EXPLORING LARVAL SETTLEMENT OF THE EASTERN OYSTER (*CRASSOSTREA VIRGINICA*) IN ATLANTIC CANADA

By

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Dalhousie University is located in Mi’kma’ki, the ancestral and unceded territory of the Mi’kmaq. We are all Treaty people.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

An ongoing issue for the Nova Scotia oyster aquaculture industry is the lack of reliable seed sources, which primarily relies on collecting wild seed. This thesis focuses on understanding and predicting the timing of settlement of the eastern oyster *Crassostrea virginica* in response to environmental drivers, which aims to help farmers and managers optimize spat collection and plan for future climate scenarios. The Growing Degree Day (GDD) framework is used to leverage the dominant effect of temperature on larval development and predict the timing of settlement. The model is calibrated with existing literature data and validated with field data collected from June to September 2022 across four estuaries in Nova Scotia. The validated GDD model could be implemented as an operational tool for farmers as the only required input is temperature, which is often already being monitored. Expanding upon the GDD model, temperature predictions from a regional climate model are incorporated to simulate conditions from three distinct timeframes: Past (1991-1995, Present (2021-2025), and Future (2051-2055). Findings suggest that rising ocean temperatures may lead to habitat expansion and earlier settlement for *C. virginica* in Atlantic Canada. However, the asynchronous phenological shift between oyster larvae and their food resources, represented by Chlorophyll-a, indicates a potential trophic mismatch that could pose challenges for predicting settlement. Outcomes from this research reaffirm our understanding of major biological drivers such as temperature and highlight avenues for further investigation of causal relationships associated with other environmental parameters, particularly potential trophic mismatch between larval presence and food availability.

LIST OF ABBREVIATIONS AND SYMBOLS

GDD	Growing Degree Day(s)
LDT	Larval Development Time
MMP	Mussel Monitoring Program
OMP	Oyster Monitoring Program
PEI	Prince Edward Island
NB	New Brunswick
°C·day	Heat units or 'Degree Day'. Units used to quantify Growing Degree Days.
(T_h)	Minimum temperature threshold for larval growth
(T_t)	Function of daily mean temperature
(GDD_t)	Growing Degree Days as a function of t (time, days)
GDD_{LDT}	GDD required to complete Larval Development Time (LDT)
RMA	Reduced Major Axis
FA	Fatty Acid(s)
EPA	Eicosapentaenoic acid
DHA	Docosahexaenoic acid
µg	Micrograms
mg	Milligrams
mm	Millimeters
Chl-*a*	Chlorophyll-*a*
POM	Particulate Organic Matter
TPM	Total Particulate Matter

mmolC	Milli mol of Carbon
m	Meter
L	Liter
°C	Degrees Celsius
h	Hour
RCP	Representative Concentration Pathway
DEB	Dynamic Energy Budget
GSL	Gulf of Saint Lawrence

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CHAPTER 1: INTRODUCTION

The ectothermic species *Crassostrea virginica* (Eastern oyster) is a commercially valuable bivalve; however, to ensure a healthy aquaculture industry, there must be a consistent and reliable source of juvenile oysters, which is often referred to as seed or spat. Oyster seed or spat refers to the post-larvae stage of the life cycle when shell length typically ranges from 0.3-10+ mm. In Nova Scotia, hatchery production of spat is insufficient to meet industry needs, therefore, this gap is commonly filled with the collection of wild spat. While the collection of wild spat can be less reliable and consistent due to uncontrolled environmental factors, it provides a cost-effective approach to the issue of seed source. Successful collection of spat requires preparation and planning prior to the summer months when oysters in Nova Scotia are expected to spawn.

Oysters are broadcast spawners meaning that both males and females release sperm and eggs into the water column. Spawning can occur at any point when temperatures are near 20 ± 2 °C, but more typically when temperatures are greater than 20 °C and during a sudden increase in temperature (Galtsoff, 1938; Medcof, 1939). Fertilization occurs in the water column, and within 24 h embryos will develop into free-swimming larvae that begin to feed on phytoplankton and organic detritus. The larval stage is the most sensitive life stage and can last from 10 to 30 days, depending on several environmental conditions, with temperature and food resources at the forefront (Davis & Calabrese, 1964; Hoegh-Guldberg & Pearse, 1995; Rico-Villa et al., 2009). At the end of the larval stage, individuals will migrate through the water column towards the bottom and search for a suitable substrate to attach to for the remainder of the life cycle. When a suitable substrate is found, the individual will metamorphose and excrete a glue-like substance to attach themselves, at which point the individual would be referred to as spat, and the settlement process is complete (Connell, 1985).

To collect spat for aquaculture purposes, a wide variety of spat collectors are utilized around the world. Regardless of the style of spat collector, an important consideration is the timing of deployment. Collectors must be deployed in advance of the expected onset of settlement to allow for the development of a biofilm consisting of bacteria and microbes that promote the settlement process (Toupoint et al., 2012b). Without the biofilm, larvae are less likely to settle on the collector. Conversely, if collectors are placed in the water column too early adverse biofouling can occur and larvae will prefer to settle elsewhere (Mallet et al., 2009). If collectors are deployed too late, the peak settlement window could be missed, resulting in little or no spat on collectors. Accordingly, for successful spat collection in the wild, the timing of collector deployment is critically important.

There are several established monitoring programs throughout Atlantic Canada (Oyster Monitoring Program (Prince Edward Island, PEI), Mussel Monitoring Program (PEI), Spat Collection Program (New Brunswick, NB)) with mandates to regularly monitor the presence of larvae in the water column and inform farmers on when larvae are likely to settle. Such monitoring programs are valuable as they provide insights to farmers on when to deploy collectors to optimize spat collection. However, these programs are costly and require expert personnel to collect and analyze samples.

Mathematical models have been used in addition to monitoring programs to predict the timing of life history events such as spawning and settlement (Dekshenieks et al., 1993). Predictive models for life history events vary in complexity but generally include the effects of several variables, including temperature, food resources, salinity, and turbidity (Dekshenieks et al., 1993; Gourault et al., 2019; Thomas et al., 2011, 2016). Models with increased complexity are valuable for developing a further understanding of life history events but less ideal for operational monitoring and predictions needed in aquaculture operations over a large spatial domain. An operational tool often used in agriculture and finfish farming for predicting growth and development of ectotherms is the thermal metric of Growing Degree Days (GDD), which considers only one variable, temperature. For ectotherms, growth is directly related to surrounding temperatures, thus GDD can be used to monitor growth and development across multiple life stages based on temperature only (Filgueira et al., 2015; Neuheimer & Taggart, 2007; Virgin et al., 2019). GDD is an integral of cumulative heat above a base temperature threshold, which is species- and process-specific. Accordingly, GDD models could offer predictions to farmers about the life history of oysters based on local water temperature, which is affordable to collect and often already monitored.

Temperatures in the future are expected to increase as a consequence of climate change. For *C. virginica* at the northern limits of their geographic habitat, rising temperatures are expected to result in increased growth rates and shorter development times. Additionally, rises in temperature are likely to result in phenological shifts in life history events such as spawning and settlement, which are integral to population dynamics of coastal bivalves (Pineda et al., 2010). Therefore, while GDD can inform farmers in the short-term about the deployment of collectors, the use of oceanographic models that predict temperature under different climate scenarios can be used in the long-term alongside GDD to predict potential changes in species distribution, which can be used by managers to plan the future of oyster aquaculture in Nova Scotia.

The goal of this thesis is to investigate the timing of oyster settlement in the short- and long-term. Modelling larvae development as a function of temperature provides the basis for both short- and long-term predictions of phenological events, which are the next steps towards improving spat collection efforts now and aquaculture planning in the future.

Chapter 2 of this thesis undertakes a literature review to collect existing data on how temperature influences *C. virginica* larval development. Subsequently, the existing literature data is used to develop a Growing Degree Day (GDD) model for *C. virginica* larvae that predicts the timing of settlement based on temperature. The GDD model was validated with data collected during a field sampling campaign carried out over four months, from June to September 2022, along the North Shore of Nova Scotia. The results from this chapter suggest that temperature had the greatest influence on larval development time and could be used to predict the timing of settlement without considering the other studied environmental parameters (food resources, salinity, or dissolved oxygen). By developing a method to predict life stage events of spawning and settlement, the model in this chapter serves as a tool for farmers and managers, providing critical information to the harvesting process of wild spat.

Chapter 3 explores phenology of the larval stage under three different timeframes, Past (1991 to 1995), Present (2021 to 2025), and Future (2051 to 2055) by coupling the GDD model developed in **Chapter 2** with temperature predictions from a regional oceanographic model. The coupled model suggests that warming temperatures experienced over time result in geographic habitat expansion and earlier settlement in existing habitats. Additionally, predictions of Chlorophyll-a from a regional biogeochemical model are included as a proxy for phytoplankton to investigate potential match/mismatch relationships between larvae development and food resources. Insights from these predictions suggest that match/mismatch trophic relationships have occurred when comparing past (1991 to 1995) and present (2021 to 2025) scenarios but are not expected to follow these patterns in the future (2051 to 2055). The outcomes from each chapter build on the current understanding of *C. virginica* larval ecology at the northern geographic range of the species distribution and provide insights into sustainable planning of the Atlantic Canada aquaculture industry.

CHAPTER 2: PREDICTING EASTER OYSTER (*CRASSOSTREA VIRGINICA*) SETTLEMENT USING GROWING DEGREE DAYS

2.1 ABSTACT

The supply of oyster spat is crucial for the sustainability and development of the oyster aquaculture industry. While hatcheries worldwide are increasing spat production, wild spat collection remains prevalent in Atlantic Canada. Existing monitoring programs aid in wild spat collection but are costly and labour-intensive, relying on fieldwork and expert personnel. To complement monitoring programs, mathematical models with varying complexity have been used to predict the settlement of commercially valuable bivalves. These models consider various environmental parameters such as temperature, winds, tides, and food concentrations. In this study, we explore the prediction of settlement in Eastern oysters (*Crassostrea virginica*) using a simple Growing Degree Day (GDD) model, which considers only one parameter, temperature. The GDD model estimates Larval Development Time (LDT) based on accumulated heat units (°C·day) above a species-specific minimum temperature threshold for growth. By calibrating the model with literature data and validating it with field observations from four estuaries in Nova Scotia, we aimed to provide a tool for farmers to predict the onset of oyster settlement based on observed seawater temperature. The model effectively predicted the onset of oyster settlement based on observed seawater temperature. The GDD model is a simple and easily implementable tool that can enhance the success of wild spat collection efforts and contribute to the robustness of the oyster aquaculture industry.

2.2 INTRODUCTION

A consistent supply of oyster seed, hereafter referred to as spat, is essential for cultivating oysters. Spat production from hatcheries is increasing worldwide, but the collection of wild spat is still a common approach in Atlantic Canada (Doiron, 2008, 2018). Proper spat collection requires placing collectors in the water as larvae are ready to settle. Additionally, collectors must be conditioned by pre-soaking in seawater before deployment, allowing for a biofilm that is required for settlement to occur (Toupoint, et al., 2012b). Monitoring programs based on the identification of larvae and the early detection of spat are in place to inform farmers on when to deploy collectors (e.g. Mussel Monitoring Program (MMP)[1] and Oyster Monitoring Program (OMP)[2] in PEI, spat monitoring program in NB[3], and the Mussel monitoring program in New Zealand[4]). However, these programs are costly as they require routine fieldwork and expert personnel to identify and count larvae and spat. Complementary to monitoring programs, mathematical models have been used to predict the settlement of commercially valuable bivalves. The prediction of settlement, defined as the point when an individual larvae

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[1].https://www.princeedwardisland.ca/en/feature/view-mussel-monitoring-results

[2].https://www.princeedwardisland.ca/en/feature/view-oyster-monitoring-results

[3].https://www2.gnb.ca/content/gnb/en/departments/10/aquaculture/content/oyster_spat_collection_updates.html

[4].https://cawthron.shinyapps.io/BMOP/

takes permanent residence on a substrate (Connell, 1985), relies on understanding two fundamental processes, spawning and larval development.

As ectotherms, the life cycle of oysters is fundamentally linked to seawater temperature (Davis & Calabrese, 1964; Dekshenieks et al., 1993; Hoegh-Guldberg & Pearse, 1995; O'Connor et al., 2007); although other environmental conditions such as trophic resources (Brown et al., 2016; Dekshenieks et al., 1993; Toupoint, et al., 2012a), salinity (Davis & Calabrese, 1964; Dekshenieks et al., 1993; Gregory et al., 2023), turbidity (Dekshenieks et al., 1993), biofilms (Toupoint, et al., 2012b), chemical cues released by mature adults (Tamburri et al., 2007), and underwater noise (Jolivet et al., 2016), among others, have also been suggested as drivers influencing the phenology of spawning, larval development, and settlement. Models that predict settlement can take different approaches, from regression models relating historical settlement data and environmental parameters such as temperature (e.g. Filgueira *et al.*, 2015) or dynamic climate conditions like winds, tides, and climate oscillation indices (e.g. Atalah and Forrest, 2019), to biological models based on laboratory data that studied the effects of temperature, salinity, food concentrations, and turbidity on larval development (e.g. Dekshenieks *et al.*, 1993), and coupled biological-hydrodynamic models predicting in space and time (e.g. Dekshenieks *et al.*, 2000).

Despite the potential influence of multiple variables in the life history of oysters, spawning of the Eastern oyster has been observed to occur when water temperatures are greater than 20°C and usually during a sudden increase in temperature (Galtsoff, 1938), although this temperature threshold could vary across latitudes and locations (Barber *et* *al*., 1991). Larval development of C. virginica has been studied in several locations in North America (Dekshenieks *et al.*, 2000); although local environmental conditions can play a role on larval development, temperature has been proposed as one of the main drivers of larval development time (Filgueira et al., 2015, 2016; Gillooly et al., 2002; O'Connor et al., 2007).

Due to the strong effect of temperature on larval development, Larval Development Time (LDT) of marine invertebrates, the period from fertilization until settlement, has been predicted using different metrics related to thermal history. For example, LDT for many marine invertebrates, including *C. virginica*, has been predicted using an exponential quadratic model with temperature as the explanatory variable (O'Connor et al., 2007). LDT for *C. virginica* has also been modeled, considering primarily the effects of temperature, with food concentration, salinity, and turbidity refining the predictions (Davis & Calabrese, 1964; Medcof, 1939). A thermal integral measure, Growing Degree Day(s) (GDD), has been used to predict the life stages of the Blue mussel (*Mytilus edulis),* specifically the timing of settlement (Filgueira et al., 2015). Generally, GDD models assume that the growth of an organism occurs above a temperature threshold, and below this threshold no growth occurs (Neuheimer & Taggart, 2007). Above the thermal threshold, GDD models assume that growth is directly proportional to temperature. Therefore, tracking exposure to temperature over this threshold using GDD models could predict growth and the phenology of life-history events of ectotherms.

To improve the robustness of the oyster aquaculture industry, a reliable and accurate method should be developed to assist the collection of wild spat. Providing farmers with a tool to predict settlement in their region based on local environmental conditions would increase the likelihood of successful spat collection. This study constructs a GDD model to predict the onset of *C. virginica* settlement. The model is calibrated with literature data and tested with settlement and temperature observations from four estuaries along the North Shore of Nova Scotia (NS, Canada) from June to September 2022. Implementing a GDD model could be an ideal tool for farmers and managers due to the limited effort required to make predictions which are easily interpretable.

