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REPRODUCTION AND RECRUITMENT OF AMERICAN LOBSTER (HOMARUS AMERICANUS) IN THE GREAT BAY ESTUARY, NEW HAMPSHIRE

BY

ELIZABETH M. MORRISSEY

B.S., University of New Hampshire, 2009

THESIS

Submitted to the University of New Hampshire

In Partial Fulfillment of

The Requirements for the Degree of

Master of Science

In

Marine Biology

May, 2016

This thesis has been examined and approved in partial fulfillment of the requirements for the degree of Master of Science in Marine Biology by:

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<u>   5/5/2016   </u>
Date

Original approved signatures are on file with the University of New Hampshire Graduate School.

DEDICATION

This thesis is dedicated to my parents, who through creativity and grit, raised a marine biologist in a landlocked part of the world.

ACKNOWLEDGMENTS

I recently learned that it takes over thirty people to produce a Taylor Swift song. It took more people to get me through a Master's degree, and I would like to recognize and thank them. First and foremost, I would like to acknowledge my committee members who shared their wisdom and love of all things oceanic; Drs. Win Watson, Jason Goldstein and Hunt Howell. My advisor, Win, taught me how to build everything out of anything, a skill that I will take with me wherever I wander. Jason provided wonderful writing advice and Hunt made sure I never left his office without a thought-provoking question. All three encouraged my curiosity, while still managing to keep me on task.

I would like to thank several UNH grad students and personnel, who among other things served as editors, divers, field technicians and boat mechanics. This includes Helen Cheng, Tom Langley, Meghan Glenn, Jenna Rackovan, Kyle Ball, Rebecca Kibler, Liz Kintzing, Nate Rennels, Dave Shay and Noel Carlson. Thanks to Josh Carloni from NHFG and several NH lobstermen who helped with seasampling. I am indebted to extremely dedicated UNH undergraduates Nate Copp, Erika Moretti and Stephanie Sykes, who worked the same early and long hours in the field, and never questioned why we chased five-gallon drifter buckets around the estuary on the boat. My "significant math other" Brian Moore, patiently walked me through script writing and kept me sane and fed, for which I am grateful. Finally, I would like to thank my family and friends who are responsible for all of this, most having been there since the beginning. A special thank you Melissa, Ian, Mom and Dad, for regularly tolerating childhood trips to the Bronx zoo and Norwalk Aquarium so that I was able to watch the sea lions swim in circles for hours (still deeply fascinating). Without your encouragement, support and spare change to feed the zoo animals, I would not be where I am today.

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ABSTRACT

REPRODUCTION AND RECRUITMENT OF AMERICAN LOBSTERS (HOMARUS AMERICANUS) IN THE GREAT BAY ESTUARY, NEW HAMPSHIRE

by

Elizabeth M. Morrissey

University of New Hampshire, May, 2016

The overall goal of this research project was to determine if lobsters reproduce and settle in the Great Bay estuary (GBE), NH. First, I mapped the distribution and abundance of ovigerous lobsters carrying late-stage eggs in the estuary, during May and June of 2015. Ovigerous lobsters were concentrated in Little Bay and adjacent sections of the Piscataqua River, with CPUE in these areas of 0.12 ± 0.02 lobsters/trap haul. Very few were found in the regions furthest from the coast. Next, egg samples were collected from these lobsters, as well as from ovigerous lobsters captured along the NH coast and their hatch dates were determined based on their stage and the rate of egg development at their respective temperatures. The mean predicted hatching date of eggs carried by GBE lobsters was June-09 ± 11.8 days (SD), while the mean predicted hatch date of eggs carried by coastal lobsters was July-01 ± 9.5 days, nearly three weeks later. The GBE eggs most likely hatched three weeks later because of the difference in water temperatures between the two areas. Plankton tows were then conducted to determine if larvae were present in the water column at the time when I predicted that the eggs carried by GBE females would be hatching. The predicted hatch dates for the 35 stage I larvae captured ranged

from May-21 through July-19, with a mean predicted hatching date of June-28 ± 17.9 days . This encompasses almost a two-month period, which is longer than either range of predicted hatch dates from eggs obtained either from estuarine or coastal lobsters. However, the larvae that hatched earliest overlapped with when ovigerous lobsters hatched their eggs in the GBE, indicating that a portion of these larvae originated in the estuary.

Strong tidal currents influence particle transport (i.e., planktonic larvae) in GBE and my next goal was to determine if these currents would retain larvae, or carry them out to the Gulf of Maine. Surface currents were characterized using surface drifters (n=21) deployed near areas with the highest densities of ovigerous lobsters carrying late stage eggs in the GBE, as well as in the Piscataqua River (n=6) to determine if larvae were transported into the GBE from areas near to the coast. Drifter movements were extrapolated over 8-16 days (when larvae develop and settle) and over this time period, drifters released from all three locations were retained in the estuary. In fact, these data suggested that the greatest abundance of juvenile lobsters should be in areas that also had the highest densities of ovigerous females. Finally, to test this prediction and to determine if lobster larvae did, in fact, settle in the GBE, the distribution, abundance and composition (size frequency, sex ratio) of juvenile lobsters in the GBE was assessed using trawls consisting of two pairs of modified ventless traps and two pairs of juvenile collector traps. Sampling occurred at six study sites on a spatial gradient, ranging from the upper Piscataqua River to Great Bay proper. The smallest lobster (38 mm carapace length (CL)) was captured in the Piscataqua River, and the average size of lobsters increased as sites furthest up into the GBE (ranging from 66.51 ± 0.78 mm CL (SEM) in the river (n=185) to 88.67 ± 2.82 mm CL, n=2, in Great Bay proper). Only adult lobsters were found at the sites furthest up in the estuary, and the

adult sex ratio also became more skewed towards males in these areas. However, the sex ratios of juvenile lobsters were 1:1 at the four sites where they were captured (Fisher's Exact test, p=0.995), indicating that the skewed sex ratios of adult lobsters were likely the result of differential movements of males and females. Taken together, these data provide support for a residential and self-recruiting lobster population in the GBE, although the timing of larvae, as well as the characterization of currents using drifters reinforces that, to an extent, the GBE lobster population is supplemented by adults that migrate into the estuary and larvae originating from coastal lobsters that are carried into the GBE by tidal currents.

INTRODUCTION

<u>Rationale and Objectives</u>

The American lobster is an important recreational and commercial fishery in the Northwest

Atlantic, generating over 450 million dollars in revenue (ASMFC 2015). Lobsters are exploited

heavily in the Gulf of Maine (GOM), and support many local New England communities,

including those in coastal New Hampshire (ASMFC 2015). Unlike other commercial fisheries,

lobster populations are not overfished in the GOM, making it a lucrative resource and fishing

effort continues to increase (ASMFC 2015). Effectively managing the GOM stock includes

identifying sources for new recruits, connectivity between stocks, and quantifying subsequent

juvenile stages, which serve as projections for harvestable lobsters (Fogarty and Idoine 1986;

Steneck and Wilson 2001; Xue et al. 2008; Botsford et al. 2009). Obtaining a better

understanding of these processes is important because stocks are not closed or discrete entities

(Harding et al. 1983; Ennis 1986; Lindegren et al. 2014); for example, new recruits drift and are

transported from many locations (Ennis 1995; Xue et al. 2008; Chassé and Miller 2010; Incze et

al. 2010; Quinn and Rochette 2015) and adult lobsters, in particular ovigerous (egg-bearing)

lobsters, can migrate long distances (Cooper and Uzmann 1971; Campbell 1986; Campbell and

Stasko 1986; Pezzack and Duggan 1986).

The American Lobster Settlement Index (ALSI) is one of several projects evaluating the fishery

at a large spatial scale, monitoring juvenile lobsters from New England to Canada (Wahle et al.

2009). However, the index excludes many inlets, bays and estuaries, which are likely contributing to the fishery. For example, ovigerous females have been found in several of these areas, including the Great Bay estuary in New Hampshire (Watson et al. 1999; Langley et al. 2014). Therefore, these inlets, bays and estuaries represent an understudied, but potentially valuable, source of recruits to the fishery.

The overall goal of this thesis was to document lobster reproduction and recruitment in the Great Bay Estuary, New Hampshire, by determining if a self-recruiting lobster population resides in estuary. The first hypothesis I tested was that ovigerous female lobsters carrying late stage eggs were present in the estuary, and as a result of warmer estuarine waters in the spring, their eggs hatched earlier than those of coastal lobsters. I accompanied commercial lobstermen on fishing trips in late spring and early summer to quantify the distribution and abundance of females with late stage eggs and then I compared the development of eggs carried by lobsters in the estuary and along the coast. In addition, I sampled for larvae with plankton tows to validate the timing of hatch and both areas and determine if the larvae captured in the estuary originated from estuarine and/or coastal females.

After confirming the presence of ovigerous females in certain areas of the estuary during the time when their eggs should hatch, and demonstrating the presence of larvae in the water column, I tested my second hypothesis, which was that lobsters recruit to the estuary. To accomplish this goal, I used drifters to determine where larvae would be transported if they hatched in specific regions of the estuary. Then I measured the abundance and distribution of juvenile lobsters in potential settlement areas. Overall, both hypotheses were supported, and there was strong evidence of larval exchange with the coast. This work has several implications for lobster management, particularly because lobsters in estuarine systems may be a source of

recruit for coastal populations as well. Understanding the population dynamics and connectivity of lobster subpopulations may better support fisheries management efforts.

Life History

Ovigerous Lobsters

Current management practices include the protection of ovigerous (egg bearing) lobsters as these lobsters are the initial source for new recruits (Little and Watson 2003, 2005; ASMFC 2015). Sexually mature females typically molt and mate in the summer, incubate their eggs for 9-11 months, and then their eggs hatch the following spring/summer (Aiken and Waddy 1976; Waddy and Aiken 1992). Arguably, there is some investment in the offspring (Attard and Hudon 1987) and ovigerous lobsters adopt strategies to speed up the growth of embryos and maximize the survival of their larvae. (Templeman 1940; Cowan et al. 2007; Moland et al. 2011). Many ovigerous females undergo seasonal migrations and it has been proposed that they do this in order to maximize the water temperatures to which their eggs are exposed and thus enhance the rate of egg development (Aiken and Waddy 1986). However, recent studies of lobsters along the coast of New Hampshire suggest that these seasonal movements do not necessarily enhance the rate of egg development and thus might serve additional roles (Goldstein and Watson 2015a). Egg development is influenced by local temperature regimes, and the initial onset of egg hatching is driven by a narrow range of surface temperatures, as waters warm to 12.5 ^{o}C (Hughes and Matthiessen 1962; Harding et al. 1983; Fogarty et al. 1991). Ovigerous lobsters display several strategies to increase the survival of their larvae, for example they hatch their clutch over a couple of weeks to drive down dispersal rates and reduce competition between larvae (Ennis 1975). In addition, ovigerous lobsters appear to be able to detect environmental conditions, and

release larvae near areas of good thermal habitat to increase their chances of survival through settlement (Miller 1997). This might be one alternative explanation for why ovigerous females along the NH coastline migrate to deeper water during the fall so their eggs will hatch the following spring in offshore waters (Goldstein and Watson 2015a).

Larval Lobsters

Initial hatching and the duration of the hatching season varies by region as a result of temperature, because the onset of hatching is driven by warming of surface water temperatures (Harding et al. 1983; Fogarty et al. 1991). As a result, there are often several large pulses of larvae during the hatching season. Typically, the first pulse occurs early in the spring when water temperatures become optimal for larval growth, and a second pulse occurs before temperatures become suboptimal for larval survival during the fall (Ennis 1975; Aiken and Waddy 1986). Broadly, hatching occurs from May-September and larvae appear as early as mid-May in Rhode Island, where waters stay warmer year-round, and as late as July in coastal Maine, where water temperatures are slower to warm (Harding et al. 1983; Wahle and Incze 1997). Lobster larvae remain above the thermocline, and generally above 3 m, while they undergo a series of molts through three planktonic stages and one post larval stage in preparation for settling on the bottom (Collings et al. 1983; Matthiessen and Scherer 1983; Harding et al. 1987; Boudreau et al. 1992).

After hatching, larval lobsters tolerate a wide range of temperatures (5-30 ^{o}C), but growth rates are negatively impacted by temperatures outside of their preferred range (Templeman 1936) and laboratory studies show that growth rates are maximized between 15-18 ^{o}C (Mackenzie 1988). Additionally, when growing in optimal environments, larvae spend less time time in the water column, and thus their time in the water column is believed to be reduced in a natural setting

(Hudon and Fradette 1988; Annis et al. 2007). The amount of time larvae spend in the water column determines, in part, where they settle, because during this time their movements are most strongly influenced by surface currents (Katz et al. 1994; Palma et al. 1999; Xue et al. 2008). Advection processes determine the distribution of larval lobsters on the large scale (Palma et al. 1999; Xue et al. 2008; Burdett-Coutts 2010), however larval behavior (i.e., swimming) influence settlement choices as well (Botero and Atema 1982; Ennis 1986; Cobb et al. 1989; Palma et al. 1999). While it is thought that recruits are typically sourced from non-local lobsters, (Incze and Naimie 2000), there is some evidence that the combination of oceanographic and behavioral factors allows lobster larvae to remain near parental grounds (Ennis 1986; Øresland and Ulmestrand 2013).

Juvenile Recruitment

Larval lobsters settle to the seafloor, immediately burrow or seek shelter, and proceed to grow quickly (Berril 1974). These early benthic phase (EBP) lobsters (size 5-40mm) are shelter restricted, and search for complex habitat while settling, such as cobble (Wahle and Steneck 1991). While in many areas higher densities of EBP lobster are found in cobble than featureless substrate, there is increasing evidence that larval lobsters are able to settle, and even grow faster, in simple substrates such as mud (Tang et al. 2015). Additionally, juvenile lobsters use peat as a nursery ground in some Cape Cod inlets (Able et al. 1988). Paired with other data, this suggests that new recruits of juvenile lobsters are able to settle in a variety of environments (Wahle 1993; Dinning and Rochette 2014). Initial recruitment occurs when larvae are retained, settle and survive to older and commercially viable stages (Harding et al. 2005; Xue et al. 2008; Cowen and Sponaugle 2009).

Survival through settlement is marked by the presence and abundance of sequential year classes (Fogarty and Idoine 1986). The presences of early stage (i.e., young of year, juvenile) lobsters indicate that they are residents of a given area, because they exhibit limited movement (Wilder 1963; Lawton and Lavalli 1995; Morse and Rochette 2012). Therefore, in this study, I sampled for juvenile lobsters as a proxy for EBP settlement.

Lobsters in Great Bay Estuary, NH

Until recently, it was believed that the use of the GBE by lobsters was seasonal, like other northeast Atlantic estuaries. The American lobster is able to utilize estuaries, because although they are stenohaline, they have limited osmoregulation capacities (Dall 1970) and can detect small changes in the salinity and temperature (Jury et al. 1994a,b; Crossin et al. 1998; Jury and Watson 2013). They use these senses to behaviorally thermoregulate, seeking their preferred temperature of ~ 16 $^{\circ}$C, and avoiding temperatures below 4 $^{\circ}$C and above 20 $^{\circ}$C (Crossin et al. 1998), and to avoid low salinities (Jury et al. 1994b), such as those that occur in the spring during the spring snowmelt, and following large storms (Jury et al. 1995).

While it is accepted that lobsters migrate on a seasonal basis to avoid harsh estuarine conditions, a recent ultrasonic telemetry tracking study revealed that some lobsters remain year round in the GBE (Langley et al. 2014). Some of these lobsters were carrying eggs, and these eggs were likely hatched directly into GBE waters. In addition, some limited data show that lobster larvae (all but stage II) were present in the GBE (NHFG 1989,1990) and EBP lobsters were captured during suction sampling studies (NHFG 1989, 1990, 2008). There is also some evidence that water currents in the GBE have the capacity to retain new recruits, as it is a well-mixed, largely recessed system (Brown and Arellano 1980; Goldstein 2012a), with a strong flood tides (Ertürk

et al. 2002). Finally, some habitats in the GBE appear to be suitable for supporting a lobster throughout its life cycle (Becker 1994; Grizzle et al. 2008; Short et al. 2001).

While juvenile lobsters have been found in the GBE, quantifying them is difficult. Juvenile lobsters are not selectively targeted by standard lobster traps and they often avoid entering traps when larger conspecifics are already inside (Miller 1995; Jury et al. 2001). Additionally, small lobsters are able to easily escape through the large mesh and escape vents of traps (Miller 1990; Tremblay et al. 1998). This makes surveying for smaller lobsters difficult, and little effort has been made to design traps to target them because they are not commercially important. Therefore, other survey methods (i.e., SCUBA surveys, sea-sampling) are often used to target them instead (ASMFC 2015). In this project I used four different types of lobster traps, including modified juvenile collectors, to try and quantify the distribution and abundance of juvenile lobsters in the GBE.

While the available data suggests that a self-sustaining population of lobsters might exist in the GBE, many of these data are from preliminary studies and are limited. Therefore, the overall goal of my thesis was to obtain sufficient data to confirm this hypothesis. The number of ovigerous lobsters has not been quantified, and the timing of hatch in the estuary is unknown. Additionally, while larval lobsters have been captured in the GBE, their presence has not yet been linked to the timing of hatch in the estuary and thus it has not been determined if they come from ovigerous females residing in the estuary, or from females in the Gulf of Maine (i.e., NH coast). While several phases of lobster life history are present in GBE, the possibility that there is a self-sustaining resident population of American lobsters in the GBE has never been rigorously explored and is the overall goal of my MS Thesis Research.

