lobsters, to contrast the depth and thermal profiles of these particular behaviors to those experienced by our tagged lobsters.

To determine which movement scenario, or combination of movement rules, best matched the depth and temperature recorded by the satellite tags attached to our two tagged lobsters, we ran linear regressions between simulated and observed values and calculated the root-mean squared error (RMSE) of each regression; the "best model" and decision rules were those with the lower RMSE. We then used the best model to hindcast potential depth and temperature profiles of ovigerous lobsters from 1978 to 2014, based on temperature at depth information extracted from FVCOM-GOM, to visualize how these profiles might vary from year to year based on inter-annual variation in temperature (assuming the same decision rules).

3.0 Results

3.1 Satellite tagging of American Lobster

3.1.1 Seasonal Movements

As planned, the two satellite tags surfaced on July 31st 2014, that is 305 days at large since the October 1st, 2013 tagging and release date (Fig. 8). The tags communicated with ARGOS Satellite Systems within at most 15 minutes from the time the tags detached from the lobsters, suggesting that the first satellite longitude-latitude record is a good proxi for where the lobsters were at that time; one lobster was in the lower Bay of Fundy, approximately 3.5 km from Beaver Harbour, New Brunswick (66°.7380W, 45°.0410N), and 33 km from where it had been tagged the previous fall (hereafter Beaver Harbour lobster, or BHL), and the other had moved into the upper Bay of Fundy, approximately 8 km from Port George, Nova Scotia (65°.2550W, 45°.0275N), and 123 km from where it had been tagged (hereafter Port George lobster, or PGL). The tag that surfaced near Beaver Harbour was physically recovered by Randy Losier, aquatic science technician in Dr. Fred Page's Oceanography group of the Department of Fisheries and Oceans at the St. Andrews Biological Station, which enabled us to access the complete record of depth and temperature (data recorded every 15 minutes) for this animal. Using this data we recalculated daily means of depth and temperature. The tag that surfaced near Port George Nova Scotia was not recovered and daily summaries of depth and temperature were recovered via satellite transmission (ARGOS Satellite Systems) for 247 days out of the 305 days at large.

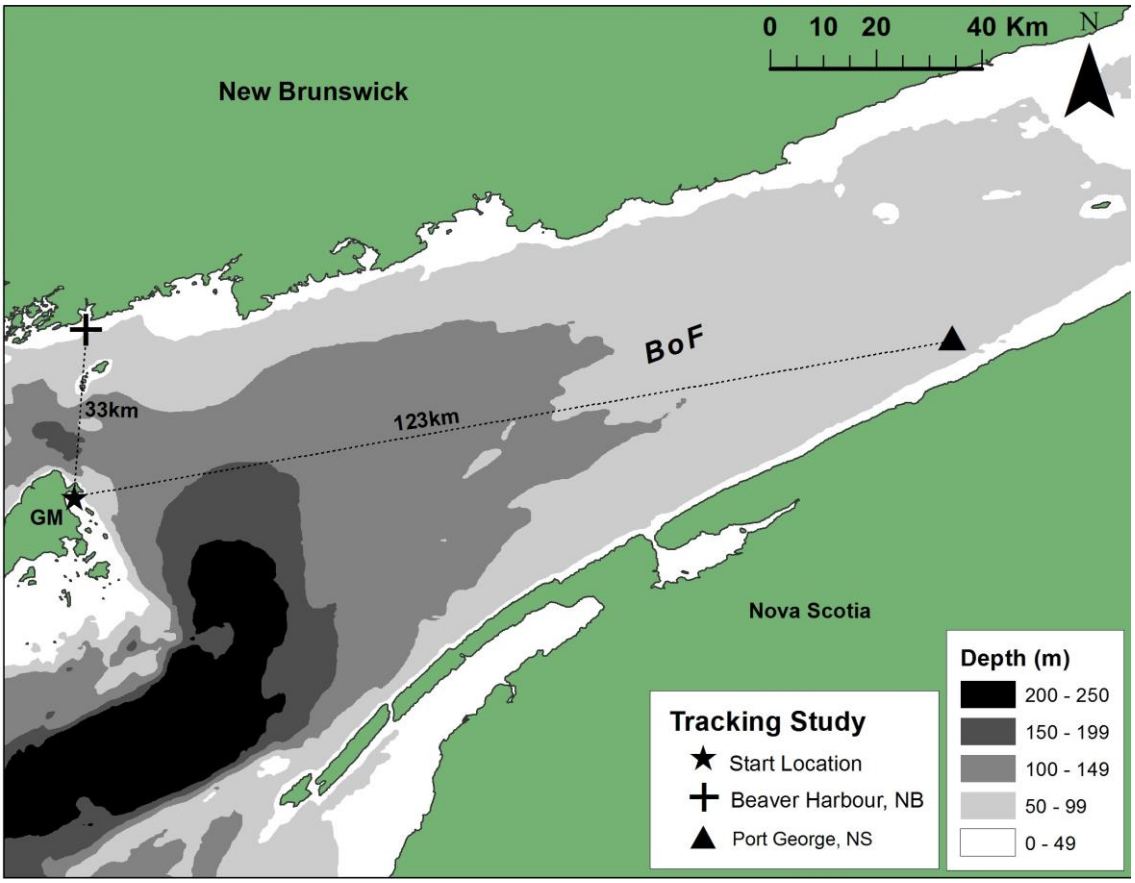

Figure 8. Map of the Bay of Fundy showing the location (North Head, Grand Manan) where two ovigerous American lobster (160 mm CL) equipped with satellite tags were released on October 1st 2013, and where tags "popped-up" on July 31st 2014 near Beaver Harbour, NB, and Port George, NS. NB: New Brunswick, NS: Nova Scotia; GM: Grand Manan; BoF: Bay of Fundy.

The depth record of the two tagged lobsters were very similar and showed three "phases of migration", a relatively rapid movement to deeper water in the fall to early winter, followed by a long period in deep water during the winter and first half of spring, and relatively rapid movement to shallower water from late spring to early summer (Fig. 9 left). More specifically, both lobsters were tagged on October 1st 2013, initiated movements (see Environmental Conditions at Migration Onset section below) to deeper water on October 29th 2013, attained an "over wintering depth" of approximately 200 m (BHL: 208.35 ± 2.30 m; PGL: 183 ± 1.40 m) by mid January 2014 (BHL: 11th, PGL: 16th), where they remained until spring 2014 (BHL: May 22nd; PGL: June 4th), before relatively rapidly moving to shallower water up to the point of tag release. From January to the end of May, lobsters in this study exhibited very little change in depth varying by only 3.1 and 6.1 m for the BHL and PGL, respectively. It is unclear whether the tagging period completely spanned the end of the tagged lobsters' seasonal movements prior to hatch. Both lobsters were initially sampled and released in shallower water than they were when their tags popped off at the end of our tagging period. Specifically, the BHL started and ended the tagging period in 28 and 45 m of water, respectively, and the PGL started and ended the tagging period in 22.6 and 65 m of water, respectively (Fig. 4, Fig. 9). The average rate of depth change observed during the fall shallow-to-deep migration was 5.92 m (± 8.04 SD) and 4.68 m (± 5.35 SD) for the BHL and PGL, respectively. The rate of depth change observed was greater during the spring deep-to-shallow migration, with the BHL and PGL making an average daily depth change of 11.08 m (± 10.99 SD) and 4.93 m (± 5.42 SD) during this period, respectively. The maximum single day depth change was similar in the fall and spring

but a decrease and a increase in depth, respectfully of 50 m by the BHL and ~32 m by the PGL.

The temperature records of the two tagged lobsters were remarkably similar (Fig. 9 right). Throughout the entire tagging period, both lobsters stayed in waters that varied between 5 and 12.7 °C. Prior to movement to deeper water in the fall, both lobsters were in 11.5 to to 12.7 °C water, and then in mid October the recorded temperature from both lobster tags started decreasing, at the same time that the animals were moving to deeper waters (Fig. 9). During the "stable phase" in the winter, both lobsters experienced very similar temperatures, which varied between 5 and 7.5 °C. The two temperature profiles did, however, show one notable difference, pertaining to the increase in temperature experienced during the spring/summer deep-to-shallow migration, with the PGL experiencing temperatures 2 to 4 °C warmer than the BHL from July 1st to the end of the record on July 31st. This difference in temperature experienced by the two lobsters during the spring/summer migration is not surprising given the different routes taken by these two lobsters, the tags of which surfaced 116 km apart (Fig. 8 right). Especially considering that the BHL returned to deep cold water in June before moving to shallow water when the tags released.

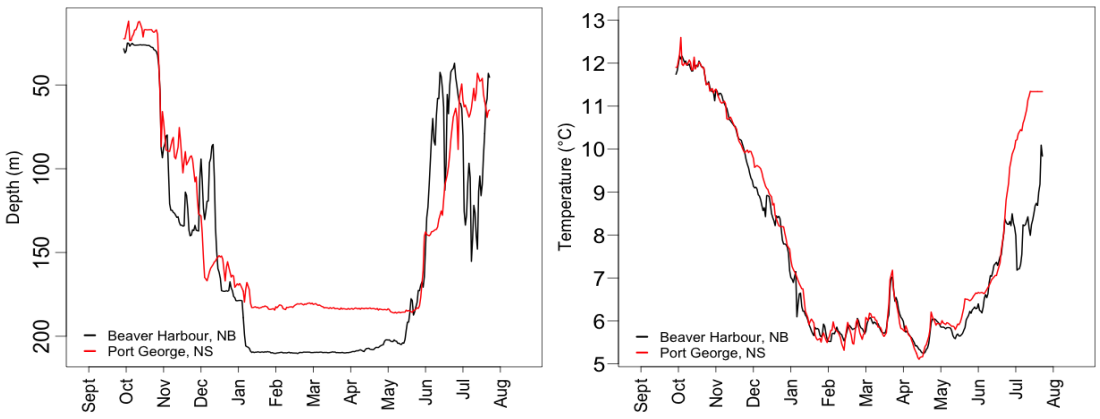

Figure 9. (Left) Depth profiles and (right) thermal histories of satellite tags attached to two ovigerous American lobster (160 mm CL) near Grand Manan Island on October 1st 2013, and that "popped-up" on July 31st 2014 near Beaver Harbour, NB, and Port George, NS.

3.1.2 Environmental Conditions at Migration Onset

Using our criterion of a 5 m depth change in a single day followed by continued movements in the same direction, we estimate that both lobsters initiated fall movements on October 29th (Julian Day 302) (Fig. 10), after spending 20 days over which changes in depth between consecutive days was generally much smaller, averaging 0.36 m (SD: ± 0.56; Range: 0 - 2.16 m) and 1.39 m (SD: ± 1.52; Range: 0 - 5.20 m) for the BHL and the PGL, respectively. Over the 20 days that preceded our estimate of "migration onset", the depth of the BHL increased slightly but significantly ($R^2 = 0.58$, $F_{1, 19} = 28.8$, $p = 3.5x10^{-5}$) from 26 to 32.10 m, whereas that for the PGL did not change significantly ($R^2 = 0.06$, $F_{1, 19} = 2.37$, $p = 0.14$). These fall shallow-to-deep movements seem to have been associated with a cooling trend (Fig. 10 top). In particular, both lobsters experienced a significant (BHL: $R^2 = 0.93$, $F_{1,9} = 129.5$, $p = 1.21x10^{-6}$; PGL: $R^2 = 0.92$, $F_{1,9} = 117.6$, $p = 1.82x10^{-6}$) decrease in temperature of approximately 0.7 °C (BHL: 12.05 to 11.36°C; PGL: 12.03 to 11.38°C) over the 10 days that preceded their movement to deeper waters. Prior to this cooling, temperature varied only by approximately 0.10 °C (BHL: 0.08 °C; PGL: 0.11 °C) with no directional trend (BHL: $R^2 = -0.07$, $F_{1,9} = 0.04$, $p = 0.55$; PGL: $R^2 = -0.10$, $F_{1,9} = 0.11$, $p = 0.70$).

Based on our criterion of a 5 m depth change in a single day, we estimate that our two tagged lobsters initiated spring deep-to-shallow movements on May 22nd (BHL: Julian Day 142) and June 4th (PGL: Julian Day 155) (Fig. 10). During the 20 days preceding migration onset, changes in depth between consecutive days were much smaller, averaging 0.62 m (SD: ± 0.63; Range: 0 - 2.21 m) with no trend ($R^2 = -0.05$, $F_{1,}$

$_{19}$ = 0.04, p = 0.84) and 0.73 m (SD: ± 1.05; Range: 0 - 4.80 m) with a slight but significant decreasing trend (R^2 = 0.59, $F_{1, 19}$ = 21.73, p = 0.0002) for the BHL and the PGL, respectively. The initiation of spring deep-to-shallow movements could not readily be attributed to changing temperature, because our two tagged lobsters seemed to experience different trends in temperature before they initiated these movements (Fig. 10 bottom). Over the 20 days that preceded movement, the BHL experienced a significant and gradual decrease (R^2 = 0.87, $F_{1,19}$ = 130, p = 6.1×10^{-10}) of 0.33 °C (from 6.02 to 5.59 °C), whereas the PGL experienced a significant increase (R^2 = 0.84, $F_{1,19}$ = 102.5, p = 4.33×10^{-9}) of 0.64 °C (from 5.93 to 6.6 ° C).

To determine whether our results here were sensitive to the criterion used to determine the day of departure, we investigated how results may change using movement criterions of a 2 m and an 8 m depth change in a single day. In particular, if we use 2 m (instead of 5 m) as a criterion, the departure day would only be shifted by one day earlier in the fall and in the spring for both lobsters. These small changes in departure day do not change results for fall and spring movements, as both lobsters still experienced a drop in temperature of the same magnitude preceding fall movements (~ 0.7 °C), but over 9 days instead of 10, and experienced opposite patterns of temperature change preceding spring movements. Similarly, if we use 8 m (instead of 5) as a criterion, the departure day would be unchanged for the BHL and would only shift by one day later for the PGL in the fall, whereas it would shift by one and four days later for the PGL and BHL, respectively, in the spring. Again these changes to departure day do not influence results obtained using a movement criterion of a 5 m depth change.

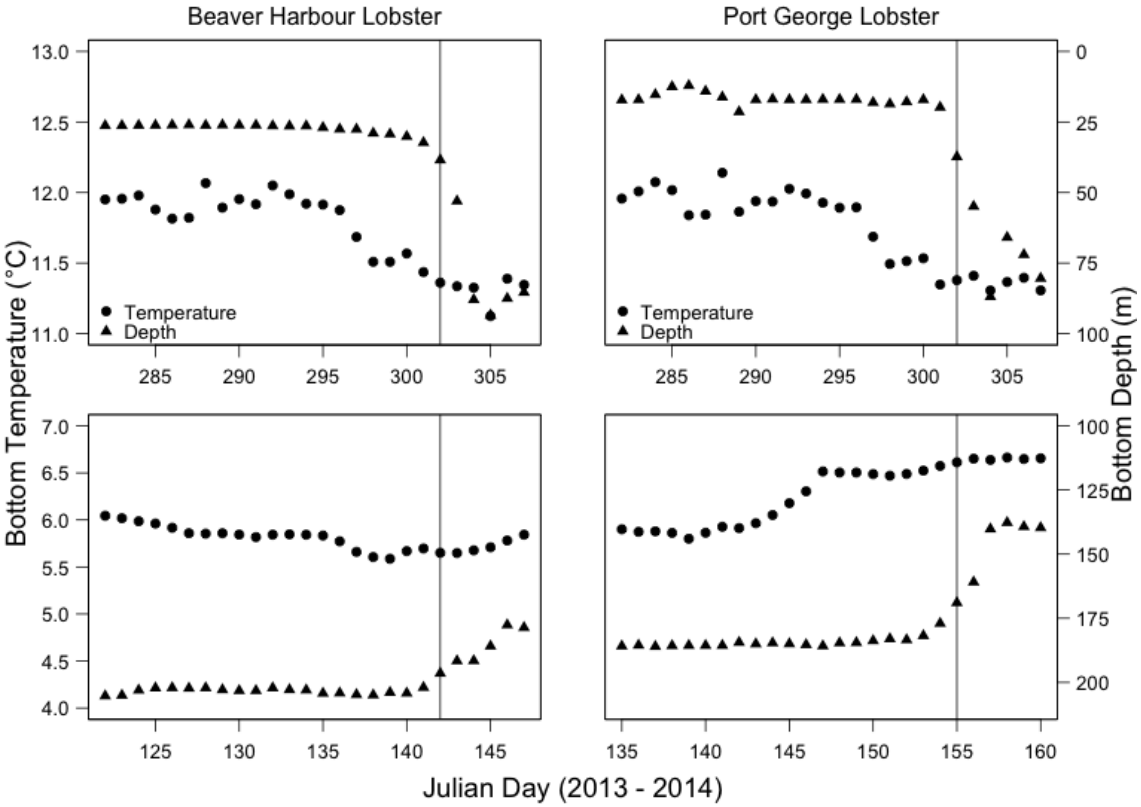

Figure 10. Bottom temperature (black circles) and depth (black triangles) of (left) the Beaver Harbour Lobster (BHL) and (right) Port George Lobster (PGL) tags during the twenty days preceding and five days following their initiation (marked by a vertical line, see Methods) of (top) shallow-to-deep migrations in the fall (Julian days 282-307, 2013) and (bottom) deep-to-shallow migrations in the spring (Julian days 122 - 147 and 135 - 160, 2014, for the BHL and PGL, respectively).