2.3 METHODS

2.3.1 Model Calibration and Validation

Heat units are expressed as Growing Degree Day(s) (GDD, °C·day), which represents the total heat over a certain threshold that is accumulated during a period of time. GDD over a certain period, between day 1 and day t, can be calculated by taking the integral of temperature above a threshold:

$$GDD_t = \int_1^t (T_t - T_h)\, dt \quad if \quad T_t < T_h; GDD_t = 0 \qquad \text{Eq. 1}$$

Where T_t is temperature over time, and T_h is the base threshold temperature below which temperature causes a minimal effect on the biological process of interest. In this case, the threshold below which larval growth is negligible. If daily temperature is less than the base threshold temperature, $T_t < T_h$, it is assumed no growth occurs, thus $GDD_t = 0$. A literature review was performed to collect information on Larval Development Time (LDT) at different temperatures that could be used to calibrate the GDD model to predict LDT as a function of temperature (Appendix A1). Only laboratory experiments that tested optimal conditions for hatchery production or studied the thermal biology of oyster larvae were included. The datasets encompassed information on oysters from different geographic locations, including Chesapeake Bay (USA), Connecticut (USA), New Brunswick (NB, Canada), and Prince Edward Island (PEI, Canada), which covers the Northern distribution range of *C. virginica*. The reported LDT ranged from 10 days at 30°C to 36 days at 20°C for oysters from Connecticut (Davis & Calabrese, 1964). Data within Atlantic Canada ranged from 14 days at 25°C in Richibucto, New Brunswick (Newkirk et al., 1977) to 30 days at 19°C in Bideford River, Prince Edward Island (Medcof, 1939). For comparison to other GDD models, it is important to specify which calibration method is used to estimate the temperature threshold for growth (T_h) and mean GDD required to complete LDT (GDD_{LDT}) since values of these estimated parameters vary considerably with each methodology. Using literature data on LDT at different temperatures, the GDD to complete LDT was calculated for each data point. The temperature threshold for larval growth (T_h) and GDD_{LDT} was estimated by optimizing a loss function that minimized the coefficient of variation for standard deviation in GDD to complete development which was obtained from each literature data point. This approach follows Ruml et al., (2010), who identified this method as the most robust for calibrating GDD models. With the calibrated threshold, the model estimates LDT in GDD units (GDD_{LDT}), or the 'heat units' (°C·day) a larva requires to become competent to settle. Statistical bootstrapping was implemented to calculate 95% confidence intervals for T_h and GDD_{LDT}. Reduced Major Axis (RMA) regression was performed on the modeled and observed LDT to verify the existence of a one-to-one relationship exists, indicating that the model perfectly fits observations.

After the calibration of T_h and GDD_{LDT}, a temperature threshold at which oysters are likely to spawn must be assumed. The reported temperature threshold that triggers spawning in *C. virginica* ranges from 15 to 28 °C (Barber et al., 1991). Since water temperatures in the study area of Nova Scotia are similar to Prince Edward Island (PEI) in that they both fall at the cooler end of the geographic range that *C. virginica* inhabits, data from PEI were used to define the spawning threshold. It has been reported that wild *C. virginica* spawns between 20.4 and 22.7 °C in PEI (Kennedy and Battle, 1964); accordingly, the approximate center of this range, 21.5 °C, was assumed to be the spawning threshold. The GDD model was validated by comparing modeled LDT with field observations of settlement.

2.3.2 Field Observations

Field observations were collected in four estuaries (sampling locations) along the North Shore of Nova Scotia (Figure 2.1) where oysters are present. Custom-built spat collectors (Appendix B) were constructed with the design based on 'spat monitors' from the New Brunswick spat collection program (Doiron, 2018). Within each sampling location, 3 collectors were placed approximately 10 m apart. Settlement was quantified by placing a scallop shell, where larvae will attach, at two depths of each collector, approximately 0.1 and 0.4 m below mean low water, hereafter referred to as shallow and deep depths, respectively. Before deployment, scallop shells were pre-conditioned in the Aquatron Laboratory at Dalhousie University by submersing them in natural seawater for one week. Two scallop shells, one per depth, were deployed weekly at each collector of all sampling locations. On each collector, settlement of *C. virginica* was monitored over two-week periods by counting the spat attached to the scallop shells; consequently, there was an overlap of one week for consecutive weekly deployments (i.e., shells deployed in Week 1 were collected in Week 3 and shells deployed in Week 2 were collected in Week 4). It was assumed that the pre-conditioning period, together with the first week of field deployment, allowed for a biofilm to develop on the shell, ensuring that the substrate was suitable for settlement during the last week of the deployment (Toupoint, et al., 2012b). During retrieval, the scallop shells were removed from the collector and preserved in 99% denatured alcohol.

Newly settled spat were counted and measured in the laboratory with a microscope equipped with an ocular micrometer following Poirier *et al.* (2019) techniques. The scallop shell area was quantified with a photograph of the shell and ImageJ software (imageJ.org). The post-larval density on each shell was determined as the total abundance of post-larvae on the shell divided by the area of the shell. Settlement at each sampling location was calculated by averaging post-larvae density across both depths and collectors (n=6 shells per sampling location). Weekly deployment of scallop shells commenced on June 7th, 2022, and continued until September 7th, 2022. Accordingly, scallop shells were retrieved weekly from June 21st, 2022, until September 21st, 2022.

Environmental variables, including temperature, salinity, dissolved oxygen, food resources, and tides were monitored to explore the potential confounding effects of these drivers on settlement. *In situ* measurements of environmental parameters began on June 7th, 2022. Temperature was recorded in 15-minute intervals at both depths using Onset HOBO U22 temperature sensors (deep) and AquaMeasure Temperature sensors (shallow) attached to each collector. Within each estuary, AquaMeasure Salinity and Dissolved Oxygen sensors (Innovasea Ltd) were placed on separate collectors at the shallow depth and recorded data every 15-minutes. A pressure sensor was fixed to a different collector (deep depth) within each estuary and used to quantify fluctuations in the tidal cycle. To characterize food resources, water samples were collected weekly from surface water at each collector location (3 samples per week per estuary). Water samples were stored in water bags (~6 L) within a cooler to avoid continued exposure to sunlight, halting photosynthesis and preserving the sample until analysis in the laboratory (3 to 6 hours post collection). At the laboratory, samples were subsampled, and gravimetric analysis was used to determine the total and organic fraction of the seston (Hawkins et al., 1999), fatty acids (Sakamaki T et al., 2020), and chlorophyll-a (Parsons, 2013). Sensor data, including temperature, salinity, and dissolved oxygen, were resolved from 15-minute intervals to daily mean values for each location. Data from water samples, including chlorophyll-a (Chl-a), Total Particulate Matter (TPM), Particulate Organic Matter (POM), and omega-3 fatty acids (FA; Eicosapentaenoic acid (EPA) and Docosahexaenoic acid (DHA)) were collected weekly at each collector. Values from each collector were averaged to a single mean value for each location. Outliers were removed before calculating the daily means.

2.4 RESULTS

2.4.1 Calibration of the Growing Degree Day (GDD) Model

Calibration of the GDD model with literature data on Larval Development Time (LDT) for *C. virginica* resulted in a threshold temperature for larval growth (T_h) of 13.5°C (95% CI: 11.66, 14.93) and a GDD_{LDT} of 193.1 °C·day (95% CI: 164.26, 230.14) to complete LDT (Figure 2.2A). The Reduced Major Axis (RMA) regression analysis between predictions and literature data (n=16, Figure 2.2B) yielded a slope of 0.91 (SE = 0.11) and an intercept of 1.87 (SE = 2.47), which are statistically similar to 1 and 0 ($p<0.05$), respectively. The results of RMA regression analysis indicate that the GDD model can accurately predict LDTs observed in the literature.

2.4.2 Field Observations and GDD model validation

Spat settlement showed a similar pattern across locations, where initially no settlement was observed. Eventually, the onset occurred, and settlement continued for a number of weeks until activity ceased (Figure 2.3). However, the timing of the onset of settlement and the duration of the settlement window varied across locations. Settlement started in Malagash on July 19th, two weeks later in Little Harbour on August 2nd, and finally in Antigonish and Tracadie a week later on August 10th. Settlement was highest in Malagash, with two similar peaks of 7.9 and 7.8 ind. cm^{-2} on July 26th and August 9th, respectively (Figure 2.3A). In Little Harbour, settlement peaked at 0.65 ind. cm^{-2} on

August 9th (Figure 2.3B); in Antigonish, settlement reached a maximum value of 0.5 ind. cm^{-2} on August 10th (Figure 2.3C); and finally, settlement in Tracadie peaked at 1.1 ind. cm^{-2} two weeks later than the other locations on August 24th (Figure 2.3D).

The predicted onset of settlement closely followed the pattern observed in seawater temperature (Figure 2.4). The assumed spawning temperature of 21.5 °C was first reached in Malagash on June 26th, followed by Little Harbour two weeks later on July 10th, then Tracadie on July 19th, and finally in Antigonish on July 20th. These dates represent the starting point of the Predicted LDT Window, depicted as the first dashed line within the time series for each location (Figures 2.3, 2.4, 2.5 and 2.6). The duration or length of the LDT window was determined by the GDD model using the observed temperature in each location after spawning was triggered. The duration of the predicted LDT window was 24 days in Malagash, 20 days in Little Harbour and Antigonish, and 19 days in Tracadie. The LDT durations reflected the temperature differences in each location. The last day of the LDT window determined by the GDD model was used as the prediction for the onset of settlement.

The predicted onset of settlement had a resolution of one day using the GDD model due to averaging temperature data into daily values; this contrasted with the weekly resolution of the observed settlement window, which was a consequence of fieldwork limitations. The GDD Model predicted the onset of settlement in Malagash on July 20th, one day after the observed settlement window, from July 12th to 19th (Table 2.1; Figure 2.3A). In Little Harbour, the predicted onset of settlement was July 30th, within the observed settlement window (July 26th – August 2nd, Table 2.1; Figure 2.3B). Similarly, in Antigonish, the

GDD model predicted the onset of settlement on August 9th, within the observed settlement window between August 3rd and 10th (Table 2.1; Figure 2.3C). Lastly, the predicted onset of settlement in Tracadie was August 7th, which also fell within the observed settlement window of August 3rd to 10th (Table 2.1; Figure 2.3D). Accordingly, the predicted onset of settlement closely corresponded with the observed settlement window for all locations.

2.4.3 Water characteristics and larval settlement

Indices of seston quality, Chl-a/POM, EPA/POM, and DHA/POM (Table 2.2) exhibited a similar pattern across all locations, which coincided with the timing of observed settlement (Figure 2.5, 2.6). The maximum value observed for each index occurred near the middle of the predicted LDT window, except for DHA/POM in Malagash, which did not show an obvious peak. Additionally, Chl-a/POM and EPA/POM in Little Harbour experienced two peaks within the LDT window, while there was only a single peak in Antigonish and Tracadie. Correlation analysis revealed strong positive correlations between Chl-a/POM (Figure 2.5) and EPA/POM (Figure 2.6) in all locations (Malagash: 0.96, Little Harbour: 0.88, Antigonish: 0.88, Tracadie: 0.99). Similarly, Chl-a/POM showed high correlation values with DHA/POM (Figure 2.6), except for Malagash (Malagash: 0.06, Little Harbour: 0.70, Antigonish: 0.89, Tracadie: 0.99). The correlation values for EPA/POM vs. DHA/POM were also high in all locations except for Malagash (Malagash: 0.10, Little Harbour: 0.84, Antigonish: 0.97, Tracadie: 0.99). In Malagash, poor correlation values resulted between DHA/POM and other seston indices because of the apparent lack of a peak in DHA on July 11th, compared to the other locations.

Other water quality parameters, such as salinity and dissolved oxygen, failed to correlate with the observed onset or peak of settlement (Appendix C1, C2). Similarly, no trends emerged between the settlement pattern and TPM or POM (Appendix C3, C4). Within the predicted LDT window, a positive correlation between TPM and POM was observed in all locations (Malagash: 0.99, Little Harbour: 0.98, Antigonish: 0.88, Tracadie: 0.98), revealing some slight fluctuation in the POM/TPM index outside of the LDT window but relatively stable within the LDT window (Appendix C5). Fluctuations of Chl-a were observed in each location except for Tracadie, where values were consistent throughout the sampling period. High values of Chl-a (> 5 µg L^{-1}) coincided with the predicted LDT window in Malagash, Little Harbour, and Antigonish; while maximum Chl-a values in Tracadie were consistently lower than the other locations and relatively constant over time, ~2 µg L^{-1}, with no evident peak throughout the sampling period (Appendix C6). As mentioned above, the EPA and DHA values followed the same pattern in all locations, except in Malagash, where there was a peak of EPA but no apparent peak of DHA on July 11th (Appendix C7). Exploring alternate seston quality indices, Chl-a/TPM (Appendix C8) and FA/TPM (Appendix C9) showed the same pattern as Chl-a/POM and FA/POM, respectively, due to the strong correlation between POM and TPM.

2.5 DISCUSSION

The life cycle of ectothermic organisms like *C. virginica* is directly influenced by environmental temperature. Given this dependence, a Growing Degree Days (GDD) model could be used in aquaculture operations to predict phenological events crucial for spat collection. Utilizing existing literature data on Larval Development Time (LDT) for *C. virginica* at different temperatures, a GDD model was constructed to predict the onset of larval settlement. Field observations of water quality parameters and oyster settlement were used to validate the model while exploring other contributing factors that could influence settlement patterns.

2.5.1 GDD Model Development

The application of Growing Degree Day(s) in the context of individual growth assumes that growth is directly proportional to temperature (Bonhomme, 2000). Although growth of ectothermic larvae has a nonlinear response at extreme temperatures (Kingsolver & Woods, 2016) and can be affected by available food resources, the assumption of linear growth holds at temperatures from 15°C to 30°C for *C. virginica* when food resources are not a limiting factor (Davis & Calabrese, 1964). However, recent studies show that elevated temperatures of 30°C resulted in slower growth than larvae reared at 25°C (McFarland K et al., 2022). Considering the temperature range experienced by larvae in this study, 18.7°C to 27.6°C during the LDT window for all study locations, it can be assumed that larval growth was within the linear portion of the thermal growth curve, enabling the use of the GDD model. The GDD model relied on available LDT datasets in which temperature was constant over time, and all other variables that could affect larval development were controlled and maintained at optimal, e.g. fed *at libitum*. Although literature data was selected from the northern range of *C. virginica*, there is no apparent latitudinal pattern within LDT literature observations, suggesting the model could be broadly applied within the regions where the literature data was collected. Despite this, local adaptations affecting *C. virginica* phenology have been identified (Barber et al., 1991; Pernet et al., 2007, 2008), which indicates the general model built in this research could be refined for a specific location by collecting and integrating local data.

In addition to data availability, the mathematical method used to calibrate the minimum temperature threshold for growth, T_h, can influence model predictions. T_h was estimated by finding the least coefficient of variation in GDD, or the CV_{GDD} method, which is a robust method for calculating T_h (Ruml, Vuković and Milatović, 2010). The CV_{GDD} method provides ease and flexibility in its implementation; however, a disadvantage is that confidence intervals (CI) must be determined separately. Statistical bootstrapping was used to estimate the CI of T_h, and through error propagation, the CI of GDD_{LDT} was determined. Providing the GDD model with CI is relevant, especially if farmers implement the model to aid in spat collection but also to assess the performance of the model.

The comparison of model predictions with literature observations by RMA regression produced a slope and intercept that suggests that the GDD model properly fits the observed data. The intercept 1.87 (SE = 2.47) implies the model maximum overestimation of LDT is ~2 ± 2.5 days. If the assumed spawning temperature is correct (see below), this overestimation could result in actual settlement occurring earlier than the model predicts. Such considerations are necessary for implementing the model as a tool to advise the timing of oyster spat collection. Growers should be advised to deploy collectors before the predicted settlement date to ensure the settlement window is not missed. The validation of the model using *in situ* temperature data from each study location as input for the GDD model indicated a general agreement between model predictions and observed settlement, validating the model.

The GDD model assumed 21.5°C as the temperature that triggers spawning (based on local data from Kennedy and Battle, 1964), which is a source of uncertainty as the model does not account for spawning at cooler temperatures, nor that a sudden rise in temperature is equally important for triggering spawning (Medcof, 1939). Marine heat waves, defined as discrete and prolonged warm water events (Smale et al., 2019), could trigger the initiation of spawning, and consequently, it is important to consider these events as potential drivers of phenological changes, especially in a changing climate. Finally, other variables besides temperature are known to affect bivalve phenology but were not included in the model because temperature is the most fundamental driver of bivalve spawning (V. S. Kennedy et al., 1996), and the ultimate goal was to develop a simple and pragmatic model that could be easily deployed in the field.

2.5.2 LDT and other Water Characteristics

Temperature plays a critical role in the phenology of marine invertebrates (O'Connor et al., 2007). In the particular case of the Eastern oyster life cycle, spawning occurs typically when temperatures are above 20°C or during a sudden increase in temperature

(Galtsoff, 1938; Medcof, 1939). The importance of when the spawning temperature is reached should not be disregarded, as this determines the beginning of the LDT prediction window. In Malagash, spawning and the onset of settlement occurred 2 weeks earlier than Little Harbour and 3 weeks earlier than in Antigonish and Tracadie. Although reaching the spawning threshold may indicate which location is likely to first observe settlement activity, it is not enough to determine the more precise timing of settlement as temperature, salinity, and food resources also play a role in development and, consequently, the timing of settlement (Gregory et al., 2023; Rico-Villa et al., 2009). For example, laboratory studies have shown sudden changes in salinity can be an effective trigger for spawning in mature oysters (Magaña-Carrasco et al., 2018), and phenological changes at extreme salinities have been recently documented for *C. virginica* in estuaries with a strong salinity gradient (Gregory et al., 2023). Salinity was not included in our analyses due to the lack of observed salinity gradient in study locations.