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CHAPTER 1

REPRODUCTIVE DYNAMICS OF LOBSTERS IN THE GREAT BAY ESTUARY

Abstract

The overall objective of this study was to determine if female lobsters are present in the Great Bay estuary (GBE) when their eggs hatch and lobster larvae are present in the water column during the hatching period, which would indicate they originated from estuarine, rather than coastal lobsters. Ovigerous lobsters were found in greatest abundances in Little Bay and the Piscataqua River (CPUE = 0.12 ± 0.02 lobsters/trap), while significantly fewer were found in the upper reaches of Great Bay (0.02 ± 0.02 lobsters/trap, Mann-Whitney p = 0.004). Lobsters in the GBE (n=58) were carrying more developed, later-stage eggs, than those carried by lobsters sampled in NH coastal waters at the same time (n=39). The hatch date of the eggs carried by estuarine and coastal lobsters was then estimated, based on water temperature and eggs stage and eggs in the GBE were predicted to hatch earlier (range May-21 to June-23; mean hatching date of June-09 ± 11.8 days (SD)) than eggs carried by coastal females (range June-11to July-23; mean hatch date of July-1 ± 9.5 days (SD)). These estimated hatch dates were confirmed by holding lobsters captured in both locations in the laboratory, at ambient temperatures, until their eggs hatched. Plankton tows were used to document when lobster larvae (n=35) were most abundant in the GBE, and their predicted hatch dates were back-calculated to determine if they were likely to have originated in the GBE.

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Stage I larval lobsters were captured from the last two weeks in May, when only estuarine eggs were hatching, to the end of sampling in late July, when estuarine eggs were no longer hatching, but coastal eggs were still hatching. The GBE warmed at a faster rate in the spring ($0.135\,^{\circ}$C / day vs. $0.117\,^{\circ}$C/day at the coast), and remained warmer than the coastal waters for the duration of the study. This was probably the cause of earlier hatching events and presence of larvae in the GBE in May. These findings provide support for a residential and self-recruiting lobster population in the GBE, although the timing of larvae indicates that coastal lobsters also provide new recruits to the estuary.

Introduction

The American lobster (*Homarus americanus*) ranges from North Carolina to Newfoundland, encompassing both inshore and offshore subpopulations. Surprisingly, given their limited abilities to osmoregulate (Dall 1970; Jury et al. 1994b; Charmantier et al. 2001), they are also found in estuaries, bays and inlets ranging from Rhode Island to Canada (Thomas 1968; Thomas and White 1969; Munro and Therriault 1983; Wahle, 1993; Howell et al. 1999). Lobsters use these warm water systems to aid in somatic growth, limb regeneration (Aiken and Waddy 1986; Moriyasu et al. 1999) and to initiate maturity and accelerate egg development (Templeman 1940; Aiken and Waddy 1986; Little and Watson 2003). Seasonally, estuaries may provide better thermal habitats, and therefore less stressful environments for larval lobsters, and in a survey of Narragansett Bay, Wahle (1993) found a gradient of early benthic phase (EBP) lobsters, with the highest abundance close to the mouth of the bay. Additionally, juvenile lobsters were documented using peat as a nursery ground in a Cape Cod inlet (Able et al. 1988) and eelgrass in Great Bay estuary (GBE), in New Hampshire (Short et al. 2001).

While estuaries often have large numbers of lobsters, it is generally accepted that these lobsters migrate there from nearby coastal waters (Templeman 1935; Watson et al. 1999). In Îles-de-la-Madeleine, Canada, lobsters have been shown to undertake seasonal migrations into, and out of, the estuary (Munro and Therriault 1981, 1983). Previous studies have demonstrated that many of the lobsters in the GBE undertake seasonal movements (Watson et al. 1999) most likely to behaviorally thermoregulate and avoid low salinities during storm events and over spring runoff (Jury et al. 1994a,b; Jury et al. 1995, Jury and Watson 2013). Therefore, it is generally accepted,

that many of the lobsters in estuaries, like the GBE, migrate there from the coast. Furthermore, given the skewed sex ratio and paucity of ovigerous (egg-bearing) females (Howell et al. 1999), it is also thought that very little lobster reproduction and subsequent recruitment occurs within the estuarine system. However, recent findings indicate that this view might not be entirely correct.

In a recent study of lobster movements in the GBE, Langley et al. (2014) discovered that many ovigerous (berried) females overwintered in certain locations of the estuary and remained there until their eggs hatched. This observation is consistent with at least one other study that examined the presence of lobsters in estuaries over the winter. Thomas (1968) found lobster buried in the mud over the winter in the Bideford River Estuary in Canada. Additionally, there is emerging evidence that lobsters, including ovigerous females do not always carry out seasonal migrations, and by remaining in local areas they maintain subpopulations (Rowe 2001; Øresland and Ulmestrand 2013; Goldstein and Watson 2015a). In particular, ovigerous lobsters might undertake large migrations before they extrude their eggs (Campbell 1986, Cooper and Uzmann 1971; Cowan 2007), but they typically do not move very far during the later stages of egg development (Saila and Flowers 1968; Jarvis 1989; Goldstein and Watson 2015a). In fact, because the location of ovigerous lobsters carrying late stage eggs is also the site where their larvae hatch, it has been proposed that movements of berried females to specific areas might have evolved to enhance the survival of hatching larvae (Jarvis 1989; Goldstein 2012b; Goldstein and Watson 2015a). Therefore, one goal of this study was to test the hypothesis that there are aggregations of berried females with late stage eggs in certain regions of the GBE.

While ovigerous lobsters have been found in certain areas of the GBE, and some evidence suggests that they are there when their eggs hatch (Goldstein 2012a; Langley et al. 2014), it is not clear if their larvae are retained within the estuary and thus serve to perpetuate a resident population of estuarine lobsters. There is some evidence for a net inward current in the GBE that is capable of retaining planktonic larvae due to strong asymmetrical flood tides (Ertürk et al. 2002). Although lobster larvae have been captured in the GBE, most of plankton tows have been taken place from late June to early September and most larvae were captured in Little Bay and the Piscataqua River (NHFG 1989, 1990). These surveys coincided with the time frame during which larvae were captured in NH coastal waters (Grabe et al. 1983; Normandeau 2014). Because the water in the estuary warms up much faster than along the coast, and lobster egg development and hatching are strongly influenced by water temperature (Templeman 1940; Hughes and Matthiessen 1962; Perkins 1972; Campbell 1986; Goldstein 2012; Goldstein and Watson 2015a,b), my working hypothesis was that the eggs carried by estuarine lobsters might hatch sooner than those along the coast and, as a result, larvae would appear in the water column sooner. One of the other major goals of this project was to determine if lobster recruits to the GBE come from larvae from coastal waters that are carried into the estuary, larvae from berried females residing in the estuary, or both. This goal was achieved by comparing the time frame during which larvae were captured in the estuary to the time frame during which the eggs carried by both estuarine and coastal lobsters hatched.

In general, the GBE offers a unique opportunity to investigate if a lobster subpopulation can reside in an estuary, whether they are self-recruiting, and if they are a source of recruits for nearby coastal populations. The first objective of this portion of my thesis was to determine where ovigerous lobsters are distributed in the Great Bay estuary and to confirm that some of

them are carrying late stage eggs in the spring when hatching most likely would occur. My second objective was to document the timing and duration of the hatching season for lobsters from the Great Bay estuary and compare it to late stage females captured along the coast of New Hampshire. My third objective was to conduct plankton tows to document when lobster larvae were present in the water column in the Great Bay Estuary. These data were compared to the times when eggs from lobsters held in captivity in the laboratory hatched. Finally, I compared the time frame when eggs hatched in both locations (coast and estuary) to the abundance of larvae captured in plankton tows to determine if the larvae captured in the estuary were more likely to have come from estuarine or coastal females.

Materials and Methods

Study Site

The Great Bay estuary (GBE) is located in southeast New Hampshire (Figure 1.1) and is comprised of three distinct bodies of water: the Piscataqua River, which articulates with the Gulf of Maine; Little Bay, which extends from the Piscataqua River to Great Bay, and Great Bay, which is approximately 25 kilometers from the coast. Seven tributary rivers provide fresh water to the GBE (Jones 2000) and due to the nature of the tides, it takes several weeks for water from Great Bay Proper to reach the coastline (Bilgili et al. 2005). There are both daily and seasonal fluctuations in water temperature and salinity in the GBE, which creates a challenging environment for lobsters (Jury et al. 1995).
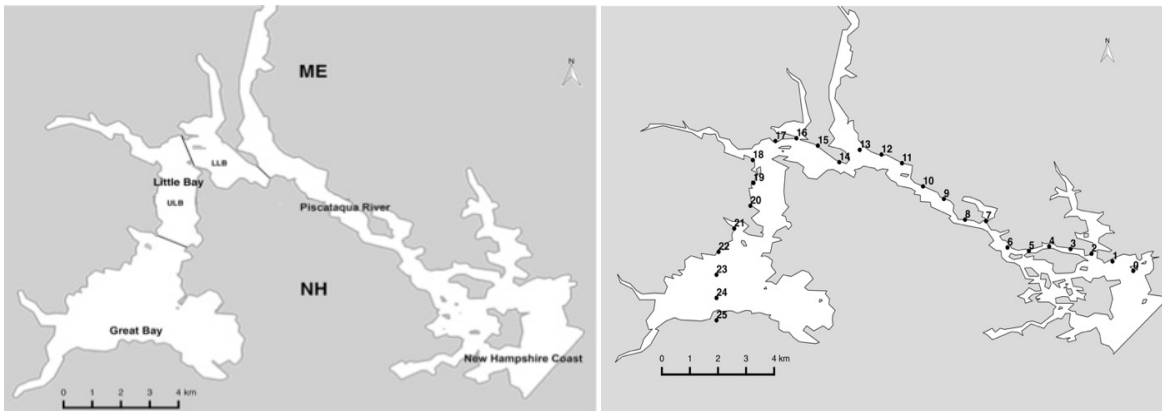
Figure 1.1 The Great Bay estuary (GBE, left panel), which is located in southeast New Hampshire and encompasses three distinct areas: The Piscataqua River, Little Bay, and Great Bay (grey lines separate the areas). For my purposes, we often divide Little Bay into upper Little Bay (ULB, closer to Great Bay) and lower Little Bay (LLB). For analyses, the GBE was "linearized" from 0-25km (right panel). The mouth of Piscataqua River is located at km 0, and the furthest point (25km) is at the edge of Great Bay.

As a result of daily and seasonal fluctuations, salinities are typically lower in the spring and higher in the summer. Generally, there is a gradient of decreasing salinity and increasing temperature as distance from the coast increases. In Little Bay, salinities and temperatures range year round from approximately 15-33 psu and 3-23° Celsius (^{o}C) and 10-30 psu and 2-24 ^{o}C in Great Bay (Fulton et al. 2013). Generally, water temperatures remain below 20 ^{o}C in both areas, except for a few weeks in the summer (Morrissey, personal obs.). Additionally, the substrate within the GBE is varied and complex (Short 1992). Nelson (1981) identified five major substrate groups in the GBE: 1) eelgrass, 2) mudflats, 3) saltmarsh, 4) channel habitat/sub tidal habitat and 5) rocky intertidal habitat. Interestingly, SCUBA and video surveys have identified certain areas within Little Bay and the Piscataqua River where the habitats are very similar to the coastal marine environment (Becker 1994; Grizzle et al.2008; Goldstein 2012a).

Egg Hatching

Sea sampling

Ovigerous female lobsters were collected during sea sampling trips with commercial lobstermen in May and June of 2015 (NHFG Permit MFD 1520) to confirm the onset of late-stage eggers in GBE and at the coast. In the GBE, sampling occurred on May-18, May-25, June-9 and June-22 and along the NH coastline on May-11, June-18 and June-25. Sea sampling trips covered most of the GBE including two kilometers of the upper Piscataqua River, but did not include the furthest sections of Great Bay (Figure 1.1). For analysis purposes, the estuary was "linearized" from the mouth of the Piscataqua River (kilometer 0 is the mouth of the Piscataqua River at the coast) to the end of Great Bay Proper (25 km; tributary rivers were not included; Figure 1.1). For each lobster captured we recorded the location, carapace length and abdomen width. In addition, 15-

20 eggs were removed from the midpoint of the ventral surface of the abdomen, between the

second and third rows of pleodpods (Figure 1.2, Helluy and Beltz 1991). Egg samples were

stored in sterilized seawater for subsequent processing in the lab. Lobsters were then
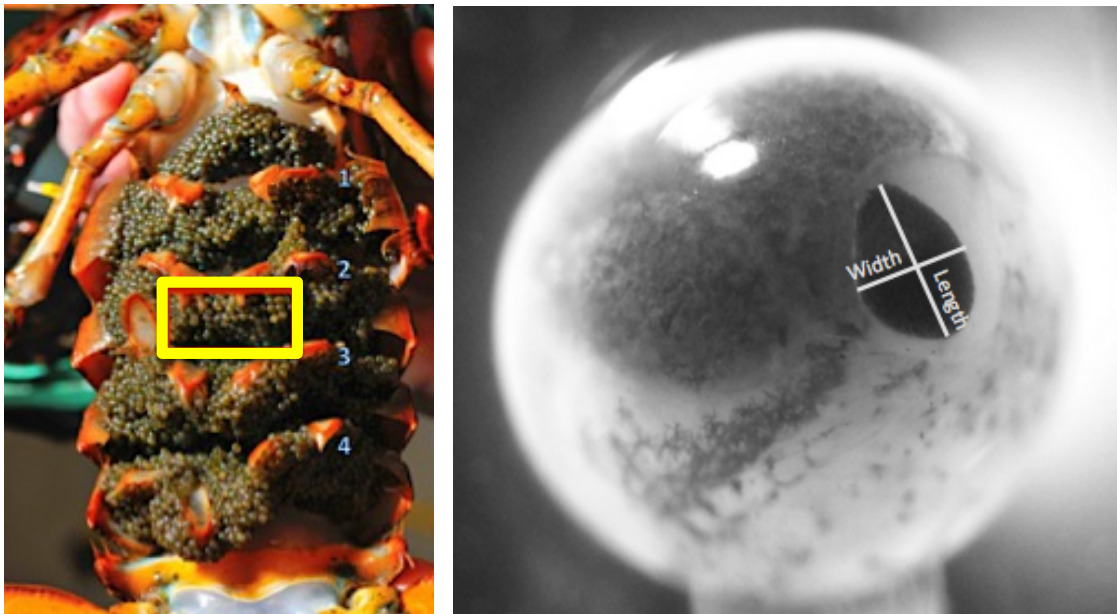
immediately released where they were captured.

Figure 1.2 The left panel shows the location from which egg samples were removed (yellow box), to keep sampling consistent. The right panel shows the technique used for determining the Perkins Egg Index. Both the width and length of eyespots were measured and these values were used to calculate the area of the eyespot (adapted from Goldstein 2012b). Length is approximately 500 microns (μm).

The abundance of ovigerous lobsters was calculated as the number of ovigerous lobsters/ trap

haul (catch-per-unit-effort, CPUE). For analysis purposes, data from all trips were tested for

assumptions of normality using JMP ver. 11.21.1 (SAS Institute, Cary, BC) and then averaged

together, because there were no significant differences between trips (Kruskal-Wallis, p=0.618).

Abundance data were not transformed, and the non-parametric Kruskal-Wallis ANOVA (α =

0.05) and the post hoc Mann-Whitney-U test were used to compare of relative abundance

(CPUE) of ovigerous females between the four regions in the estuary; the river, lower Little Bay,

upper Little Bay and Great Bay. Standard error of the means (SEM) were used as the measure of variance, and was incorporated for all other analyses unless otherwise noted The density and distribution of ovigerous lobsters were mapped using QGIS software (ver 2.12, QGIS Geographic Information System. http://qgis.osgeo.org).

Egg Development and Hatch Predictions

A subset of 10 eggs from each egg sample were selected haphazardly and used to determine developmental status, as described in Goldstein and Watson (2015b). Only embryos visibly enclosed in egg envelopes were used for analysis and hatching or hatched pre-larvae were excluded from analysis. Digital pictures were taken of each egg using an Olympus SZX7 dissecting scope and Nikon camera (SMZ 2T), at 3.2x magnification. Egg images were uploaded to Image J software (http://imagej.nih.gov/ij) to measure the size of the eyespots (Figure 1.2). Eyespots tended to have an oval shape and so I calculated an "average diameter" for each eyespot to the nearest 0.01 micron for each sample using the equation $W_{i=}$ (L+W)/2, where L= longest length of the eyespot and W= longest width of the eyespot (Perkins 1972). Linear regression analyses (as done in Perkins 1972) were used to ensure that only normally shaped eggs were used in subsequent analysis. All egg measurements outside of the 95% confidence interval were excluded from further analysis.

One goal of this study was to determine if the eggs carried by estuarine lobsters hatch earlier than those carried by coastal females. To estimate when the eggs obtained from females during sea sampling would have hatched we used a modification of the Perkin's Eye Index (PEI, Perkins, 1972):

$$Z_{i \to h} = \frac{W_h - W_i}{-8.3151 + 2.6019T_{i^\circ C}} - \frac{(\Delta T * W_h/W_i) * (W_h - W_i)}{7}$$

where $Z_{i \text{-} h}$ is the number of weeks for hatching, W_i is the average diameter of the eye

(calculation shown above), W_h is the size at which egg development is complete; and $T_{i^\circ C}$ is the

average temperature regime (Helluy and Beltz 1991). The term W_h was standardized to 570 μm,

because it represents the size when lobster eggs in New Hampshire complete development

(Goldstein and Watson 2015a). Weekly temperatures (starting with the week prior to the first sea

sample date) were used to calculate T, as it reflected the most realistic thermal regime change

that lobsters were exposed to during the spring and summer. In addition, the PEI equation was

modified by adding a term to compensate for the effects of rate of temperature change (ΔT) on

the rate of egg development. The rate of temperature change was calculated by taking the slope

of temperature change from May-July at both the coast and estuary. Once predicted hatch dates

were obtained for all egg samples, the range was compared between the estuary and coast using

nonparametric Kruskal-Wallis ANOVA ($\alpha = 0.05$) and the post hoc Mann-Whitney-U test using

the statistical package JMP ver. 11.2.1 (SAS Institute, Cary, NC), as the data did not meet

parametric assumptions of normality and homogeneity. Additionally, the progress (%

development) of egg development was compared between the two locations.