3.2 Individual-Based Modelling

3.2.1 FVCOM-GOM bottom temperature validation

The regression analyses showed positive and significant correlations between observed (DFO trawl surveys) and modeled (FVCOM-GOM) bottom temperature in both 2013 ($R^2 = 0.72$, $t_{23} = 7.845$, $p = 5.99 \times 10^{-08}$) and 2014 ($R^2 = 0.61$, $t_{20} = 5.78$, $p = 1.19 \times 10^{-05}$) (Fig. 11 top). The mean absolute error of bottom temperature predictions was 0.45 °C (± 0.84 SD) (2013) and 0.32 °C (± 0.89 SD) (2014), and the maximum absolute error was 1.90 °C (2013) and 1.97 °C (2014). The regression slopes and intercepts were not significantly different from 1 and 0, respectively, for 2013 (intercept: $t_{23} = 1.48$, $p = 0.152$; slope: $t_{23} = -1.79$, $p = 0.087$) and 2014 (intercept: $t_{20} = 0.819$, $p = 0.422$; slope: $t_{20} = 1.07$, $p = 0.297$) data, suggesting that temperature predictions were not significantly biased relative to observed values. However, direct comparison of observed and predicted values did suggest that modeled temperatures underestimate real temperatures, with the difference being significant in 2013 ($t_{24} = 2.71$, $p = 0.006$) and non-significant in 2014 ($t_{21} = 1.69$, $p = 0.053$). Though we did not find a significant relationship between error and depth in either 2013 ($R^2 = 0.01$, $F_{1, 23} = 1.25$, $p = 0.27$) or 2014 ($R^2 = -0.04$, $F_{1, 20} = 0.21$, $p = 0.65$), the model seems to over-estimate temperature at depths around 50 m and generally under-estimate temperatures at greater depths in both years (Fig. 11 bottom).

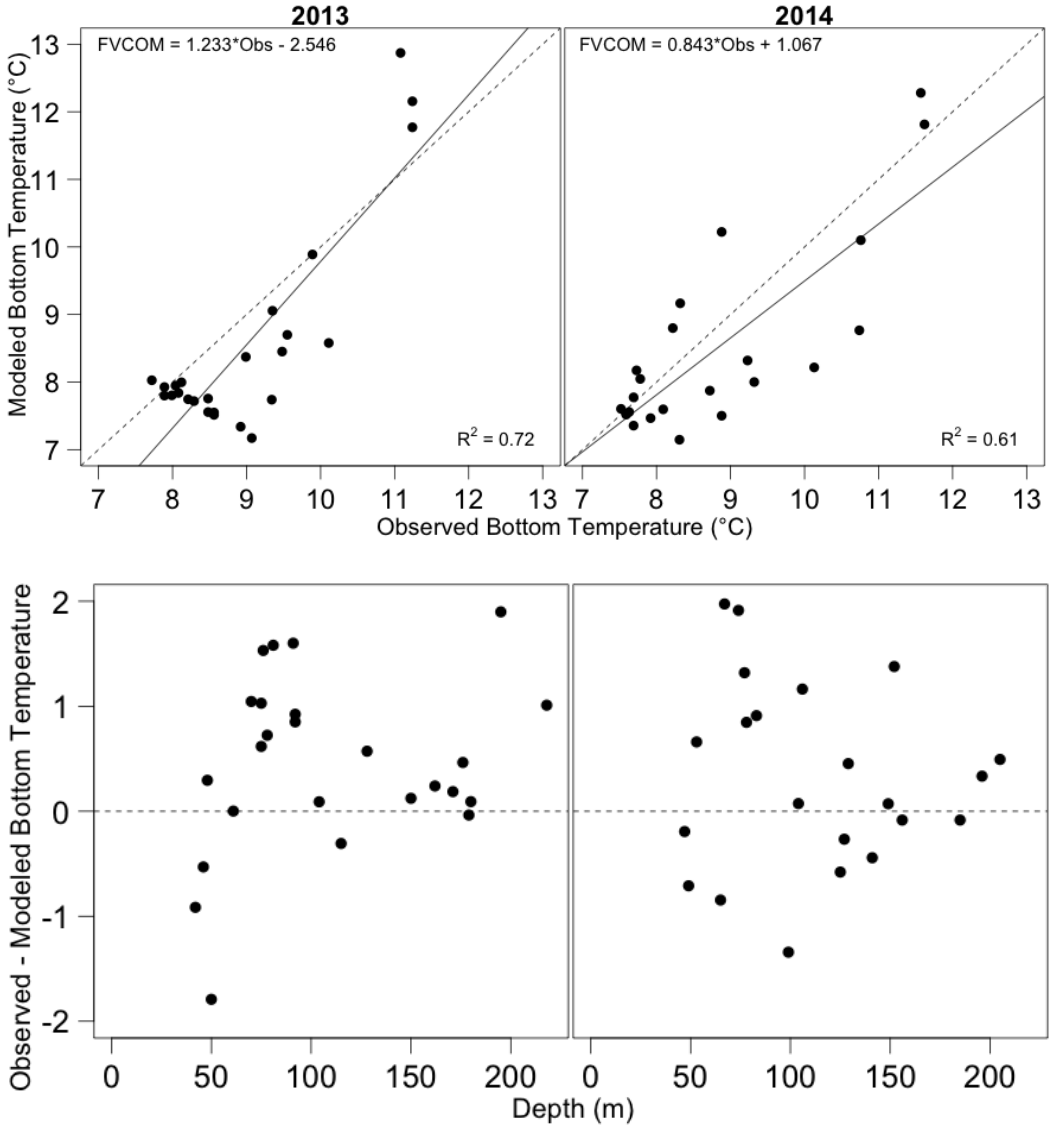

Figure 11. (Top) Linear regressions (solid line) between observed (Department of Fisheries and Oceans' groundfish survey, Fig. 3) and modeled (FVCOM) bottom temperature for (left) July 2013 and (right) July 2014, including correlation coefficient (R^2) and the regression equation. The dash line represents a 1:1 relationship. (Bottom) Difference between these observed and modeled bottom temperatures in relation to depth.

3.2.2 One-dimensional depth-based spatial domain

The mean daily bottom temperature of the satellite tags attached to our two lobsters was significantly and strongly associated with the mean daily temperature of model grid cells that were at the same depth as the tag (BHL: $R^2 = 0.81$, $F_{1, 302} = 1218$, $p = 2.2x10^{-16}$; PGL: $R^2 = 0.82$, $F_{1, 302} = 1380$, $p = 2x10^{-16}$) (Fig. 12). There were, nevertheless, considerable differences between modeled and tag temperature, as regression slopes were significantly different from 1 (BHL: $t_{302} = -3.41$, $p = 0.0007$; PGL: $t_{302} = -3.23$, $p = 0.0014$) and intercepts from 0 (BHL: $t_{302} = 5.60$, $p = 0.0001$; PGL: $t_{302} = 3.69$, $p = 0.0003$). For the Beaver Harbour lobster, modeled temperature overestimated recorded temperature for much of the fall and winter, but there was no obvious bias during the spring (Fig. 12 top left), whereas for the Port George lobster, modeled temperature also overestimated tag temperature for much of the fall but it underestimated tag temperature in the spring (Fig 12 top right).

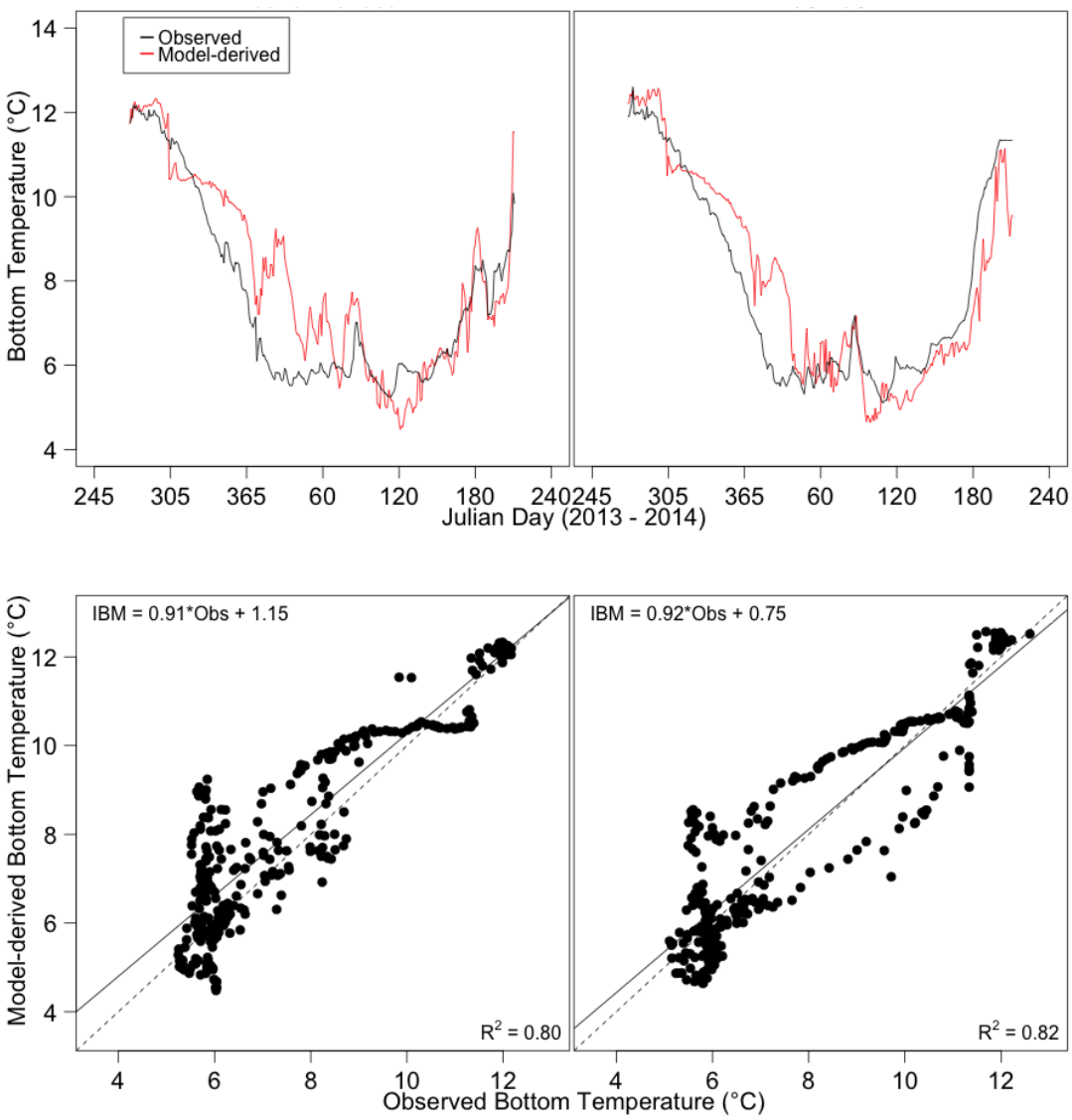

Figure 12. Observed (black lines) and model-derived (red lines) temperature experienced by two ovigerous American lobster tagged in coastal waters of Grand Manan on October 1st 2013 (Julian day 274), and tracked until July 31st 2014 (Julian Day 212) when the tags "popped-off" in (left) Beaver Harbour, New Brunswick and (right) Port George, Nova Scotia. The observed temperature was the mean daily temperature recorded by the satellite tag, and the modeled-derived temperature was the mean bottom temperature predicted by the FVCOM model for all model grid cells at the depth recorded by the satellite tag on a given day. These figures show the ability of the one-dimension depth-based reconstruction of temperature used in our individual-based model to mimic the thermal environment of the Bay of Fundy to which these tagged lobsters were exposed.

3.2.3 Movement scenarios

We were able to simulate the main features of the movement of our two lobsters with our individual-based model using a temperature-driven movement scenario with particular combinations of values of Vertical Movement Scope (VMS), Temperature Information Range (TIR), and Temperature Sensitivity (TS). These particular temperature-driven movement rules produced depth/temperature profiles that were much more similar to those of our two tagged lobsters than were profiles obtained using a random walk and no-movement scenarios. The step-wise exercise undertaken to assess the role of these different decision rules demonstrated the important influence of migration on the temperature history experienced by virtual lobster as well as indicating that if the virtual lobster were motivated by seeking warmer temperatures they could achieve a depth migration similar to what is observed.

When the virtual lobster's VMS and TIR were set at ± 15 m a day, we found that the depth profiles of virtual lobsters increasingly resembled those of our two tagged lobsters as the value of the TS increased from 0 (random) to 0.05 (a degree of directedness), and that no improvements were made when the TS was increased further to 0.075 and 0.1 (Fig. 13). In particular, the speed of the fall shallow-to-deep migration displayed by virtual lobsters, as well as the depth at which they spent winter, increasingly matched the depths of tagged lobsters with TS increasing from 0 to 0.05; note that lobster with a TS of 0 (random walk) still showed a tendency to move, on average, to deeper water over time, because their movement in the opposite direction was constrained by the shoreline (depth = 0). The one important exception is that virtual

lobsters (with VMS and TIR set at ± 15 m) failed to display the spring deep-to-shallow migration undertaken by our two lobsters at all values of TS, only showing the beginning of these movements late in the summer. The absence of spring migration by virtual lobsters occurred because bottom temperature was relatively constant at that time within the 15 m depth range detectable by virtual lobsters.

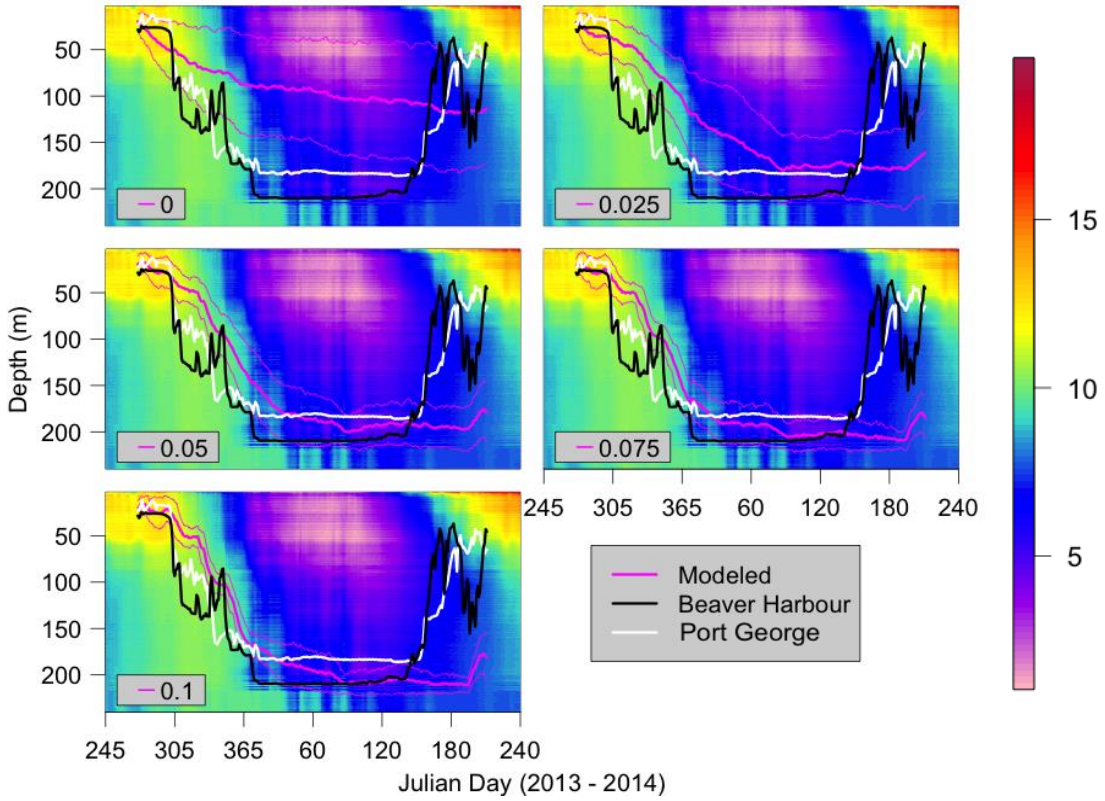

Figure 13. Observed (black and white lines) and mean modeled (± SD) (magenta line) depth of ovigerous American lobster with different temperature sensitivity coefficients (TS) plotted over the one-dimensional thematic map of 2013 - 2014 bottom temperature extracted from FVCOM. The observed depths are average daily depths recorded by satellite tags of the two ovigerous lobsters that were tagged in this study. The modeled depths are the mean daily depths (± SD) of 100 lobsters simulated in our individual-based model, where the lobsters' Temperature Information Range (TIR) and Vertical Movement Scope (VMS) were restricted to ± 15 m/day. The different panels illustrate virtual lobsters possessing a range of Temperature Sensitivity (TS) coefficients varying from (top left) 0, where lobsters have no affinity to move towards warmer temperature (i.e. random walk), to (bottom left) 0.1, where lobsters will move to the depth with highest temperature within their VMS and TIR (see Methods).