Food resources also affect the growth of bivalve larvae and thus the length of LDT and settlement phenology. In general, oyster larval growth is directly related to food availability up to a maximum food density at which larval ingestion and growth rate plateau (Rico-Villa et al., 2009). Additionally, bivalve larvae can withstand periods of starvation (McFarland et al., 2020) by halting growth and utilizing their lipid reserves (Kheder et al., 2010). Furthermore, if the starvation period falls within the first few or last few days of the larval cycle, LDT is not expected to change since young larvae do not appreciably feed due to an underdeveloped esophagus and competent larvae preparing to metamorphose reduce feeding rate until settlement is completed, as shown for *C. gigas*

(Kheder et al., 2010; Rico-Villa et al., 2009) and *M. mercenaria* (Gallager, 1988). In addition to quantity, seston quality must meet the species-specific nutritional requirements or risk a slower growth rate resulting in a prolonged LDT. It has been suggested that seston must include high EPA and DHA content as these fatty acids are essential to bivalve larval development (Pernet & Tremblay, 2004; Rico-Villa et al., 2006). Results from the current research show the onset of settlement followed conditions where seston indices describing the quality of food resources (chlorophyll-a/POM, EPA/POM) reached maximum values. In fact, it has been suggested that a phytoplankton bloom rich in EPA acted as a trigger for bivalve larvae to settle (Androuin et al., 2022; Leal et al., 2018; Toupoint, et al., 2012a). The 'trophic settlement trigger' (TST) hypothesis has been explored for different species of bivalves and it is understood that trophic cues that trigger settlement are likely species-specific (Androuin et al., 2022; Leal et al., 2018). Species-specific trophic cues for *C. virginica* are not well documented in the literature. Our results show DHA and EPA have a strong correlation in Little Harbour, Antigonish, and Tracadie, but contrasting results show a weak correlation between EPA and DHA in Malagash, suggesting that DHA is unlikely to act as a TST or other additional factors are at play. Although the existence of a TST related to EPA is possible in our results, causal relationships cannot be verified since this work does not include information on larvae in the water column nor monitor enough environmental parameters to rule out other possible factors.

In addition to local variables modulating the timing of phenological events (e.g. settlement), hydrodynamic processes could be a significant driver for larval dispersal and population connectivity (Pineda et al., 2010). This study did not account for larval dispersal, although it could be assumed that advected larvae would come from nearby sources exposed to similar thermal regimes. While this study focused on larval development time (LDT), investigations of recruitment would depend on mortality and should include effects of advection from ocean currents, which determine coastal connectivity and influence the larval thermal history. Finally, although other variables could impact the timing of settlement, this study demonstrates the strong effect of temperature, suggesting that it could be used to predict oyster life history events such as spawning, larval development and settlement at the Northern end of their distribution range.

2.6 CONCLUSIONS

The life cycle of ectothermic organisms is highly influenced by temperature. Although temperature is fundamental to *C. virginica* phenology, influencing significant life history events like spawning and settlement, other environmental factors such as marine heat waves, sudden shifts in salinity, and food resources, notably fatty acids like EPA and DHA, can be significant. Despite the influence of multiple drivers, the developed GDD model, calibrated using data across the Northern distribution of *C. virginica*, has proven effective in predicting larval settlement based on temperature. The lack of correlation between EPA and DHA, as seen in the Malagash location, emphasizes the intricate interactions of factors and suggests potential trophic triggers for settlement. Beyond these local environmental variables, the role of local adaptation and hydrodynamic processes affecting larval dispersal could impact oyster settlement. Nevertheless, the present study emphasizes the primary role of temperature in predicting the life history events of *C. virginica*, highlighting the potential for using the GDD model as a pragmatic tool to aid oyster farmers in optimizing spat collection.

2.7 TABLES

Table 2.1: Predicted spawn date, duration of predicted LDT, predicted settlement date, and observed settlement window in each sampling location.

	Predicted LDT window			
Location	Predicted spawn date	Duration (days)	Predicted Settlement date	Observation window
Malagash	Jun 26	24	Jul 20	Jul 12 - 19
Little Harbour	Jul 10	20	Jul 30	Jul 26 - Aug 2
Antigonish	Jul 20	20	Aug 9	Aug 3 - 10
Tracadie	Jul 19	19	Aug 7	Aug 3 - 10

Table 2.2: Average, standard deviation, and range of environmental variables over the full study period. Temperature (n=107), Salinity (n=107), Dissolved Oxygen (DO) (n=107), chlorophyll-a (Chl-a) (n=14), Total Particulate Matter (TPM) (n=14), Particulate Organic Matter (POM) (n=14), fatty acid EPA (n=14), and fatty acid DHA (n=14) across the four field sampling location during the study period.

		Malagash		Little Harbour		Antigonish		Tracadie	
Parameter	Units	avg±sd	range	avg±sd	range	avg±sd	range	avg±sd	range
Temp	°C	21.6±2.6	15.0-26.9	21.1±2.8	14.2-27.6	20.3±2.9	12.6-26.5	20.6±2.7	14.2-26.8
Salinity	PSU	19.8±8.0	6.8-28.9	28.7±1.3	23.7-29.9	26.5±3.0	18.9-29.9	26.3±4.7	5.6-29.9
DO	% Sat.	114.1±7.4	93.9-136.6	106.1±7.6	84.5-130.8	127.0±12.0	103.1-148.9	106.9±7.2	82.0-121.4
Chl-a	$\mu g\ L^{-1}$	3.0±1.6	1.4-6.4	3.5±2.3	1.1-9.6	4.7±2.7	1.2-11.4	1.6±0.5	0.8-2.3
TPM	$mg\ L^{-1}$	10.5±12.4	3.3-46.6	8.8±4.9	3.0-18.0	21.6±24.0	3.4-81.9	17.1±30.1	2.2-106.4
POM	$mg\ L^{-1}$	4.8±3.0	0.7-10.6	5.9±4.0	1.6-12.5	9.2±7.9	2.1-29.3	7.0±7.4	1.3-26.3
FA-EPA	$\mu g\ L^{-1}$	1.9±1.3	0.9-4.6	2.7±2.6	0.4-8.9	3.5±2.2	1.3-8.1	0.7±0.4	0.4-1.7
FA-DHA	$\mu g\ L^{-1}$	1.2±0.4	0.4-1.8	1.5±1.0	0.4-4.0	3.1±1.6	0.9-5.1	0.8±0.6	0.2-2.0

2.8 FIGURES

Figure 2.1: Field sampling locations along the North Shore of Nova Scotia, Canada. Locations in the top pane from left to right are Malagash, Little Harbour, Antigonish, and Tracadie.

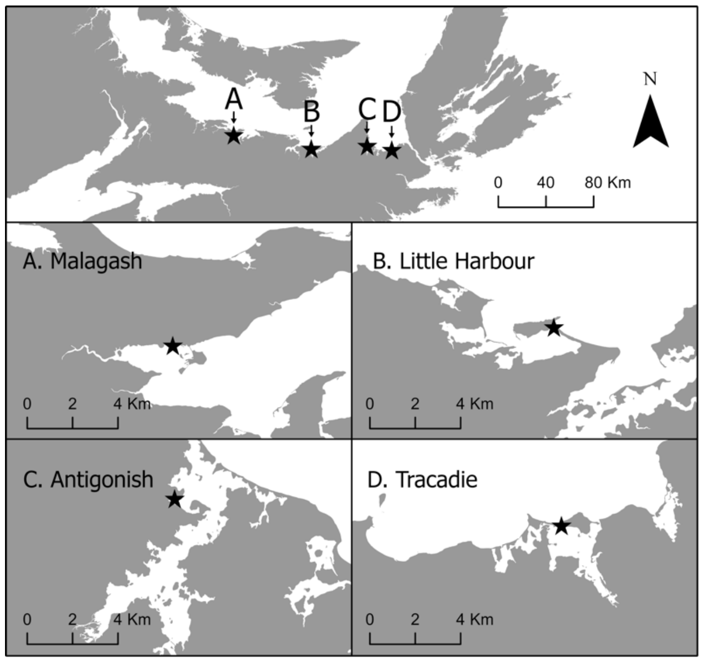


Figure 2.2: (A) Observed Larval Development (LDT) at different experimental temperatures for *C. virginica* and predicted LDT using the Growing Degree Day (GDD) model. (B) Reduced Major Axis (RMA) regression (solid line) between observed and modeled LDT (R^2 of 0.75) alongside of a one-to-one relationship (dashed lined).

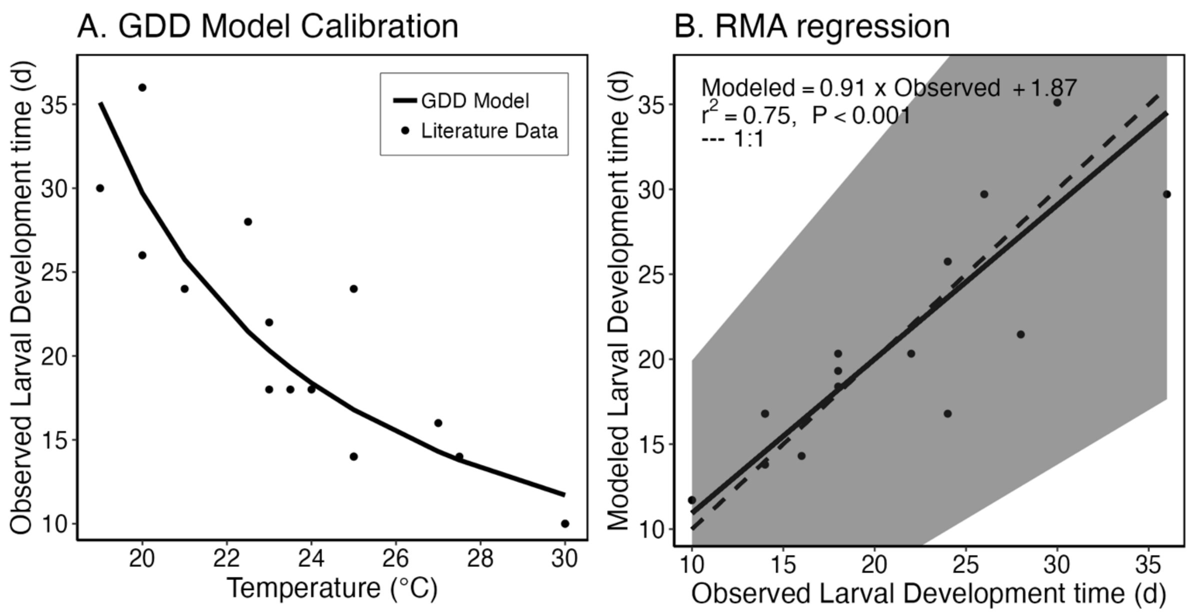


Figure 2.3: Observed settlement (mean and standard deviation, n=6) in each of the four field sampling locations. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement could first occur in each location. The settlement window is a one-week period, reflecting the one-week sampling interval. Due to significantly higher settlement in Malagash, Figure 2.3A has a separate vertical axis than 2.3B, 2.3C, and 2.3D to visualize the temporal trend in each location.

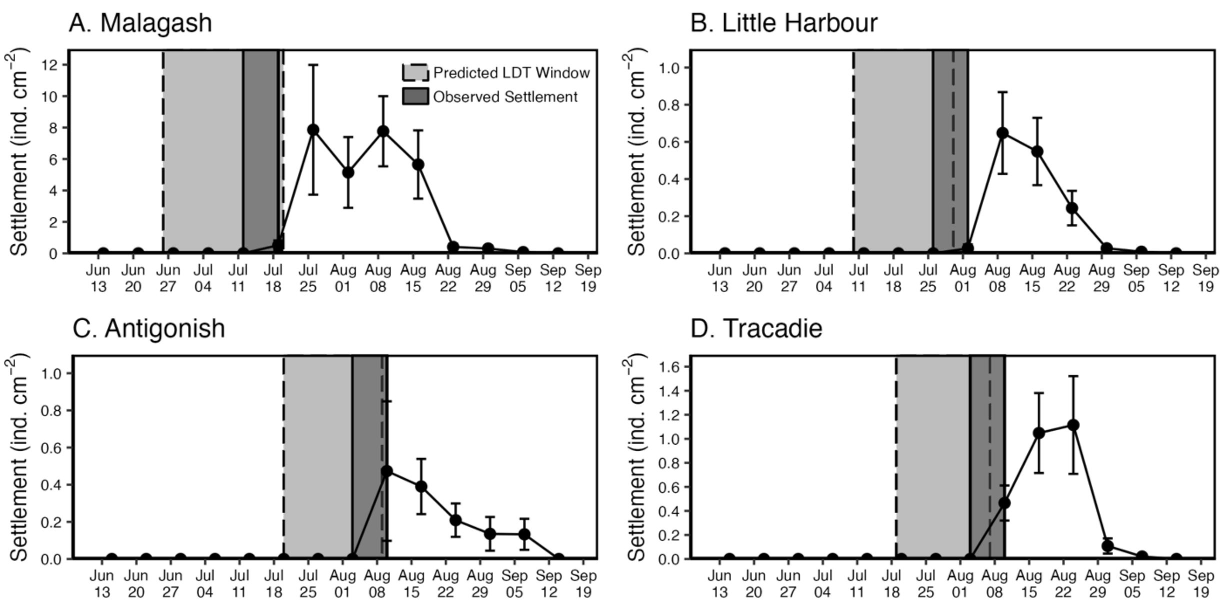


Figure 2.4: Observed temperature (daily mean and standard deviation, n=144) in the four field sampling locations. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement was first observed in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.

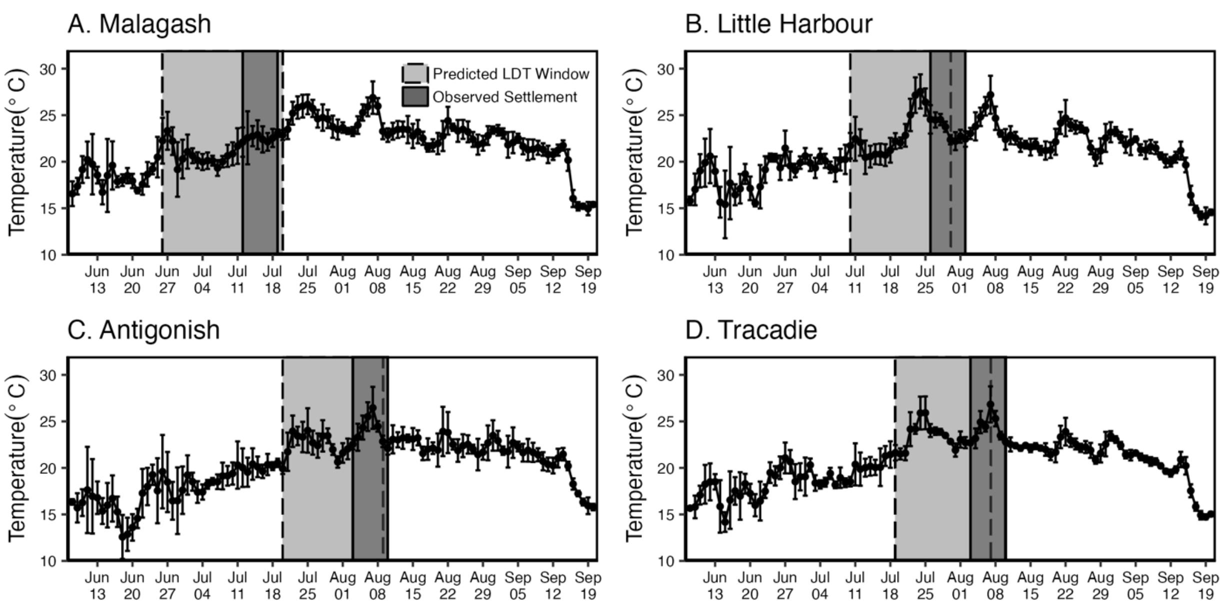


Figure 2.5: Seston quality index (mean and standard deviation, n=3) defined as observed chlorophyll-a, (Chl-a, µg L^{-1}), divided by observed Particulate Organic Matter, (POM, mg L^{-1}), in each of the four field sampling locations. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement was first observed in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.