Development of eggs in the laboratory

A subset of nine lobsters, obtained during the Great Bay sea sampling trips, were held at the

Jackson Estuary lab (JEL) in Durham, NH from June-18 to June-30. A second subset of seven

lobsters were obtained from NHFG during coastal sea sampling trips and were held at the

Coastal Marine Lab (CML) in Newcastle, NH from May-12 to July-20. All lobsters were

measured, tagged with sphyrion tags, and held in a 0.9 meter round fiberglass tanks supplied with ambient seawater. Lobsters were partitioned into separate areas of the tank, and provided with shelters, a natural cobble bottom and were exposed to natural light conditions. They were feed live mussels, rock crabs and Atlantic herring weekly. Onset Hobo temperature loggers (model UA-002-64, Onset Computer, Bourne, MA) were used to record both tank temperature and ambient water temperatures at both locations.

Weekly subsamples of five eggs were obtained from each female to monitor egg development using the methods described above. Egg clutches were checked visually each week for signs of hatching and once they were near hatching, they were checked more regularly. Larvae were retained in tanks by placing fine mesh over the outflow in the center of the tank. I designated the date when larvae were first observed in the water as the hatch data for the clutch of eggs carried by each lobster.

The development of the eggs carried by the lobsters held in this incubation study were used to calibrate the new term for the PEI index. The PEI index is effective for predicting hatch dates of eggs at a given temperature, however it is not as useful for predicting the hatch dates of lobster eggs exposed to a more naturally changing temperature regime (Goldstein and Watson 2015b). As the objective of this study was to predict hatch dates accurately, regardless of the effect of temperature, an additional term was added to the PEI index and then this modified equation was used to predict when an egg of a given stage, exposed to a given thermal history, would hatch. The term derived to account for the effects of temperature change on egg development was as follows:

$$\frac{(\Delta T * {}^{W_h}\!/\!_{W_i}) * (W_h - W_i)}{7}$$

This term was derived from comparing the rate of development to the rate of temperature change

of lobsters from the incubation study (Figure 1.3).
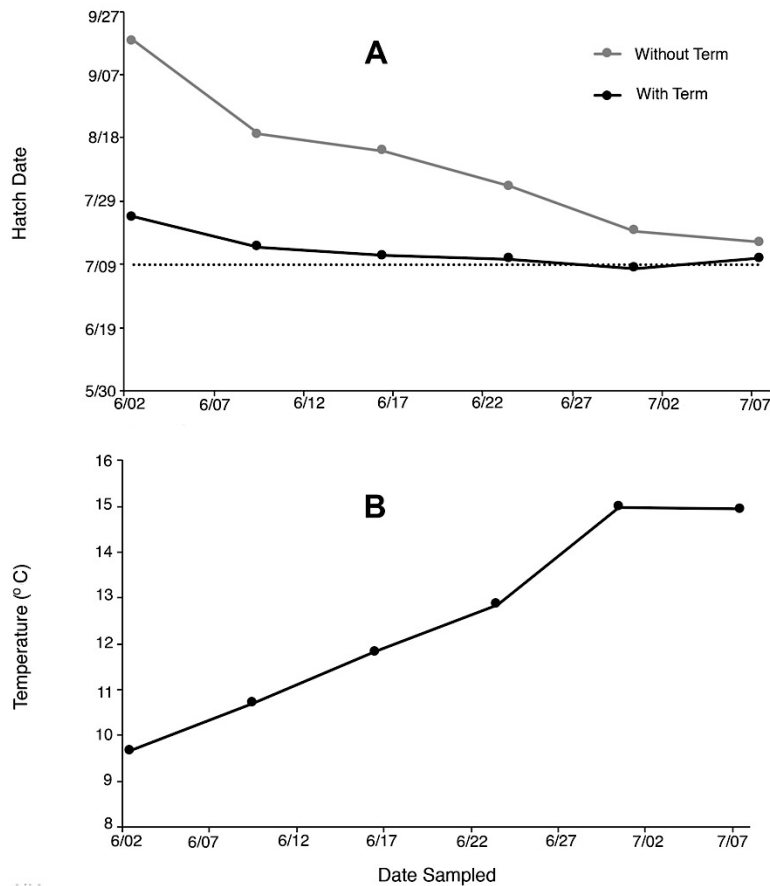
Figure 1.3 Modified method for predicting hatch dates based on modified PEI and water temperature. A) The closer in time samples were obtained to the actual hatch date (dashed line), the better the match between predicted and actual hatch dates. B) This was due, in part, to the fact that water temperatures were increasing each week. However, when the PEI equation was modified to take changing water temperature into account, it was possible to more accurately predict hatch dates with egg samples obtained early in the season. These data represent hatch predictions for one lobster.

Temperature rates were measured over the time frame of 5/6- 7/6. The rate of temperature change was 0.147 degree/day in the tanks at the estuary and 0.117 degree/day in the tanks at the coast. The term allowed for a more accurate hatch date prediction, despite temperature change.

The accuracy of using this modified equation was tested using egg samples from ovigerous lobsters held at the coast, and compared against their known hatching dates. The modified index provided more accurate predictions of hatch dates (Figure 1.3), regardless of which week eggs were sampled (Figure 1.4).
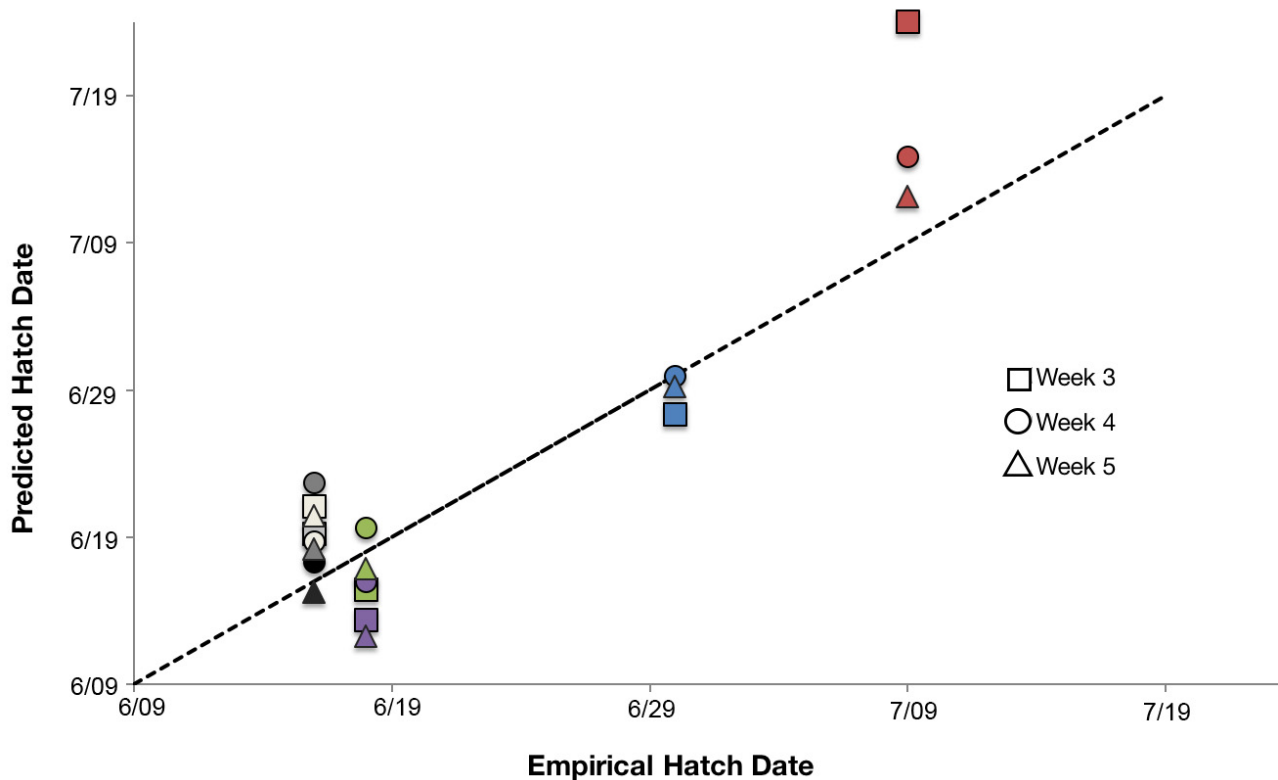
Figure 1.4 Comparisons between predicted hatch dates (using the modified PEI equation) and empirical (actual) hatch dates of lobsters (n=7) held at the coast. It was determined that modified PEI equation accurately predicted hatch dates. Additionally, predicted hatch dates remained constant from the third week that egg samples were obtained (June 2) to the fifth week (June 16). When comparing weekly hatch dates predictions to the empirical data, there were no differences (p=0.81, df =3). Each color represents one lobster, and the dotted line represents a perfect fit to the empirical hatch dates.

Larval Studies

Plankton tows

Plankton tows were conducted in lower Little Bay and upper Little Bay from 5/27- 7/29/15 to sample for larval lobsters in the water column during the time of year that lobster eggs were likely to be hatching in the estuary (Figure 1.5).
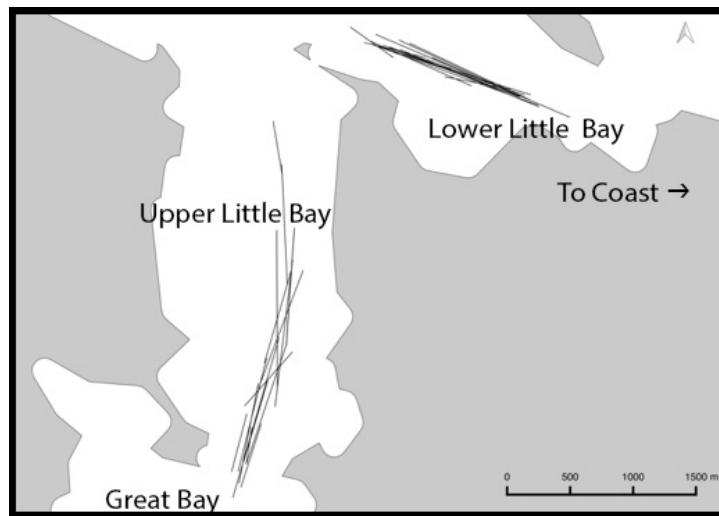
Figure 1.5 The location of plankton tows carried out in the GBE. A total of 38 tows were conducted, and each line on the map represents one tow.

Tows occurred twice weekly during morning and evening hours, for a total of four tows a week. Two 15' 500 micron 1m diameter neuston nets were towed 0.5m below the surface for 30 minutes. Due to variable weather conditions, sampling did not always take place on the same days of the week. A General Oceanics flowmeter (model 2030R) was attached to the mouth of one net, and the volume of water sampled was calculated for each tow using the following equation:

$$m^3 = \frac{(3.14 \text{ x Net Diameter}^2) * \text{ Tow Distance}}{4}$$

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Coordinates of the start and end of a tow, weather conditions, phase of the tide cycle, distance

traveled (km) and boat speed (kts; boat speed was kept consistent during sampling, so overall

average boat speed was used when these data were missing) were recorded during each tow.

Temperature data were obtained from a YSI Sonde (model 6600 V2-4, YSI Inc.,Yellow Springs,

Ohio) located in upper Little Bay (Figure 1.6). The abundance of larvae was quantified as the

number of larvae per 1000 meter^3 of water passing through the net. Larvae abundance was

calculated by dividing the total number of larvae captured per week by the sum of water volume

sampled per week at each site. The geometric means of the catch data were calculated, and the

abundance of larvae was compared over time (per week/month) using a non-parametric Kruskal-

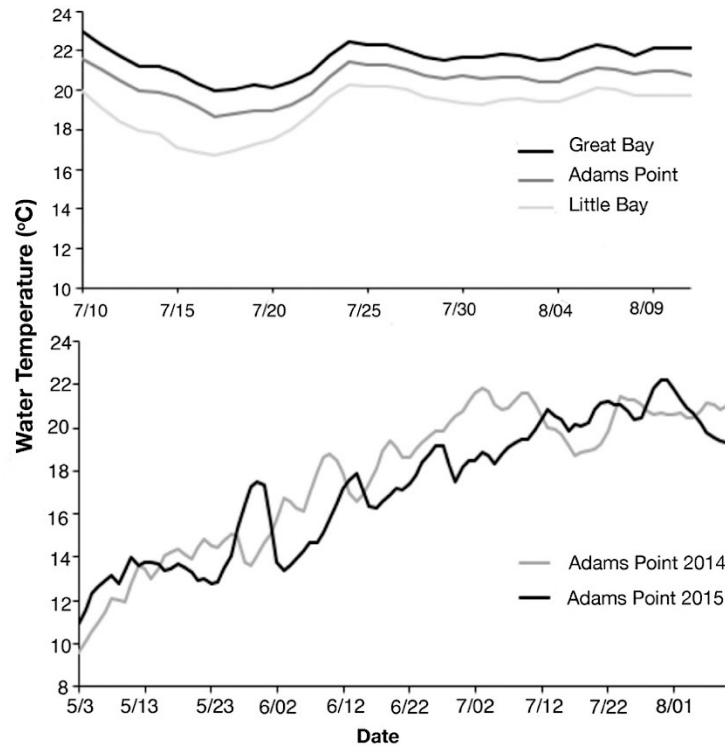Wallis ANOVA test (the data failed tests of normality and heterogeneity).

Figure 1.6 Water temperatures in the GBE (2014 and 2015). A) Water temperatures from July to October 2014 in upper Little Bay, Adams Point (which separates Little Bay from Great Bay) and a Great Bay site. B) Water temperatures from the Adams Point site in 2015, when plankton tows took place. Temperatures were not obtained from the other two sites in 2015, but temperature trends remained similar at the Adams point site.

Hatch prediction

Larvae captured during plankton tows were photographed, and the photos were then used to determine stage using the methods outlined by Aiken and Waddy (1986). Additionally, intermediate stages were noted using personal observations. For instance, while stage I larvae were identified by poorly defined chelae, a triangular, underdeveloped tail and lack of pleopods on the abdomen, Intermediate late stage I larvae were identified by better defined chelae, and small pleopod buds. The capture date and larval stage were then used to predict a hatch date using a formula derived from Harding et al. (2005) and adapted from Mackenzie (1985, 1988). The equation was used to calculate the duration in days from hatch up to stage II (i.e., all the way

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through Stage I) where Days $=1305T^{-2.02}$ (where T is temperature). Average weekly water temperatures were obtained from the YSI probe in upper Little Bay, as described above. While many larvae hatched in Little Bay where the water was slightly colder, the location of the YSI probe likely represented temperatures that free floating larvae were exposed to (Figure 1.6). The resulting data provided an estimate of when the captured larvae first hatched, and these data were then compared to the predicted hatch dates for eggs carried by the ovigerous females sampled at sea. These comparisons were used to determine if larvae obtained in plankton tows were more likely to have originated from the estuary, the coast, or both.

Egg Hatching

Sea sampling

A total of 64 ovigerous lobsters were captured during four sea sampling trips in the Great Bay estuary and 39 were caught during three trips along the NH coast. The average carapace length (CL) of the ovigerous lobsters obtained in the estuary was 85.08 ± 0.56 mm (range 78-100 mm CL) while the coastal females averaged 86.13 ± 1.77 mm (range 70- 134 mm CL). Size did not differ significantly between the two areas (unpaired t-test, $p = 0.58$). Of the lobsters captured in the estuary, six were already hatching (visually assessed), while none of the coastal females were in this condition until the June-18 trip (although observations were limited to one prior sea sampling trip on May-12).

The abundance of ovigerous lobsters did not differ over the four sampling trips and therefore catch data were pooled for further analysis (Table 1, $p = 0.62$, df $= 3$).

Table 1.1 Average CPUE of ovigerous lobsters from sea sampling trips in the estuary. Catch from the third trip was lower because only half of the trawls were fished. Either 10 or 20 traps were fished per trawl.