When the virtual lobsters' VMS was set at ± 15 m a day and the TS was set to 0.05, we found that as the TIR increased from ± 5 to 220 m, the fit of observed and simulated depth profiles improved, but not uniformly with increasing TIR and mainly due to effect on the simulated spring (not fall) migrations (Fig. 14). In particular, the fall shallow-deep migration by virtual lobster and the depth at which they overwintered matched relatively well the depth of our two tagged lobsters, and this match did not improve markedly with increasing TIR. TIR did, however, have an important effect on the spring deep-shallow migration of virtual lobsters. More specifically, TIR values of ± 15 to 100 m resulted in incomplete migrations very late in summer, with the magnitude of these migrations increasing only marginally with increasing TIR within this range. In contrast, a TIR of ± 220 m resulted in a complete spring migration by virtual lobsters that was relatively well timed with that of our two tagged lobsters. The mismatch of spring migration by virtual lobsters when TIR was set to values less 220 m occurred because temperature was relatively uniform at that time within 100 m of the overwintering depth. Interestingly, virtual lobsters with TIR of ± 220 m moved somewhat shallower into warmer water than our two tagged lobsters.

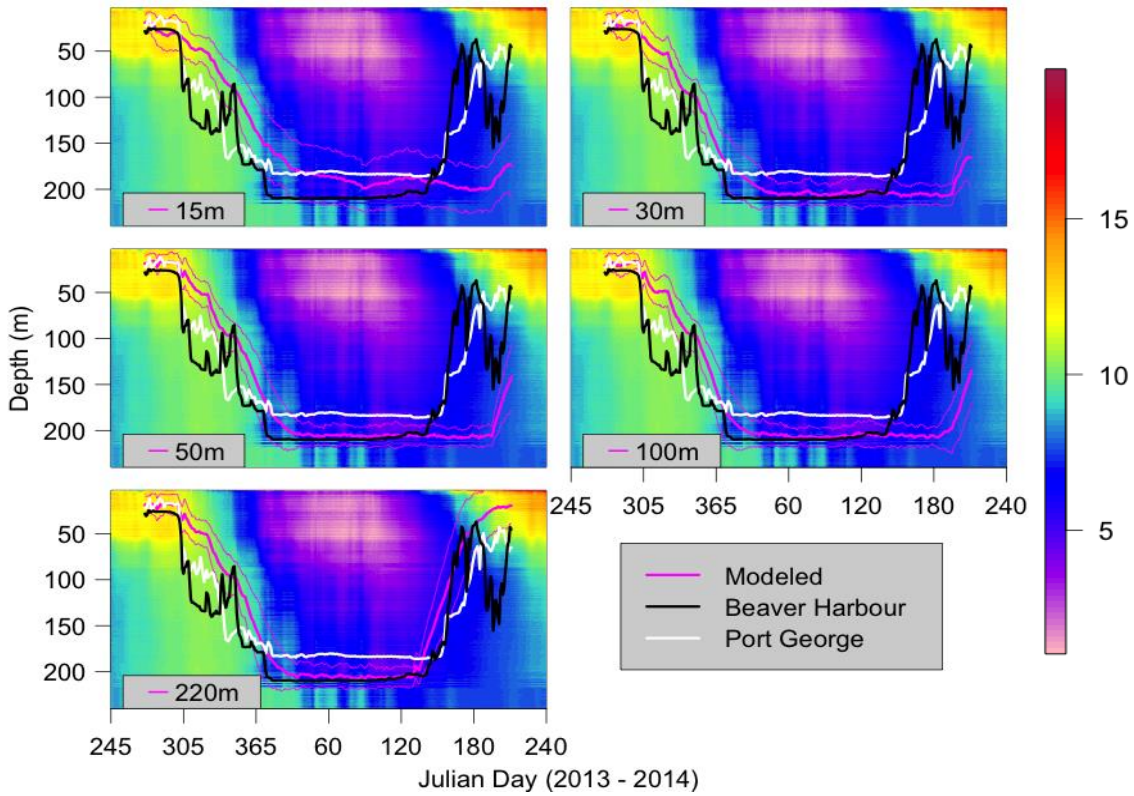

Figure 14. Observed (black and white lines) and mean modeled (± SD) (magenta line) depth of ovigerous American lobster plotted over the one-dimensional thematic map of 2013 - 2014 bottom temperature extracted from FVCOM. The observed depths are average daily depths recorded by satellite tags of the two ovigerous lobsters that were tagged in this study. The modeled depths are the mean daily depths (± SD) of 100 lobsters simulated in our individual-based model, where the lobsters' Vertical Movement Scope (VMS) was restricted to ± 15 m/day and the lobster's Temperature Sensitivity (TS) coefficient was set to 0.05. The different panels illustrate virtual lobsters possessing a range of values of Temperature Information Range (TIR), varying from (top left) ± 15 m/day, where lobsters have access to temperature information from - 15 to + 15 m from their current depth every day, to (bottom left) ± 220 m/day, where lobsters have access to temperature information over the entire depth range every day (see Methods).

When the virtual lobsters' TIR was set to ± 220 m per day and the TS was set to 0.05, we found that the fit between observed and modeled depth trajectories increased as VMS increased from ± 5 to 15 m, but did not improve with further increases of VMS (Fig. 15). In particular, a VMS smaller than ± 15 m did not give the virtual lobsters enough movement range to reach the overwintering depths of our tagged lobsters (VMS = 5 m), or to reach them as early in the year (VMS = 10 m). The best-fit model was when the VMS was set to ±15 m, which resulted in the depth profile of virtual lobsters displaying a shallow-to-deep movement in the fall, overwintering depth, and shallow-to-deep movement in the spring that closely matched those of our two tagged lobsters. Note that this best-fit model positioned the virtual lobsters in shallower and warmer water in the summer at the end of the migration compared to our tagged lobsters. When the VMS was increased to ± 30 and 45 m, the virtual lobsters completed the spring deep-to-shallow migration markedly earlier than our two tagged lobsters. To make a depth change of ± 15 m, lobsters only need to move a horizontal distance of 0 - 6 km in the majority of locations within our study domain (Fig. 16).

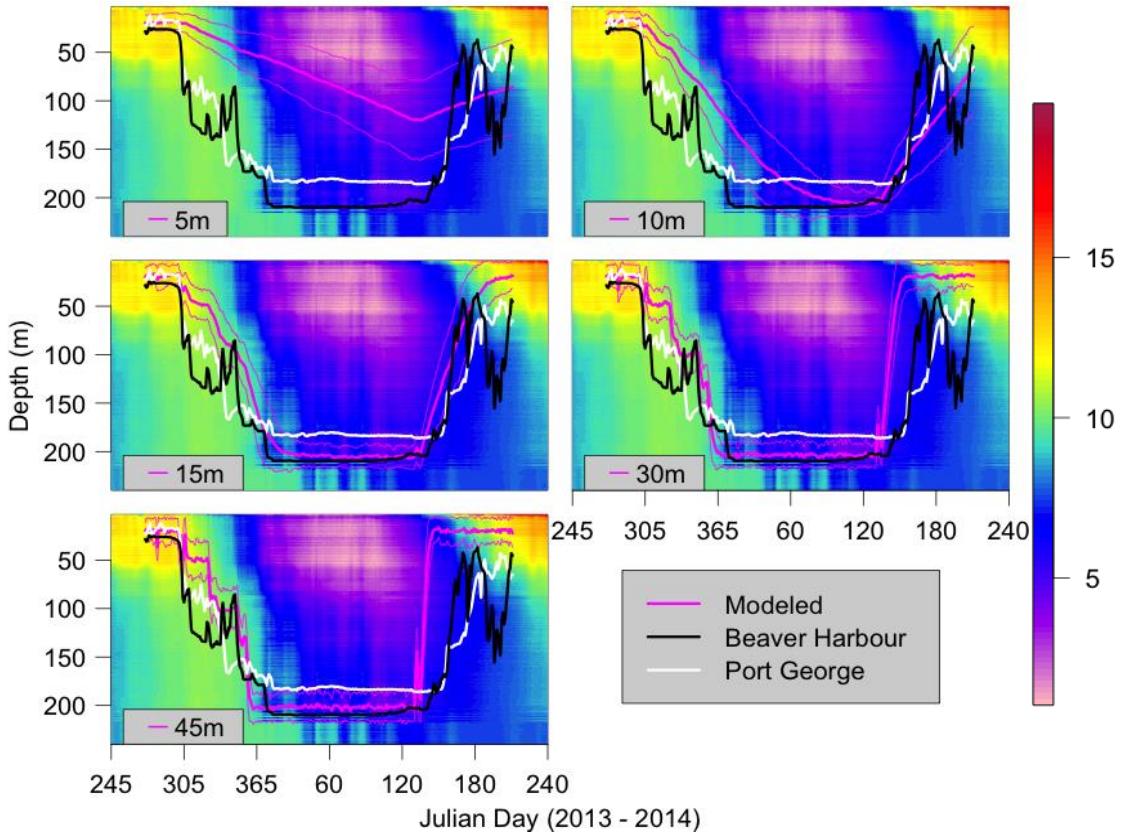

Figure 15. Observed (black and white lines) and mean modeled (± SD) (magenta line) depth of ovigerous American lobster plotted over the one-dimensional thematic map of 2013-2014 bottom temperature extracted from FVCOM. The observed depths are average daily depths recorded by satellite tags of the two ovigerous lobsters that were tagged in this study. The modeled depths are the mean daily depths (± SD) of 100 lobsters simulated in our individual-based model, where the lobsters' Temperature Information Range (TIR) was set to ± 220 m/day and the lobsters' Temperature Sensitivity (TS) was set to 0.05. The different panels illustrate virtual lobsters possessing a range of Vertical Movement Scope (VMS), varying from (top left) ± 5 m/day, where lobsters can move up or down 5 m from their current depth every day, to (bottom left) ± 45 m/day, which allows lobsters quicker access to different depths and associated temperature (see Methods).

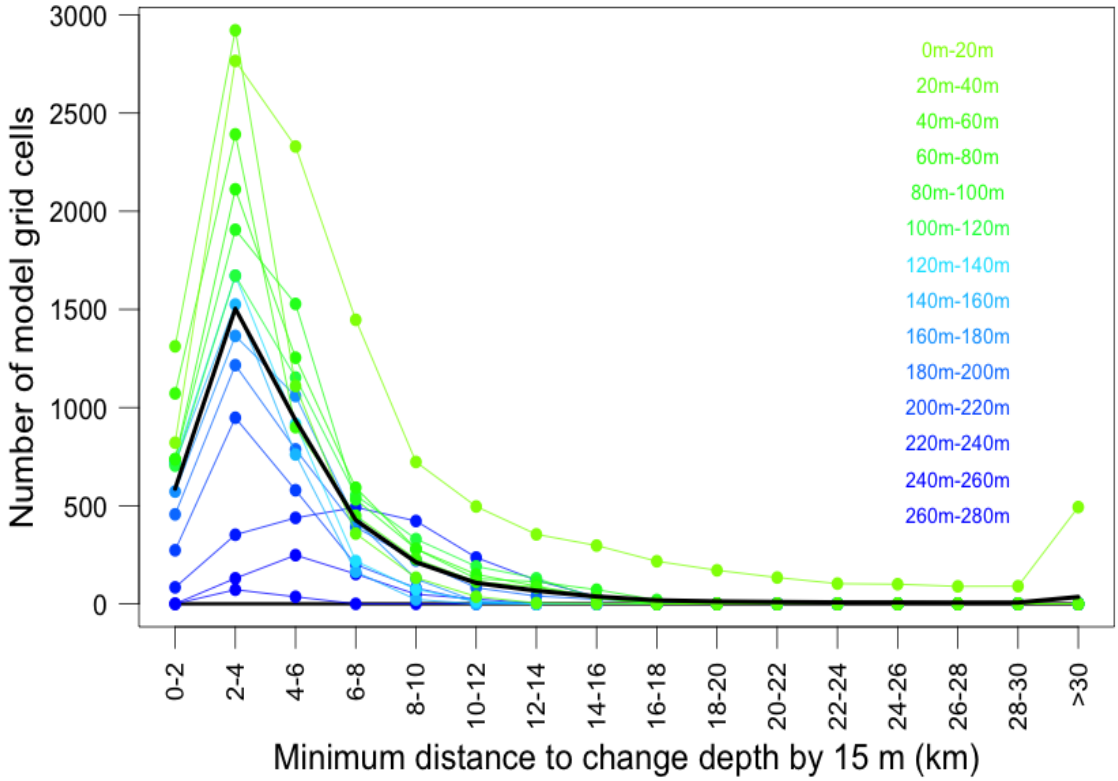

Figure 16. Number of FVCOM-GOM grid cells in each 20 m (0 – 280 m) depth bin requiring a minimum horizontal distance of X km to change depth by 15 m. The bolded black line is the mean of all model grid cells.

Among the parameter combinations considered above, the virtual lobster possessing a VMS of ± 15 m per day, TIR of ± 220 m per day and a TS of 0.05, hence a temperature-driven scenario, resulted in a depth profile that reflected that of our tagged lobsters remarkably well (Fig. 17). As evidenced by the smallest root-mean-squared error, this model produced depth and temperature profiles that best matched those of our tagged lobsters (Fig. 17), and will hereafter be referred to as our "temperature-driven" scenario. Virtual lobsters simulated to achieve the maximum temperature without constraints (VMS and TIR = ± 220 m, TS = 1), hereafter referred to as "maximized temperature" scenario, produced a depth and temperature profile that fit our tagged lobsters' profiles well, and better than random walk or no-movement, but less well than the temperature-driven model (Fig. 17). In comparison to our tagged lobsters, maximized temperature lobsters (i) stayed in shallower and warmer water longer before the fall shallow-to-deep migration, (ii) reached overwintering depth sooner, and seemed to overwinter deeper, and (iii) completed the deep-to-shallow spring migration markedly sooner. The virtual lobsters simulated in the random walk scenario (VMS and TIR = ± 15 m, TS = 0) produced a depth and temperature profile that fit our tagged lobster's profiles markedly better than the no-movement scenario, but also markedly more poorly than the temperature-driven or maximized temperature scenarios. Given that virtual lobsters in the random walk scenario were constrained by the shoreline (depth = 0), their mean movements were towards deeper water, which coincidentally avoided the coldest water in shallows during the winter. The virtual lobsters simulated in the no-movement scenario (VMS, TIR, and TS = 0) produce depth and temperature profiles that were the poorest fit to our tagged lobsters' profiles. These virtual lobsters stayed in shallow water

throughout the migration period, experiencing colder water in the winter and warmer water in the spring and summer compared to our tagged lobster that completed their deep-to-shallow and shallow-to-deep migrations in the fall and spring, respectively.