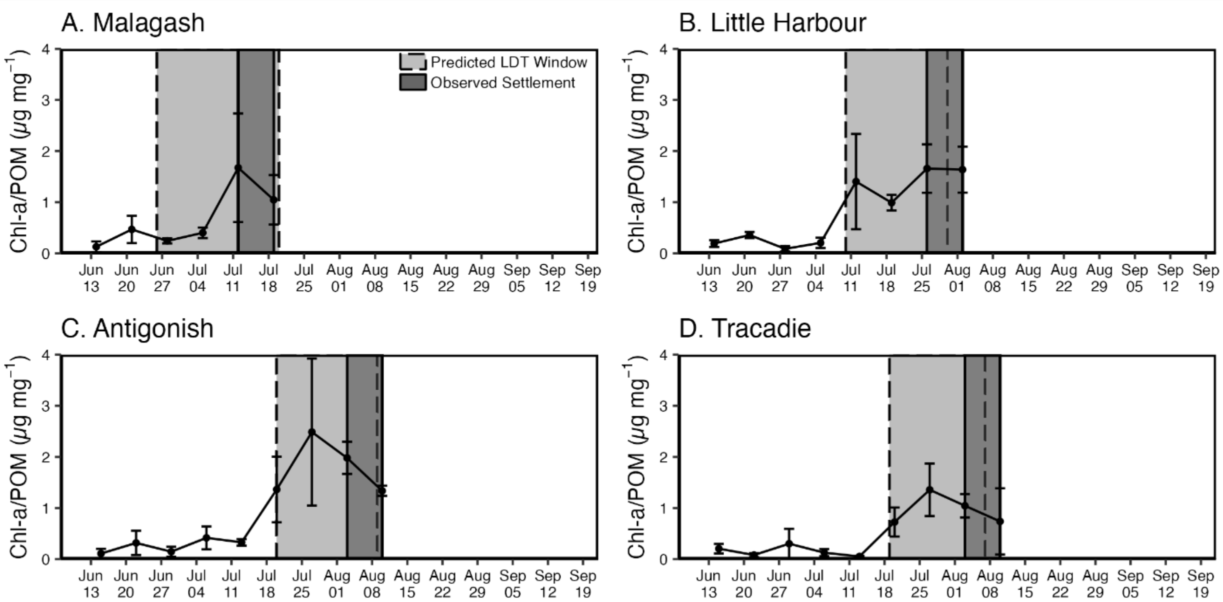
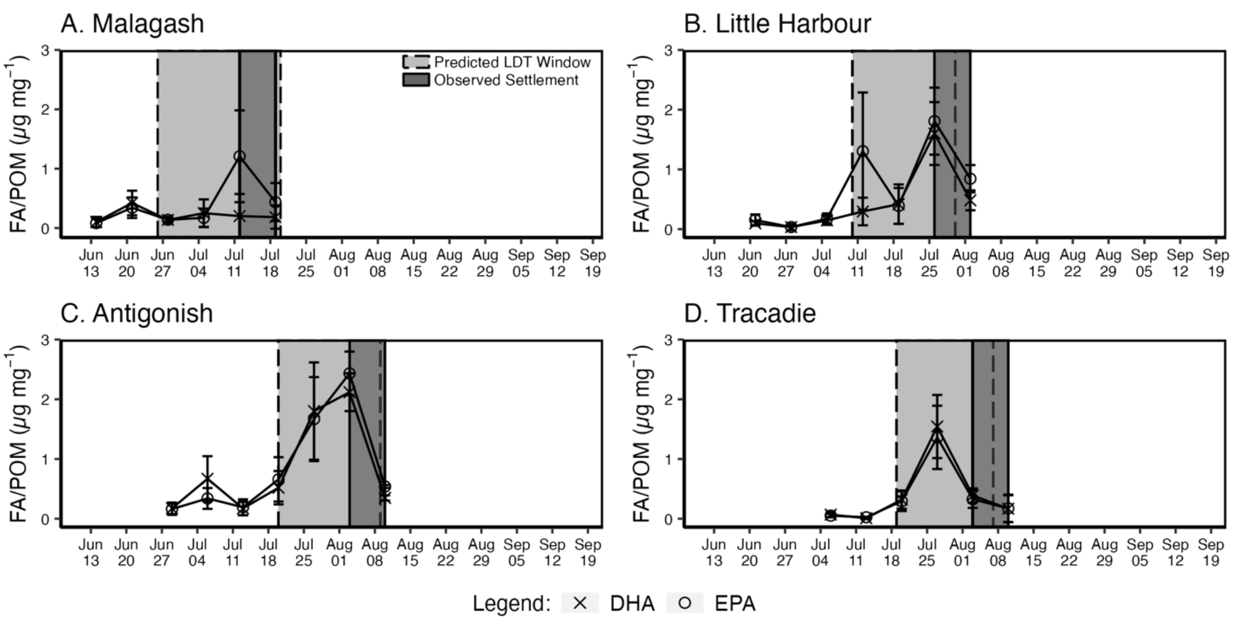


Figure 2.6: Seston quality index (mean and standard deviation, n=3) defined as observed Seston Fatty Acids (EPA and DHA, μg L^{-1}) divided by Particulate Organic Matter (POM, mg L^{-1}) in each of the four field sampling locations. DHA (denoted by "x" markers) and EPA (denoted by "o" markers) are two of the most important essential fatty acids (EFA) for developing oyster larvae. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement was first observed in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.



CHAPTER 3: PAST, PRESENT AND FUTURE OF EASTERN OYSTER (*CRASSOSTREA VIRGINICA*) SETTLEMENT IN ATLANTIC CANADA

3.1 ABSTRACT

Temperature fundamentally influences the life cycle of *Crassostrea virginica* (Eastern Oyster), impacting the timing and growth for all life cycle events. With climate change associated with increasing ocean temperatures, understanding settlement phenology becomes vital for oyster aquaculture sustainability. This chapter investigates *C. virginica* settlement trends in Atlantic Canada for different timeframes using a Growing Degree Days (GDD) model for larval development and the outcomes of a regional oceanographic model. The Canadian Regional Climate Model (CRCM) integrated with CANadian Océan PArallélisé (CANOPA) provide localized ocean temperature estimates for different climate scenarios. The study area includes the Gulf of St. Lawrence's (GSL) shallow coastal regions, known for wild and cultured *C. virginica* populations. Model simulations cover the Past (1991-1995), Present (2021 – 2025), and Future (2051 – 2055) under the A1B, Representative Concentration Pathway (RCP) 8.5 high emissions scenario. Increasing temperatures predicted by the climate model for future scenarios are expected to result in oyster habitat expansion and earlier settlement dates. As a proxy for food resources, predicted Chlorophyll-*a* over the same timeframes suggests that phytoplankton will not experience the same phenological shift as oysters, resulting in potential match/mismatch trophic relationships. Insights from this research can aid

stakeholders in adapting aquaculture practices to address climate change challenges and promote sustainable development within the industry.

3.2 INTRODUCTION

Climate change is expected to cause an increase in ocean temperature across the globe, particularly in Atlantic Canada where the rate of ocean warming is above the global average (Saba et al., 2016). Temperature is a key driver for ectothermic organisms such as the bivalve species *Crassostrea virginica* (Eastern oyster) as it affects nearly every aspect of their life cycle such as phenological traits (e.g. spawning and settlement) (Galtsoff, 1938; Steeves et al., 2018), larval development (Davis & Calabrese, 1964; Hoegh-Guldberg & Pearse, 1995), growth and development (Galtsoff, 1964; Steeves et al., 2018). Ocean warming also affects the phenology of spawning and settlement for other marine bivalves such as *Crassostrea gigas* (Gourault et al., 2019; King et al., 2021; Thomas et al., 2016), *Mytilus edulis* (Filgueira et al., 2015), *Geukensia demissa* (Virgin et al., 2019), and a number of other marine species (Edwards & Richardson, 2004; Laliberté & Larouche, 2023; Thackeray et al., 2010). Post fertilization, bivalve larvae exposed to warmer waters will experience an increase in growth rate (MacInnes & Calabrese, 1979), thus allowing larval development to occur over a shorter period of time (Davis & Calabrese, 1964). Consequently, the timing of larval settlement, defined as the step when a larva takes permanent residence on a substrate (Connell, 1985), would likely occur earlier in the year due to warmer seasonal temperatures. Such phenological changes are critical for the development of wild oyster populations (Toupoint et al., 2012) and oyster farming. For oyster farmers, knowledge of larval settlement determines the moment in which to place spat collectors in the water to harvest newly settled oysters (Doiron, 2008), to be raised in an aquaculture setting.

Variations in phytoplankton assemblages are likely to have an additional effect on bivalve populations since phytoplankton is the primary food source of bivalves (Galtsoff, 1964). The phenology and population dynamics of phytoplankton are significantly affected by light availability (Edwards & Richardson, 2004), but also by temperature (Pepin & Jamieson, 2013). Given the different drivers of phenology between bivalves and the phytoplankton they feed on, it is possible that climate change could exert species-specific effects on their phenology. For example, spawning of oysters is likely to occur earlier in the year, mostly driven by increased temperature, while the effect on phytoplankton production is not as clear, as both light and temperature play a role. Varying changes to the phenology of oysters and phytoplankton could introduce a match/mismatch situation between larval presence and food availability (*sensu* Cushing, 1990). The match/mismatch hypothesis, which suggests that changes in trophic resources can impact the performance of larvae by synchronizing or de-synchronizing periods of phytoplankton production with periods when larvae are present in the water column and feeding on seston. Accordingly, the interaction between temperature and light could result in a mismatch between larval presence and food resources, impacting larval development and settlement, with negative consequences for recruitment in wild populations and the aquaculture industry (Toupoint et al., 2012).

In the context of a changing climate, several studies couple biological models to climate scenarios to explore potential effects experienced by bivalve populations. Most of these studies found that a changing climate has significant effects on individual biology which can also be used to explain phenological changes at the population level. For instance, bioenergetic frameworks such as the Dynamic Energy Budget (DEB) have been coupled to *in situ* measurements and simulations of sea surface temperature to predict growth of *C. virginica* (Steeves et al., 2018), *Mytilus edulis* (Steeves et al., 2018; Thomas et al., 2011) and model the expanding distribution of *Crassostrea gigas* along the European Atlantic coast (Gourault et al., 2019; King et al., 2021; Thomas et al., 2016). In the context of life history events of ectotherms, the Growing Degree Day (GDD) framework has been used to quantify the thermal history and predict the growth and development of different life stages of ectothermic species (Broell et al., 2017; Neuheimer & Taggart, 2007; Steele & Neuheimer, 2022). For bivalves, general GDD models have been shown to accurately reflect growth of *Geukensia demissa* larvae (Virgin et al., 2019) and used to predict the onset of settlement for *M. edulis* (Filgueira et al., 2015). Additionally, heuristic approaches like GDD models offer a pragmatic method for predicting life history stages of ectotherms and can provide information to bivalve farmers crucial for collecting wild seed.

In this investigation, the most recent iteration of a fine-scale regional climate model (Long et al., 2016) will be coupled to the GDD model constructed in **Chapter 2**, to characterize the thermal exposure of *C. virginica* larvae and investigate how the timing of larval settlement of oysters in the Gulf of St. Lawrence could be affected by varying increases in temperature predicted within a changing climate. Additionally, the most recent iteration of a biogeochemical model that predicts Chlorophyll-a for the same region (Lavoie et al., 2021) will be used to assess food resources available to larvae and explore the match/mismatch hypothesis between the timing of larval development and food availability. With an improved understanding of how these important life history events will be affected by climate change, stakeholders (farmers and managers) will be able to plan and adjust aquaculture practices to changing conditions to ensure the sustainability of the oyster aquaculture industry.

3.3 METHODS

3.3.1 Study area

This study focuses on the shallow coastal regions within the Gulf of St. Lawrence (GSL) where oysters are known to inhabit. Large amounts of freshwater are discharged into GLS through the St. Lawrence River and from the many smaller rivers that flow into GLS, affecting the structure of water masses. During late fall and winter, water temperatures cool, and from January to March, most of the GSL estuary is covered in ice. As the seasons change, the relatively shallow waters warm quickly and by late June, small coastal basins can reach temperatures above 20ºC and last until September. The GSL region supports extensive bivalve aquaculture operations and in 2022 accounted for the majority of Canada’s cultured shellfish with approximately $95 million dollars in production value compared to the $125 million dollars produced nationally (Statistics Canada, 2022).

3.3.2 Climate Model

The climate model used in this study is an operational model developed by Fisheries and Oceans Canada with the capability to predict ocean temperature by coupling existing atmospheric and ocean models. The Canadian Regional Climate Model (CRCM) (Caya & Biner, 2004; Caya & Laprise, 1999) representing the atmospheric component is a downscaled version of the second generation Canadian Global Climate Model (CGCM2) (McFarlane et al., 1992). Representing the ocean component, the CANadian Océan PArallélisé (CANOPA) ocean model (Brickman & Drozdowski, 2012) is based on the Océan PArallélisé model (Madec et al., 1997) and the Louvain-la-Neuve ice model (Bouillon et al., 2009). CANOPA is used for its ability to predict ocean temperature with grid cells of a horizontal spatial resolution of 1/12º. For this study, outputs from the CANOPA model were sub-set to include a smaller domain that included the southern GSL region. Model simulations cover the time period of 1970-2100 and operate under the Representative Concentration Pathway (RCP) 8.5 scenario to account for the higher levels of warming that is expected for Atlantic Canada, compared to other regions (Saba et al., 2016). Mean temperatures were calculated for 1991 - 1995, 2021 - 2025, and 2051 - 2055 to represent the Past, Present, and Future climate scenarios, respectively. A full description of the model can be found in (Long et al., 2016). Comparing the model data to observations of temperature in four reference locations (study locations from **Chapter 2**) with Reduced Major Axis (RMA) regression, revealed the need for a correction factor to coastal cells of the CANOPA temperature data (Appendix D1). Otherwise, the model would underestimate temperature when compared to temperature observations, likely because the spatial resolution of the model is too coarse to reflect the sub-scale processes occurring in shallow coastal cells.

3.3.3 Biogeochemical Model

The recently developed Gulf of St. Lawrence Biogeochemical Model (GSBM; Lavoie et al., 2021), is built upon the CANOPA model that provides temperature data and thus has the same 1/12° spatial resolution and grid. The GSBM simulates the biogeochemical cycles of dissolved oxygen, nutrients, and biological components that determine phytoplankton dynamics. Biological variables such as algal biomass are calculated in nitrate units, which were converted to chlorophyll-a units. Chlorophyll-a values from the same Past, Present, and Future timeframes were extracted from the model over the same GSL domain and used as a proxy for phytoplankton abundance (Laliberté & Larouche, 2023) representing the food sources available for oyster larvae (Thomas et al., 2016).

3.3.4 Growing Degree Day (GDD) Model

The growing degree day (GDD) model used in this study was constructed in **chapter 2**. In brief, Growing Degree Day(s) is a time-based integral of heat available for growth. Such metric has been successfully employed to explain and predict growth and development for many species of marine organisms (Bonhomme, 2000; Filgueira et al., 2015; Neuheimer & Taggart, 2007). This GDD model is used to predict larval development time of *C. virginica* larvae. To initiate the model, temperature is assumed to be the main driver that triggers spawning, however, this is a simplifying assumption since spawning is not explicitly determined by exceeding a certain temperature threshold. Within the model, the minimum temperature threshold for larval growth (T_h) is set at 13.5ºC based on data from the literature (Calabrese & Davis, 1966; Davis & Calabrese, 1964; Dupuy et al., 1977; Loosanoff & Davis, 1963; Medcof, 1939; Newkirk et al., 1977) and calibration is performed by minimizing the coefficient of variation in GDD (Ruml et al., 2010). The GDD target to complete the larval development time (GDD_{LDT}, ºC·day) is set at 193 ºC·day (**Chapter 2**). GDD calculations follow the integral:

$$GDD_t = \int_1^t (T_t - T_h)\, dt$$

where GDD_t (ºC·day) is growing degree day at time *t* (day), T_t is average daily temperature (°C), and T_h is the threshold temperature for larval growth to occur (°C). For $T_t < T_h$ it is assumed that $T_t = T_h$, resulting in zero GDD units accumulated towards GDD_{LDT}.

3.3.5 Coupled Climate-GDD Model

The GDD model of *C. virginica* larvae was coupled to the high resolution CANOPA ocean model directly via water temperature. Daily predictions of sea surface temperature were used as T_t, the average daily temperature in the GDD model. In all locations, or grid cells of the model, that reached the temperature required to initiate spawning, GDD was calculated from spawning date to GDD_{LDT} and used to explore phenological changes. A fully crossed scenario analysis was carried out to understand the sensitivity of the model to the following factors:

- Thermal regimen: Past (1991-1995), Present (2021 – 2025), and Future (2051 – 2055) climatology scenarios were determined by averaging daily temperature within all locations for the 5-year periods. The dataset for each timeframe was used to explore how the timing of settlement varied and evaluate the impact of warming waters.
- Spawning temperature: 20ºC, 21.5ºC, and 23°C as thresholds that trigger spawning.
- Minimum temperature threshold for growth (T_h): Cooler (11.8ºC), moderate (13.5ºC), and warmer (14.9ºC) threshold temperatures.
- Larval Development Time (LDT) in 'heat units' (GDD_{LDT}, ºC·day): Short (164.2 ºC·day), average (193.1 ºC·day), and long (227.6 ºC·day) LDT predictions for the GDD model.