Date	Trawl Hauls (n)	Average CPUE $\pm$ SEM
5/18	21	0.057 ± 0.021
5/25	24	0.063 ± 0.014
6/9	16	0.034 ± 0.011
6/22	30	0.060 ± 0.021

Ovigerous lobsters were not evenly distributed within the estuary, and the greatest abundance was in Little Bay (Figure 1.7). There were significantly fewer ovigerous lobsters found in the upper reaches of Great Bay (Great Bay and upper Little Bay combined, 0.02 ± 0.02 lobsters/trap), compared to the lower sites (lower Little Bay and river combined, 0.12 ± 0.02 lobsters/trap, $p = 0.004$, df $= 1$, Figure 1.7). In contrast, the CPUE from the coastal sites (the lower part of the Piscataqua River to Seabrook, NH) was approximately twice as high (0.24 ovigerous lobsters/trap over the same time frame of May-June, NHFG 2015).
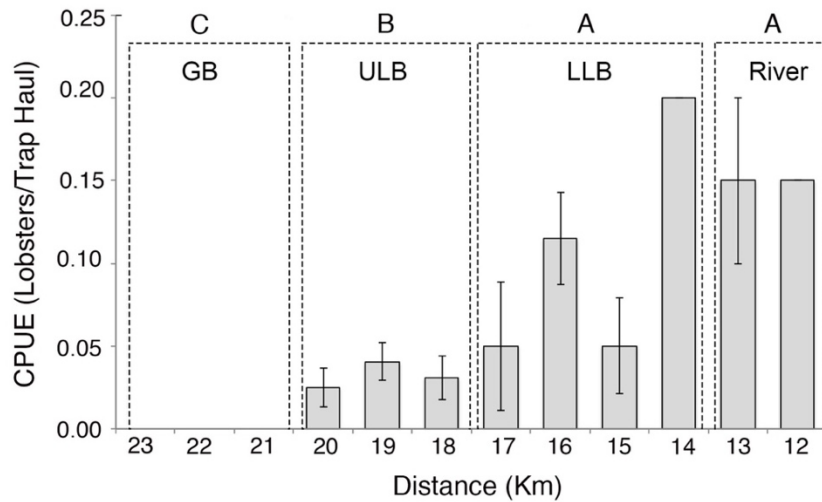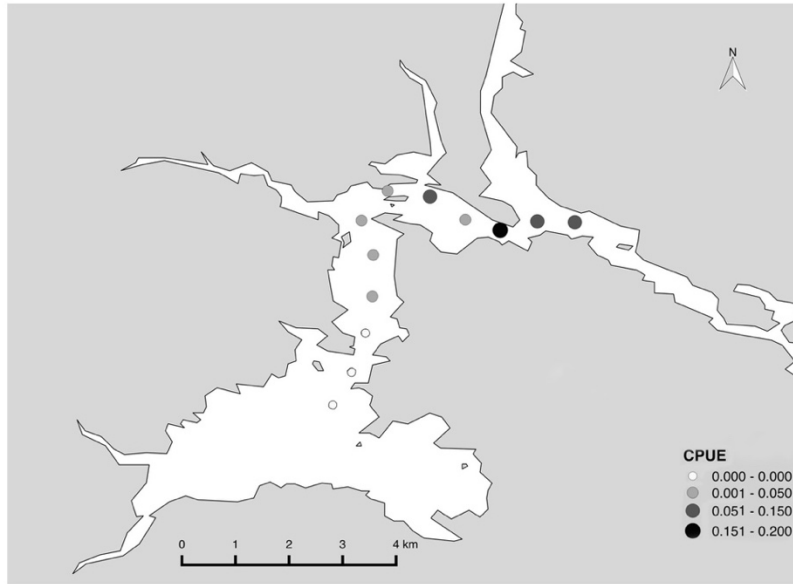
Figure 1.7 The distribution of ovigerous females in the Great Bay Estuary, based on sea sampling. A) Abundance (ovigerous lobsters/trap haul) overlaid on a map of the estuary. Every km that was sampled is indicated, regardless of whether ovigerous females were captured or not. Darker circles indicate higher abundance of ovigerous females. White points indicate areas that were sampled but no ovigerous lobsters were captured B) Distribution of ovigerous females, broken down into four regions: the river, lower Little Bay (LLB), upper Little Bay (ULB) and Great Bay (GB). Kilometer 23 is the furthest area up estuary sampled, and is in Great Bay. Above letters (A-C) indicate locations with significantly different densities. There were similar number of lobsters in the river and LLB (p=0.182, but significantly fewer lobsters in upper Little Bay than the two sites closest to the coast ($P_{ULB,LLB}$=0.003; $P_{ULB,River}$=0.003) and none were found in Great Bay. Letters above the regions represent post-hoc differences.

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Hatching dates of eggs carried by lobsters held in the laboratory

The average size of the ovigerous lobsters captured and held at the coast (CML) was similar to the size of those captured in the estuary and maintained at JEL (coast=87.4 ± 4.7mm CL, estuary=83.2 ± 1.4 mm CL; unpaired t-test, p= 0.44). Additionally, the overall thermal regime that lobsters experienced in the laboratories did not differ from ambient conditions at each location over the 7-10 weeks that they were held for the incubation study, although initially, water temperatures were warmer in the lab at the estuary (unpaired t-test, p_{coast}= 0.84; $p_{estuary}$= 0.75, Figure 1.8).
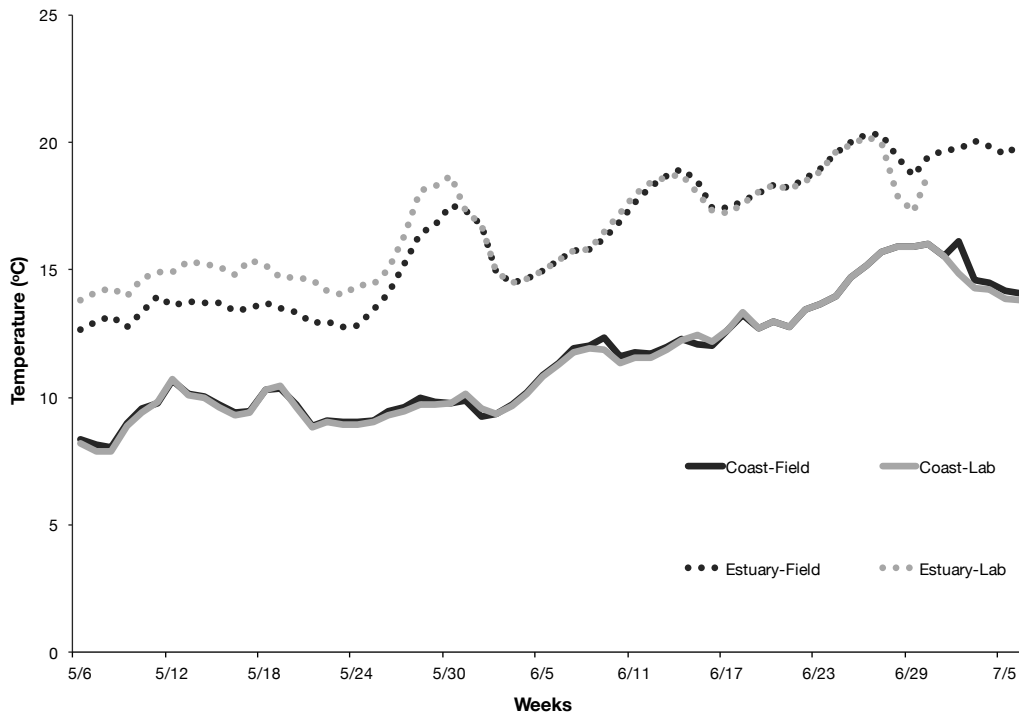
Figure 1.8 A comparison of water temperatures between the coast and the estuary, and between the field and the laboratory holding tanks. At the coast, tank and ambient temperatures were very similar, and ranged from 9.4 ^{o}C in May to 14.8 ^{o}C in July. In the estuary, tank temperatures (15.2 ^{o}C) were significantly warmer than natural conditions (14.0 ^{o}C unpaired t test, p < 0.001) during the week of 5/19-5/26, when lobsters were initially held. In June, water temperatures were very similar (both about 17.6 ^{o}C). Temperatures were not measured in July from the tanks. Water temperature differed significantly when comparing the ambient and tank temperatures of the estuary to the coastal conditions in May, June and July (unpaired t-tests, P<0.001).

The eggs carried by lobsters held at JEL hatched between May-25 to June-22, with a mean hatch date of June-02 ± 7.9 days (SD) while lobsters held at the coast hatched between from June-16 to July-09 with a mean hatch date of June-22 ± 9.1 days (SD). Thus, eggs from lobsters held in the estuary hatched a full three weeks earlier and hatching was completed two weeks earlier than coastal lobsters (Figure 1.9).
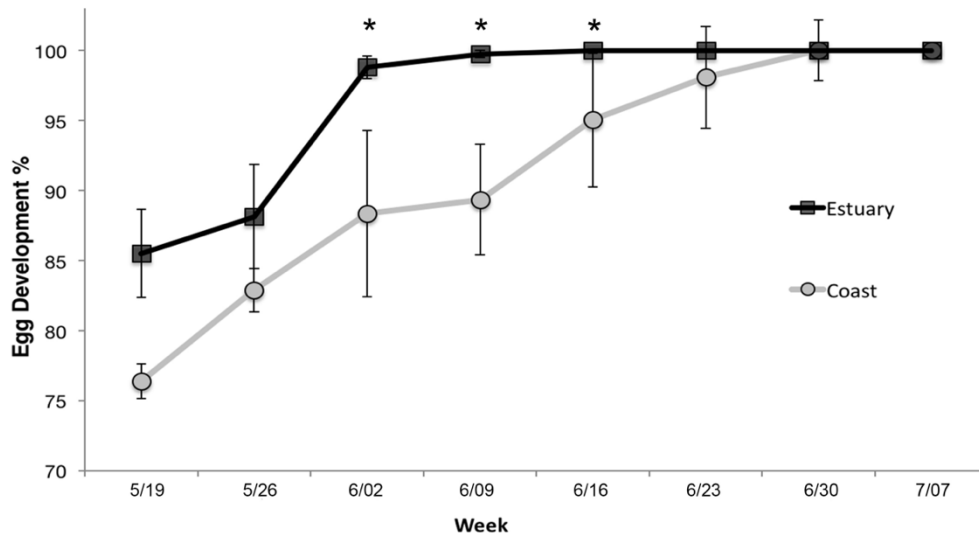
Figure 1.9 Comparison of the rate of development of eggs incubated at CML (coast, n=4) vs. JEL (estuary, n=7). Eggs exposed to estuarine water temperatures were always more advanced in development than eggs held at coastal water temperatures and were significantly more developed during several weeks (denoted by asterisk, 6/02 p = 0.008, 6/09 p=0.006, and 6/16 p=, 0.004). The first eggs from an estuarine female hatched on day 5/25 and the first coastal lobster eggs hatched three weeks later. The eggs carried by ovigerous females at JEL had all hatched by 6/16, whereas eggs did not finish hatching at the coast until 6/30, two weeks later. Only lobsters held for the same exact time frame were used in this analysis.

Hatch Predictions for Eggs carried by Lobsters during Sea Sampling

Water temperatures in the Great Bay estuary warmed at a faster rate in the spring (0.135 °C / day vs. 0.117 °C/day), and remained warmer than the coastal waters for the duration of the study (Figure 1.8, p=<0.0001). The estuary reached a daily average temperature of 12.5 °C in early May (5/6) while temperatures did not reach that point until more than a month later at the coast

(6/17). Most likely, due to these temperature differences, the eggs carried by ovigerous females

in the estuary had developed more, on any given date, than those carried by coastal lobsters

(Figure 1.10). In addition, estuarine lobster (n=58) eggs probably hatched earlier (5/21-6/23;

mean hatching date of 6/9 ± 11.8 days (SD); Figure 1.11) than those carried by coastal females

(n=39; mean hatch date of 7/1 ± 9.5 days (SD), range 6/11-7/23).
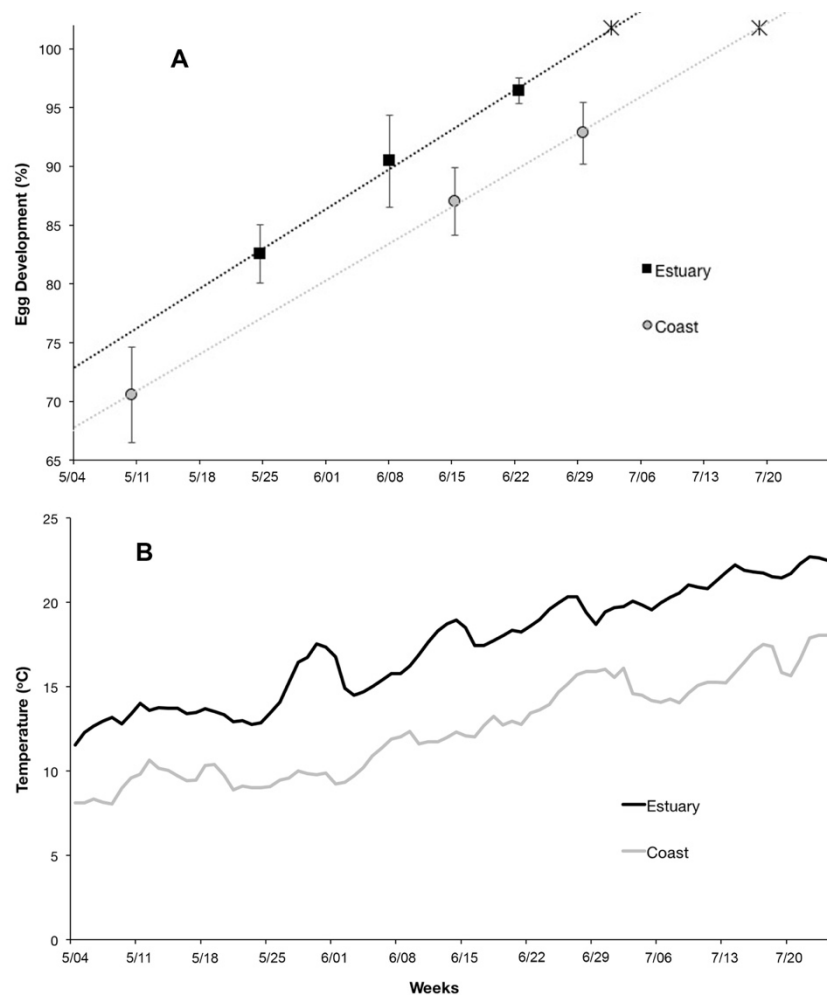
Figure 1.10 A) The rate of development of eggs obtained from estuarine (n=47, one trip excluded) and coastal lobsters (n=39) during sea sampling trips. A regression line was fit to the data and was used to predict when lobsters would be carrying 100% developed eggs; which was two weeks earlier for estuarine vs coastal lobsters. The equation of the line used to predict 100% hatch was y=0.469 + 14.12 (R^2=0.993) at the estuary and y=0.433 + 13.8 (R^2=0.999) at the coast, where the slope was daily egg development (%) B) Egg development is strongly influenced by water temperature and it is evident that the estuary warmed up at a faster rate, and was consistently warmer, than at the coast.

The modified Perkins Equation was used to predict when eggs collected from lobsters while sea-sampling would hatch. The eggs carried by estuarine and coastal lobsters in situ were predicted to hatch over significantly different time frames; hatching was predicted to occur 21 days earlier at the estuary than the coast (Figure 1.11). When comparing the ranges of predicted hatching, estuarine lobsters hatched their eggs significantly earlier ($p < 0.001$, df $= 1$). In addition, based on the ovigerous lobsters sampled, the range of hatching in the estuary was predicted to occur over a concentrated and shorter time frame than the coastal hatching period (34 as opposed to 42 days) therefore hatching in both regions overlapped by only 12 days (Figure 1.11).
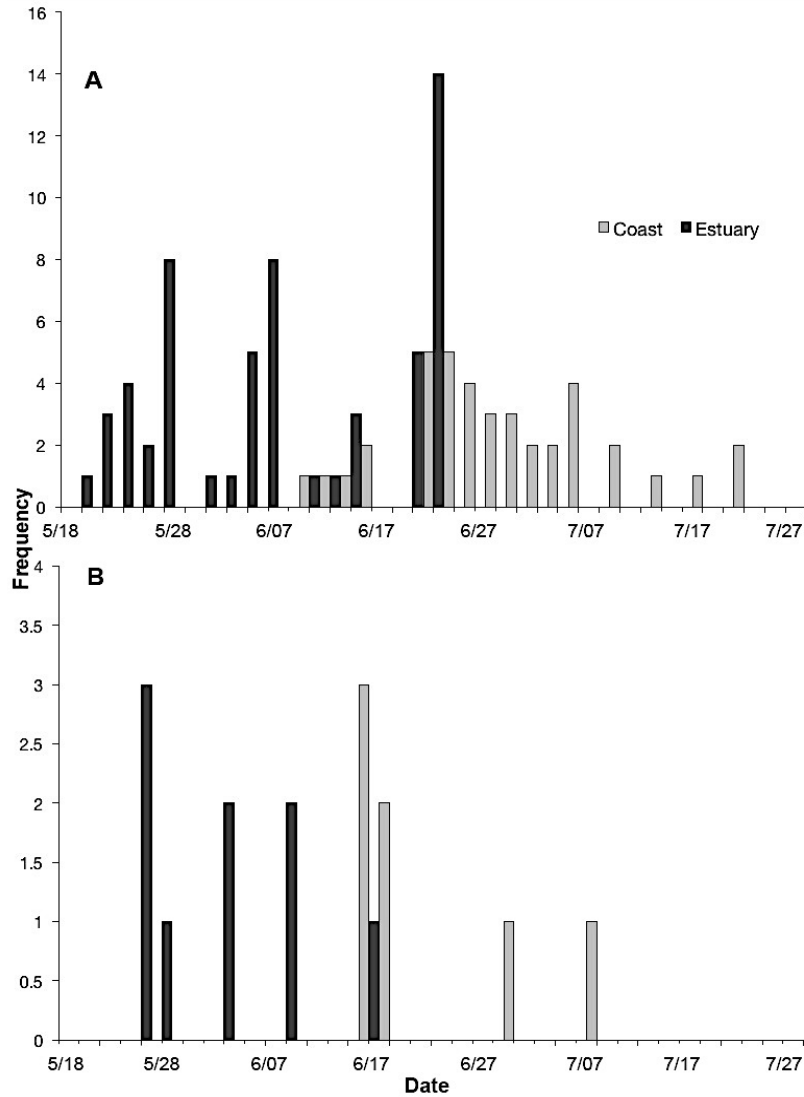
Figure 1.11 A) Predicted hatch dates based upon eggs obtained from ovigerous lobsters during sea sampling. The eggs carried by estuarine lobsters hatched sooner than those carried by coastal females. Also note there was some overlap in June. B) Empirical hatch dates of the 16 lobsters held at the estuary and coast.