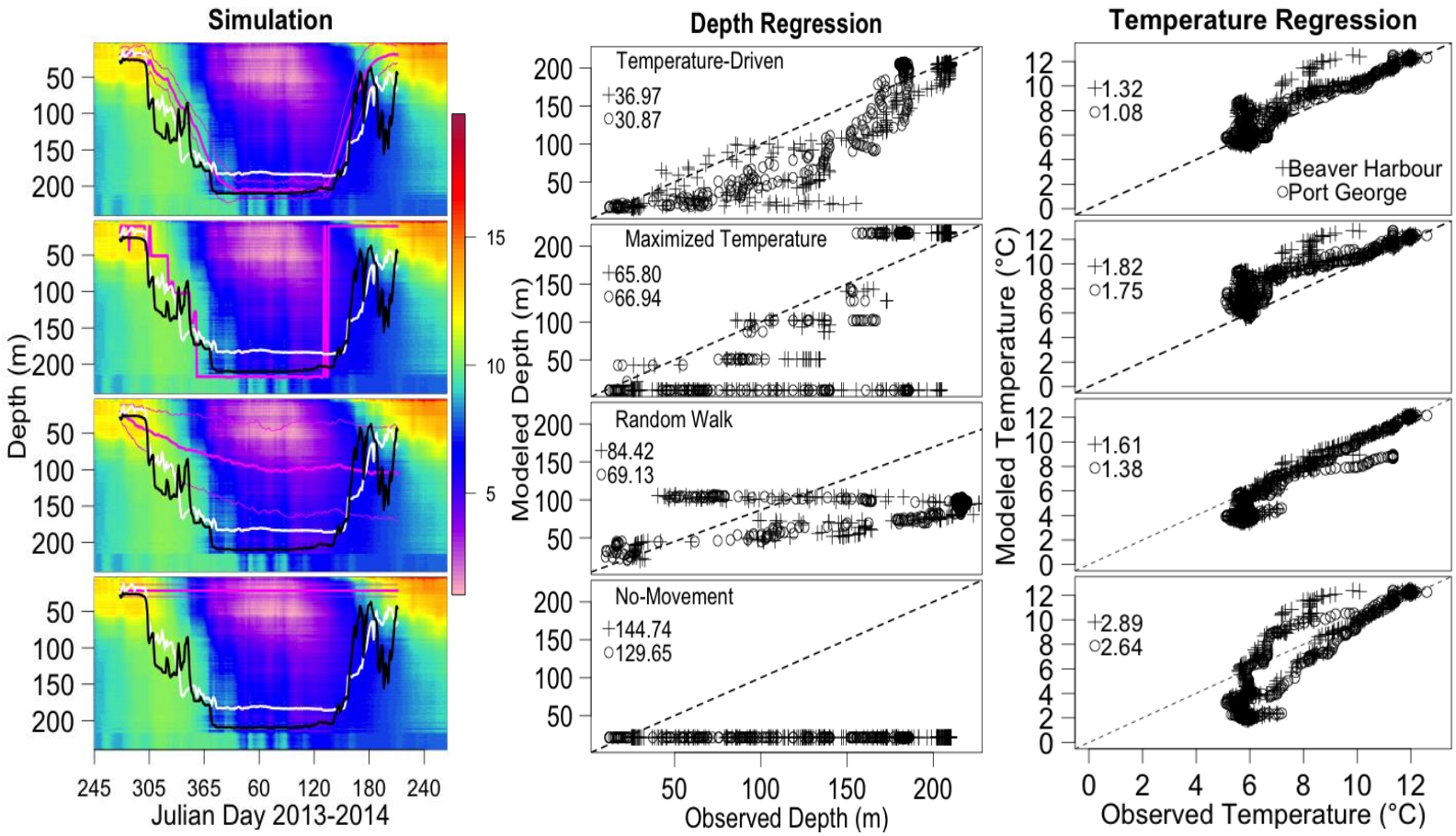
Simulation
Depth Regression
Temperature Regression
Depth (m)
Julian Day 2013-2014
245 305 365 60 120 180 240
Temperature-Driven
+36.97
○30.87
Maximized Temperature
+65.80
○66.94
Random Walk
+84.42
○69.13
No-Movement
+144.74
○129.65
Modeled Depth (m)
Observed Depth (m)
+1.32
○1.08
+1.82
○1.75
+1.61
○1.38
+2.89
○2.64
+Beaver Harbour
○Port George
Modeled Temperature (°C)
Observed Temperature (°C)

Figure 17. (Left Column) Observed (black and white lines) and mean modeled (± SD) (magenta line) depth of ovigerous American lobsters plotted over the one-dimensional thematic map of 2013 - 2014 bottom temperature of our study area, and relationship between the observed and modeled average daily (Middle Column) depth and (Right Column) temperature of these lobsters (Fig. 12). Observed values are values recorded by satellite tags attached to the two ovigerous lobsters that were tagged in this study (+ and ○). Modeled values are the mean of 100 simulations of our individual-based model, in each of four scenarios: (First Row) temperature-driven scenario, where VMS was ± 15 m/day, TIR was ± 220 m, and TS was 0.05; (Second Row) maximized temperature scenario, where VMS and TIR were ± 220 m/day and TS was 1; (Third Row) random walk scenario, where VMS and TIR were ± 15 m/day and TS was zero; (Fourth Row) no-movement scenario, where VMS, TIR, and TS were zero (see Methods). Dotted lines represent the 1:1 relationship, and values in each panel are the root-mean-squared-errors calculated from the regressions between modeled and observed values for tagged lobsters that ended in Beaver Harbour (+) and Port George (○).

The growing-degree-days (GDD) accumulated by embryos of our two tagged lobsters between October 1st 2013 and July 31st 2014 were similar, despite these lobsters having ended in very different locations following their spring deep-to-shallow migration; the lobster that travelled to Beaver Harbour, N.B. (BHL), accumulated 2300 GDD and the lobster that travelled to Port George, N.S. (PGL), accumulated 2394 GDD (Fig.18). These GDD estimates, directly derived from the lobsters' tag data, were somewhat lower than estimates derived from our model (2445 and 2430 GDD for the BHL and PGL, respectively) (Fig. 18), where daily temperatures were estimated as the model temperature at depths derived from the tag. To facilitate comparisons of GDD of our tagged lobsters to GDD accumulated by virtual lobsters under different scenarios, hereafter to represent tagged lobsters we will use GDD calculated using modeled temperature at the tag depth, thus 2445 and 2430 GDD for the BHL and PGL, respectively.

For approximately the first 75 days of the study, virtual and tagged lobsters accumulated a similar number of GDD, including those that were simulated to move randomly or not at all (Fig. 18). The similarity in GDD over this time period occurred because bottom temperature did not vary much (10.82 - 11.47 °C) across the range of depths (10 - 50 m) (Fig. 4) used by our tagged and virtual lobsters under different movement scenarios. At approximately Julian day 350, however, the mean bottom temperature started to vary more markedly (3.5 - 7.4 °C) among the depths utilized (21 - 210 m) by tagged and virtual lobsters, and therefore the GDD accumulation trajectories started to diverge (Fig. 18).

Virtual lobsters accumulated either more or fewer GDD than tagged lobsters depending on the movement scenario. Virtual lobsters in the no-movement scenario stayed in shallow water and endured the lowest temperatures during the winter, however they did benefit from a rapid increase in temperature in the spring (Fig. 17). The rate of GDD accumulation for these virtual lobsters reduced markedly during the winter, and these lobsters overall acquired the lowest number of GDD (2034 ± 42 GDD) of all movement scenarios and tagged lobsters (Fig. 18). Virtual lobsters in the random walk scenario avoided the lowest temperatures in shallow water in the winter, but they experienced cooler water throughout the winter compared to our tagged lobsters (Fig. 17). Moreover, these lobsters stayed deeper and experienced cooler temperatures in the spring and summer compared to virtual lobsters not moving at all. Overall, the virtual lobsters in the random walk scenario accumulated a much lower number of GDD (2123 ± 175 GDD) than our tagged lobsters, but a greater number of GDDs than virtual lobsters in the no-movement scenario (Fig. 18). Lobsters that moved to deep water in the fall, stayed deep over winter, and returned to shallow water in the spring (temperature-driven, maximized temperature and tagged lobsters) avoided the cold shallow waters in the winter and benefited from warm shallow waters in the spring, summer and early fall (Fig. 17). The temperature-driven scenario and our tagged lobsters made similar migratory movements (Fig. 17), with exception that temperature-driven lobsters followed the highest temperatures into shallower water in the summer while our tagged lobster did not, resulting in them accumulating 95 and 111 GDD more (2541 ± 40 GDD) than the BHL and PGL, respectively. Virtual lobsters in our maximized temperature scenario occupied greater depths with warmer water over winter months than our tagged

lobsters, and they moved sooner to shallow and warm water in the spring, resulting in them accumulating 313 and 328 GDD more (2758 ± 6 GDD) than the BHL and PGL, respectively.

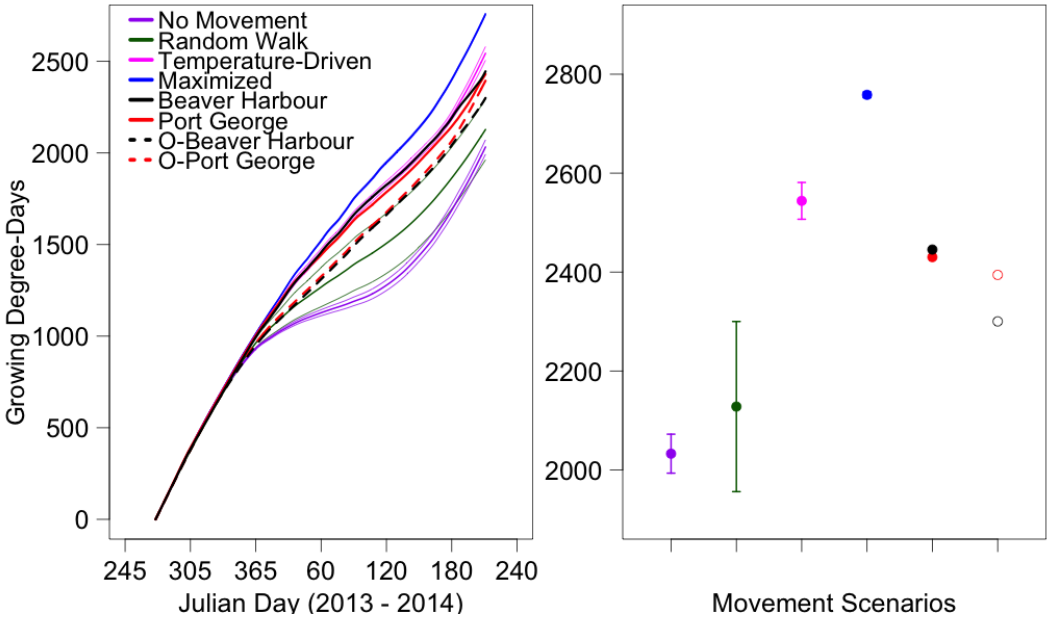

Figure 18. (Left) Time-based trajectories and (right) endpoints of cumulative growing degree-days (GDD) (± SD) estimated for our two study lobsters (red and black lines [left] and circles [right]) and for lobsters simulated under different scenarios in our individual-based model (blue, magenta and green lines [left] and circles [right]). GDD for the tagged lobsters were estimated by summing over the tagging period (Julian day 274 in 2013 [October 1st] to 212 in 2014 [July 31st]) the average daily temperatures recorded by the satellite tags (black and red stippled lines [left] and open circles [right]), or average modeled temperatures across FVCOM grid cells at the average daily depth recorded by the satellite tags (black and red solid lines [left] and circles [right]). GDD values for virtual lobsters are the mean of 100 simulations of our individual-based model, in each of four scenarios: temperature-driven scenario, where VMS was ± 15 m/day, TIR was ± 220 m/day, and TS was 0.05 (magenta lines and point); maximized temperature scenario, where VMS and TIR were ± 220 m/day and TS was 1 (blue lines and point); random walk scenario, where VMS and TIR were ± 15 m/day and TS was zero (green lines and point): no-movement scenario, where VMS, TIR, and TS were zero (purple lines and point) (see Methods).

3.2.4 Hindcast inter-annual variability in the timing of migration and thermal histories

When we ran our temperature-driven model using hindcast bottom temperatures from 1978 to 2014, virtual lobsters consistently displayed shallow-to-deep migrations in the fall, overwintered in deep water and then migrated back to shallow water in the spring, although there was considerable variation in the timing of the fall descent and spring ascent (Fig. 19). Whereas the onset of the fall descent varied considerably from year to year, it did not become progressively earlier or later over the time period investigated (R^2 = -0.02, $F_{1, 34}$ = 0.37, p = 0.55). The onset of spring ascent did show a significant positive relationship with years (R^2 = 0.15, $F_{1,34}$ = 7.35, p = 0.01), but this relation became clearly non-significant (R^2 = -0.03, $F_{1, 31}$ = 0.015, p = 0.90) when we removed three of the earlier years (1979, 1980, 1981) where the onset of spring ascent was predicted to have been exceptionally early (Fig. 19). The number of GDD accumulated by virtual lobsters also varied considerably among years, but we found no significant relationship between GDD accumulated and year (R^2 = 0.026, $F_{1, 34}$ = 1.93, p = 0.17) (Fig. 20).

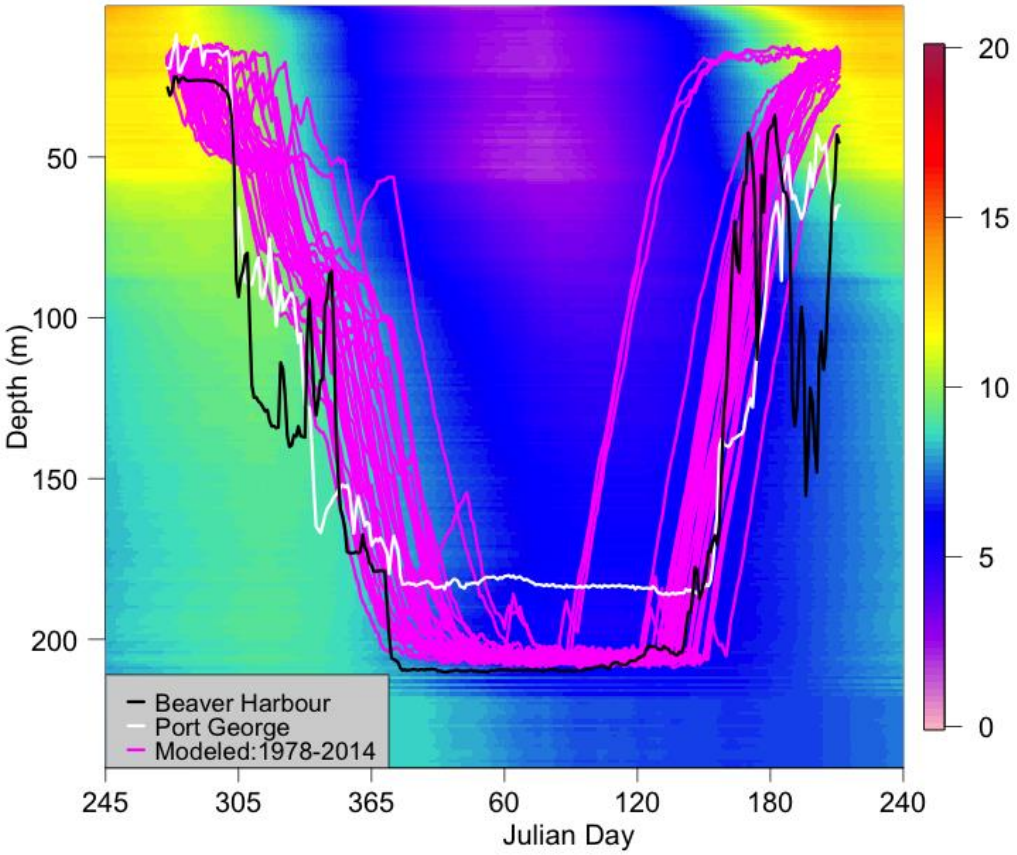

Figure 19. Observed (black and white lines) and modeled (magenta lines) depth of ovigerous American lobster plotted over the one-dimensional average bottom temperature at depth climatology using bottom temperature extracted for our study area (Fig. 3) from the FVCOM model from 1978 to 2014. The observed depths are average daily depths recorded by satellite tags attached to the two ovigerous lobster that were tagged in this study. The modeled average daily depths are the result of 100 lobsters simulated in our individual-based model of the temperature-driven scenario (VMS = ± 15 m/day, TIR = ± 220 m/day, TS = 0.05; see Methods) run using bottom temperature extracted from FVCOM over different sets of years from 1978 to 2014 (i.e. 1978 - 1979, 1979 -1980, 1980 - 1981, and so forth).