The fully crossed scenario analysis was carried out in each of the previously mentioned reference locations (shown as black dots in Figure 3.1) from **Chapter 2** and resulted in a total of 324 simulations. Comparison between simulations was achieved by extracting key traits from each model scenario such as Day of year (DOY) that spawning is assumed to occur, predicted DOY for the onset of settling, and LDT. ANOVA was used to quantify the influence of different factors on the prediction of settlement from the 324 simulations. Then, a 'base' scenario defined by the most likely values for parameters of Spawning temperature: 21.5°C, T_h = 13.5°C, and GDD_{LDT} = 193.1°C·day, was used to explore broader spatial patterns across the GSL in phenology between the Past, Present, and Future scenarios. Additionally, average chlorophyll concentrations during the predicted larval development time of each cell were estimated across Past, Present, and Future scenarios to explore the match/mismatch that may occur between larval presence and food resources.

3.4 RESULTS

3.4.1 Climate scenarios

The average temperature from July 21st to August 11th, when oyster larvae were normally present in the water column in the model domain for the current years, increased over the three considered timeframes, Past (1991-1995), Present (2021-2025), and Future (2051-255) (Figure 3.1). In the Past scenario, the average temperature for the model domain was 17.9±1.6°C (Figure 3.1A), while it increased up to 18.9±1.7°C in the Present (Figure 3.1B), and up to 20.0±1.7°C in the Future (Figure 3.1C). Both minimum and maximum temperatures followed a similar warming trend, with minimum values of 15.6ºC, 16.8ºC, and 17.6ºC and maximum values of 23.2ºC, 24.6ºC, and 25.2ºC, for Past, Present and Future scenarios, respectively.

Across the model domain, average temperature rose ~1.0ºC from the Past to the Present scenario (Figure 3.1D) and is predicted to increase by ~1.1ºC from the Present into the Future (Figure 3.1E), for a total average increase of ~2.1ºC, over the 60 years that the model spans. However, this change was not consistent everywhere. Between Past and Present, predicted increases were ~2.2ºC for some regions in the southern extent of the study areas while other regions further north only increased by ~0.3ºC (Figure 3.1D). From the Present to Future scenarios, predictions ranged from a temperature increase of ~0.4ºC in open water locations to ~2.0ºC in the coastal waters surrounding PEI (Figure 3.1E). Overall, in 60 years, temperature changes were predicted to increase between ~1.1ºC and ~3.2ºC across locations.

3.4.2 Prediction of larval settlement

The 324 simulations produced by the fully crossed scenario analysis were analyzed with ANOVA to assess the influence of predefined factors on the prediction of larval settlement in the reference locations (Table 3.1). The analysis revealed that the Timeframe (Past, Present, and Future) was the most significant predictor, accounting for 47.3% of the variation in settlement dates. Spawning temperature and station location contributed 21.6% and 17.7% to the variation in settlement dates, respectively. Finally, variations in the temperature threshold for growth to occur, T_h, and GDD_{LDT}, only contributed 4.1% and 3.3% of the variation in settlement dates, respectively.

The four reference locations that were selected to investigate the performance of the Climate-GDD model did not always reach the assumed spawning temperature (Figure 3.2A). Whether spawning was assumed to occur at 20ºC, 21.5ºC, or 23ºC, Malagash was the only reference location to reach all three spawning thresholds for each Past, Present, and Future scenario (Figure 3.2A). Comparatively, in the Past, Antigonish only reached the 20ºC spawning threshold, in the Present, both 20ºC and 21.5ºC, and in the Future, all three spawning temperatures (Figure 3.2A). Little Harbour and Tracadie followed the same pattern, where 20ºC and 21.5ºC spawning thresholds were reached in the Past and Present, but all three 20ºC, 21.5ºC, and 23ºC spawning thresholds were only reached in the Future (Figure 3.2A). There was a noticeable trend towards earlier spawning over time in all reference locations (Figure 3.2B). Consistently, Malagash was the first location that reached spawning temperatures (Figure 3.2B), followed by Little Harbour, Antigonish, and Tracadie, where similar spawning dates generally occurred later, with some variation between them. Similarly, settlement date also tended to occur earlier over time across all temporal scenarios (Past, Present, and Future), with the earliest settlement in Malagash (Figure 3.2C). Furthermore, there was a decrease in predicted larval development time (LDT) over the temporal scenarios (Figure 3.2D). Malagash consistently recorded the shortest LDT among the reference locations. For the Past, Present, and Future scenarios, the median LDTs in Malagash were 23, 21, and 20 days, respectively (Figure 3.2D). The other reference locations displayed slightly longer LDTs than Malagash but were quite comparable to one another. For instance, Little Harbour had a median LDT of 26.5, 23.5, and 22 days across the three scenarios, while in Antigonish median LDT was 27, 23.5, and 22 days for the same respective scenarios (Figure 3.2D). In Tracadie, LDT was slightly shorter than both Little Harbour and Antigonish, with median LDTs of 26, 23, and 21 days for the Past, Present, and Future scenarios (Figure 3.2D).

Outside of the reference locations, GDD predictions that consider the 'base' model parameters (Spawning temperature: 21.5°C, T_h = 13.5°C, GDD_{LDT} = 194.6°C·day), were calculated throughout the model domain to depict the spatial pattern of how oyster phenology changed across Past, Present, and Future scenarios in the model domain. Spawning and thus settlement was predicted to occur in increasingly more locations over time. The base spawning temperature of 21.5°C needed to be reached in a location for settlement to occur, thus for all 189 coastal cells in the model domain, there were 83 cells that reached the spawning threshold in the Past (Figure 3.3A), 146 locations in the Present (Figure 3.3B), and 183 cells in the Future (Figure 3.3C). In the Past, settlement occurred along the shorelines of protected waters in the GSL, and first occurred within the innermost region of the Northumberland Straight, followed by less protected bays and shorelines of the GSL or not at all (Figure 3.3A). In the Present scenario, settlement was predicted to occur along more shoreline locations within the GSL (Figure 3.3B). The change in settlement day from Past to Present was greater in locations in the east than in the west (Figure 3.3D). For all locations where settlement occurred in the Past and Present scenarios, average settlement date was predicted to occur ~14.6 days earlier in the Present than in the Past (Figure 3.3D). Future predictions suggested settlement will occur in nearly all shoreline locations in the GSL (Figure 3.3C). Across the model domain, settlement date in the Future was predicted to be ~8.8 days earlier than in the Present (Figure 3.3E). For locations that experienced settlement in the Past, Present, and Future scenarios, comparison over the 60 year period indicated settlement date was on average ~20.6 days earlier in the Future than in the Past.

3.4.3 Match/Mismatch between Larval Development and Food resources

For all locations where spawning and settlement occurred within the model domain, chlorophyll-a values between these two events, i.e. during LDT, were averaged to represent food resources available to planktonic larvae. Across the model domain, average chlorophyll-a available to larvae was 2.2 (mmolC m^{-3}) in the Past (Figure 3.4A), 1.9 (mmolC m^{-3}) in the Present (Figure 3.4B), and 2.0 (mmolC m^{-3}) in the Future (Figure 3.4C). Although average values were similar, spatial patterns emerged when comparing Past, Present, and Future. In the Past, relatively high values of chlorophyll-a were present in the more eastern locations where settlement occurred. Heading west, the amount of chlorophyll-a continued to decrease (Figure 3.4A). From the Past to Present, most locations experienced a decrease in Chlorophyll-a (Figure 3.4D), with the largest decreases in eastern locations, yet these locations still recorded the highest relative values of chlorophyll-a in the Present scenario (Figure 3.4B). Contrarily, some of the westernmost locations experienced a slight increase in chlorophyll-a (Figure 3.4D). In the Future, chlorophyll-a increased for some locations that previously experienced a decrease but slightly decreased in other locations (Figure 3.4E).

The analysis of settlement date and available food resources between the Past and Present scenarios revealed a prominent East-West pattern (Figure 3.5A). The model predicted earlier settlement and less available food in the eastern locations in the Present than the Past. Moving west, settlement still emerges earlier, but in contrast, these regions experience a slight increase in chlorophyll-a levels, signifying a richer food environment

(Figure 3.5A). This turning point between increasing and decreasing values of Chlorophyll-a is pronounced around the -64.5°W longitude mark. Locations west of this longitude experienced an increase in chlorophyll-*a* of up to ~0.5 mmolC m^{-3}, while a linear decrease, to as much as ~1.2 mmolC m^{-3}, was observed to the east (Figure 3.5B).

From the Present to Future timeframe, for most locations earlier settlement days were forecasted, with an average advance of approximately ten days (Figure 3.5C). However, the distinct longitudinal patterns seen in the Past-Present were less apparent. The availability of food resources, represented by chlorophyll-a, remained relatively consistent across regions with minor fluctuations (Figure 3.5D). As stated previously, chlorophyll-*a* increased by ~0.5 mmolC m^{-3} in locations where it had previously decreased and decreased by up to ~0.5 mmolC m^{-3} in other locations (Figure 3.4E); however, these changes did not emerge with a longitudinal pattern (Figure 3.5D).

3.5 DISCUSSION AND CONCLUSIONS

In this study, a Growing Degree Day(s) model was coupled with temperature data from a high-resolution climate model to predict the timing of settlement for *C. virginica* in Past, Present, and Future scenarios. When comparing scenarios, the coupled model predicted an increase in suitable areas for settlement over time and earlier in the year for locations that had already experienced settlement. Additionally, chlorophyll-a was used as a proxy for food resources available during the predicted larval development time, revealing varying food resources between the Past, Present and Future scenarios that could result in a potential phenological match or mismatch between larval presence and food availability, which may have positive or negative effects on larval development.

While the spatial resolution of the model (1/12°) is considered fine-scale for climate models, there are many shallow bays within the model domain that are smaller than the ~6 by ~8 km model grid cell and consequently not accurately represented in the model. Additionally, coastal geomorphology and bathymetry can have a large impact on water circulation and consequently on temperature of coastal areas (Filgueira et al., 2016; Laignel et al., 2023). To overcome these limitations, the original climate data was calibrated using *in situ* data collected during the summer months of 2022 (Appendix D1&2). The calibrated temperature data predicted an increase in average temperature of ~3.2ºC by 2051-2055 compared to current temperatures, which fits with the prediction for this area in future climate scenarios as discussed by Long et al. (2016). This model was driven by the RCP 8.5 scenario, which is the most extreme climate scenario and it was included in this work to account for higher levels of warming expected in Atlantic Canada in comparison with other regions (Saba et al., 2016). While some studies modeling reproductive traits of bivalves in the context of climate change considered multiple RCP scenarios (e.g. Gourault et al., 2019), this study and others (e.g. King et al., 2021; Klinger et al., 2017) only considered the RCP 8.5 scenario to represent temperature in biological models. Accordingly, this could be considered the worst-case scenario from the RCP choice perspective; however, stochastic events such as marine heatwaves and hypoxic conditions that usually co-occur with heatwaves have not been included in the model but they can play a major role in bivalve ecophysiology and mass mortalities (Carneiro et al., 2020; Correia-Martins A et al., 2022; Talevi et al., 2023) and are expected to increase in frequency and severity (Oliver et al., 2019). Despite the lack of extreme stochastic events, the current model provides information about the general phenological changes caused by temperature, the most relevant driver for a commercially valuable ectothermic species under future scenarios.

The coupled climate-GDD model projections indicate an increase in the geographic range of suitable areas for settlement over time. This predicted expansion can be attributed to the progressive achievement of spawning temperature in more locations, which suggests that the habitat range for Eastern oysters is likely expanding in Atlantic Canada. The simulations suggest that the increase in habitat is mostly along a latitudinal gradient, with predictions of spawning and the concomitant settlement expanding northward. Similar northward habitat expansion has been documented for the invasive species *Crassostrea gigas* in European waters in relation to ocean warming (King et al., 2021; Laugen et al., 2015; Shelmerdine et al., 2017; Thomas et al., 2016). However, for other bivalve species that occupy habitats close to their upper thermal limits, it is expected that warming temperatures will result in a reduction of suitable habitat (Canu et al., 2010; Deutsch et al., 2015; Steeves et al., 2018). The coupled climate-GDD model also suggests that warming temperatures will result in phenological shifts of key life history traits such as earlier spawning and settlement in existing oyster habitat, which aligns with current literature surrounding climate impacts on *C. gigas* and *C. virginica* (Gourault et al., 2019; Steeves et al., 2018; Thomas et al., 2016).

The effect of warming temperatures that can lead to *C. virginica* habitat expansion and phenological shifts is of interest from economic and management perspectives, particularly for the aquaculture sector in Atlantic Canada where the growing season is limited by low temperatures during the winter (Comeau et al., 2012). These shifts suggest an increase in the potential for growth, both at the level of individual organisms and for the industry as a whole, potentially influencing future investment, regulations, and cultivation strategies (Reid et al., 2019). Nevertheless, other factors, such as the risk of heatwaves or the potential alteration of biological processes and functioning driven by climate change and the culture itself, should not be overlooked when considering the future of the aquaculture industry.

While warming temperatures are likely to result in favorable conditions for *C. virginica* in Atlantic Canada, changes in food resources may impose stressors on oyster populations. The patterns of chlorophyll-a concentrations in the model domain, serving as a proxy for food resources for planktonic larvae of *C. virginica*, revealed spatial and temporal variation. Spatial and temporal trends in food available to larvae could be explained by shifts of the LDT window associated with temperature fluctuations, or by phenological changes experienced by phytoplankton populations (Edwards & Richardson, 2004). While this study did not directly investigate changes in phytoplankton phenology related to climate change, it has been predicted that phytoplankton phenology in the study area will vary with location and species (Laliberté & Larouche, 2023). Exploring the spatio-temporal predictions of oyster life history events and variations in the food available to larvae across three different timeframes produced results that indicate the potential for match/mismatch relationships (*sensu* Cushing, 1990), which could vary across locations and timeframes. While examining the ecological implications of Chl-a variations from the past to present during LDT, the greatest decline was in eastern locations, which began at ~3.1 mmolC m-3 in the past and decreased to ~1.9 mmolC m-3 in the present. Given that any shift in Chl-a represents a change in phytoplankton abundance, it could be ecologically significant by influencing larvae growth, survival, and phenology. Further research would be required to determine the threshold levels of Chl-a that would significantly affect oyster ecology. Locations where the change in food resources is the most pronounced are where match/mismatch relationships are most likely to occur. Where future changes result in a favorable increase in temperature and a concurrent increase in available food, such conditions promote the expansion of the species geographic distribution. Similar instances are reported for *C. gigas* along the European coast, where increases in temperature and food resources during larval development likely aided in the species northward expansion (Thomas et al., 2016). Alternatively, in locations with a mismatch relationship where less food is available to larvae, the larval phase may be prolonged by reduced growth and/or delay of metamorphosis until reaching a specific settlement cue. The effects of the phenological mismatch relationship could have significant implications for larval survival rates and the overall success and timing of settlement, as observed for *M. edulis* in Îsles de la

Madeleine, an archipelago appearing in the northern portion of the study area (Toupoint et al., 2012). Further research is needed to understand and model the dynamics of phytoplankton in relation to temperature and other drivers, which will be crucial in predicting the impacts of climate change on oyster larval development and settlement.

The current study enables the prediction of the future outlook for the settlement and potential spatial distribution of *C. virginica*, but the intrinsic uncertainties of modeling estimations should be considered. As previously stated, the spatial resolution of the model is too coarse to accurately reflect conditions within narrow bays and waterways. Additionally, the parameterization of the GDD model relies on a limited set of laboratory studies, and the spawning threshold, 21.5 °C, is not necessarily only triggered by reaching a certain water temperature; instead, several factors can interact to influence the timing of spawning. Furthermore, our GDD model assumes that growth is directly proportional to temperature and that food is not a limiting factor, assumptions that could be violated under specific conditions. Regarding the potential match/mismatch implications, the use of chlorophyll-a as a proxy for food resources neglects the omnivorous nature of oyster larvae. Besides model uncertainty, oyster adaptation driven by climate change stressors could impact future phenology and spatial distribution (Barber et al., 1991; Casas et al., 2018). While this study focuses on the timing of larval development, to fully understand how recruitment is affected, considerations should include mortality and larval thermal history both of which depend on ocean transport processes of advection. Despite these sources of uncertainty, the current model has offered insights into the possible phenological changes of oyster larvae settlement across varying climate scenarios, suggesting habitat expansion and earlier settlement as a consequence of warming temperatures. Further work is required to understand the emergence of match/mismatch trophic relationships between larvae and food resources. These insights contribute to improving knowledge of the interactions between climate change and *C. virginica* in Atlantic Canada and provide valuable information for stakeholders to plan the future of oyster aquaculture in the region.