When comparing the mean empirical hatch date (June-22 ± 9.1 days SD) of lobsters held in the

laboratory to the predicted mean hatch date from eggs collected in the field (July-01 ± 9.5 days

SD), the empirical hatch date at the coast was nine days earlier than the predicted hatch date

(p=0.027, df = 1, Figure 1.11). In the estuary, the mean empirical hatch date of lobster held in

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captivity was June-02 ± 7.9 days (SD), 7 days earlier than the predicted mean hatch date from the field (June-09 ± 11.8 days SD, p = 0.13, df = 1, Figure 1.11). Ovigerous lobsters held in captivity represent a small subsample of each area, and those held at the estuary hatched during as similar time frame as ovigerous lobsters sampled in the field. Additionally, held lobsters exhibited a similar trend; eggs carried by estuarine lobsters hatched much earlier (approximately 20 days) than those at the coast (Mann-Whitney, p = 0.005).

Larval Studies

Plankton Tows in the Great Bay Estuary

Over 19 trips, a total of 38 plankton tows were carried out in upper and lower Little Bay. On average tows covered 0.92 ± 0.05 km (see Figure 1.5). The average volume of water sampled per tow (both nets) was 2116.27 ± 148.35 m^3, and there were some differences in volume of water sampled by week. For example, the volume water sampled during the second week was 874.80 ± 282.87 m^3, and was significantly less than all other weeks, while the volume of water sampled during the eighth week (3066.44 ± 222.21 m^3) was significantly more than two other weeks (one-way ANOVA p = 0.023, df = 9). The average volume of water sampled per tow during the upper Little Bay transects was 2110.01 ± 205.27 m^3, which did not differ from the volume of water sampled in lower Little Bay (2122.48 ± 219.86 m^3, p = 0.97, df = 35.8). Overall, the average weekly water volume sampled was 8041.74 ± 934.67 m^3 and ranged from 3499.21 to 12265.75 m^3. Larvae were captured in similar densities during evening and morning tows (Mann-Whitney, p = 0.22), and these data were combined for further analysis.

All 35 larvae that were captured in the GBE were identified as stage I, although some ranged

from recently hatched to late stage I. Of the 35 larvae, 23 were captured in lower Little Bay, and

12 were captured in upper Little Bay. Larvae were first captured in May, and the geometric mean

of larvae abundance ranged from 0 larvae/1000 m^3 to 3.7 larvae /1000 m^3, however there were

no significant peak in abundance (Figure 1.12). Although more larvae were captured in lower

Little Bay, and there was no significant difference in the average number of larvae captured at

lower Little Bay (0.82 ± 0.36 larvae/1000m^3) and upper Little Bay (0.29 ± 0.08 larvae/ 1000m^3;

p = 0.35, df = 1), and weekly larval abundance was highly variability. Additionally, there were

no significant differences in larval catch between the two locations in June (Mann-Whitney, p =

0.33) or July (Mann-Whitney, p = 0.31).
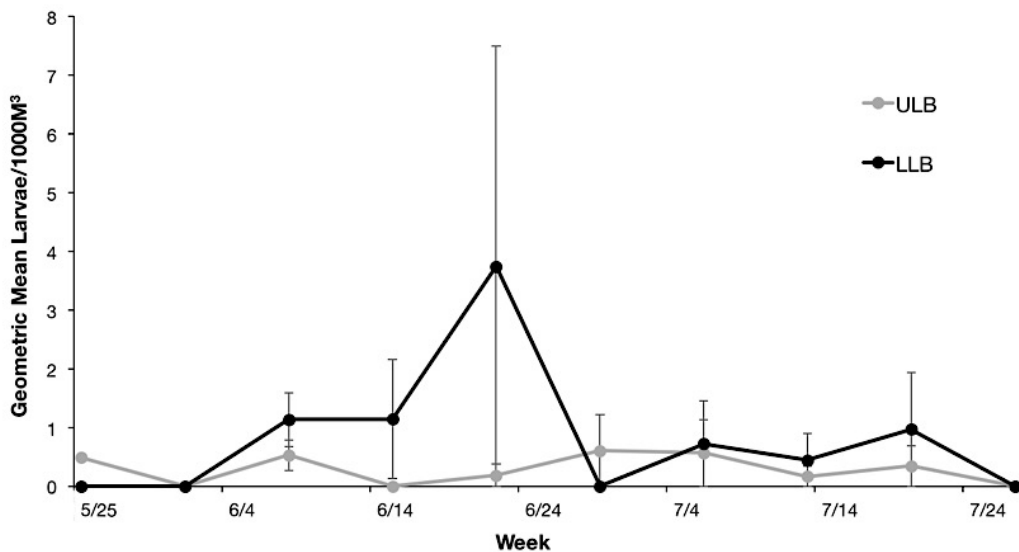
Figure 1.12 Geometric means of larvae captured during plankton tows in upper Little Bay (ULB) and lower Little Bay (LLB.) Larval abundance remained similar over each week, and there was no distinct peak (p = 0.380, df = 9). Error bars are standard error mean.

Predicted hatch dates of larvae captured in the field

The putative hatch dates for the 35 larvae captured during plankton tows were calculated based on their stage and the water temperature, and ranged from May-21 through July-19, with a mean predicted hatching date of June-28 ± 17.91 (SD) days (Figure 1.13). This range encompasses nearly two months, which is longer than the hatch range predicted from the eggs obtained either from estuarine or coastal ovigerous lobsters (one month and six weeks, respectively). Importantly, larvae were captured in the estuary from the time when eggs were hatching in the estuary until the time when eggs stopped hatching along the coast. The larvae that hatched earliest likely overlapped with when ovigerous lobsters hatched their eggs in the estuary. The larvae that hatched later occurred after lobster hatched their eggs in estuary (estimated to occur by July, Figure 1.10.), but overlapped with lobster hatching at the coast.
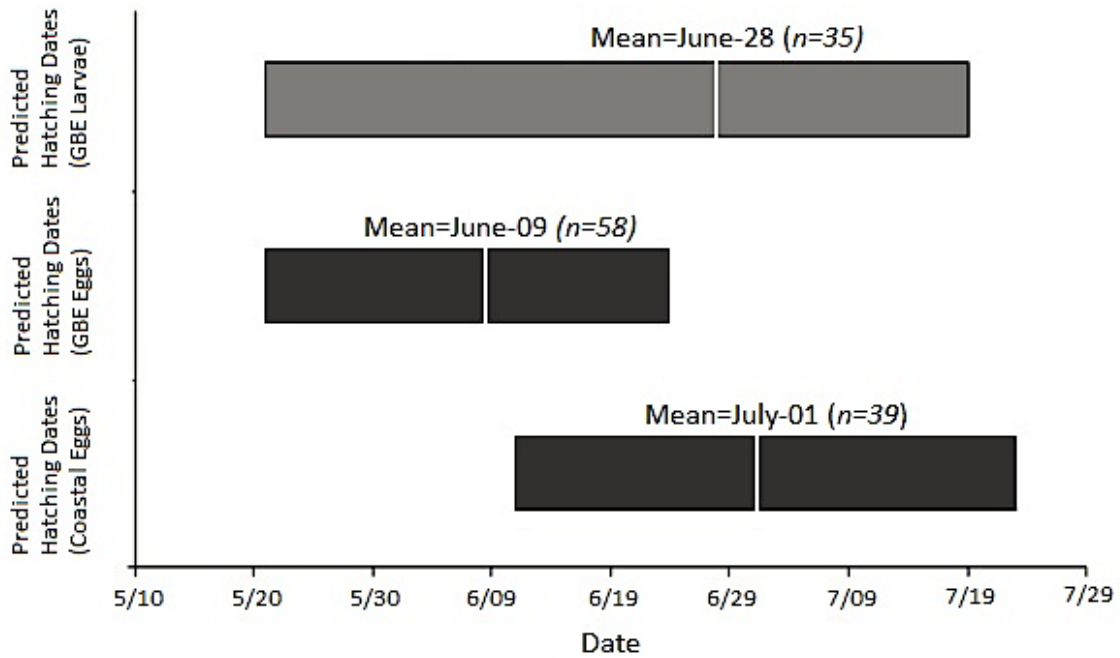
Figure 1.13 The predicted hatch dates of eggs collected from ovigerous females (black bars) captured during sea sampling trips in the estuary (n = 58) and the coast (n = 39), compared to the predicted hatch dates (back-calculated) of larvae (n = 35) captured in plankton tows in the estuary (light grey bar). These data indicate that larvae captured during plankton tows in the estuary likely originating both from females residing in the estuary and from those along the coast. Larvae caught earlier in the season are probably from estuarine residents, while those captured later in the season most likely came from coastal lobsters. Vertical white bars indicate mean hatch dates.

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Discussion

Previous tracking studies have shown that some American lobsters, including berried females, overwinter in the GBE. Thus, it is likely that these females are present in the GBE when their eggs hatch. The overall goal of this study was to more thoroughly examine the reproductive dynamics of lobsters in the GBE to test the hypothesis that it contains a resident and self-recruiting lobster population. The data from seasampling, both egg development and plankton tow studies all support this hypothesis. However, this study also revealed that the GBE lobster population is also subsidized by some coastal lobsters whose larvae are likely carried up into the estuary by tidal currents.

Abundance and distribution of ovigerous females

Ovigerous lobsters, with late stage eggs, were captured in relatively high densities in some areas of Little Bay and the Piscataqua River in the late spring and early summer. This is consistent with previous data and also with data showing that areas of the GBE that are furthest from the coast have the largest proportion of males compared to females (Howell et al. 1999; NHFG 2010; Langely et al. 2014). Reproductive females may avoid these areas because of suboptimal conditions (i.e., warm temperatures and low salinities), which are not favorable for larval and juvenile survival (Templeman 1936; Ennis 1975; Goldstein and Watson 2015a).

While it is likely that many of the female lobsters captured during this study overwintered in the GBE (also verified in Langley et al. 2014), it is also possible that they migrated into the estuary from the coast. Watson et al. (1999) demonstrated that there is a considerable amount of

exchange of estuary and coastal lobsters, due to seasonal migrations. Moreover, the spring is when most of the up-estuary, up-river migrations take place. This hypothesis is supported by the fact that, in late June, a few lobsters carrying egg clutches that were less than 80% developed were observed (pers. obs). A majority of lobsters from the estuary were predicted to have hatched all of their eggs but this time, so it is likely that the females observed with less developed eggs moved into the estuary from the coast (Figure 1.12).

Egg development and hatching season

Generally, the eggs carried by lobsters in the GBE developed and hatched earlier than those carried by coastal lobsters. In the spring, ovigerous lobsters were also carrying late stage eggs at a time of the year when it is unlikely that coastal lobsters had started to migrate inshore or up into the estuary (Figure 1.11, Goldstein and Watson 2015a,b). Eggs carried by estuarine lobsters were further along in their development for the entire duration of the hatching season, and as a result their mean hatching date was two weeks earlier than the mean hatching date of the eggs carried by coastal lobsters (Figure 1.10). The entire hatching season was also shorter in the estuary; 33 days vs 42 days at the coast, and two estuarine lobsters completed hatching all their eggs on May-25 (pers. obs.), well before hatching at the coast was predicted to have started (June-11; Figure 1.11).

One of the most important environmental factors that influences egg development is temperature (Templeman 1936; Hughes and Matthiessen 1962; Perkins 1972; Sastry and Vargo, 1977; Goldstein and Watson 2015b). As a result, hatching events differ regionally, with eggs carried by lobsters in colder waters experiencing a delayed hatch (Templeman 1940; Aiken and Waddy 1986; Quinn, et al. 2013). In GBE, water temperatures increased at a higher rate than at the coast

(0.135 °C/day vs 0.117 °C/day) and thus lobster eggs in the estuary were exposed to significantly warmer temperatures throughout the hatching period (Figure 1.8). In some lobster populations, peak hatching has been linked to high summer temperatures, and has been predicted to reach a maximum a month after hatching starts (Harding and Trites 1988; Burdett-Coutts 2010). Hatching in GBE started when water temperatures exceeded 12°C, and while peak hatching was observed about a month after initial hatch (June-23, Figure 1.11), water temperatures still had not peaked. This suggests that hatching is more dependent on the rate of temperature change than overall higher summer temperatures. This is also the conclusion reached by Goldstein and Watson (2015b) when they compared the rate of development of eggs from coastal lobsters with those that overwintered offshore. They found that, even though mean temperatures during egg incubation were similar, eggs carried by inshore lobsters hatched several weeks earlier than offshore eggs because the rate of warming of inshore waters in the spring was much greater. Templeman (1940) also observed a difference in egg development and hatching at two adjacent areas (Grand Manan and West Northumberland strait in Canada) that experienced different temperature regimes, and hatching occurring earlier, and over a shorter time period, in the warmer area.

While water temperature appears to have the greatest impact, other variables may also have an influence on rate of egg development, such as lobster size. For example, it has been observed that larger lobsters hatch their eggs earlier than smaller lobsters (Attard and Hudon, 1987). However, in this study the estuarine lobsters were roughly the same size (85.08 ± 0.56 mm CL) as the coastal lobsters (86.13 ± 1.77 mm CL , p = 0.58), so this could not have been the cause of the differences in egg development and hatching we observed.

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Lobster larvae distribution and abundance

Larvae were captured over a period of time that spanned the hatching periods of eggs in the estuary and the coast. Lobster larvae were first captured in the estuary at the end of May (May-27) and then consistently captured there until sampling ended at the end of July, and the relative abundance of larvae remained constant in June and July (data were insufficient for comparisons with May). In comparison, based on lobsters held in the laboratory, the egg stages of lobsters obtained while sea sampling, and the predicted time of hatching of these eggs, stage I larvae from estuarine lobsters would have first appeared in the water column at the end of May and then only been present until the middle of June. In contrast, coastal larvae should have first appeared around the middle of June, and been present until the middle of July. Previous studies reported that larvae were captured along the NH coast starting in early June (Grabe et al. 1983; Normandeau 2014), while we demonstrated larvae in the GBE in May. Thus, taken together, the egg development, hatching, and plankton tow data strongly suggests that larvae captured at the beginning of the season originate from estuarine lobsters, and those obtained later in the season were probably of coastal origin. Moreover, because the period of hatching of coastal and estuarine eggs overlapped, the highest abundance of larvae was in the estuary during this time, when there was a confluence of both sources of recruits. It is common for regions that receive larvae from multiple sources to have a prolonged larval season (Fogarty 1998).

Capturing early stage larvae at a time of year when hatching occurs exclusively in the estuary supports the hypothesis that some new recruits to the estuarine population originate from reproductive females within the estuary. Furthermore, all the larvae captured in the GBE were stage I. At the temperatures they experience in the GBE they may quickly molt to stage II larvae

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in 4-6 days (Mackenzie 1988; Annis et al., 2007). Thus, the young larvae captured in the GBE most likely originated there.

Support for a resident population

Several of my findings support the hypothesis that there is a resident, self-recruiting, lobster population in the GBE. First, the relative densities of late stage ovigerous lobsters were similar to densities of ovigerous females found on the Canadian coast (Gendron 2005), and represent a robust broodstock population. Additionally, these ovigerous females carry eggs that are more developed than those carried by coastal lobsters over the same time frame. This suggests that lobsters would have to overwinter in the GBE because ovigerous coastal lobsters do not start migrating inshore at this time (Goldstein and Watson 2015a) and those that did migrate would have eggs that are not as developed as those that experienced the rapidly warming estuarine waters in the spring. Finally, each type of egg development data obtained indicated that the eggs carried by estuarine lobsters develop faster and hatch earlier than those being carried by coastal lobsters and this early hatch corresponds to the first appearance of stage I larvae in the water column.

However, while the data clearly support the hypothesis that the GBE most likely supports a resident, self-recruiting subpopulation of lobsters, it is also apparent that there is a considerable amount of mixing of the estuarine and coastal populations. Larvae were captured during the time of year when estuarine lobsters were exclusively hatching as well as later in the summer when the eggs of coastal lobsters were hatching. Thus, it is possible that new recruits to the estuary come from both estuarine and coastal females and there is considerable connectivity between the two populations (Scheltema 1986; Sponaugle et al. 2002; Cowen and Sponaugle 2009).

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Sustainability of resources may be dependent on understanding source-sink dynamics, in particular the link between dispersal (i.e., larval pathways and connectivity) and subpopulations (Fogarty 1998). Source-sink dynamics in part facilitate the long-term survival of populations, and it is imperative for management to be aware of these dynamics, particularly in systems where monitoring population growth is difficult. Additionally, differences in larval survival and location of settlement depend on the duration of time spent in the water column, and larvae from GBE may have the advantage. The local, short, early and discrete hatching season in the estuary may provide a robust source of larvae that are able to settle faster and survive better due to getting a head start (Scarrat 1964; Pandian 1970; Caddy 1979; Harding et al. 1983). Future genetic studies should probe the source-sink dynamics of GBE, and determine if lobsters in the estuary are a completely self-sustaining population, or if they are supported from migrants during seasonal migrations. Several studies have suggested that subpopulations arise from, and are supported by, several sources, and in particular may be supported by larvae of 'mixed origin' (Roughgarden and Iwasa 1986; Botsford et al. 1994).