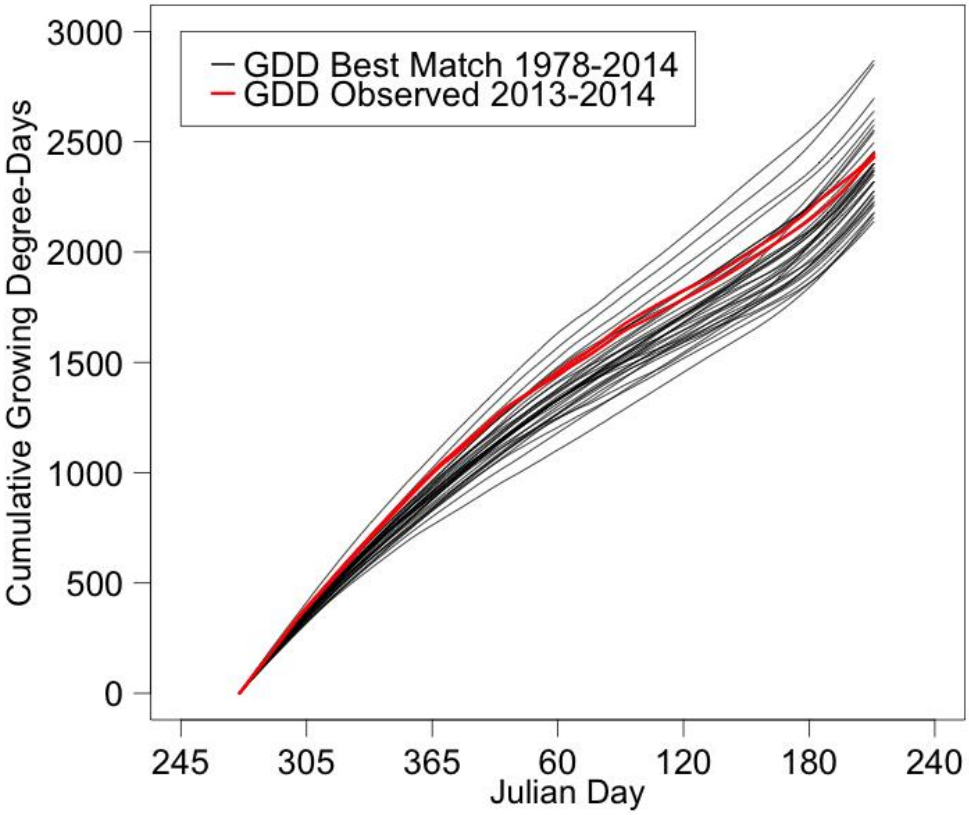

Figure 20. Mean cumulative growing degree-days (CGDD) of our two lobsters tagged from October 1st, 2013 (Julian day 274) to July 31st, 2014 (Julian Day 212) (red lines) and of 100 virtual lobsters (black lines) simulated by our individual-based model over the same Julian days of different sets of years from 1978 to 2014 (i.e. 1978-1979, 1979-1980, 1980-1981, and so forth). CGDD was calculated by summing the degrees Celsius experienced by lobster embryos each day after subtracting a 0°C temperature threshold of development. CGDD of tagged lobsters was based on the average modeled temperature across FVCOM grid cells at the average daily depth recorded by the satellite tags. CGDD of virtual lobsters was obtained using the model scenario that best matched the temperature experienced by our tagged lobsters in 2013-2014 (VMS = ± 15 m/day, TIR = ± 220 m/day, TS = 0.05; see Methods).

4.0 Discussion

This project used a combination of satellite tagging and an individual-based model (IBM) to advance our understanding of the patterns and causes (proximate and ultimate) of seasonal migrations by ovigerous American lobsters, *Homarus americanus*, in the Bay of Fundy, Gulf of Maine.

4.1 What we learned from satellite tagging American lobster

4.1.1 Seasonal Movements

This study documented, with an unprecedental level of detail, the deep-shallow migrations of two ovigerous American lobster undertake in the Bay of Fundy, Gulf of Maine, including daily estimates of the depth and the temperature they experienced. The two tagged lobsters initiated movements to deep water on the same day in the fall of 2013 (October 29th), attained an "overwintering depth" of approximately 200 m by mid-January 2014 (BHL: 11th, PGL: 16th), and then initiated rapid movement back towards shallow water in spring 2014 (BHL: May 22nd; PGL: June 4th). Earlier tag-recapture studies, which provided much more limited information concerning these migrations (but on a greater number of individuals), suggest movements of ovigerous females that are consistent with those documented in this study. In particular, analysis of pooled single and multiple recaptures of 1046 ovigerous females tagged and recaptured in the northern Gulf of Maine between 1982 and 1983 revealed these females moving from shallow to deep water between November and January, remaining deep (~ 200 m) during January to June, and returning to shallow water from July to September

(Campbell, 1986). Similar timing of fall departure from shallow water was noted further south in the Gulf of Maine, off the coast of New Hampshire, where the mean date tagged lobsters left the range of detection of a fixed-array radio-acoustic positioning system was November 1st (95% CI = October 22nd to November 11th; Goldstein and Watson, 2015a).

The continuous depth data afforded by the satellite tags yielded novel insights into the seasonal movements of ovigerous lobsters. In the fall, our two ovigerous lobsters moved from shallow to deep water with a vertical displacement of almost 200 m in 74 and 79 days for the "Beaver Harbour lobster" (BHL) and the "Port George lobster" (PGL), respectively. The PGL's vertical trajectory in the fall was mostly gradual, with very few "ups and downs", and this female reached her overwintering depth of ~ 185 m in 79 days. In contrast, the BHL encountered more ridges and valleys, which led her down to ~ 140 m in only 27 days, then back up to ~ 85 m in 19 days, before she made it down to her overwintering depth of ~ 200 m 28 days later. Our study is the first to report direct evidence that lobsters stay at a relatively constant depth throughout the winter. From January to the end of May, lobsters in this study exhibited very little change in depth (max. 6.1 m). It is likely that horizontal movements were also limited during this time given the low temperatures over this period in the winter (5.11 - 7.18 °C). Lobster activity levels are known to decline markedly below 10 °C, with lobsters capable of little activity only while at temperatures between 2 and 5 °C (Mcleese and Wilder, 1958). The spring deep-to-shallow migration resulted in a vertical displacement of ~ 150 m in 70 and 57 days for the BHL and PGL, respectively, a rate that was similar to that

observed for the females' fall shallow-to-deep migration. The PGL's vertical ascent was mostly regular, and she was in 65 m of water when the tag detached after 57 days. In contrast, the BHL encountered more hills and valleys during its ascent, which lead this female up to ~ 40 m in only 41 days, then back down to ~ 150 m in only 14 days, before she made it to ~ 45 m when the tag detatched 15 days later. Our two lobsters were in deeper water than they were captured when the tags detached from them, which may be because this occurred earlier (one month and 22 days) than a full year at large. Differences observed in depths encountered between the two tagged lobster reflect different paths - and thus bathymetry- taken by the two females. It is noteworthy that even though these two lobsters took different pathways during their fall and spring migrations, their thermal regimes were remarkably similar up until July 1st, from which point the PGL experienced warmer waters than the BHL. By the end of the 305-day tagging period the two lobsters were 116 km from one another, one near the mouth, and the other the upper-part, of the Bay of Fundy, but the difference in their "heat exposure" was only 94 Growing Degree Days (GDD). These similar thermal histories, despite markedly different movement pathways, suggest that lobsters in different regions could hatch their eggs at similar times if their migrations are adjusted to local bathymetry.

We are unable to confirm when, where and at what depth our tagged lobster's embryos hatched. Our tags detached from the lobsters on July 31st, and we do not know whether the embryos had hatched at that time because only the data and not the lobsters were collected. We were unable to assess the development status of the young embryos upon lobster tagging, and hence were unable to use the females' temperature records to

predict embryo development and hatch. Hatching in the Bay of Fundy starts in July and can extend to September, but peaks the second half of August (Campbell, 1986; Factor, 1995). During an experimental trapping study off the coast of Grand Manan, Bay of Fundy, in August 1982 and 1983, large numbers of ovigerous lobsters carrying developed embryos were caught at depths of 1 to 20 m (Campbell, 1990). It is unknown whether these aggregations are unique to Grand Manan, but this finding could suggest that in the Bay of Fundy ovigerous lobsters hatch their eggs close to the coast in August. This information suggests we may have missed the final shoreward movements of migration of our tagged lobster, as their tags detached at the end of July while they were still in slightly deeper water (45 and 65 m, for the BHL and the PGL, respectively). Though we are unable to say precisely where or when our two females hatched their eggs, what is clear is that spring inshore movements of these lobsters varied sufficiently to cause differences in eggs' hatch location (116 km Euclidian distance at time of tag release in lower and upper parts of Bay of Fundy) and hence potential larval transport and subsequent settlement (Incze *et al.*, 2006). This observation has implications to connectivity among lobster sub-populations and management areas. In particular, connectivity is increased by the movement of reproductive individuals among coastal areas for larval release. In particular, the timing and location of when and where eggs are hatched will subject larvae to paticular sets of environment factors (e.g., currents and temperature) that will affect where they disperse, the time they spend in the plankton, and subsequently where they settle (Xue *et al*., 2008).

4.1.2 Environmental Triggers

Our two tagged ovigerous lobsters showed remarkable synchrony in the timing of their fall shallow-to-deep migration- seemingly initiating these on the same day- and this synchrony may have been triggered by a relatively abrupt decrease in temperature of ~ 0.7 °C in 10 days. The environmental cues that trigger seasonal vertical movements in ovigerous lobsters are poorly understood. It has been hypothesized that declines in water temperature and an increase in storm events may both trigger fall offshore movements of lobsters (Goldstein and Watson, 2015a). Laboratory experiments have demonstrated that lobsters can sense changes in temperature as small as 0.15 °C, and move towards preferred thermal environments (Reynolds and Casterlin, 1979; Crossin *et al.*, 1998; Jury and Watson, 2000; Jury and Watson, 2013). However, we are the first to document an observed decrease in temperatures directly experienced by ovigerous lobster in nature preceeding the initiation of movements to deep water in the fall.

In comparison to the fall shallow-to-deep movements, the spring deep-to-shallow movements of our two tagged ovigerous lobsters were not as synchronous (thirteen days apart), nor were they clearly related to temperature. One might expect these migrations to be associated with warming atmospheric temperature, which lobsters could perceive (with some delay) via changes in temperature at depth. Based on a time-series of sea surface and bottom temperatures recorded at the long-term monitoring station “Prince 5” in the Bay of Fundy (66°.85W, 44°.93N), surface temperature starts increasing in April and continues to increase until September, and bottom temperature (100 m) also starts to

increase in April, albeit at a slower rate (Petrie and Jordan, 1993). The bottom temperature at ~ 200 m, where our lobsters were in the spring, presumably starts increasing shortly thereafter. Therefore, we expect that an increase in temperature experienced by deep-water lobsters in the spring would indicate that shallow water is warming, and that this warming could act as a trigger for movements into shallow water in late-May and early-June. However, unlike the rapid and marked cooling event that coincided with movements to deep water in the fall (0.7 °C in 10 days), in the spring the two lobsters experienced opposite patterns (-0.17 °C and +1.3 °C in 10 days; -0.64 and +0.54 °C in 20 days) preceding movements, and no marked change from these general patterns in the 2 to 3 days immediately preceding initiation of movements, arguing against temperature being a trigger for deep-to-shallow movements in the spring. Both lobsters did experience a very slight warming of approximately 0.1 °C during 2 to 3 days immediately preceding their vertical movements, but this change in temperature is likely too small for the lobsters to have perceived (Jury and Watson, 2000), and even if it had been perceived it is unlikely that it would have triggered the lobsters' movements to shallower water given that no vertical displacements were made by either lobster when they experienced a spike in temperature of approximately 1.4 °C (BHL: 5.71 to 7.02 °C; PGL: 5.64 to 7.18 °C) that lasted ~ 6 days in late-March. Importantly, if tagged lobsters had initiated movements at this time they would have been met with very cold temperatures in shallower water.

One important consideration related to our ability to assess the link between temperature and seasonal migrations is whether the estimated date of departure is

“correct”, and how inferences may change if this date was different. We estimated the day vertical migrations were initiated based on a one-day change in depth of magnitude of 5 m or more. This 5-m criterion was selected based on consideration of bathymetry and published estimates of lobster movements, but it is somewhat arbitrary. Importantly, however, our estimate of departure date is not overly sensitive to changes in this criterion. As using a smaller (2-m) or larger (8-m) depth change in a single day as our movement criterion resulted in small changes in departure day and did not change our conclusion that temperature change may have contributed to the initiation of fall, but not to spring.

Deciphering the cues that trigger movements is difficult, because (i) more than one can be involved, (ii) these can be correlated, (iii) we often do not know exactly when animals start moving, and (iv) we generally do not know abiotic/biotic conditions when they do so. Other possible environmental cues that could trigger lobster vertical movements in the fall and spring include photoperiod, storm events, or changes in water chemistry caused by spring blooms. It has been hypothesized that an increase in storm events may trigger fall offshore movements of lobsters (Jury *et al.*, 1995; Goldstein Watson, 2015a). Off the coast of New Hampshire, the initiation of offshore movement by ovigerous and non-ovgierous lobster coincided with a 36% increase in wave height (proxy for storm events) between spring-summer (May 1st - August 31st) and fall-winter (September 1st - December 31st) (Goldstein and Watson, 2015a). The data presented in this study supports the argument that these movements result in less exposure to waves/storms, but it is not clear that storms initiated these movements because we do

not know whether the lobsters experienced a change in wave action prior to moving offshore. We did not measure wave height or other proxies for storm events experienced by lobster, and are therefore unable to say whether storm events may have contributed to initiating movements of tagged lobsters in our study. Photoperiod is an important cue to time vitellogenesis (yolk deposition) in American lobster, however little evidence exists to support its role in migrations (Nelson, 1986). Furthermore, in the Bay of Fundy green light penetrates to a greater depth than red and blue light, and only 2.5% of light at the sea surface is detectable at 10 m (Klugh, 1927). It is unlikely that photoperiod plays a role in triggering spring movements, considering that our tagged lobsters were in ~185 and ~200 m of water. In the fall lobsters are at depths likely penetrated by light, however the influence of photoperiod on the timing of fall movements to deep water remains unclear. Phytoplankton cues from spring blooms are used by many species as cue for spawning, to synchronize larvae with zooplankton (Himmelman, 1975). Presumably, this cue would not work to initiate lobster spring migrations, as relying on detection of dead plankton cells to initiate movement would bring the lobsters to their in inshore hatch locations too late in the season for the match of larvae and their food to occur. In the fall an increase in storm events, decrease in temperature and shortening of photoperiod potentially all play roles in inciting movements to deep water in lobster. Future work should place emphasis on how lobsters directly experience these parameters to determine their importance to the timing of movement. In the spring we were unable to show a link between temperature and initiation of movements to shallow water and it is unlikely that photoperiod or plankton blooms serve as cues. Further

consideration is needed to determine cues that could trigger lobster movement to the shallows when lobsters are at ~200 m depth.

4.1.3 Advantages and Disadvantages of Satellite Tags to Track the Movement of Ovigerous Female American Lobster

This is the first study to use satellite tag technology to track American lobsters. This novel technology has allowed us to generate daily estimates of depth and temperatures experienced throughout an entire 10-month migration with relatively little effort on our part. However, satellite tags are expensive to purchase and operate, difficult to secure to lobsters because of the tag size relative to the lobster size, and are not guaranteed to return data. Therefore, even though satellite tags allowed us to overcome difficulties and biases associated with traditional tag-recapture or telemetry tracking of lobster, they present different obstacles.