3.6 TABLES

Table 3.1: ANOVA results from the fully crossed scenario analysis. Treating Settlement date as the dependent variable, station locations were selected to be the same as the four field sampling locations in Chapter 2. Spawning temperature, an independent variable considered in the model that has three threshold levels to mark different spawning at different temperatures. GDD_{LDT} and T_h are factors that are independent of the predicted settlement data but non-independent of each other since they originate from the calibration process. Timeframe is the final independent variable which has 3 levels (Past, Present and Future) to characterize the difference in conditions through time.

Parameter	Sum of Squares	df	F-statistic	PR(>F)	% variation
Station	11665.47	3	245.47	4.57E-74	17.72
T_h	2676.65	2	84.49	9.86E-29	4.07
Spawning Temp	14250.27	2	449.79	2.17E-83	21.64
GDD_{LDT}	2160.15	2	68.18	2.43E-24	3.28
Timeframe	31149.13	2	983.19	6.58E-119	47.31
Residual	3944.37	249	-	-	5.99

3.7 FIGURES

Figure 3.1: (***A***) Past, (***B***) Present, (***C***) Future SST during 3 weeks that larvae are common. (***D***) Temperature difference between past and present. (***E***) Temperature difference between present and future. Four reference locations in Nova Scotia are shown as black dots.

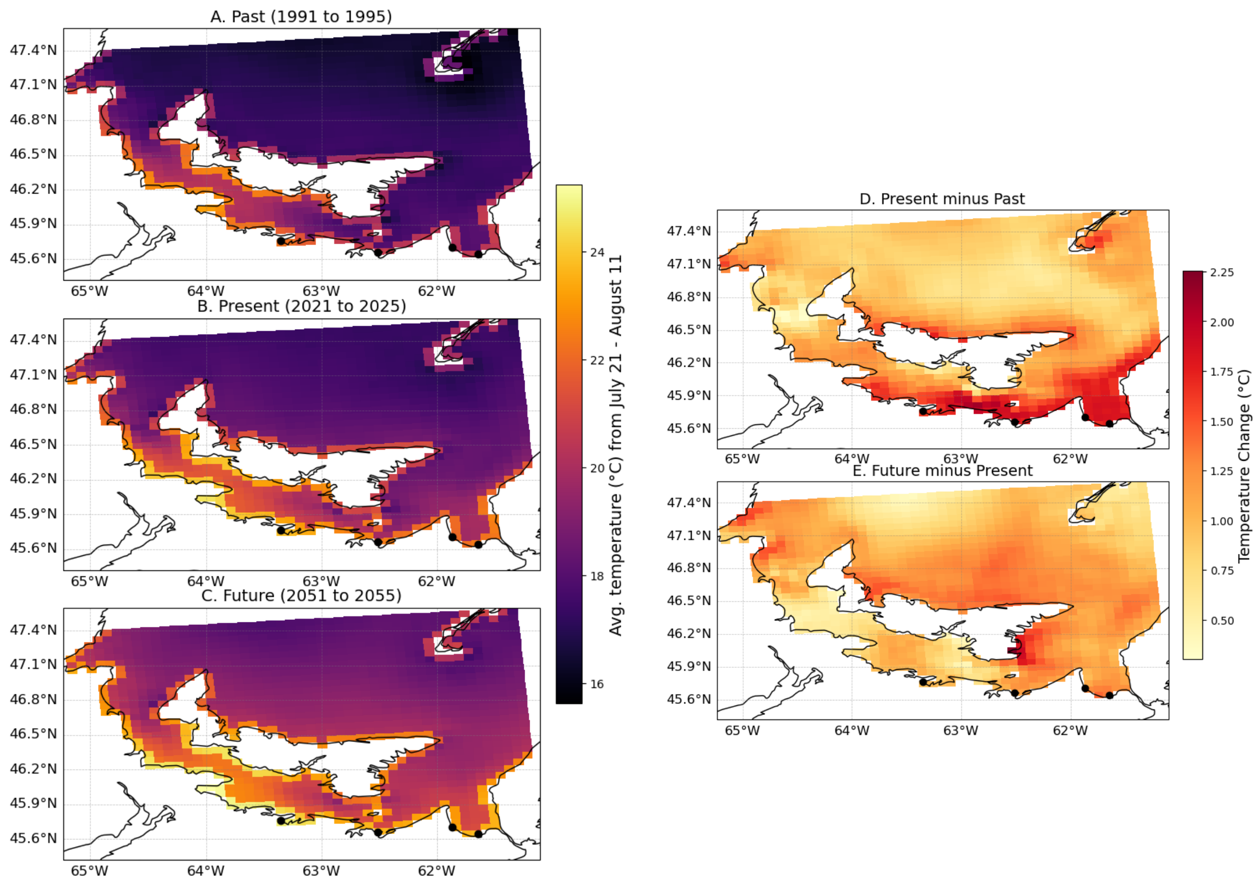


Figure 3.2: GDD model performance illustrated by plots of model values in the four reference locations and across the Past Present and Future scenarios. The maximum of three spawning thresholds (20ºC, 21.5ºC, and 23°C) can be reached in each location (Figure 3.2A). The date on which spawning threshold(s) were reached (Figure 3.2B). The date of predicted settlement incorporates variability for T_h and GDD_{LDT} (Figure 3.2C). Larval development time is the number of days between spawning and settlement (Figure 3.2D).

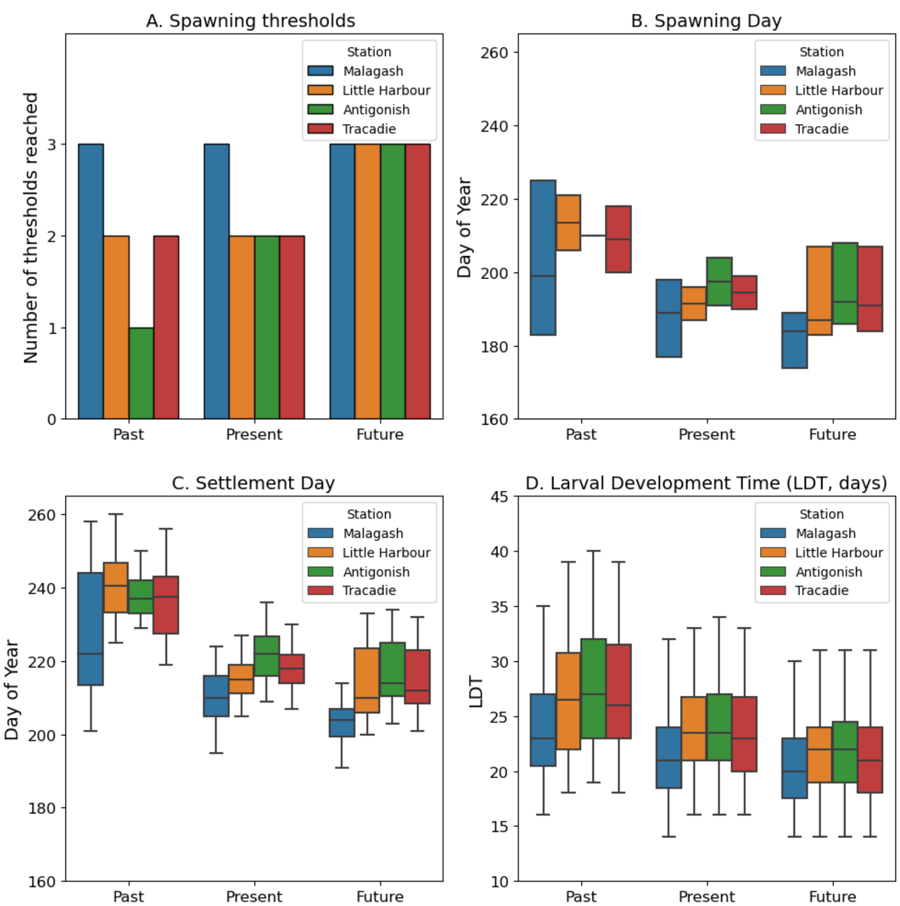


Figure 3.3: Map of Settlement date for (***A***) past, (***B***) present and (***C***) future. Difference in set day for (***D***) present minus past, (***E***) future minus present.

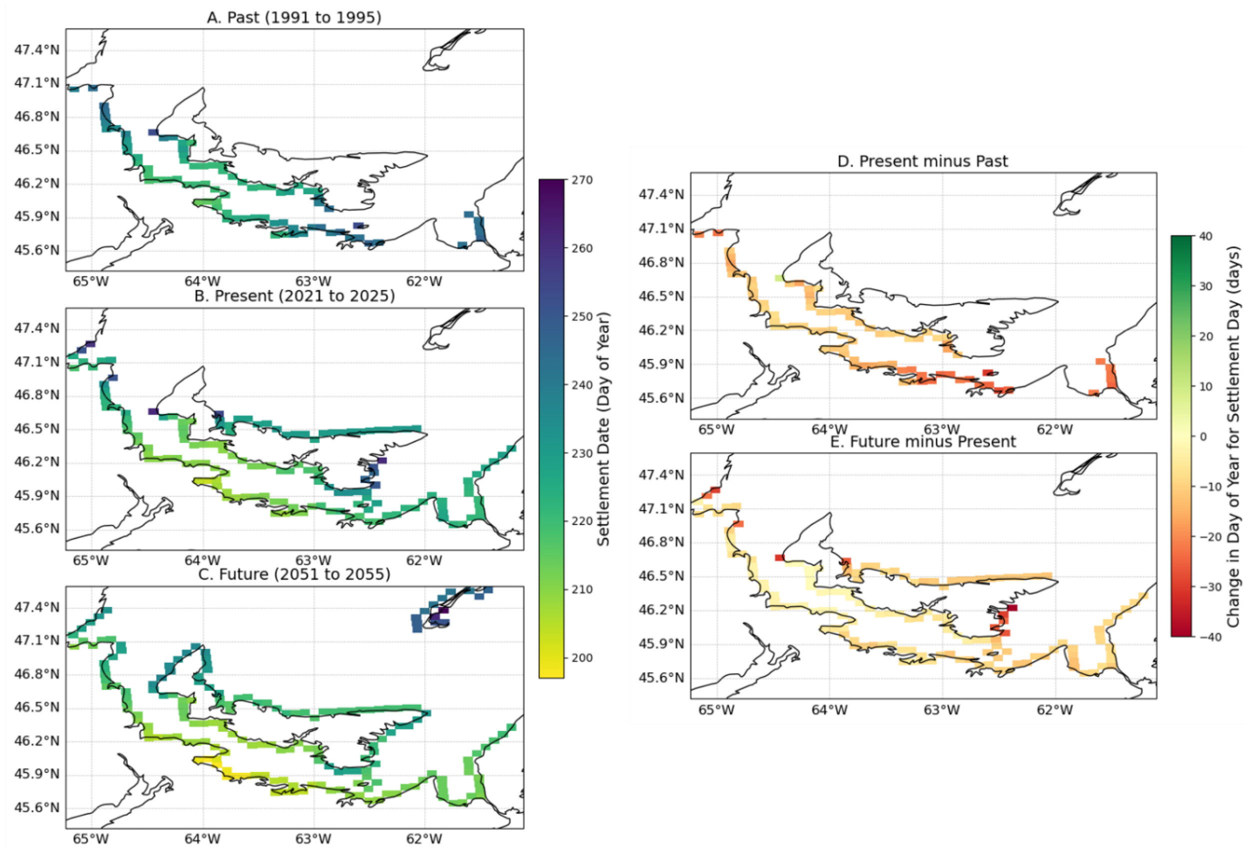


Figure 3.4: Average Chlorophyll-a during LDT window of each cell for (A) Past, (B) Present, (C) Future. (D) Change in Chlorophyll-a from Past to Present. (E) Change in Chlorophyll-a from Present to Future.

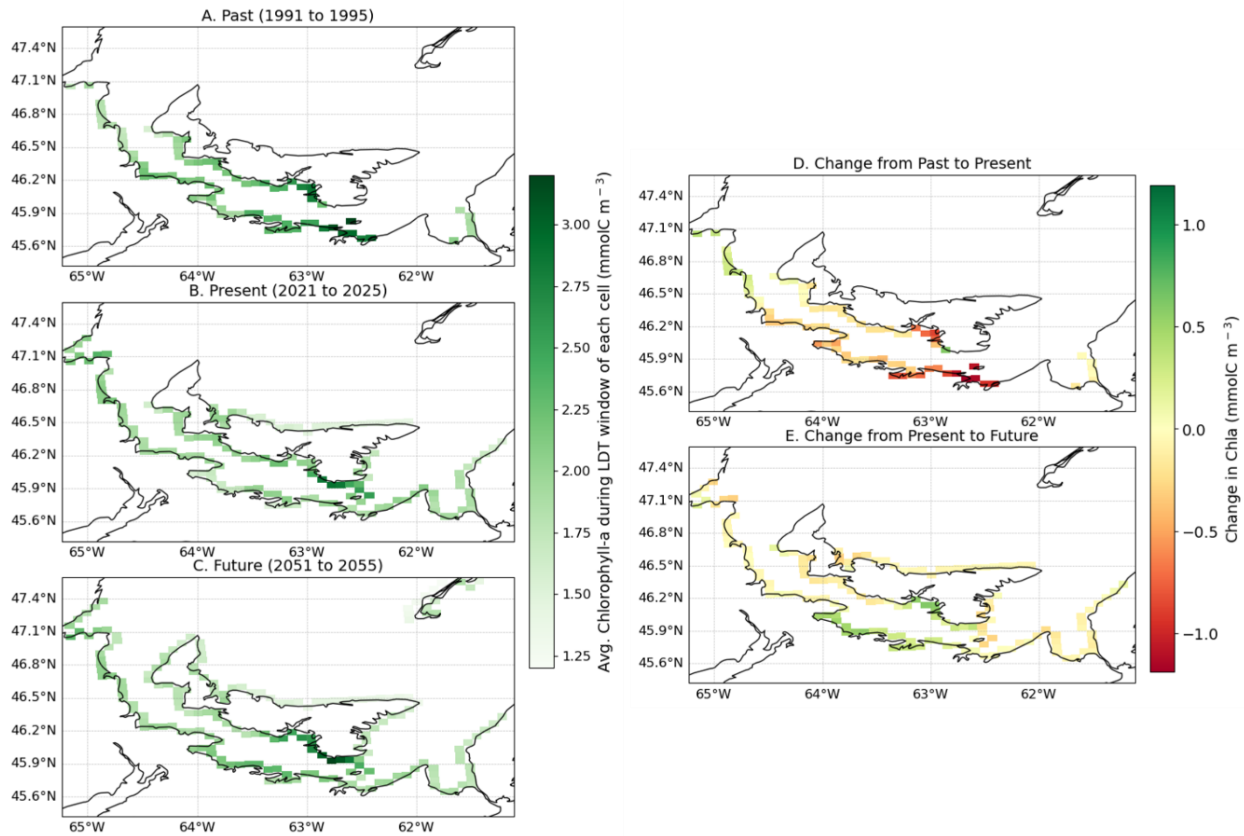
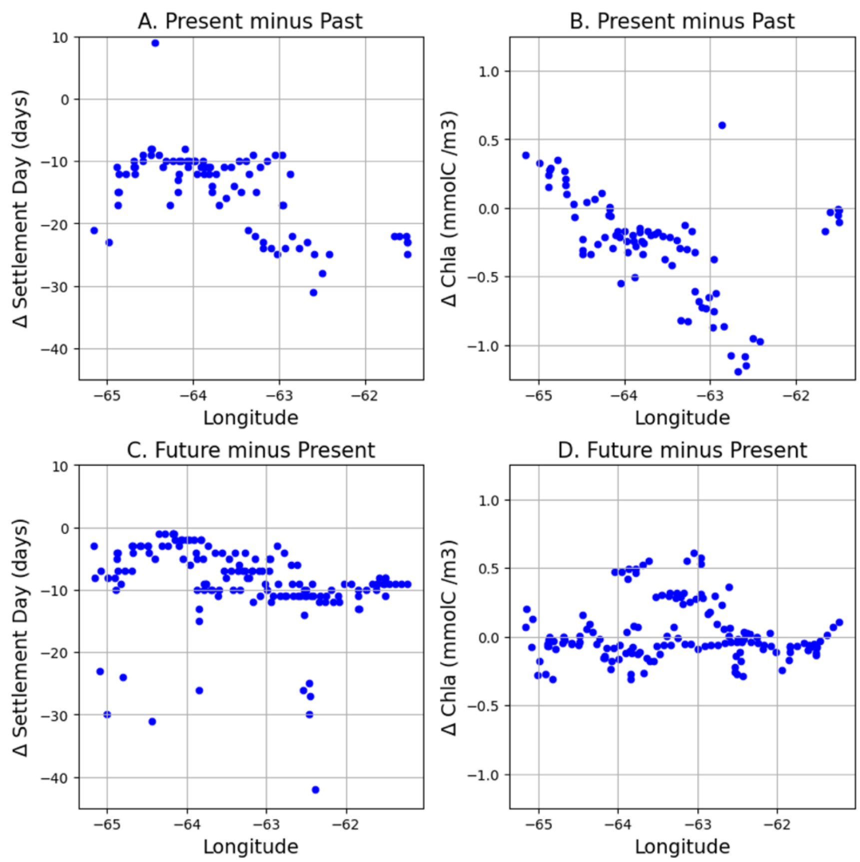


Figure 3.5: Change in Settlement Day across longitude (A and C) from Present to Past and Future to present, respectively. Differences in Chlorophyll-*a* concentrations across longitude (B & D) during larval development from the same respective timeframes. Negative values in A and C indicate a reduction in the number of days between settlement dates from the later time period compared to the earlier one. Changes in Chlorophyll-a in B and D reflect the differences in available food for oyster larvae between the compared timeframes.