While the data reported in this Chapter demonstrate that larvae are present in the GBE, it is possible that they are exported to coastal waters by the strong currents in the GBE. One of the goals of the work summarized in Chapter 2 of this thesis was to test this hypothesis by releasing drifters and tracking their trajectories. These data provided evidence that larval retention was possible. The second goal of the research described in Chapter 2 was to determine if these newly settled lobsters could survive in the estuary. I was able to collect a number of small juvenile lobsters in the estuary, indicating that subsequent stages settled and survived (Chapter 2). Therefore, I conclude that there is a self-sustaining population of lobsters in the GBE that are

linked through migrations and larval transport, with the lobsters that reside along the NH

coastline.

CHAPTER 2

REPRODUCTIVE DYNAMICS OF LOBSTERS IN THE GREAT BAY ESTUARY

Abstract

In Chapter 1, I presented data indicating that there are areas within the GBE where ovigerous

lobsters overwinter and that in the spring their eggs hatch, releasing larvae into the estuary

approximately three weeks earlier than larvae appear along the NH coast. The objective of the

research presented in this chapter was to determine if these larvae would be retained in the

estuary and eventually settle within the GBE. This overall goal was achieved by characterizing

currents that possibly retain larvae in the estuary, and quantifying the distribution of non-

migratory juvenile lobsters (<60mm CL), which serve as proxies for successful settlement. To

characterize currents, passive surface drifters (n = 21) were deployed from two known hatching

sites in the in GBE from 2008-2015. Drifters were also deployed in the Piscataqua River (n = 6)

to determine if larvae could be transported into the estuary from areas near the mouth of the

Piscataqua River. Drifters released in the river moved a net distance of 8.65 ± 0.72 km into the

estuary after 24 hours. Drifters released in lower Little Bay moved 5.16 ± 0.25 km into the

estuary over 24 hours, and drifters released in upper Little Bay moved 1.87 ± 0.37 km down

estuary during the same timeframe. These movements were extrapolated over the two-week time

frame it takes larvae to develop and settle, and even after this series of tidal cycles, drifters

released from the three locations were retained in the estuary. In 2014, the abundance and

distribution of juvenile lobsters in six different study sites was assessed using four-trap trawls consisting of two pairs of modified ventless traps and two pairs of juvenile collector traps). Sampling occurred on a spatial gradient, ranging from the Piscataqua River to Great Bay proper.

The smallest lobster (38 mm) was captured in the Piscataqua River, and the average size of lobsters increased at sites furthest up into the estuary, while the abundance of lobsters decreased in these areas. Juvenile lobsters were not captured in Great Bay, and the CPUE of juvenile lobsters was similar in the river, lower Little Bay and upper Little Bay ($p = 0.66$, $df = 3$). While the sex ratio of adult lobsters varied in the estuary, juvenile lobsters maintained even sex ratios at the four sites where they were captured (Fisher's Exact test, $p = 0.995$), as expected from the non-migratory juvenile size class of residential lobster populations. Overall, these findings confirm the retention and settlement of larvae that originate in the GBE. Taken together with the findings presented in Chapter 1, it is likely that there is a self-sustaining population of lobsters in the GBE, that is also subsidized by a flow of larvae into the estuary from the NH coastline.

Introduction

The Great Bay estuary (GBE) in New Hampshire is characterized as a large, tidally-mixed system with freshwater input from seven river systems. The upper reaches of GBE are 23-25 km from the ocean, making it highly insulated and increasing the possibility for the retention of meroplanktonic (free swimming) larval lobsters (Bilgili et al. 2005; Goldstein 2012a). Within GBE, there is strong evidence for a resident population of American lobsters, as summarized in Chapter 1. Ovigerous female lobsters overwinter and hatch their eggs in the estuary (Chapter 1, Langley et al. 2014), and there are limited data indicating the presence of small (10-60mm) juvenile lobsters in certain areas of the GBE (NHFG 1989, 1990, 2008; Becker 1994; Short et al. 2001). Lobster larvae have also been captured using plankton tows at the same time that the eggs carried by estuarine females are hatching (Chapter 1). The overall goal of this portion of my thesis research was to test the hypothesis that, given the prevailing currents in different areas of the GBE, lobster larvae originating in the GBE are retained and in settle in certain areas of the estuary. To accomplish this goal, I conducted two different studies. The rationale for both studies are summarized below.

Estuarine systems are important transitional areas to the open ocean, and often have complex hydrography. In the GBE, Bilgili et al. (2005) built a Lagrangian model to predict the amount of time that particles were retained in the estuary and the length of time it took these particles to move from the estuary to the coast. From the area farthest from the coast (Great Bay proper), it was predicted that particles would arrive at the coast after 20.5 days (39.3 tidal cycles) and from the Piscataqua River 7.5 days (14.4 tidal cycles, from Trowbridge 2007 based on data from Bilgili et al. 2005). More recent studies (Goldstein 2012a), using passively floating 'drifter' units

deployed in Little Bay, which lies between Great Bay and the river, and is the source of many lobster larvae in the GBE (Chapter 1), yielded a retention time surpassing 16 days, or approximately 30 tidal cycles (Goldstein 2012a). These data showed that over the same amount of time, particles did not leave the estuary, and is the opposite of results from the Bilgili model, which predicted that it would take 15.7 days for water from this region to be flushed from the GBE entirely. These two studies describe different characterizations of currents in GBE, and suggest two different endpoints for settlement should larvae remain in the surface currents. Both stage I and IV lobster larvae are influenced by surface currents for their transport and remain in the top three meters of the water column for approximately 11-50 days until they settle, (Templeman 1936; Mattheisen and Scherer 1983; Hudon and Fradette 1988; Mackenzie 1988; Annis et al. 2007),

There are data presented in this chapter that suggest a portion of larvae, particularly those that originate in Little Bay, are retained in GBE. To confirm that lobsters are recruited to an area, it is necessary to demonstrate that juvenile lobsters are present in the GBE, and I test the hypothesis that the most juveniles will be present in areas where the drifter data predict the advection of larvae and where early benthic phase (EBP) lobsters will settle. Previous attempts to use suction sampling or settlement collectors to survey for EBP were not successful in GBE. Therefore, in this study, juvenile lobsters less than 60 mm in carapace length (CL) were targeted as a proxy for lobster settlement within the estuary. These lobsters serve as a proxy for successful settlement because they exhibit limited movement (Wilder 1963; Cooper and Uzmann 1980) and are considered to be residential (Morse and Rochette 2012). In GBE, the abundance, distribution, size and sex composition of juvenile lobsters has not yet been rigorously quantified and thus

their distribution has not been linked to areas where larval settlement is predicted to occur (as driven by surface currents).

In summary, the objectives of Chapter II were to: 1) characterize currents within the GBE and Piscataqua River to determine if larvae that originate in the GBE are likely to be retained there and; 2) quantify the abundance, distribution, size and sex composition of the juvenile lobsters that reside in the GBE to determine if larvae settle in the estuary and grow to adulthood, suggesting that there could be a self-sustaining population of lobsters in the GBE.

Larval Retention

Drifters

Various methods have been developed to characterize where larvae might be passively transported by oceanic currents. For this study, 'Paul' drifters with satellite (GPS) transmitters (for design to to: http://www.nefsc.noaa.gov/drifter) were used to quantify the putative passive movements of early and late stage larvae that stay in the top 3 meters of the water column (Figure 2.1, Harding et al. 1987).

Figure 2.1 A Paul drifter. The GPS unit is placed into the otter box on the top part of the drifter unit, and remains above the water for transmission purposes. The inside of the bucket contains both weights and floatation devices, so that it floats with about ¼ of the drifter above water.

To best identify where larvae were carried after hatching, drifters were deployed at two known

hatching grounds in Little Bay (identified in Chapter I). Drifters were also released at a site in the lower Piscataqua River in an attempt to determine if larvae hatched along the coast could be transported into the estuary (Figure 2.2). Drifters were deployed periodically during the summers of 2008-2015, (excluding 2010, when no drifters were released), and deployments in the river were limited to two years; 2008 and 2015. Drifters were only deployed during weeks when normal weather patterns occurred (i.e., were not released during heavy rain or high wind in order to eliminate influences of unusual currents). Daily tide heights were recorded from NOAA stations closest to the site of each release (https://tidesandcurrents.noaa.gov), and included tide data for all dates that drifters were at large. Tide data were not normally distributed, and when compared for each region by year and tide, did not differ (Kruskal-Wallis, $p > 0.06$). High tides in GBE ranged from 1.89 ± 0.04 meters (m) to 2.11 ± 0.04 m ($p = 0.11$, $df = 5$) and low tides ranged from 0.05 ± 0.03 m to 0.14 ± 0.0 4m ($p = 0.06$, $df= 5$) from mean low water. In the river, tides ranged from 2.35 ± 0.18 m to 2.49 ± 0.05 m ($p = 0.35$, $df= 1$) and low tides ranged from -0.02 ± 0.05 m to 0.27 ± 0.12 m ($p = 0.21$, $df = 1$) from mean low water. Drifters were typically deployed at the start of either an incoming or outgoing tide, although a few releases ($n = 7$) occurred more than two hours after the start of a tide. Positional "fixes" (latitude and longitude) were obtained at ~30 minute intervals, and drifters were left at large for a minimum of 3 hours or until they ran aground and needed to be recovered. Approximately 48 fixes were obtained daily, and the accuracy of each fix was estimated to be within 0.07 km (determined from specifications of GPS unit). Data were subsequently edited to remove data during times when drifters had run aground and moved less than 0.14 km over several hours (over the range of -0.07 to 0.07 km to account for both the position in the estuary and the accuracy range of side to side motion).

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To determine the spatial patterns and directions of drifter movements and to create individual "drifter tracks" (a complete series of fixes over time) for each trial, a model was created in python (Python Software Foundation, version 2.7. Model scripts at https://github.com/ bmoore/earth-vector/). To create the model, the estuary system (including Piscataqua river) was divided into two regions along the longitude line W -70.853216°, which divided Little Bay, which runs E-W from the river and Great Bay, which run N-S, from the river. The estuary and river were then further partitioned into a grid, so each "fix" could be assigned a position in the estuary that could then be used to determine if the drifter moved up or down estuary in-between each fix. Subsequently, the direction (degrees), distance (km) and velocity (cm · s^{-1}) were calculated for each "step" between two consecutive fixes. Negative distance and velocities indicated down estuarine movements (towards the coast), while positive metrics indicated up estuarine movements (away from the coast).

Drifter tracks were pooled by release site and tide cycle after determining that there was no effect of year and tide. The sum of distance (km) and average velocity (cm · s^{-1}) were calculated for each one-hour interval for every trial (n = 27). Overall net distance traveled (km), linear position within the estuary (km) and net velocity (cm · s^{-1}) were calculated for the time periods 6, 12 ,18 and 24 hours (corresponding to changing tidal cycles) for the three release locations.
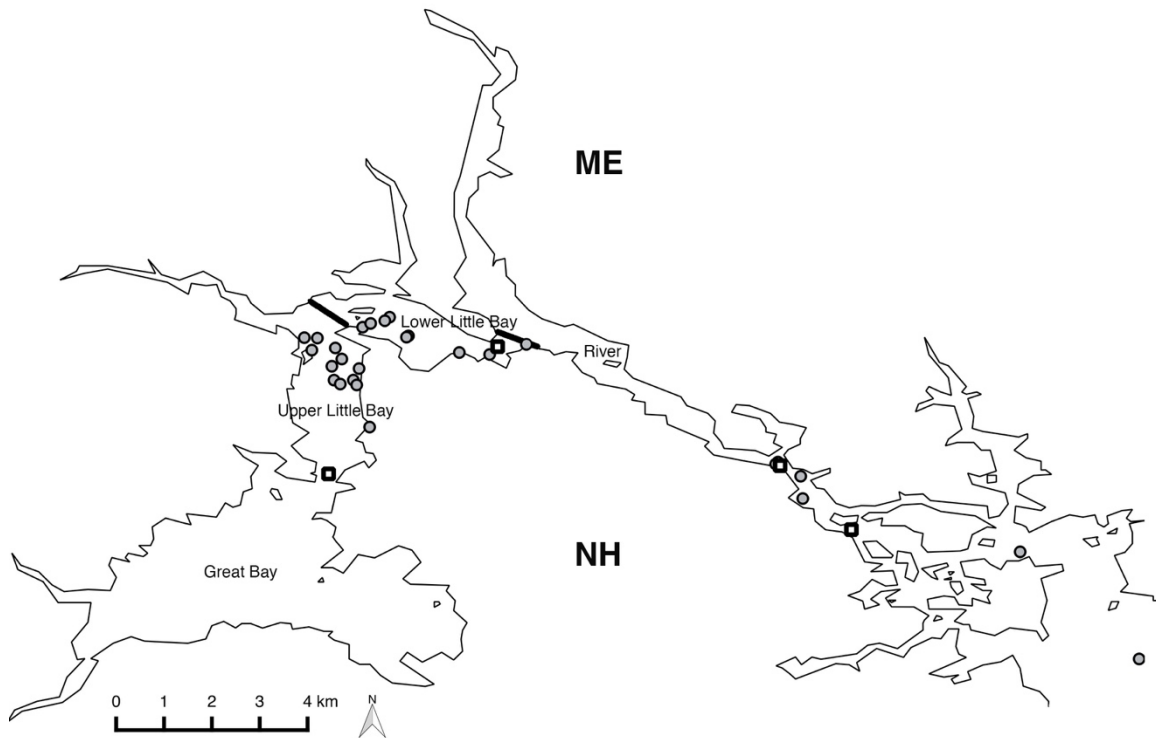
Figure 2.2 The release sites (grey circles) of all drifters (n = 27) deployed during 2008-2015. Release locations ranged from the mouth of the Piscataqua River to upper Little Bay. The black lines delineate the three regions where drifters were deployed: Piscataqua River (6 deployments), lower Little Bay (LLB, 9 deployments) and upper Little Bay (ULB, 12 deployments). The current profiler sites (black squares) are also shown on an estuarine gradient. In the river, they overlay on two drifter deployments.

Great Bay Currents

To determine if the drifters moved in a manner that would be predicted by the currents in the GBE, hourly velocity and linear position data were compared against data taken from the 2007 NOAA current study, which involved measuring currents at 11 locations in the Piscataqua River and GBE (Kammerer 2007). For my comparisons, only four of the 11 sites were used because three sites were very close to the drifter release locations (Figure 2.2), and the fourth was close to the mouth of the river. Although current profilers were deployed at several depths for the current study, only data from the shallowest sampling strata (between 0.55 - 0.70 meters) were used to

compare against the drifters. All current data were taken from the month of July (May was used

at one site where the current profiler was removed before July), and average velocity was

calculated over a 24-hour tide cycle for a total of 30 tide replicates. A model was then built to

determine the distance (in km) a particle would be carried for each hour of the tide cycle, up to

24 hours. The station closest to the water parcel was used to determine the distance the parcel

traveled over the proceeding hour. Due to the paucity of stations in from the upper Piscataqua

River into Great Bay Proper, a midpoint was established between each of the three sites furthest

into the estuary, and was used to determine which station to reference. The linear position of

water parcels within the estuary was predicted from these data, and was then compared to the

empirical linear positions of drifters over a similar time frame. These models were then used to

extrapolate where drifters and parcels of water would move to, for 8-16 days, which is the

amount of time larvae are likely in the water column before they settle, given the water

temperatures in the GBE (Templeman 1936; Mackenzie 1988; Annis et al. 2007).

Juvenile Recruitment

Trap Study

The goal of this part of the study was to quantify the abundance and distribution of juvenile

lobsters (< 60 mm CL, Lawton and Lavalli 1995) residing in GBE through a fishery independent

survey using modified lobster traps. Trap trawls were composed of a juvenile collector, a small-

mesh juvenile collector, a, ventless lobster trap and a small-mesh ventless lobster trap (4 traps

total). Juvenile collectors were small, 30" single-parlor ventless lobster traps with 1.4" mesh and

1.88 x 1.88" modified square entrance heads (Protoco Enterprises, Inc., North Plains, OR).

Ventless lobster traps consisted of 36" single-parlor traps with 1" mesh. Both trap types were

fished in pairs, and one of each trap type was wrapped in ½" mesh to help retain small lobsters (Figure 2.3).
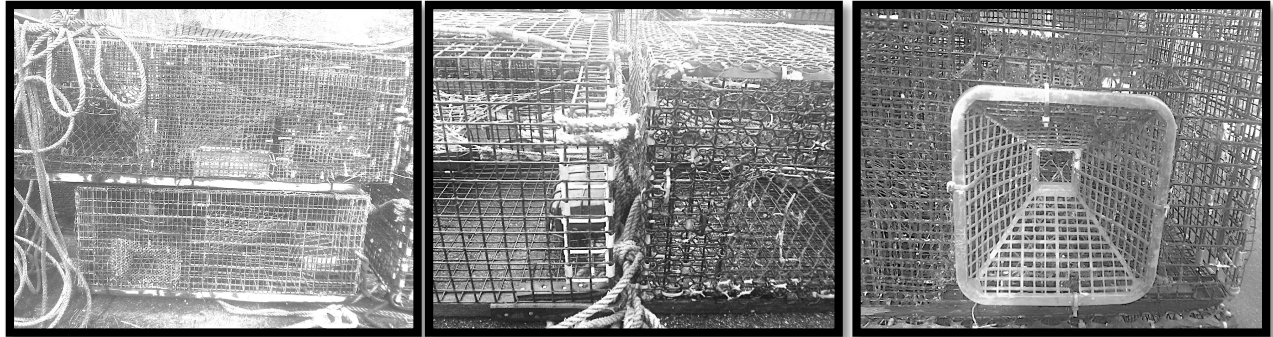

Figure 2.3 Trap configurations used in the 2014 trap study. The left panel shows the difference in size of standard traps and juvenile collectors; the middle panel shows regular mesh (left) as compared to with traps wrapped in smaller mesh (right). The modified entrance heads used on juvenile collectors are shown in panel on the far right.