Traditional tag-recapture methods used to track lobsters require animals to be physically recaptured after being tagged and released in their environment. Common tags that have been used in such studies include knuckle bands, which consist of plastic, or elastic bands that are placed around the lobster's knuckles, and anchor tags, which are anchored into the lobster's tissues and comprise a "streamer" portion that extends out of the animals' body and contains an individual identifier. Anchor tags overcome one of the main obstacles for tracking crustaceans, which is that they lose externally-attached (e.g., knuckle banks, acoustic tags, satellite tags) tags when they molt. The principal

limitation of traditional tag-recapture methods is that they generally do not allow robust inferences at the population level, because (i) in most studies the majority of tagged individuals are not recaptured, and (ii) those that are recaptured likely do not represent a random sample of the individuals that were tagged. The average recovery rate for traditional tag-recapture studies involving marine organisms is approximately 5% (Thomson, 1962), and that for American lobster is approximately 21% (review: Haakonsen and Anoruo, 1994; Pezzack and Duggan, 1986; Campbell and Stasko, 1985; Campbell, 1986; Estrella and Morrisey, 1997). Importantly, these studies almost always rely on lobster fishermen to recover tagged animals during the fishing season, resulting in recoveries being biased to areas of high fishing effort and to lobsters that move less (Cooper and Uzmann, 1971; Campbell and Stasko, 1985; Campbell, 1986; Campbell and Stasko, 1986; Pezzack and Duggan, 1986; Estrella and Morrisey, 1997; Comeau and Savoie, 2002). In addition to this difficulty of making population-level inferences, the movement information obtained from individuals that are recaptured is generally limited to two or a few points over time. This type of data prevents inferences concerning pathways between release and recovery location and almost invariably underestimates movements made.

Ultrasonic telemetry is a more recent technology used to track a great diversity of animals, and which is increasing in popularity, including the study of movement in American lobster (Goldstein and Watson, 2015a; Morse and Rochette, 2016). This technology is based on acoustic tags that are attached to an animal, and which emit ultrasonic sound pulses that are detected by either stationary moored receivers or by

mobile handheld receivers (Cowan *et al.* 2007; Goldstein and Watson, 2015a). In comparison to traditional tag-recapture methods, ultrasonic telemetry generates more highly-resolved data on movement. However, because of the relatively short distances over which sound pulses from acoustic tags used on lobster can be detected by receivers (fixed receivers: 400 - 500 m; handheld: 20 - 100 m), the range over which individuals can be tracked is limited (Klimley *et al*. 2001; Goldstein and Watson, 2015a). Moreover, the number of individuals that can be tracked using fixed-array systems is also limited due to collision among acoustic "pings" emitted by different tags. This technology has been particularly useful to study small-scale movements, including daily excursions, foraging habits, shelter use, and predator-prey interactions (Golet *et al.* 2006; McMahan *et al*, 2013; Morse and Rochette, 2016). It can, however, also be used to study broader movement patterns- including migrations- by deploying fixed receivers to form "gateways" to movement. However, this method is generally limited to areas that have geomorphological features that naturally constrain the movements of animals, enabling the establishment of "gateways" that will have a high likelihood of detecting the tagged animals. For instance, this approach has been used to determine when lobsters in the southern Gulf of Maine initiate offshore movements and when they return inshore (Goldstein and Watson, 2015a). It affords limited information on movement, simply providing time stamps of when the tagged animal(s) was(were) in proximity to one or several of the receivers that make up the curtain. If moored receivers are used in conjunction with hand-held receivers, researchers can obtain additional positional information during short-distance migrations (Goldstein and Watson, 2015a). Acoustic telemetry can thus be used to ask questions about migrations, especially when different

types of instruments are used in combination. However, this technology is not particularly useful in instances when animals move long distances (e.g., 123 km during this study) and do not return to the same area the following year, as observed in this study.

Pop-up Satellite archival tags (PSAT) enable large-scale ocean migration studies (Thorstad *et al*., 2013). One of the main advantages is that, in addition to a start and an end location of migration, the tag collects information about the environment experienced by tagged individuals (Gunn and Block, 2001), such as detailed records of depth and temperature. In this study we obtained 305 days of depth and temperature information for our two lobsters. Movements between start and end locations can be estimated by matching daily depth and temperature to bathymetry and modelled temperature in the area (Bjorkstedt *et al*., In Prep). Since the tags are pre-programmed to detach from the animal after a certain period, and the buoyant tag floats to the surface and starts transmitting the subset of the archived data to a base station on earth through ARGOS satellites, tags do not have to be recovered to retrieve data. Importantly, the ultimate advantage of satellite tags is arguably that the data is not biased in relation to the distance or location moved by a tagged individual, as is the case for traditional tagging studies based on fishery recaptures.

The main limitation to satellite tags is arguably that transmission success is dependent on a variety of factors, including weather, remaining battery life, surrounding topography, obstructions such as seaweed, debris, or rocks, and damage to the tag.

Usually not all collected data is successfully transferred to ARGOS satellites (Thorstad *et al*., 2013), often leaving holes in the dataset and sometimes resulting in no recovered data at all. A second challenge associated with PSAT is that the tags are relatively large, which limits the size of animals that can be tagged and can affect the ease with which they can be secured to smaller-bodied animals. Since this study we have made two other attempts to tag ovigerous lobsters, and both mostly failed (results not reported here). In the fall of 2015 and spring of 2016, we satellite tagged seven and four ovigerous lobsters, respectively, ranging in size from 140 to 183 mm CL. The tags were programmed to remain on the lobsters for eleven or five months for individuals tagged in the fall or spring, respectively. Seven of the eleven tags detached prematurely, from days up to a bit over one month after release; the most succesful was a tag that stayed on a lobster from October 6th to November 20th, which provided spotty data, but suggested movement to deep water in 2015 by this lobster was between October 26th and November 9th, which is consistent with observations in this study from 2013 (October 29th). We believe that these premature releases were due to the adhesive used to attach the tag to the lobster's carapace being defective. In hindsight, a stringent test for glue quality should have been performed prior to tagging. The remaining four tags were never heard from after release, for reasons that are unknown to us, but could be related to obsruction of the signal either at the surface (e.g. seaweed, debris, cliff), underwater (e.g. rock or trap), or ashore (e.g. under boulder). One tag was found washed ashore in north western Nova Scotia and was returned to us, but the tag was too damaged to recover data.

Satellite tag technology is relatively expensive, which limits the number of individuals that can be tagged in a particular study, and hence limits generalizations that can be made at a population level. This study was the first attempt to use satellite tags to track the movement of a marine invertebrate, and given the data uncertainty, costs, and tagging problems, we only successfully tagged two ovigerous lobsters. The satellite tag used in our study costs 2,500 USD, to which must be added costs related to data collection through satellite transmissions. The cost of satellite use is directly proportional to the amount of data transmitted, which is a function of the number of days the tag records data as well as its frequency of sampling. In total the cost of data acquision, including daily averages of depth and temperatures, start and end locations, and the monthly active platform fee in this study were relatively inexpensive, at approximately 253 USD per tagged animal. Using satellite tags to track lobster in a larger study, for example involving 30 lobsters, would cost approximately 82,590 USD including additional charges. This cost is not insignificant, especially if we consider uncertainties surronding the recovery of data.

Another major limitation of pop-up satellite archival tags, which has already been alluded to, is that they are relatively large and have to be attached externally, which limits the size to only large individuals and could impair movement. A satellite tag with a low-drag float, battery and release section is 230 mm long. To properly anchor the tag to a lobster, the lobster's carapace needs to be large enough to support the tag at two points of attachment sufficiently spaced on the lobsters carapace to hold the tag. Therefore, satellite tags are not suitable to study movements of juvenile or small

mature lobster. In this study we tagged the largest ovigerous lobsters (160 mm CL) we could find to reduce the likelihood of impediment to movement and capture by fishermen traps.

Another consideration of satellite tags, and tagging studies in general, is the effect of the tag on movement of the target animal. Although we can not unequivocally say that the satellite tags had no impact on the activity of the two lobsters tagged in the study, we believe that if they did have some effect it was minimal. First, observations by SCUBA divers following release revealed no evident effect of the tags on the lobsters' behaviour and maneuverability. Secondly, the large net (euclidian) distances the two lobsters moved from their tagging site (33 and 123 km) provides evidence that movements were not markedly hindered by the tags, if at all. Finally, studies in this area have shown lobster utilising depths similar to those used by our tagged lobster (Campbell, 1986; Campbell and Stasko, 1986), again suggesting that movements observed during our study were "normal" and not markedly affected by the relatively large tag.

This study provides compelling evidence for the usefulness of satellite tags to track the movements of large lobsters, because data on depth and temperature is continuous, highly detailed, and non-biased in space or time. However, for these tags to become more useful to study movements of lobster in general, work should be done to devise the most-effective and reliable attachment method. Satellite tag technology is continuing to develop and is becoming cheaper and smaller, which will make it an even more desirable method to track animals such as lobsters and other marine invertebrates.

4.2 What we learned from the individual-based model

4.2.1 Navigation

Ovigerous lobster's affinity for warmer water seems to have played a role in navigation during the shallow-to-deep movements in the fall, but not the deep-to-shallow movements in the spring. In our individual-based model (IBM), we were able to recreate with high fidelity the observed movements from 20 m down to 200 m in the fall, by requiring virtual lobsters to move to the depth of maximum temperature each day when their Temperature Information Range (TIR) and Vertical Movement Scope (VMS) were +/- 15 m. This finding suggests that ovigerous lobster could complete their fall movements to deep water solely by relying on temperature within +/- 15 m of their depth. This behavioural thermoregulation in lobster, selecting preferred thermal conditions, has been demonstrated under laboratory conditions (Reynolds and Casterlin, 1979; Crossin *et al*., 1998).

We were not able to recreate deep-to-shallow movements observed in the spring in our IBM using the same movement rules (TIR and VMS +/- 15 m) that successfully recreated fall shallow-to-deep migrations. Only when the virtual lobsters were given information on temperature across all depths (TIR +/- 200 m) were we able to recreate the observed deep-to-shallow movements in the spring, which provides strong evidence that lobsters were not using temperature as a navigational cue during spring migrations. This conclusion is also consistent with the conclusion made on the basis of temperature data recorded by the animals' tags that a change in temperature was not responsible for

initiating spring shoreward movements. Furthermore, their movements persisted through isobaths where water was colder, and in the summer vertical movements ceased when lobsters were at 45 and 65 m when warmer water was available at shallower depths (< 25 m).

Other cues that could orient deep-shallow migrations in ovigerous lobsters that were not investigated in this study include, but are not limited to, hydrostatic pressure, chemicals, wave surges, and magnetic fields. Hydrostatic pressure would seem to be an obvious candidate given its reliability as a proxy for depth. Hydrostatic pressure is used by Crustacean larvae (Knight-Jones and Qasim, 1955, Knight-Jones and Morgan, 1966, Naylor and Atkinson, 1972), including American lobster (Ennis, 1975), to adjust their depth in the water column. It is also used by adult crabs (*Carcinus maenas*) making vertical migrations related to circatidal rhythms (Naylor and Atkinson, 1972; Reid and Naylor, 1990; Fraser and Macdonald, 1994), and this possibility should be investigated for American lobsters, although there is evidence that young stage V (1st benthic phase) lobster lose this ability (Ennis, 1975). In controlled conditions, American lobsters have shown their ability to navigate to shelter, food and other animals using chemical cues (Atema, 1995). In nature, lobster have demonstrated that they can detect baited traps from distances of 11 ± 0.7 m (Watson *et al.*, 2009), however it is unlikely that chemotaxis plays a major role in long-distance navigation over 200+ m of vertical migration (Basil and Atema, 1994). Spiny lobster (*Panulirus argus*) have demonstrated their ability to navigate using wave surge, the horizontal movement of water near the ocean floor (Herrnkind, 1970; Herrnkind and McLean, 1971: Walton and Herrnkind,

1977; Herrnkind, 1983), and magnetic fields (Lohmann *et al.* 1995), however it has yet to be determined whether American lobster have these abilities. In order to understand the environmental cues used by lobsters to navigate during seasonal migrations, we need a more complete characterization of the physical environment on the spatial and temporal scales that are relevant to these migrations. Presently, our IBM only uses temperature as a potential navigational cue, but it could be expanded to include additional environmental parameters such as those mentioned above.

4.2.2 Function of Seasonal Migration

This study is the first to demonstrate that seasonal movements made by ovigerous lobsters in the Bay of Fundy increase the temperatures they and their embryos experience in comparison to temperatures that they would experience if they moved at random or remained in shallow coastal waters year round. Data collected here provides the best empirical evidence that these seasonal movements are driven, from a functional standpoint, by temperature. Given the seasonal variation in temperature-depth profile in our individual-based model (IBM), virtual lobsters in temperature-directed scenarios, having temperature information for all depths (TIR = ± 200 m) and Vertical Movement Scopes ≥ ± 15 m, as expected, consistently moved from shallow to deep water in the fall, stayed deep over winter, and then return to shallow water in the spring. The movements of our tagged lobster were surprisingly similar to the temperature-driven scenario where the VMS was ± 15 m, likely because daily depth changes greater than this is unrealistic for a lobster in nature. This finding suggests that the movements the

tagged lobster displayed position them at the right depth most of the year to experience the warmest water available. More specifically, we show that ovigerous lobster accumulate between ~ 421 and ~ 404 additional GDD above 0 °C by moving to deep water in the fall and returning to shallow water in the spring than if they moved at random or stayed inshore, respectively. Though our sample size is low (n = 2), these findings represent the most direct and detailed empirical evidence for the hypothesis that seasonal movements by ovigerous lobster function to increase temperature experienced by developing embryos (Campbell, 1986).

Contrary to our study in the northern Gulf of Maine, two studies in the southern Gulf of Maine found no evidence that ovigerous females undertake seasonal vertical migrations to increase the temperature they and their embryos experience. The first study to document temperatures experienced by ovigerous lobsters during brooding was a mark-recapture study done in Muscongus Bay, Maine, in which temperature data loggers were glued to the carapace of females (Cowan *et al*., 2007). In this study larger females (> 93 mm CL) experienced less variable temperatures throughout the brooding period than smaller (< 93 mm CL) individuals, but there was no significant difference in the average number of GDD experienced by the two groups of females (953 and 984 GDD above 3.4 °C, respectively). Although this study generated little data on the location or depth of females, the temperature patterns observed suggest that smaller females tended to spend the entire brooding season in shallow coastal areas, where temperature is more variable, and larger individuals spent much of the fall and spring in deep water, where temperatures is less variable. The second study was done off the coast

of New Hampshire. In this study the movement of ovigerous lobsters was again not monitored and instead caged ovigerous lobsters underwent different “simulated seasonal movements” based on previous tracking studies in this area (Goldstein and Watson, 2015b). In this study, females that were caged “offshore” in ≈ 30 m of water from fall to winter, and then moved “inshore” in ≈8 - 10 m in the spring, accumulated (840 GDD above 3.4 °C) a similar number of GDD from September to June compared to lobsters that were kept inshore (938 GDD above 3.4 °C) or offshore (905 GDD above 3.4 °C) (Goldstein and Watson, 2015b). Note that the offshore location in which these lobsters spent their winter was not as deep as in our study (30 vs. 200 m), and the thermal conditions weren’t as different from their inshore location as was the case in ours, meaning that the thermal benefit incurred through seasonal movements is less evident compared to our study.

The thermal benefit associated with seasonal deep-shallow migrations differs among regions due to differences in seasonal changes in bottom temperature and the local bathymetry. For instance, in the Bay of Fundy, shallow inshore areas experience prolonged cold water during the winter that is caused by cold atmospheric temperatures and high levels of mixing, but lobsters can move down to 200 m depth relatively easily given the bathymetry and significantly increase their thermal conditions for the winter (as shown in this study). In contrast, further south along the coast of the Gulf of Maine, coastal waters are not as cold in the winter and the slow sloping shelf makes it difficult for a lobster to access deep water that would markedly increase their thermal regime in the winter (Mountain and Holzwarth, 1989). These conditions of the southern Gulf of

Maine, may explain why the two studies just mentioned done in these regions found no evidence that seasonal migrations increase thermal conditons experienced by lobsters. Further north in the Gulf of St. Lawrence, ovigerous lobsters are confronted with a three-layer stratification of the water column, which involves a cold intermediate layer of approximately -1 to 2.5 °C year round (moves from the surface in winter to 40 m in the summer) that acts as a barrier to the deeper warmer waters (Gilbert and Pettigrew, 1996). Not surprisingly, ovigerous lobster in the Gulf of St. Lawrence move little year round with no particular patterns relating to depth (Comeau and Savoie, 2002).