CHAPTER 4: DISCUSSION

This thesis relies on the influence of temperature on bivalve physiology to develop a Growing Degree Day (GDD) model that can be used in the short-term to predict the optimal timing for spat collection or in the long-term to predict phenological changes associated with climate change, both useful to farmers and managers to develop operational management plans that must account for such variations in population dynamics.

Chapter 2 leveraged existing literature data to build the foundation for a species-specific growing degree day model of the larval stage. Average daily temperatures at each field site informed the GDD model, which was used to predict settlement dates at these locations. The settlement date predicted by the model agreed with field observations, which indicates the model performed well during the field validation. While investigating other water parameters collected as field data, food resources (Chlorophyll-a, fatty acids EPA and DHA) and seston composition (TPM and POM) showed correlations to settlement, but salinity and dissolved oxygen showed no correlation with settlement. Although food resources have been shown to affect settlement in bivalves (Toupoint *et al*., 2012a) our results suggest that temperature was the dominant factor influencing the timing of settlement. Additionally, bivalve settlement may be influenced by salinity, but it is suggested that the combined effect of salinity and POM is what contributed significant influence (Leal *et al*., 2019).

By combining the GDD model (**Chapter 2**) with regional oceanographic model, we explored shifts in phenology and species distribution through multiple scenario analysis (**Chapter 3**). Since *Crassostrea virginica* is a temperate bivalve that thrives in warmers temperatures, the cooler waters of Nova Scotia are the most significant limitation to growth due to their ectothermic nature. In the context of warming temperatures associated with climate change, our results share similarities with investigations of *Crassostrea gigas* in European waters, showing earlier settlement and habitat expansion to higher latitudes (King *et al*., 2021; Thomas *et al*., 2016). However, as temperatures rise, the effect of food resources available to larvae gains complexity in the form of potential asynchronous phenological shifts between larvae and their primary food source of phytoplankton. The predicted phenological shifts suggest locations in Atlantic Canada could have varying responses to future climate change scenarios, as suggested by Feindel et al., 2013, with potential mismatch conditions between larvae and phytoplankton.

4.1 FUTURE DIRECTIONS

While some studies have explored the biological mechanism that triggers spawning such as genetics (Barber *et al*., 1991), temperature (Magaña-Carrasco *et al*., 2018), food resources (Barber, 1996), salinity (Gregory *et al*., 2023), and chemical cues released by adults (Galtsoff, 1938), the complexity of the natural environment and confounding variables increases the uncertainty on predictions of spawning in wild populations. Spawning date is a significant parameter that initiates the GDD model, so it is important to reduce the uncertainty of the spawning date parameter as much as possible. To overcome the limitation of a complex spawning threshold in wild oysters, conducting a meta-analysis of data from existing monitoring programs could provide insights towards a more defined threshold for spawning. Additionally, future investigations could work towards further understanding uncertainty within the model by comparing various methods for sensitivity analysis with the statistical bootstrapping method used in this study. To refine the GDD model for a specific region, future experiments could further investigate the duration of the *C. virginica* larval stage in the laboratory under constant and fluctuating conditions (mimicking the natural environment) by using broodstock from the region of interest.

4.2 CONCLUSIONS

Understanding how development is influenced by environmental factors is critical to predicting the life history events of ectotherms, such as the spawning and settlement of *Crassostrea virginica*. This thesis contributes to our understanding that temperature is the predominant factor influencing the timing of settlement. The field data collected as part of this thesis illustrates that settlement can be predicted for wild bivalve populations by considering temperature as an integral variable. Development of monitoring programs, like those in neighboring provinces would be beneficial to the oyster aquaculture industry in Nova Scotia but would come with a high dollar cost. As an alternative to extensive monitoring, the GDD model could provide this essential information to farmers in a timely and cost-effective manner. As temperatures are expected to rise in the future, the model predicted more suitable habitat and a longer growing cycle for oysters, suggesting opportunities to expand oyster aquaculture in the Gulf of St. Lawrence. Finally, the information presented in this thesis is useful to farmers, managers, and researchers because it collects and provides information, in the form of short- and long-term predictions, on larval phenology in a region with little existing documentation.

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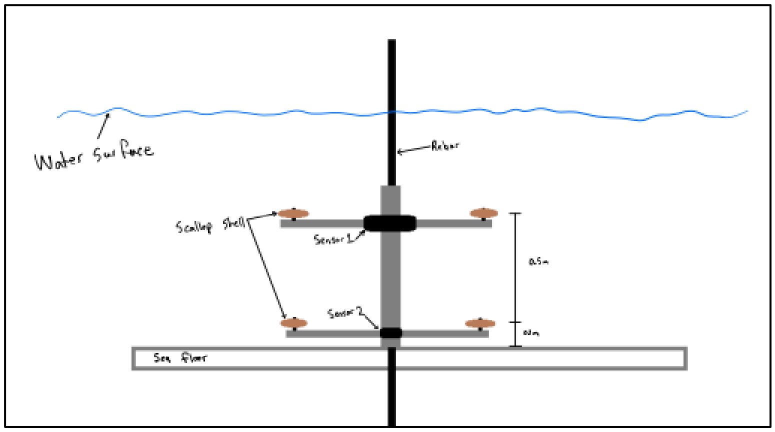
APPENDICES

APPENDIX A

Table A1: Literature results of Larval Development Time (LDT) at different temperatures. For comparison, the number of days to complete the larvae stage according to the model is included.

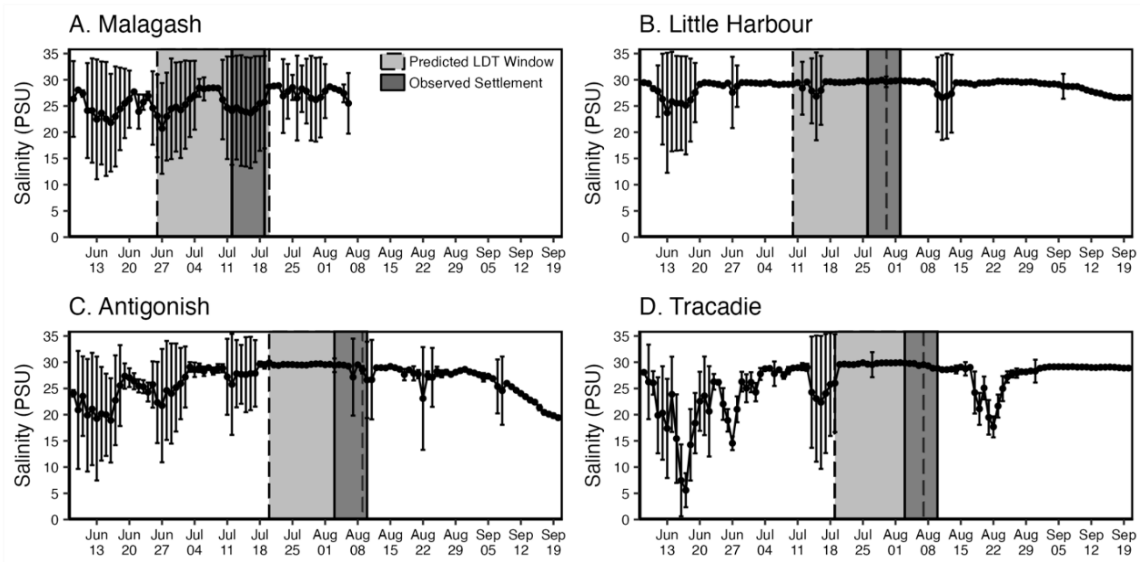
		Observations	Model
Source	Temperature	LDT (days)	Days till GDD=193.1 (°C·day)
Medcof (1939)	19	30	35.1
Medcof (1939)	20	26	29.7
Calabrese (1964)	20	36	29.7
Medcof (1939)	21	24	25.7
Calabrese (1964)	22.5	28	21.5
Newkirk (1977)	23	22	20.3
Loosanoff,Davis (1963)	23	18	20.3
Loosanoff,Davis (1963)	23.5	18	19.3
Newkirk (1977)	24	18	18.4
Calabrese (1964)	25	24	16.8
Calabrese, Davis (1966)	25	14	16.8
Newkirk (1977)	25	14	16.8
Dupuy (1977)	27	16	14.3
Calabrese (1964)	27.5	14	13.8
Calabrese (1964)	30	10	11.7
Loosanoff,Davis (1963)	30	10	11.7

APPENDIX B

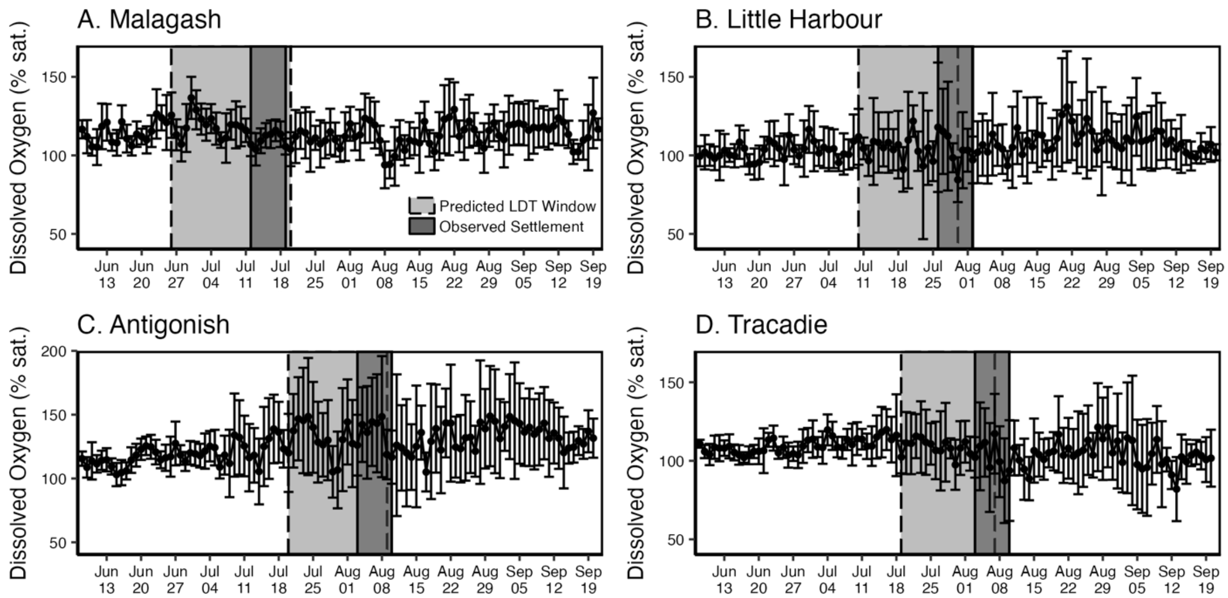


B1: Diagram of spat collector. Design based on NB Spat collection program.

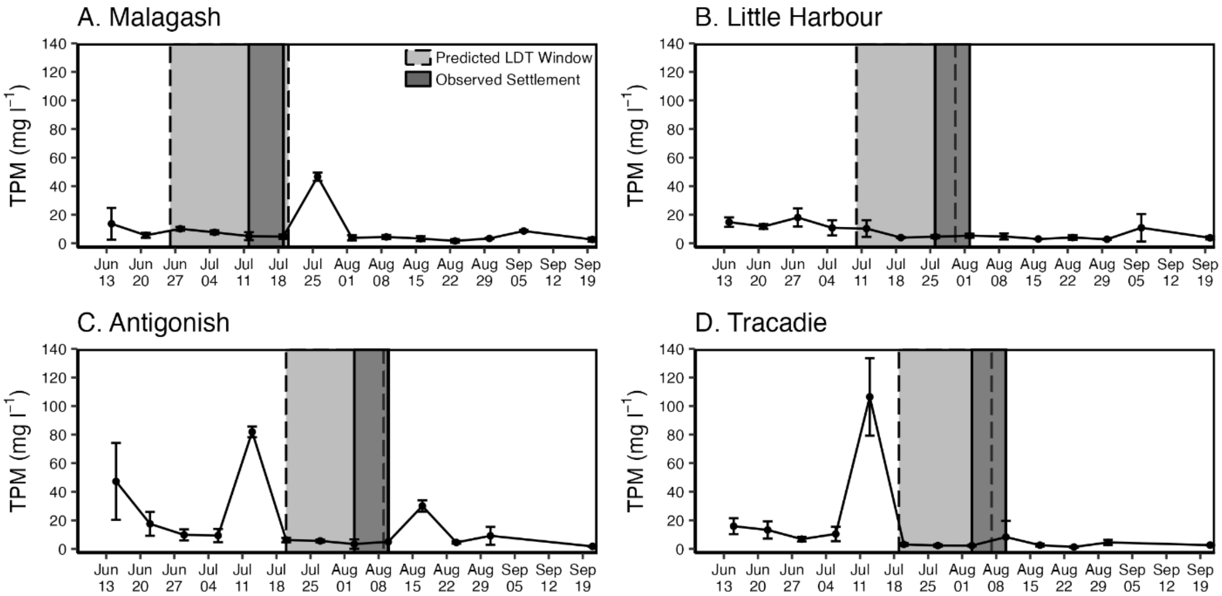
APPENDIX C



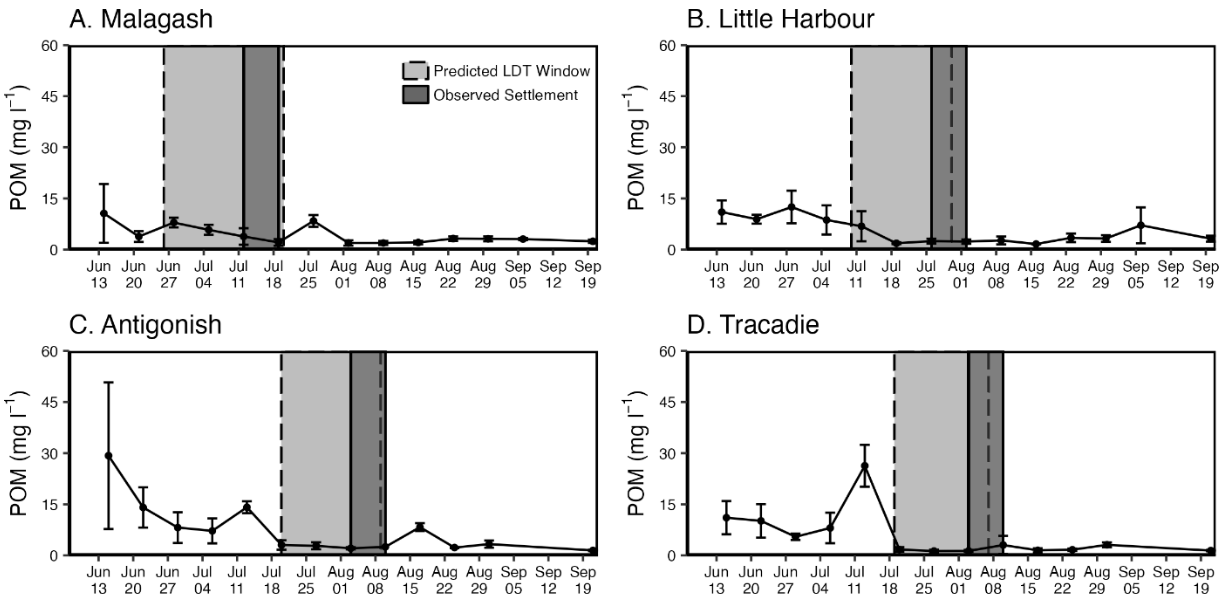
C1: Salinity values (daily mean and standard deviation, n=144) in the four sampling locations. The salinity probe in Malagash malfunctioned, resulting in no measurements during the last half of the sampling period. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement first occurred in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.