The four trap-trawls were fished at six fixed sites within the GBE along a 14 km long gradient (Figure 2.4). All trawls were fished from June-August of 2014 at depths of less than eight meters, and were hauled every 1-7 days. Traps were re-baited each time with equal amounts of herring. Lobster catch was enumerated, and the sex and carapace length (to the nearest millimeter) of each lobster was recorded. Lobster abundance was then quantified in terms of the number of lobsters / trap (catch per unit effort, CPUE). Onset HOBO units (Onset Computer Corp., Bourne, MA) were fixed to each trawl to log temperature and light levels every 30 minutes.
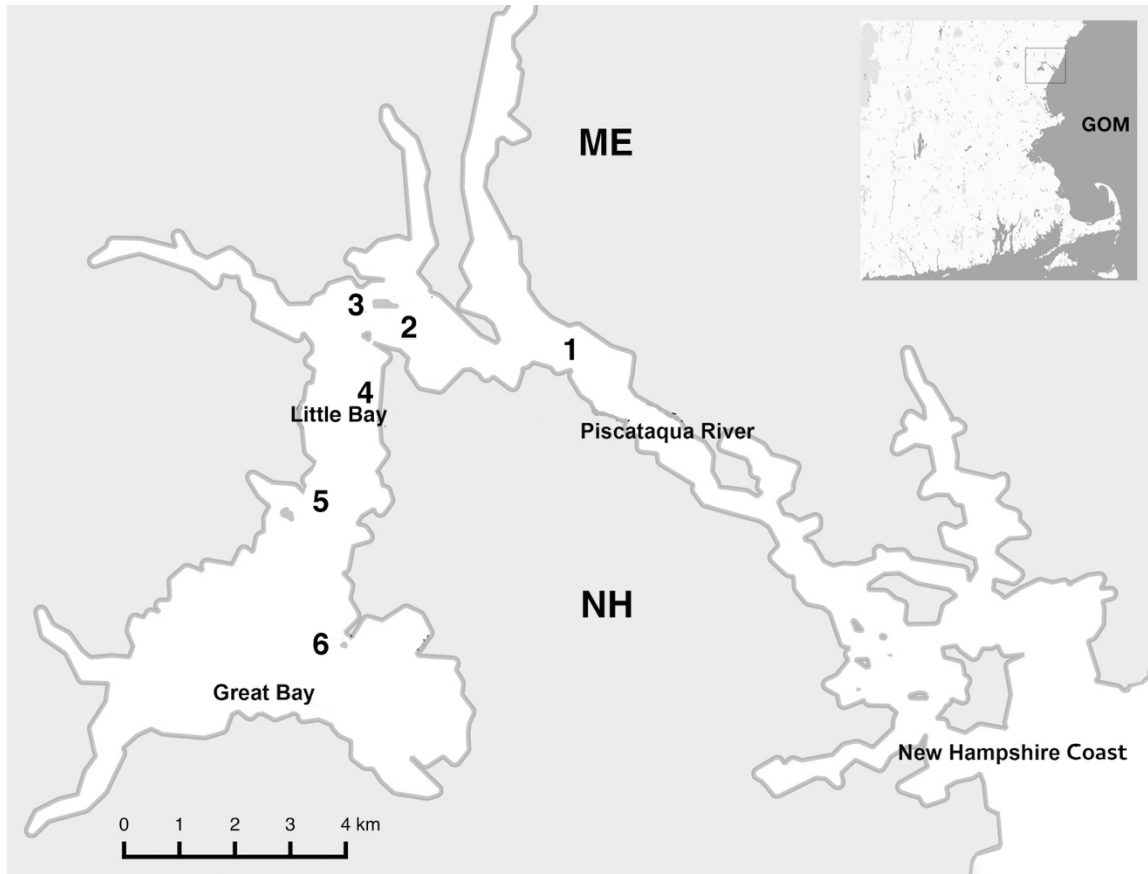
Figure 2.4 The Great Bay estuary (GBE) is located in southeast New Hampshire and encompasses three distinct areas: the Piscataqua River, Little Bay, and Great Bay. For my purposes, Little Bay was divide into upper Little Bay (ULB) and lower Little Bay (LLB). The locations of study sites are labeled 1-6, and are on a coastal-to-estuarine gradient: (1) River; (2) LB1 (3) LB2 (4) ULB (5) GB1 and (6) GB2.

Data Analyses

Catch data were sorted into adult (>60mm) and juvenile (<60mm) size bins, and the relative

abundance, size structure and sex ratio of these categories were compared at each of the six study

sites. Catch (CPUE) data were tested for, and failed, assumptions of normality using JMP

11.21.1 (SAS Institute, Cary, BC). Due the presence of many "no catch" events (i.e., zeroes

made up the mode and minimum value), the catch data were not transformed, and instead the

non-parametric Kruskal-Wallis ANOVA ($\alpha = 0.05$) and the post hoc Mann-Whitney-U test were

used to compare of relative abundance (CPUE) of juvenile and adult lobsters between the six

study sites in the estuary. The size frequencies of catch were examined by site, and the average carapace length (mm) size was calculated for each site. The sex ratios were calculated as the number of males to females (M:F), and then expressed as the percentage of males/site. The sex ratios of adult and juvenile lobsters were compared between sites using the Fisher's Exact Test, to account for the small number of observations.

<center>**Results**</center>

Larval Retention

Drifters

A total of 27 drifters were released mid-channel and tracked during 2008-2015; six were released in the Piscataqua River, nine in lower Little Bay and twelve in upper Little Bay (Figure 2.2). Drifters released in the Piscataqua River remained at large, before running aground or being retrieved, for 10.0 ± 2.4 hrs (range 5.6 - 21 hrs). In contrast, drifters released in lower Little Bay and upper Little Bay were at large for a much longer period of time (lower Little Bay 50.5 ± 18.3 hrs, range 4.5-179.5 hrs; upper Little Bay 49.0 ± 16.7 hrs, range 3.7-171.4 hrs). For most comparative analyses only the first 24 hrs of data from each release were used because over half of (56%) of the drifters ran aground by the completion of the first full semi-diurnal tidal cycle (four tides in 24 hrs). However, full tracks were used for modeling tracks over two weeks, because drifters generally behaved similarly at each release location (Figure 2.5)
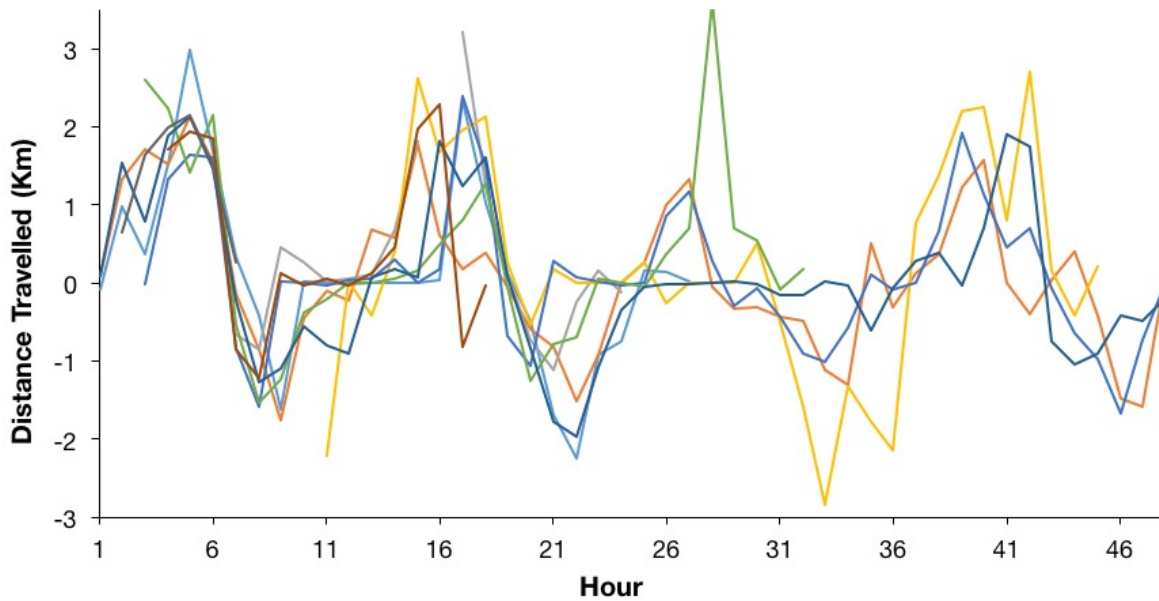
<center>58</center>

Figure 2.5 The distance traveled for drifter deployed (n = 9) in lower Little Bay over 48 hours. Drifter trajectories 'behaved' in a similar fashion during each tide cycle, regardless of the duration of each trial, or the timing of their release. Each colored line represents one drifter release.

The drifters released in the Piscataqua River and lower Little Bay tended to move further into to the estuary than the initial release site, regardless of when they were released relative to the tide cycle, or the amount of time they were at large (Figure 2.6). In contrast, those released in upper Little Bay did not travel as far and moved in a net down-estuary direction (Figure 2.7).
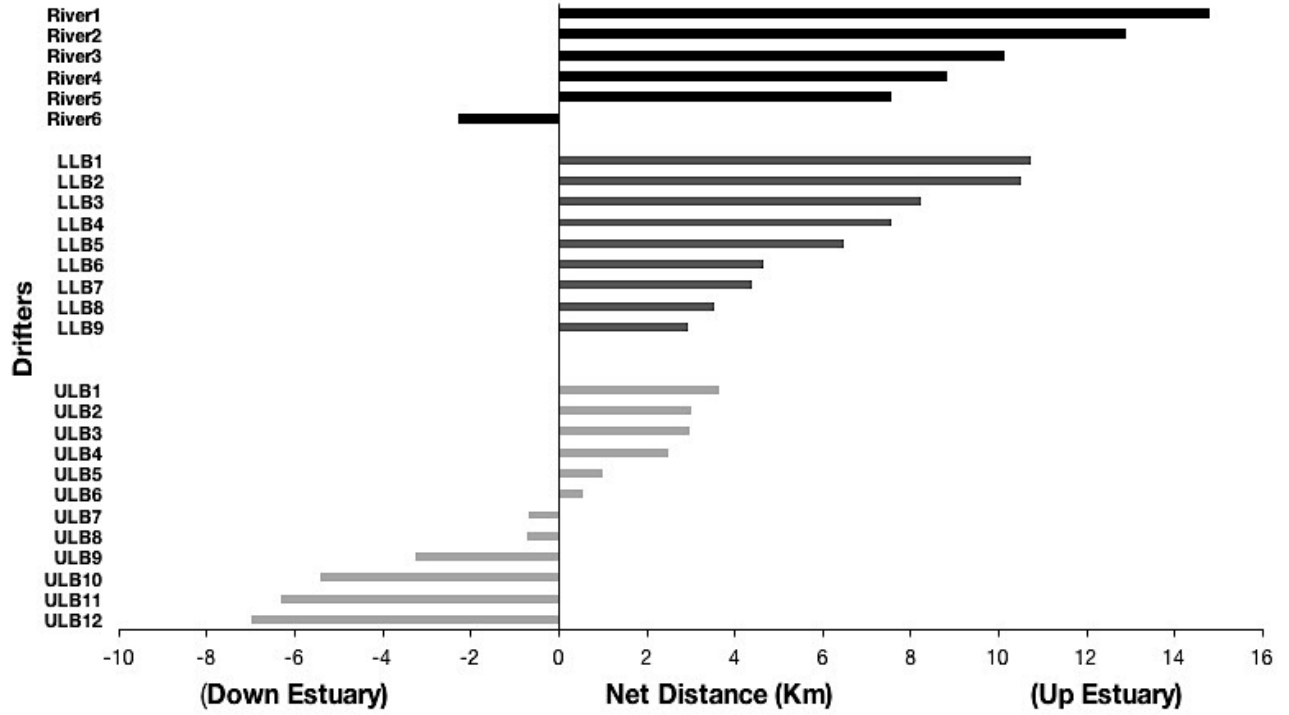
Figure 2.6 The net distance that each drifter (n = 27) traveled. Light grey bars are drifters released in the upper Little Bay, medium grey are lower Little Bay releases and black bars are releases in the river. Each bar represents the net distance moved by a single drifter during a single release.

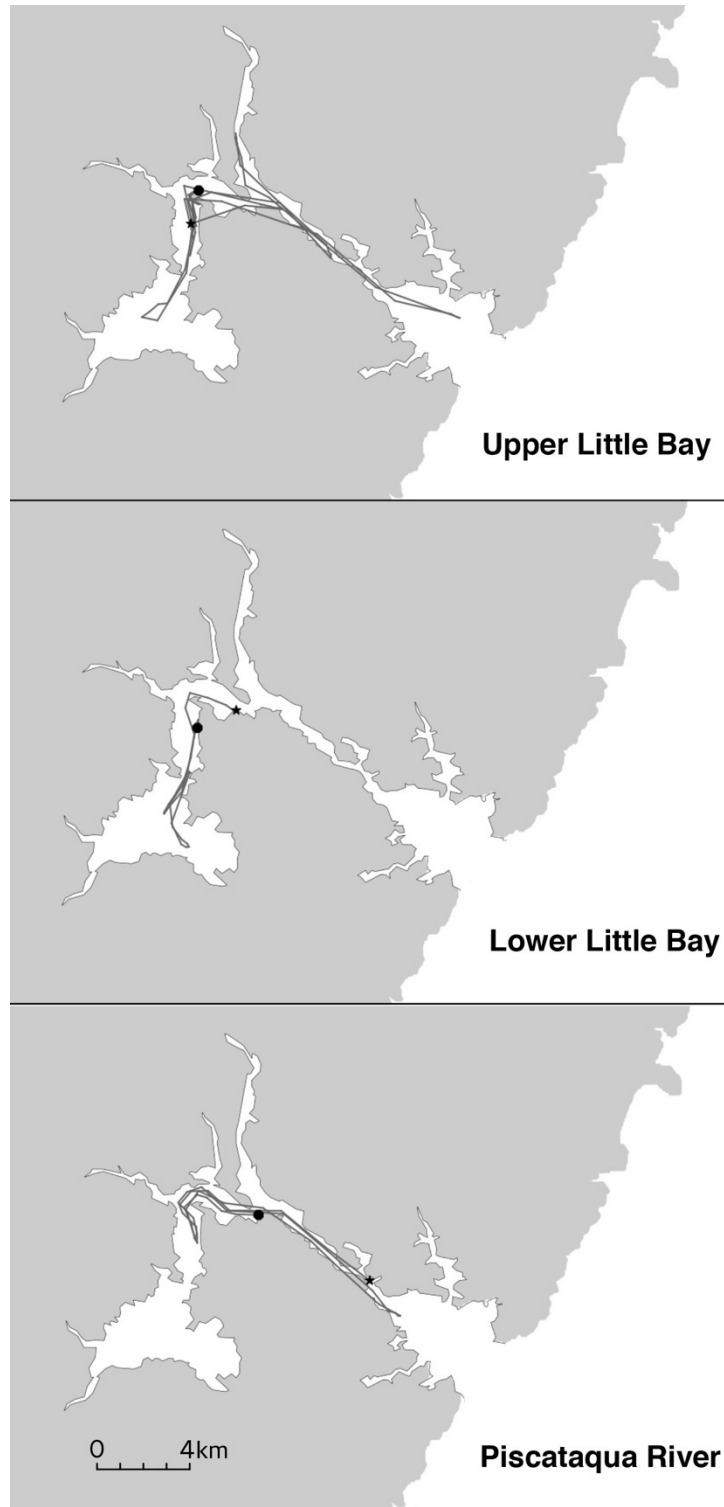**Figure 2.7** Example trajectory plots of the tracks taken by an individual drifter released in A) upper Little Bay and recovered after 28 hours B) lower Little Bay and recovered after 26 hours (middle) and C) the river and recovered after after 8 hours (bottom). The star symbol indicates the location of the start of each trial and the circle indicates where the drifter ran aground and the trial ended.

Drifters released in the river moved the most per hour; while currents did not carry drifters in Little Bay and Great Bay as far from their points of origin (Figure 2.8). The drifters released in the river moved an average net distance of 8.65 ± 0.72 km into the estuary after 24 hours, while drifters released in lower Little Bay moved an average net 5.16 ± 0.25 km km inward. Drifters released in upper Little Bay (closer to Great Bay) only moved an average net 1.87 ± 0.37 km down estuary in 24 hours (Figure 2.9). For drifters released in the estuary, there was a generally initial large movement up estuary, and less movement over subsequent tides (Figure 2.9). Drifters released at all three locations were retained in the estuary, even after several tide cycles. In addition, drifters converged in similar areas because drifters released near the coast moved up estuary, and those released at the higher reaches moved further down estuary. Thus, after 24 hours, drifters released from all three sites were in the general Little Bay area.