Although the movements of ovigerous lobster tagged in the Bay of Fundy increased the temperatures experienced by their embryos compared to females moving randomly or not at all, they did not appear to maximize the temperatures females experienced, considering temperatures available. Virtual lobsters in our IBM that moved to warmest water available each day (maximized temperature scenario) moved to deep water much faster in the fall, to shallow water earlier in the spring, and to shallower depths in the summer compared to tagged ovigerous lobster. These differences in movements resulted in an average of 321 GDD above 0 °C more (13% more) than observed for tagged lobsters. In this “maximized temperature” scenario, the virtual lobsters were able to move to the depth of maximum temperature with no constraints to movement, which can in and of itself explain part of the difference in GDD between virtual and our tagged lobsters, as they clearly have limits to the speed at which they can change depth. However, tagged lobsters also experienced a lower number of GDD (103 GDD, 4 %) than virtual lobsters in the “temperature-driven” scenario, which had

strongly directed movements towards the depth of maximum temperature but had restraints to movement of ± 15 m/day. It is reasonable to assume that our lobsters were able to change depth by up to 15 m each day, or at least most days, considering that they were observed changing depth by as much as 50 m (BHL) and 32 m (PGL) in a single day during their shallow-to-deep migration in the fall. More generally, to make a depth change of ± 15 m in the Bay of Fundy, lobsters need to move a horizontal distance of less than 10 km in the majority of locations within our study domain, with many locations only requiring 2 - 4 km. The prevalence of 'flat' bathymetry, which requires greater horizontal distances to be covered to change depth by 15 m, is greater in the deep basins (> 200 m depth). Such 'flat' areas do also occur in shallower water, but less frequently. Moreover, the slopes leading to basins are relatively steep from where these lobsters were in the fall, which enables lobsters to make marked changes in depth by moving relatively limited horizontal distances. We are unable to estimate the speed of our tagged lobster in horizontal space, but in a lab experiment lobsters 85-100 mm CL walked on a treadmill at a speed of up to 8 m per min for 30 min without reaching the point of exhaustion (no longer able to walk) (Rose *et al*, 1998). It is unknown how long a lobster can sustain a speed of 8 m per min, but even at half this speed a lobster could cover approximately 5.75 km in one day. Thus the discrepency in GDD between our tagged and the “temperature-driven” virtual lobsters is likely not due to an unrealistic assumption concerning movement rates of real lobsters, but rather likely reflects decisions by the tagged lobsters not to move to areas of highest temperature at certains times of the year. That lobsters made such a choice was evident in the summer at least, when virtual lobsters continued movements to shallow depths (~ 20 m) where water was

warmest, while tagged lobster at some point stopped their ascent and stayed in water deeper than 45 and 65 m in cooler water for 30 - 32 days. This finding strongly suggests that tagged lobsters were not maximizing temperature within their ability, especially in the summer.

We hypothesize that our two ovigerous lobsters postponed returning to inshore coastal areas in the summer to avoid exposing their embryos to high temperatures that could have triggered hatch. Not only do migrations play a role in ensuring embryos get sufficiently high temperatures for development, but they could also act to regulate hatch time (Hare, 2014). Embryos were too early in development to stage them at the time of tagging, therefore we were unable to forecast egg development, and estimate when hatching occurred. It is possible that hatch had not yet occurred when tags detached from our lobsters on July 31st, considering hatching in the Bay of Fundy peaks in the second half of August, starting in July and extending to September (Campbell 1986; Factor, 1995). High concentrations of ovigerous lobster carrying developed eggs have been observed in August in 1 - 20 m of water off Grand Manan (Campbell, 1990), whereas when the tags detached at the end of July, our tagged lobsters were still in 45 and 65 m of water. Moreover, considering the bathymetry in this area tagged lobsters could have easily been in warmer shallower water by this time, if they “wanted” hatch to occur suggesting that they were “not ready” to hatch their embryos. Hatch time ideally would synchronize the presence of lobster larvae and the plankton they feed on (critical period hypothesis: Hjort, 1914, 1926; match-mismatch hypothesis: Cushing, 1990), and it may be that females delayed return to shallow water (and hatch) to increase the

likelihood of such a match. The “Prince 5” fixed monitoring station in the Bay of Fundy (66°.85W, 44°.93N) showed that between 1999 - 2015, zooplankton biomass has been highest from July to September, peaking in August (Johnson *et al.*, 2017; Martin, 2017). If the timing of hatch were to successfully “match” with the presence of zooplankton prey, hatching in these two lobsters would occur not long after tags detached. What is clear is that the lobsters that underwent deep-shallow migrations in this study did not move into shallow water in the summer where water was warmest as early as they could have, suggesting that seasonal migrations also function to regulate hatch time.

This study shows that seasonal movements made by ovigerous female lobsters have direct implications to the temperatures experienced by embryos throughout brooding, and hence to the development of these embryos. We are, however, unable to confirm the extent to which the temperatures experienced by the embryos affected their development time, given that we did not directly monitor embryo development (only the temperature they were exposed to) and there is evidence that the relation between temperature and embryo development is not constant throughout the brooding period nor over the entire range of temperatures experienced (Gendron and Ouellet, 2009). Therefore, we can assume that the increase in temperature experienced by embryos carried by ovigerous lobster undertaking seasonal movements had an effect on their development, likely an acceleration effect, but to what extent is unclear. Moreover, we are unable to confirm whether the main or only function of these seasonal movements by ovigerous lobster is to influence the progression of embryo development, given that these could also be associated with temperature requirements of molting, growth, or

gonadal development and there exists evidence that non-ovigerous male and female lobsters might also occasionally undertake such migrations in the Gulf of Maine (Factor, 1995).

4.2.3 Hindcast Inter-Annual Variability in the Timing of Migration and Thermal Histories

Using our temperature-driven model and hindcast bottom temperature for 1978 to 2014, virtual lobsters were found to consistently display the seasonal migration between shallow and deep water reported for our two tagged lobsters, although there was considerable variation in the timing of the fall descent and spring ascent. Our temperature-driven scenario assumes that lobsters always move towards warmer temperatures, and therefore variability in the timing of shallow-to-deep and deep-to-shallow movements of virtual lobsters in the fall and spring, respectively, are directly related to that year's vertical variation in bottom temperature at those times. We did not detect a gradual shift in the timing of either the fall or the spring migration over the years. This finding was somewhat surprising, considering the recent and marked warming observed in the Gulf of Maine (Mills *et* al., 2013; Hebert *et al.*, 2014; Pershing *et al*., 2015; Kavanaugh *et al*., 2017). Specifically, average daily sea surface temperature (satellite-derived) in the Gulf of Maine has risen at a rate of 0.03 °C yr^{-1} between 1982 and 2013 (Pershing *et al*., 2015), and at a rate of 0.23 °C yr^{-1} between 2004 and 2013, with 2012 and 2013 being the two warmest years in the time series (Pershing *et al*., 2015). In general, during warm years spring warming occurs earlier and fall cooling

occurs later (Pershing *et al*., 2015). However, our model did not predict trends in the timing of fall movements that match these temperature trends. For example, for 2012, which was an exceptionally warm year for sea surface temperature, our model predicts that movements to deep water in the fall occurred earlier than in 2004, which was a relatively cold year for sea surface temperatures. The reason for this discrepancy is unclear, but may be related to the temperature information used in these different exercises. In particular, warming trends in the Gulf of Maine are based on average annual sea surface temperature, and these trends may or may not be well correlated with inter-annual trends in bottom temperature during the few weeks in the fall and spring when migrations occur. But also, migration decisions in our IBM are a function of patterns in variation of temperature with depth, and not only temperature at a particular depth, and these may be even further removed from annual trends in average sea surface temperature. To determine how warming oceans may affect migrations of lobsters and other benthic organisms we need a better understanding of how temperature is changing near the sea floor, and whether sea surface temperature is a good proxy of these trends, as well as a better understanding on the environmental cues lobsters use during these movements and the flexibility of their behaviour to changes of the cues.

4.2.4 Bottom Temperature Assumptions in Individual-Based Model

The FVCOM bottom temperature predictions show considerable error, however these likely had little impact on the individual-based model simulations, which depend on the large-scale seasonal cycle of bottom temperature. Comparing FVCOM modeled

bottom temperature to spatially and temporally matched observations from the July 2013 and 2014 groundfish surveys conducted by the Canadian Department of Fisheries and Oceans, we found a positive correlation between modeled and observed bottom temperature in both years. The correlation coefficients (R^2 of 0.72 and 0.61), however, indicate that the FVCOM model is not very good at making point predictions of bottom temperature, showing relatively large error in both years (up to 1.97 °C). A much better fit (R^2 of 0.87) between observed and modelled temperatures was found in a recent study in the northwest Atlantic region that used $2x10^6$ pairs of FVCOM-observation records (Manning, 2012) to quantify the spatial and temporal accuracy and precision of the modeled data (Li *et al.*, 2017). The differences in correlations coefficients observed in this study and ours is potentially due to our observations having been made in July, when FVCOM's skill to predict bottom temperature is poorest (Li *et al.*, 2017). FVCOM has reasonable skill at predicting bottom temperature in the Gulf of Maine, especially in our study area, because waters are reasonably well mixed, are near shore and in the northern range of the model where it performs best (Li *et al*., 2017). Moreover, bottom temperatures used in the individual-based model are averaged across FVCOM model grid cells, and if there is unbiased error around the regression line reduces error, and since the number of estimates for each depth is large given the number of grid cells, the mean error should be markedly reduced.

We found some indication that the FVCOM makes somewhat biased temperature predictions, but these did not alter the natural structure of the seasonal bottom temperature cycle. Our low number of observations at only one point in time used to

validate the FVCOM's skill at predicting bottom temperature (2013: 23 sites; 2014: 25 sites over 3 - 4 days in July), limits our ability to evaluate biases across spatial and temporal scales relevant to the period over which we tracked lobsters. Our results suggest that the FVCOM under-estimated temperature in 2013 but not in 2014, whereas Li *et al*. (2017) concluded that the model over-estimates temperatures under 9.9°C and under-estimates those above 9.9°C. In terms of bias with depth, though no significant pattern was found, results suggest that temperature may be over-estimated at 50 m and under-estimated at greater depths, but confidence in this pattern is somewhat limited given the small number of observations. Unfortunately, the study by Li *et al*. (2017), which was based on a much larger number of observations, did not investigate bias with regard to depth or season. A bias in FVCOM model prediction is potentially more concerning than prediction errors for our inferences, but only if the bias alters the true ordinal-scale gradient of the vertical temperature profile. More specifically, if the bias alters where the depth of maximum temperature is located at any time during the study period, this would affect the virtual lobster's movement decision and temperature experienced. This, however, does not appear to have occurred, because the seasonal bottom temperature structure (Fig. 4), which is composed of the daily vertical temperature profiles that drive movement (Fig. 6), clearly reflects the correct seasonal bottom temperature cycle with respect to depth. In particular, vertical profiles of bottom temperatures indicate that temperature is higher at shallow compared to deep depths from April to October and the opposite (warmer in deeper water) from November to March, which is consistent with our understanding of the seasonal cycle of bottom temperature in this area (Richaud, 2016).

The conclusion from our study and Li *et al*. (2017) concerning error and bias in FVCOM's bottom temperature predictions is that large-scale seasonal oceanographic variability in bottom temperature is accurately modeled using FVCOM, but localized high-frequency dynamics in vertically stratified summer conditions are less skillfully handled (Li *et al*., 2017). This study was the first effort to validate FVCOM bottom temperature predictions in the Bay of Fundy, however we decided not adjust modelled temperature for use in our IBM based on these validations. Correspondence between the modeled and observed bottom temperature over our IBM's domain was of some assurance, but the limited scope of the validation data made it difficult to justify adjusting modelled temperatures, considering the validation was based on sampling at a small number of locations over a short period of time (over 3-4 days in July in 2013 and 2014, respectively) whereas the IBM required data from grid cells over a much longer time period (Sept 2013 to August 2014). Moreover, we acknowledge that the simplified temperature field of our IBM does not represent the lobster's environment entirely accurately, but it is a good method for addressing questions on how particular movements either modeled or observed affect thermal history, which require large spatial and temporal information on bottom temperature. Moreover, it gives us a foundation on which to produce hypotheses to be tested more empirically.

4.3 Summary and future directions

This project investigated seasonal deep-shallow migrations of ovigerous American lobster, *Homarus americanus*, in the Bay of Fundy, Gulf of Maine. For the first time, satellite tags were used to track in greater detail than before seasonal migrations of ovigerous lobsters from fall to summer, including daily records of depth and temperature. Temperature records suggest that fall migrations are triggered by a relatively rapid decrease in temperature (~ 0.70 °C in 10 days) in shallow coastal areas, but that spring migrations do not appear to be associated with a change in temperature. A simple individual-based model was built to simulate lobster movement in a 1-dimensional daily temperature-at-depth space, to contribute to our understanding of proximate and ultimate causes of these migrations. This modelling work supports the hypothesis that ovigerous lobster in the Bay of Fundy move to deep water in the fall and return to shallow water in the spring to increase exposure to warm waters while they brood their embryos. It also showed, however, that seasonal migrations made by our two tagged lobsters did not maximize the temperature they (and their embryos) experienced, as they moved to deeper water sooner in the fall and to shallow warmer water later in the spring than expected under this hypothesis.

Before we can improve our ability to predict the timing of lobster seasonal migrations, the timing and location of hatch, and implication of these to connectivity, further work is needed to determine what environmental cues lobsters respond to. Part of this work will involve laboratory experiments to test lobsters' responses to specific environmental cues in controlled conditions, such as chemical cues, wave surges,

photoperiod, hydrostatic pressure, magnetic fields and temperature. Once we have a better understanding of which of these cues could be used in seasonal migrations, they can be incorporated into the individual-based model created for this study and through step-wise analyses we can evaluate how and which of these are important to seasonal movements. Moreover, future versions of this individual-based model could incorporate a sensitivity parameter that would account for the magnitude of the temperature variability the lobsters are exposed to rather than basing movement solely on the location of maximum depth, regardless of the magnitude of difference. Further developments of this model would ideally investigate temperature-driven movements in a two-dimensional environment accounting for horizontal distance needed to change depth. Satellite tags are useful to validate predictions made by such models (as shown here), as they can provide continuous data on several environmental parameters (magnetic field, light, depth and temperature) over relatively unconstrained spatial and temporal ranges. Knowledge of where and when lobsters move in relation to temperature and other environmental parameters is desirable to fine tune practices already in place to protect ovigerous lobster, but moreover will be essential to predict changes in population dynamics, especially as our oceans change as a result of climate change.

5.0 References

Aiken, D. E. (1977). Molting and growth in decapod crustaceans with particular reference to the lobster, *Homarus americanus*. *Div. Fish. Oceanogr. Circ*. **7**: 41-73.

Aiken, D. E. and Waddy, S. L. (1980). Reproductive biology. *In* The Biology and management of lobsters (Cobb J. S., Phillips, B. F., eds), Vol 1. Academic Press, New York, p. 215-276.

Atema, J. (1995). Chemoreception. *In* The biology of the lobster *Homarus americanus*. (Factor, J. R., ed) Academic Press, San Diego, C.A. p. 330-335.

Basil, J. and Atema, J. (1994). Lobster orientation in turbulent odor plumes simultaneous measurement of tracking behavior and temporal odor patterns. *Biol. Bull*. **187**: 272-273.

Bjorkstedt, E., Hanley, P., and Rochette, R. (In prep).Virtual walking tours of the Bay of Fundy: combining archival tag data and an ocean circulation model to infer individual migration paths of lobster (Homarus americanus) in the Bay of Fundy.

Campbell, A. (1986). Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand-Manan, Eastern Canada. *Can. J. Fish. Aquat. Sci*. **43**: 2197-2205.

Campbell, A. (1990). Aggregations of berried lobsters (*Homarus americanus*) in shallow waters off Grand Manan, eastern Canada. *Can. J. Fish. Aquat. Sci.* **47**: 520-523.

Campbell, A. and Stasko, A. B. (1985). Movements of tagged American lobsters, *Homarus americanus*, off Southwestern Nova Scotia. *Can. J. Fish. Aquat. Sci.* **42**(2): 229-238.

Campbell, A. and Stasko, A. B. (1986). Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. *Mar. Biol.* **92**: 393-404.

Chassé, J., Lambert, N., Comeau, M., Galbraith, P.S., Larouche, P., and Pettipas, R.G. (2014). Environmental conditions in the southern Gulf of St. Lawrence relevant to lobster. *DFO Can. Sci. Advis. Sec. Res. Doc*. 2014/031. v + 25 p.

Chen, C., Beardsley, R. C., and Cowles, G. (2006). An unstructured grid, finite-volume coastal ocean model (FVCOM) system. *Oceanography*. **19**: 78-79.

Chen, C., Huang, H., Beardsley, R. C., Liu, H., Xu, Q., and Cowles, G. (2007) A finite volume numerical approach for coastal ocean circulation studies: comparisons with finite difference models. *J. Geophys. Res*. **112**. C03018

Comeau, M. and Savoie, F. (2002). Movement of American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. *Fish. Bull*. **100**: 181-192.