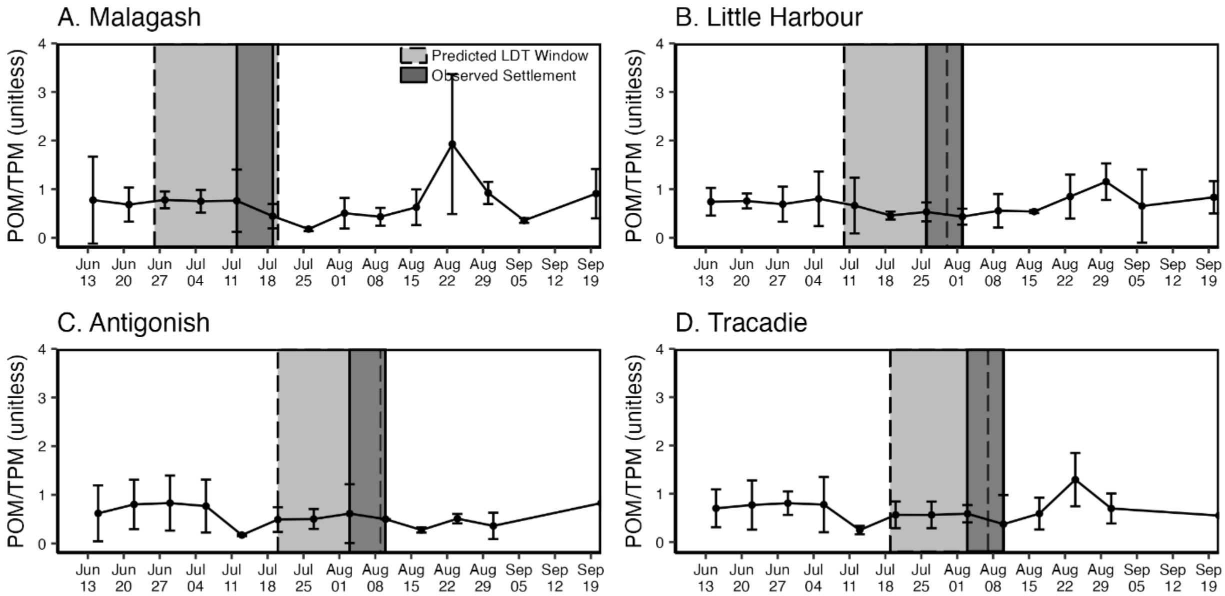
C2: Dissolved Oxygen (daily mean and standard deviation, n=144) in each of the four sampling locations. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement first occurred in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.



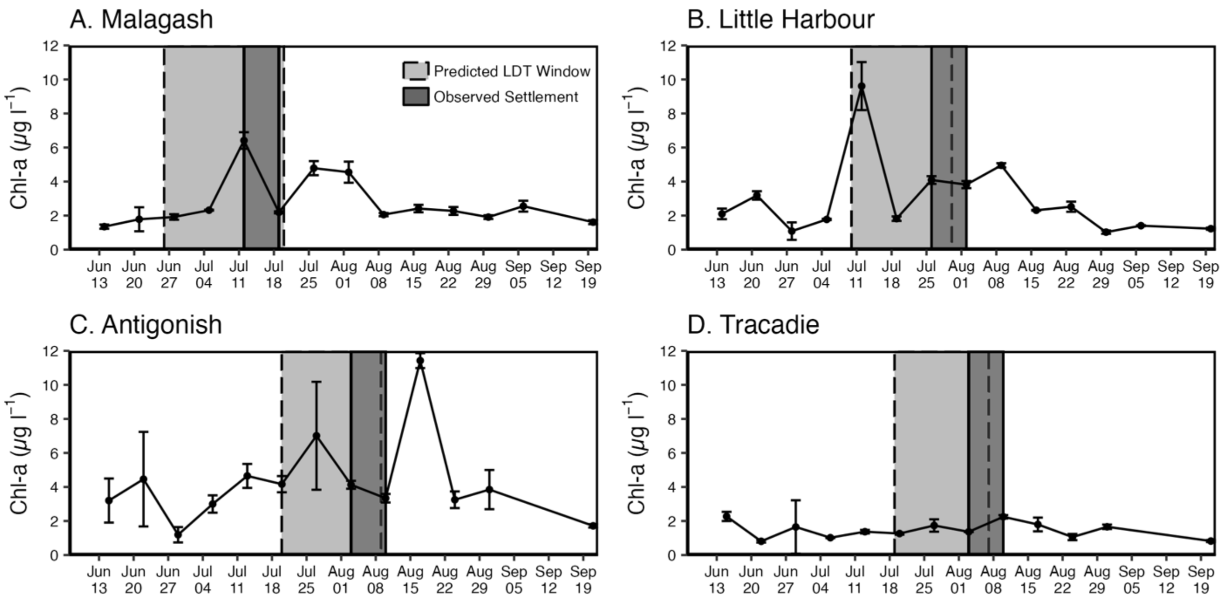
C3: Total Particulate Matter (TPM) values (mean and standard deviation, n=3) are determined by averaging triplicate water samples within each of the four study locations. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement first occurred in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.



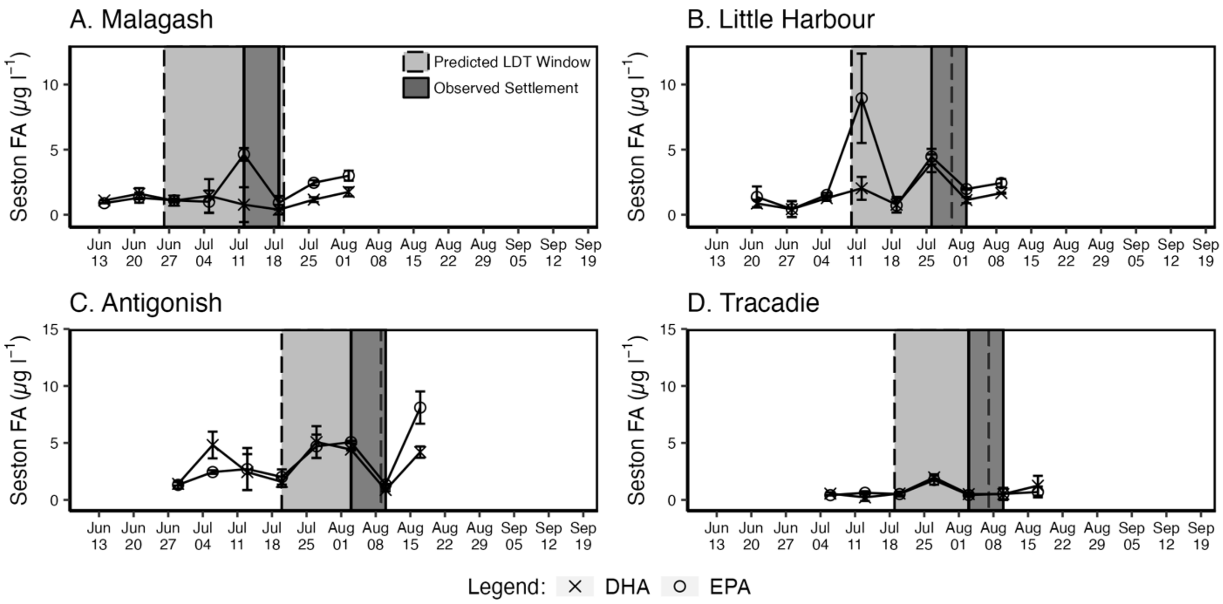
C4: Particulate Organic Matter (POM) values (mean and standard deviation, n=3) are determined by averaging triplicate water samples within each of the four sampling locations. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement first occurred in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.



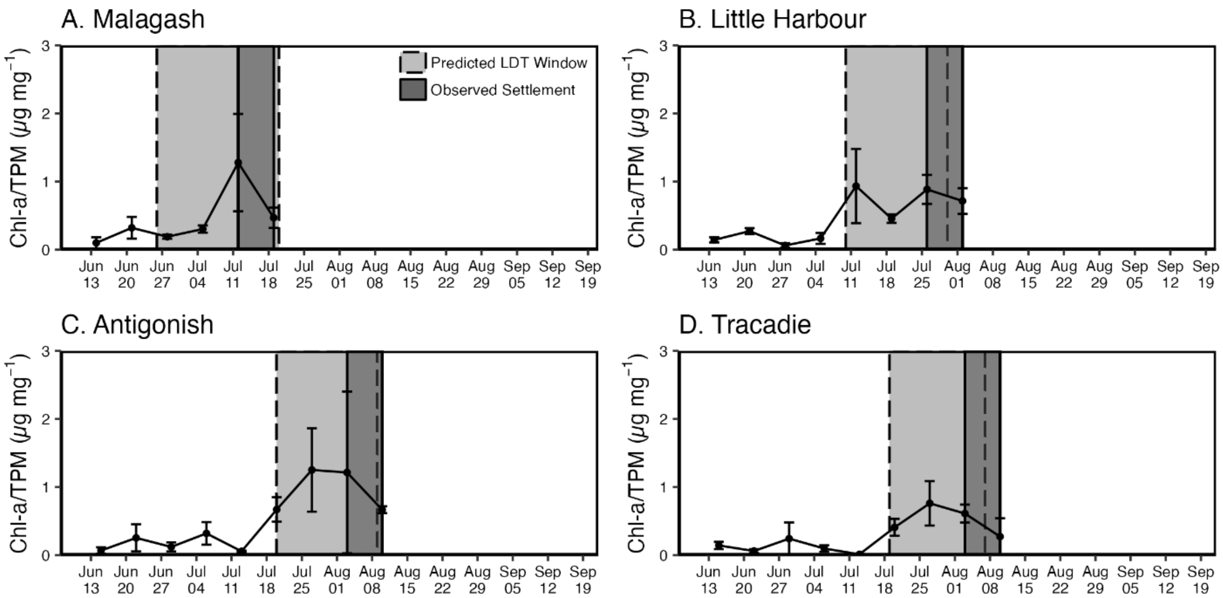
C5: POM/TPM index is a common measurement in the study of seston that shellfish consume. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement first occurred in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.



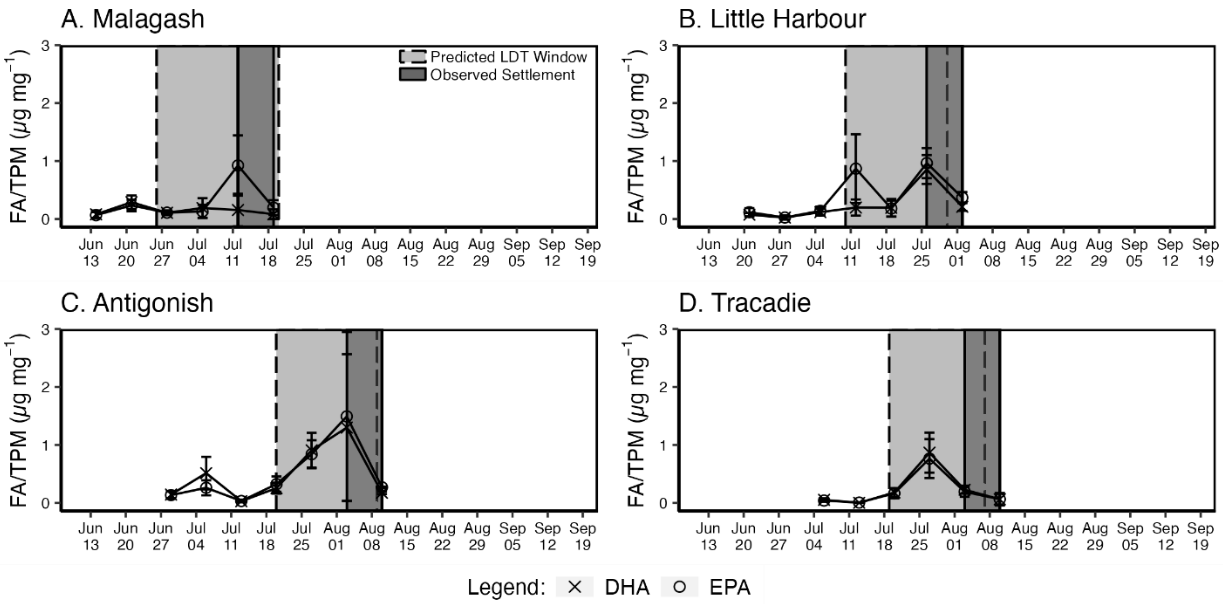
C6: Chlorophyll-a values (mean and standard deviation, n=3) are determined by averaging triplicate water samples. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement first occurred in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.



C7: Seston Fatty Acids (mean and standard deviation, n=3) are determined from triplicate water samples within each sampling location and then analyzed with gas chromatography. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement first occurred in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.



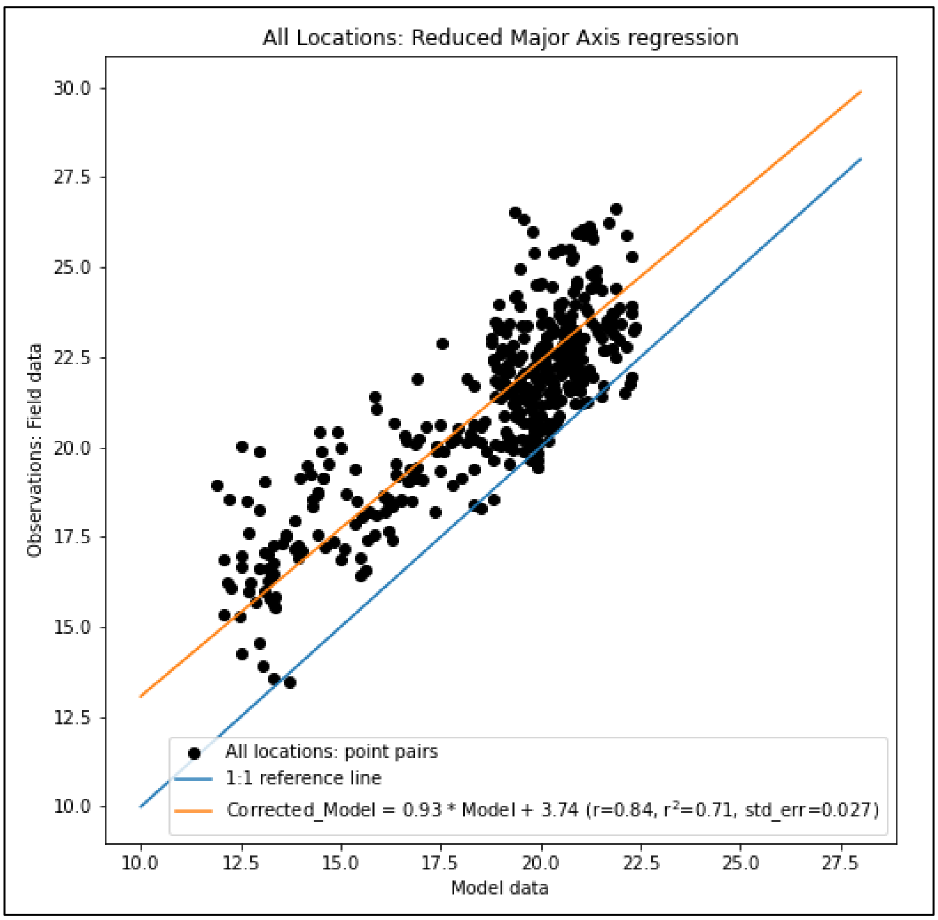
C8: Seston quality, defined as Chlorophyll-a per Total Particulate Matter (TPM), is determined by dividing each Chl-a value by each TPM value within the four study locations. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement first occurred in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.



C9: Seston quality, defined as Fatty Acids per Total Particulate Matter (TPM), is determined by dividing each Fatty Acid value by each TPM value for each of the four study locations. The dashed light grey box represents the larval development window predicted by the GDD model, and the dark grey solid-lined box represents the temporal window when settlement first occurred in each location. The settlement window is a one-week period, reflecting the one-week sampling interval.

APPENDIX D

D1: Utilizing observations of temperature, previously collected during a 2022 field campaign, RMA regression was used to compare modeled data with observations and further refine the climate model before making predictions of settlement. The additional refinement of the model applied a linear relationship, determined by RMA regression, to all coastal cells to account for the considerable warming that occurs in shallow bays where oysters inhabit.



D2: Time series of model original data, model corrected data, and real observations from 2022 at each sampling location to show what the coastal correction is doing.