Cooper, R. A. and Uzmann, J. R. (1971). Migrations and growth of deep-sea lobsters, *Homarus americanus*. *Science.* **171**: 288-290.

Cooper, R. A., Clifford, R. A., and Newell, C. D. (1975). Seasonal abundance of the American lobster, *Homarus americanus*, in the Boothbay region of Maine. *Trans. Am. Fish. Soc*. **104**: 669-674.

Cousineau, J., Nistor, I., and Cornett, A. (2012). Hydrodynamic impacts of tidal power lagoons in the Bay of Fundy. *Coast. Eng. Proc*. **33**, p. 69.

Cowan, D. F., Watson III, W. H., Solow, A. R., and Mountcastle, A. M. (2007). Thermal histories of brooding lobsters, *Homarus americanus*, in the Gulf of Maine. *Mar. Biol*. **150**: 463-470.

Crossin, G. T., Al-Ayoub, S., Jury, S., Howell, W. W. (1998). Behavioral thermoregulation in the American lobster *Homarus americanus*. *J. Exp. Biol.* **201**: 365-374.

Cushing, D. F. (1990). Plankton production and year-class strength in fish populations: an update of the match-mismatch hypothesis. *Adv. Mar. Biol.* **26:** 249-239.

Department of Fisheries and Oceans Canada. (1997). State of the Ocean: Scotian Shelf, Bay of Fundy, and Gulf of Maine. DFO. Sci. Stock Status Report G3-0.

Drinkwater, K. F. and Gilbert, D. (2004). Hydrographic variability in the waters of the Gulf of St. Lawrence, the Scotian Shelf and the Eastern Gulf of Maine (NAFO Subarea 4) during 1991-2000. *J. Northw. Atl. Fish*. **34**: 83-99.

Ennis, G. P. (1975). Behavioral responses to changes in hydrostatic pressure and light during larval development of the lobster *Homarus americanus*. *J. Fish. Res. Board Can*. **32**: 271-281.

Ennis, G. P. (1984). Small-scale seasonal movements of the American lobster *Homarus americanus. Tans. Am. Fish. Soc*. **113**: 336-338.

Estrella, B. T. and Morrisey, T. D. (1997). Seasonal movement of offshore American lobster, *Homarus americanus,* tagged along the eastern shore of Cape Cod, Massachusetts. *Ocean*. *Lit. Rev.* **95**: 466-476.

Factor, J. R. (1995). The biology of the American lobster, (*Homarus americanus*). Academic Press, San Diego, C.A.

Fitzpatrick, J. J. (2009). Assessing skill of estuarine and coastal eutrophication models for water quality managers. *J. Mar. Syst*. **76**: 195-211.

Fogarty, M. J. and Borden, D.V.D. (1980). Movements of tagged American lobster, *Homarus americanus,* off Rhode Island. *Fish. Bull*. U.S. **78**: 771-780.

Fraser, P. J. and Macdonald, A. G. (1994). Crab hydrostatic pressure sensors. *Nature.* **371**: 383-384.

Gendron, L. and Ouellet, P. (2009). Egg development trajectories of early and late – spawner lobsters (*Homarus americanus*) in the Magdalen Islands, Quebec. J. *Crust. Biol*. **29**: 356-363.

Gilbert, D. and Pettigrew, B. (1996). Interannual variability (1948 – 1994) of the CIL core temperature in the Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* **54**: 57-67.

Goldstein, J. S. and Watson III, W. H. (2015a). Seasonal movements of American lobsters in southern Gulf of Maine coastal waters: patterns, environmental triggers, and implications for larval release. *Mar. Ecol. Prog. Ser*. **524**: 197-2011.

Goldstein, J. S. and Watson III, W. H. (2015b). Influence of natural inshore and offshore thermal regimes on egg development and time of hatch in American lobsters, *Homarus americanus*. *Biol. Bull*. **228**: 1-12.

Golet, W. J., Scopel, D. A., Cooper, A. B., and Watson III, W. H. (2006). Daily patterns

of locomotion expressed by American lobsters (*Homarus americanus*) in their natural habitat. *J. Crust. Biol*. **26**: 610-620.

Gunn, J. and Block, B. (2001). Advances in acoustic archival, and satellite tagging in Tuna. *In* Tuna: Physiology, Ecology, and Evolution. (B. A. Block and E. D. Stevens, eds) San Diego: Academic Press. 167 -224.

Han, G., Loder, J. W., Smith, P. C. (1999). Seasonal-mean hydrography and circulation in the Gulf of St. Lawrence and on the Eastern Scotian and Southern Newfoundland Shelves. *Am. Meteor. Soc*. **29**: 1279 - 1301.

Haakonsen, H. O. and Anoruo, A. O. (1994). Tagging and migration of the American lobster *Homarus americanus*. *Rev. Fish. Sci*. **2**: 79-93.

Hare, J. A. (2014). The future of fisheries oceanography lies in the pursuit of multiple hypotheses. *J. Mar. Sci.* **71:** 2343-2356.

Hebert, D., Pettipas, R., Brickman, D., and Dever, M. (2014). Meteorological, sea ice, and physical oceanographic conditions on the Scotian Shelf and in the Gulf of Maine during 2013. DFO. N6157.

Herrick, F.H. (1909). Natural history of the American lobster. Bull. *U.S. Bureau Fish.* **29**: 148-408.

Herrnkind, W. F. (1970). Migration of the spiny lobster. *Nat. Hist.* **79**: 36-43.

Herrnkind, W.F. (1983). Movement patterns and orientation. *In* The biology of Crustacea (F.J. Verngerg and W.B. Wernberg, eds), Vol **7**, p.41-105. Academic Press, New York.

Herrnkind, W. F. and Mclean, R. (1971). Field studies of homing, mass emigration and orientation in the spiny lobster, *Panulirus argus*. Ann. N.Y. Acad. Sci. **188**, 359-377.

Himmelman, J. (1975). Phytoplankton as a stimulus for spawning in three marine invertebrates. *J. Exp. Mar. Biol. Ecol.* **20**: 199-214.

Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P. - V. Réun*. **20**: 1-228.

Hjort, J. (1926). Fluctuations in the year classes of important food fishes. *J. Con. Int. Exploit. Mer.* **1:** 5-38.

Hughes, J. T. and Mathiessen, G. C. (1962). Observations on the biology of the American lobster, *Homarus americanus. Limnol. Oceangr*. **7**: 414-421.

Incze, L. S., Wahle, R. A., Wolff, N., Wilson, C., Steneck, R., Annis, E., Lawton, P., Xue, H., and Chen, Y. (2006). Early life history and a modeling framework for lobster (*Homarus americanus*) populations in the Gulf of Maine. *J. Crust. Biol*. **26**: 555-564.

Johnson, C., Devred, E., Casault, B., Head, E., and Spry, J. (2017). Optical, chemical, and biological oceanographic conditions on the Scotian Shelf and in the eastern Gulf of Maine in 2015. CSAS. DFO.

Jury, S. H. and Watson, W. H. (2000). Thermosensitivity of the lobster, *Homarus americanus*, as determined by cardiac assay. *Biol. Bull*. **199**: 257-264.

Jury, S. H. and Watson, W. H. (2013). Seasonal and sexual differences in the thermal preferences and movements of American lobsters. *Can. J. Fish. Aquat. Sci.* **70**: 1650-1657.

Jury, S. H., Howell, W. H., and Watson III, W. H. (1995). Lobster movements in response to a hurricane. *Mar. Ecol. Prog. Ser*. **119**: 305-310.

Kavanaugh, M. T. Rheuban, J. E., Luis, K. M. A., and Doney, S. C. (2017). Thirty-three years of ocean benthic warming along the U. S. northeast continental shelf and slope: patterns, drivers, and ecological consequences. *J. Geophys. Res*. **122**: 9399-9414.

Klimley, A. P., Le Boeuf, B. J., Cantara., K. M., Richert, J. E., Davis, S. F., Sommeran, S. V. (2001). Radio-acoustic position as a tool for studying site-specific behaviour of the white shark and other large marine species. *Mar. Biol*. **138**: 429-446.

Klugh, A. B. (1927). Light penetration into the Bay of Fundy and into Chamcook Lake, New Brunswick. *Ecol. Soc. Am*. **8**: 90-93.

Knight-Jones, E. W. and Morgan, E. (1966). Responses of marine animals to changes in

hydrostatic pressure. Ann. Rev. Ocean. *Mar. Biol*. **4**: 267-299.

Knight-Jones, E. W. and Qasim, S. Z. (1955). Responses of some marine plankton animals to changes in hydrostatic pressure. *Nature.* **175**: 941-942.

Krouse, J. S. (1981). Movement, growth, and mortality of American lobsters, *Homarus americanus,* tagged along the coast of Maine. U.S. Dept. Com. NOAA Tech. Rep. NMFSSRF. **747**: 12.

Lavalli, K. L. and Lawton, P. (1996). Historical review of lobster life history terminology and proposed modifications to current schemes. *Crustaceana*. **69**: 594-609.

Lawton, P. and Lavalli, K. L. (1995). Postlarval, juvenile, adolescent, and adult ecology. *In* Biology of the lobster Homarus americanus (J. R. Factor, ed.), p. 47–88. Acad. Press, San Diego, CA.

Li, B., Tanaka, K. R., Chen, Y., Brady, D. C., and Thomas, A. (2017). Assessing the quality of bottom water temperatures from the Finite-Volume Community Ocean Model (FVCOM) in the Northwest Atlantic Shelf region. *J. Mar. Syst*. **173**: 21-30.

Lohmann, K. J., Pentcheff, N. D., Nevitt, G. A., Stetten, G. D., Zimmer-Faust, R. K., Jarrard, H. E., and Boles, L. C. (1995). Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. *J. Exp. Biol.* **198**: 2041-2048.

Manning, J. (2012). Environmental monitors on lobster traps, phase VII: Validating ocean models. Final Report. NOAA/NEFSC. 07-051

Martin, J. (2017). *Bay of Fundy- Western Isles*. Retrieved March 24, 2017 from http://www.st.nmfs.noaa.gov/copepod/time-series/ca-50501/html/yearbox-qual2015.html.

Mcleese, D. W. and Wilder, D. G. (1958). The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. *J. Fish. Res.* **15**: 1345-1354.

McMahan, M.D., Brady, D.C., Cowan, D.F., Grabowski, J.H., Sherwood, G.D. (2013). Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*). *Can. J. Fish. Aquat. Sci*. **70**: 1625–1634.

Mills, K. E., Pershing, A., Brown, C., Chen, Y., Chiang, F.-S., Holland, D., Lehuta, S., Nye, J., Sun, J., Thomas, A., and Wahle, R. (2013). Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave. *Oceanography*. **26**: 191-195.

Morrisey, T. D. (1971). Movements of tagged American lobsters, *Homarus americanus*, liberated off Cape Cod, Massachusetts. *Trans. Am. Fish. Soc*. **100**: 117-120.

Morse, B. and Rochette, R. (2016). Movements and activity levels of juvenile American lobsters *Homarus americanus* in nature quantified using ultrasonic telemetry. *Mar. Eco. Prog. Ser*. **551**: 155-170.

Mountain, D.G. (2003). Variability in the properties of the shelf water in the Middle Atlantic Bight, 1977–1999. *J. Geophys. Res.* **108**: 3014.

Mountain, D. G. and Holzwarth T. J. (1989). Surface and bottom temperature distribution for the northeast continental shelf. U.S. Department of Commerce. NOAA/NEFSC

Munro, J. and Therriault, J.-C. (1983). Migrations saisonnieres du homard (*Homarus americanus)* entre la cote et les lagunes des Iles-de-la-Madeleine. *Can. J. Fish. Aquat. Sci*. **40**: 905-918.

Naylor, E. and Atkinson, J. A. (1972). Pressure and the rhythmic behavior of inshore animals. *Symp. Exp. Biol*. **26:** 295-415.

Nelson, K. N. (1986). Photoperiod and reproduction in lobsters (*Homarus*). *Amer. Zoo.* **26**: 447-457.

Neuheimer, A. B. and Taggart, C. T. (2007). The growing degree-day and fish size-at-age: the overlooked metric. *Can. J. Fish. Aquat. Sci*. **64**: 375-385.

Perkins, H. C. (1972). Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). *Fish. Bull*. **70**: 95-99.

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A., Record, N. R., Scannell, H. A., Scott, J. D., Sherwood, G. D., and

Thomas, A. C. (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science.* **350**: 809-812.

Petrie, B. and Jordan, F. (1993). Nearshore, shallow-water temperature atlas for Nova Scotia. Canadian Technical Report of Hydrography and Ocean Sciences. **145**.

Pezzack, D. S. and Duggan, D. R. (1986). Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian Shelf. *Can. J. Fish. Aquat. Sci*. **43**: 2206-2211.

Reid, D. G. and Naylor, E. (1990). Entrainment of bimodal circatidal rhythms in the shore crab *Carcinus maenas*. *J. Biol. Rhythms*. **5**: 333-347.

Reynolds, W. W. and Casterlin, M. E. (1979). Behavioral thermoregulation and activity in *Homarus americanus*. *Comp. Biochem. Physiol*. **64**: 25-28.

Richaud, B., Kwon, Y.-O., Joyce, T. M., Fratantoni, P. S., and Lentz, S. J. (2016). Surface and bottom temperature and salinity climatology along the continental shelf off the Canadian and U.S. East Coasts. *Cont. Shelf. Res.* **124**: 165-181.

Rose, R. A., Wilkens, J. L., and Walker, R. L. (1998). The effects of walking on heart rate, ventilation rate and acid-base status in the lobster, *Homarus americanus*. *J. Exp. Biol*. **201**: 2601-2608.

Stasko, A. B. (1980). Tagging and lobster movements. *Can. Tech. Rep. Fish. Aquat. Sci.* **932**:141 - 150.

Templeman, W. (1940). Lobster tagging on the west coast of Newfoundland 1938. *Nfld. Dept. Nat. Res. Fish. Res. Bull*. **8**: 16.

Thorstad, E. B., Rikardsen, A. H., Alp, A., and Okland, F. (2013). The use of electronic tags in fish research- an overview of fish telemetry methods. *Turk. J. Fish. Aquat. Sci.* **13:** 881-896.

Tlusty, M., Metzler, A., Malkin, E., Goldstein, J., and Koneval, M. (2008). Microecological impacts of global warming on crustaceans – temperature induced shifts in the release of larvae from American lobster, *Homarus americanus*, females. *J. Shellfish. Res*. **27**: 443-448.

Uzmann, J. R., Cooper, R. A., and Pecci, K. J. (1977). Migration and dispersion of

tagged American lobsters, *Homarus americanus,* on the southern New England Continental Shelf. U.S. Dept. Com. NOAA Tech. Rep. NMFSSSRF. **705**: 92.

Waddy, S. L. and Aiken, D. E. (1986). Multiple fertilization and consecutive spawning in large American lobsters, *Homarus americanus*. *Can. J. Fish. Aquat. Sci*. **43**: 2291-2294.

Waddy, S. L. and Aiken, D. E. (1990). Mating and insemination in the American lobster, *Homarus americanus*. *In* Crustacean Sexual Biology (R. T. Bauer and J. W. Martin, eds), pp. 126-144. Columbia Univ. Press, New York.

Walton, A. S. and Herrnkind, W. F. (1977). Hydrodynamic orientation of the spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): wave surge and unidirectional currents. Memorial University of Newfoundland Marine Sciences. *Res. Lab. Tech. Rep*. **20:** 184-211.

Watson III, W. H., Golet, W., Scopel, D., and Jury, S. (2009). Use of ultrasonic telemetry to determine the area of influence and trapping area of American lobster, *Homarus americanus*, traps. *New Zeal. J. Mar. Fresh.* **43**: 411-418.

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

Wilder, D.G. (1963). Movements, growth and survival of marked and tagged lobster liberated in Egmont Bay, Prince Edward Island. *J Fish, Res. Bd. Can*. **20**: 305-318.

Wilder, D. G. and Murray, R. C. (1958). Do lobster move offshore and onshore in the fall and spring? *Fish. Res. Bd. Can. Atlant. Prog. Rep*. **69**: 12-15.

Xue, H., Incze, L. S., Xu, D., Wolff, N., and Pettigrew, N. R. (2008). Connectivity of lobster populations in the coastal Gulf of Maine, Part I: circulation and larval transport potential. *Ecol. Mod*. **210**: 193-211

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