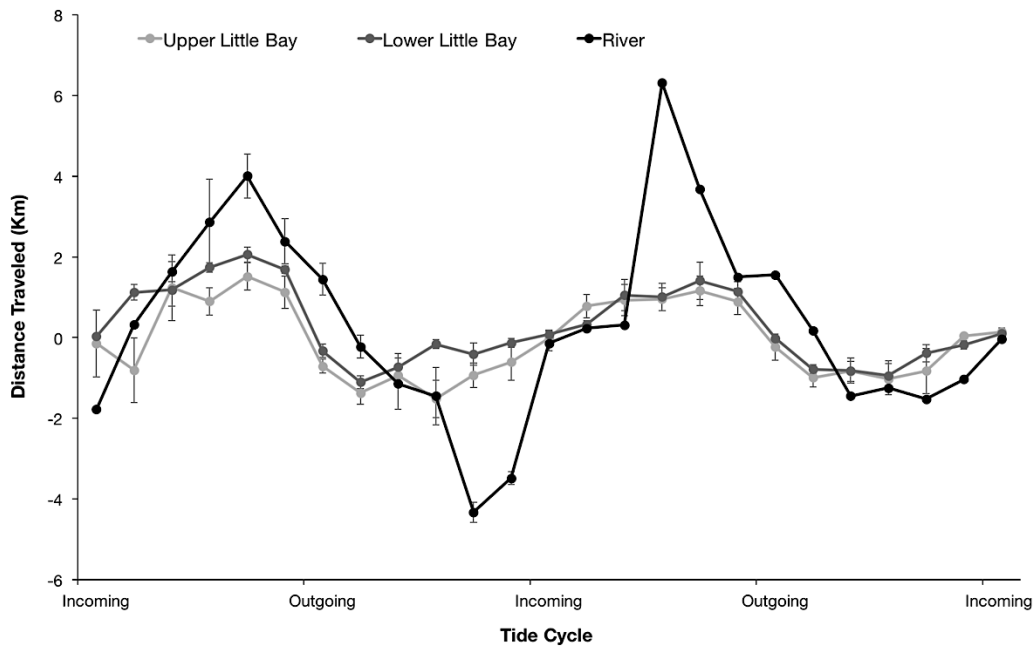**Figure 2.8** Average hourly distance (± SEM) traveled by drifters (n = 27) over one full semidiurnal tidal cycle (4 tides in 24 hours). Drifters were released in upper Little Bay (light grey), lower Little Bay (dark grey) and the Piscataqua River (black line). Those released in the river traveled further on both incoming and outgoing tides than those released in the estuary. Observations range n = 1-11 for each hour.
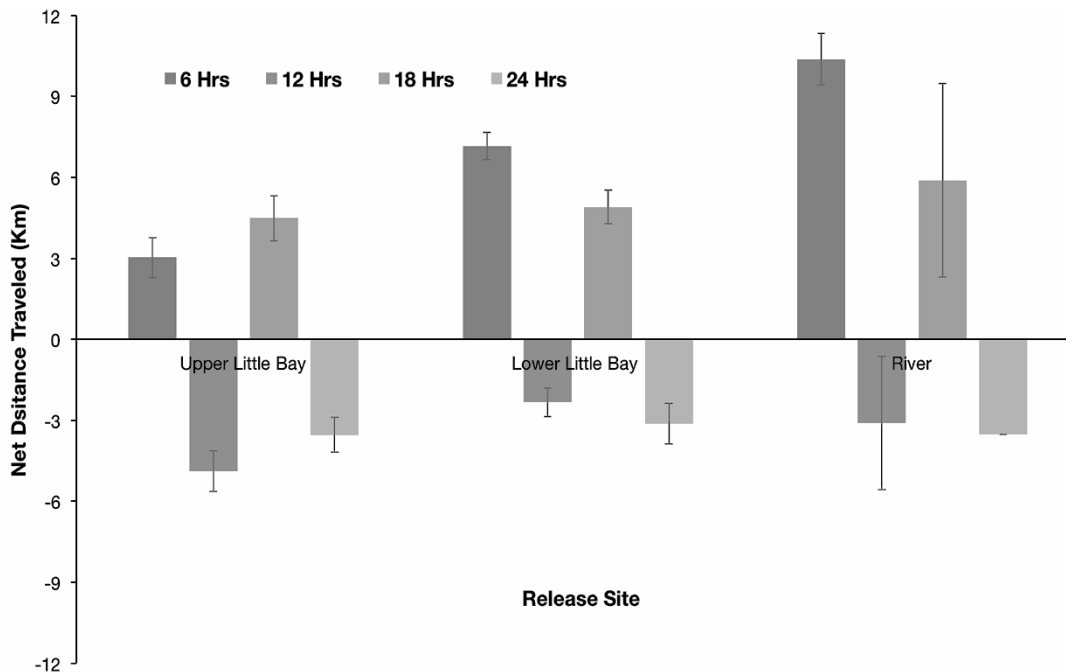
Figure 2.9 The average distance that drifters deployed in each of the three release locations traveled in six hour increments over 24 hours (n = 27, observations ranged from 1-12 for each 6-hour interval). Each six-hour increment represents an incoming and an outgoing tide, and starts on an incoming tide. Positive values are up estuary and negative values are down estuary movements.

Great Bay Currents

When comparing the movements of drifters to water currents measured during the 2007 current study, the general direction of trajectories was similar. However, drifters moved at a slower speed (Figure 2.10). When comparing the movements of water predicted from current data to the actual positions where drifters ended up, only drifters released in the river exhibit a similar pattern (Figure 2.11). For example, drifters released in the estuary were not carried very far, whereas the current data predicted they would move toward the coast. This was also true when extrapolating both drifter position and predicted current position to the amount of time that larvae remain in the water column (8-16 days, Figure 2.12). As drifters ratcheted up-estuary with each tide cycle, they were exposed to slower, more equivalent, ebb and flow currents (Figure

2.10) and therefore they were retained in the estuary. In contrast, current models predicted that

they should consistently move toward the coast with every outgoing tide.
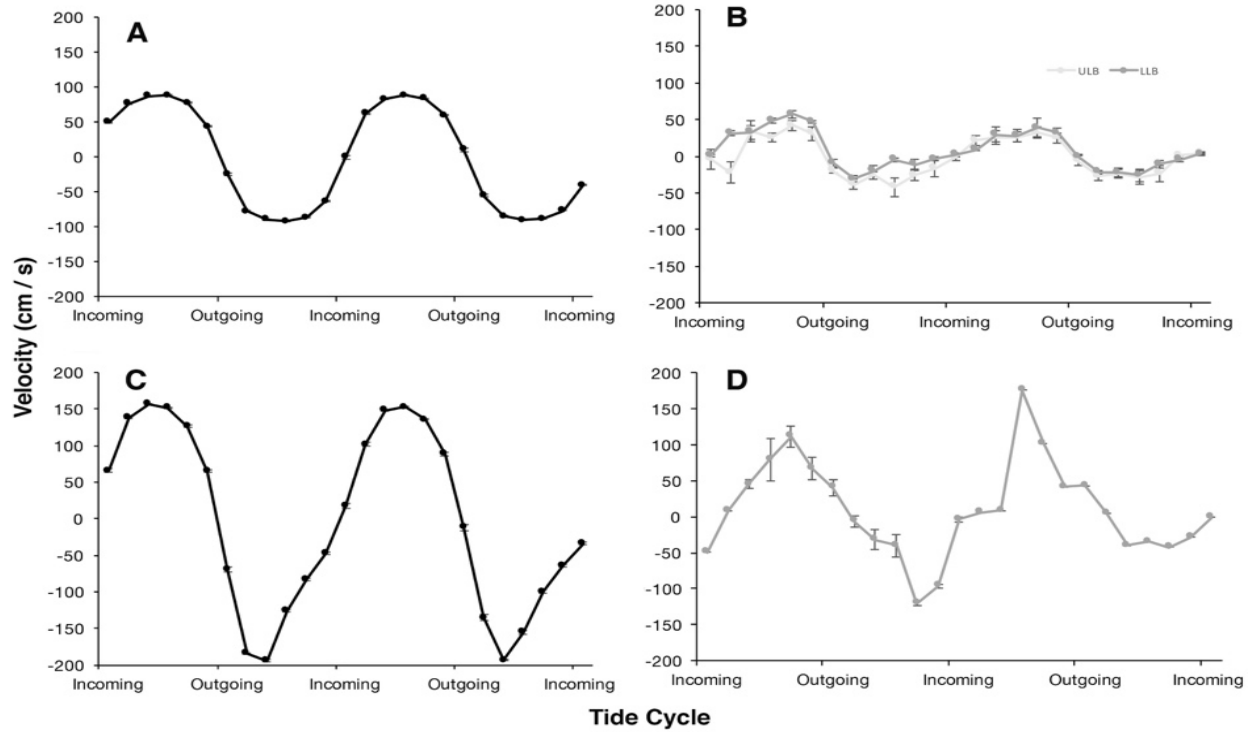
Figure 2.10 Comparing the velocity of drifters released at three release locations to currents measured during the 2007 NOAA current study. A) Water currents as measured by a current profiler in upper Little Bay. This was compared to B) drifters released in lower and upper Little Bay (ULB, LLB). C) Water currents measured by a current profiler at the midpoint of the Piscataqua River. This was compared to D) drifters released in the river.
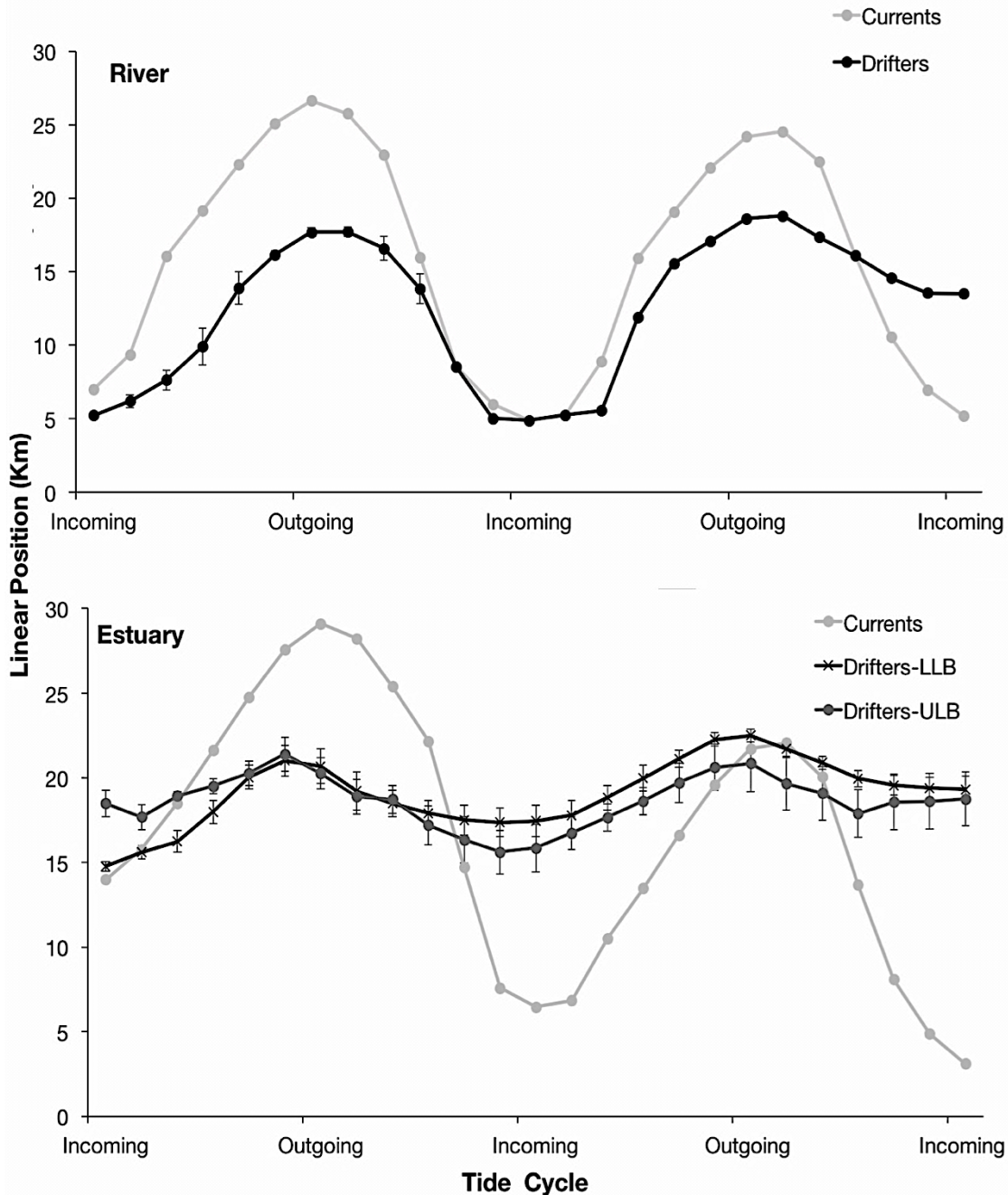
Figure 2.11 A comparison of the movements of drifters (n = 25) released in different locations to movements of a hypothetical parcel of water in the same areas, as predicted from current data. The y axis represents the linear "position" within the GBE system. The 0 - 14 km range includes the Piscataqua River (the mouth of the river is 0km), 14-18km = lower Little Bay (LLB), 18-21km = upper Little Bay (ULB) and 21-25km = Great Bay Proper. Generally, drifters remained in the lower parts of the estuary (15km-20) after a full tidal cycle, regardless of where they were released. Observations ranged from 1-11 for each hour for the drifters. The predicted linear 'position' was modeled using current data from the 2007 NOAA study. Each tide represents a six hour increment, and calculations were made every hour .
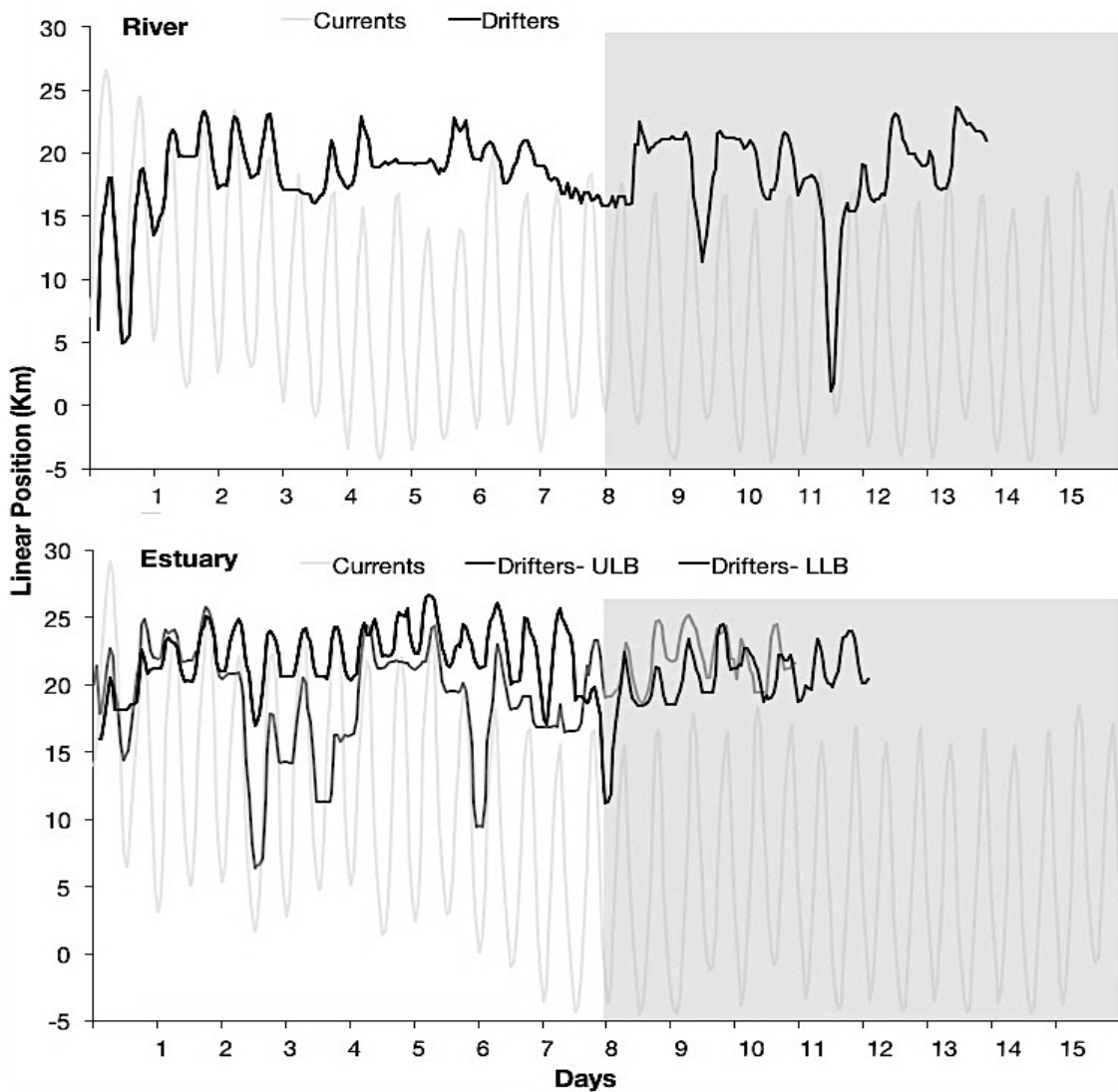
Figure 2.12 The linear position of drifters compared to their locations predicted by currents, over a 16-day time period. The shaded grey area highlights the time frame during which larvae would likely settle in the estuary if they hatched on day 0 (Hudon and Fradette 1988; Annis et al. 2007). Either the entirety or parts of several trials (ranging from 4-6 trials) were used to construct the drifter tracks for the time frame that larvae should be settling. The drifter data indicate that larvae that hatch in the estuary probably stay in the estuary, although the current data suggest they might be slowly transported towards the coast (located at 0 km).

Juvenile Recruitment

Catch composition in different types of traps and collectors

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Trawls were treated as replicates when comparing catch between sites (CPUE = lobsters/trawl /haul). When combining data from the six study sites, soak duration did not significantly influence the number of lobsters captured, and therefore data from all trawls, regardless of soak time, were for further analyses (Figure 2.13).
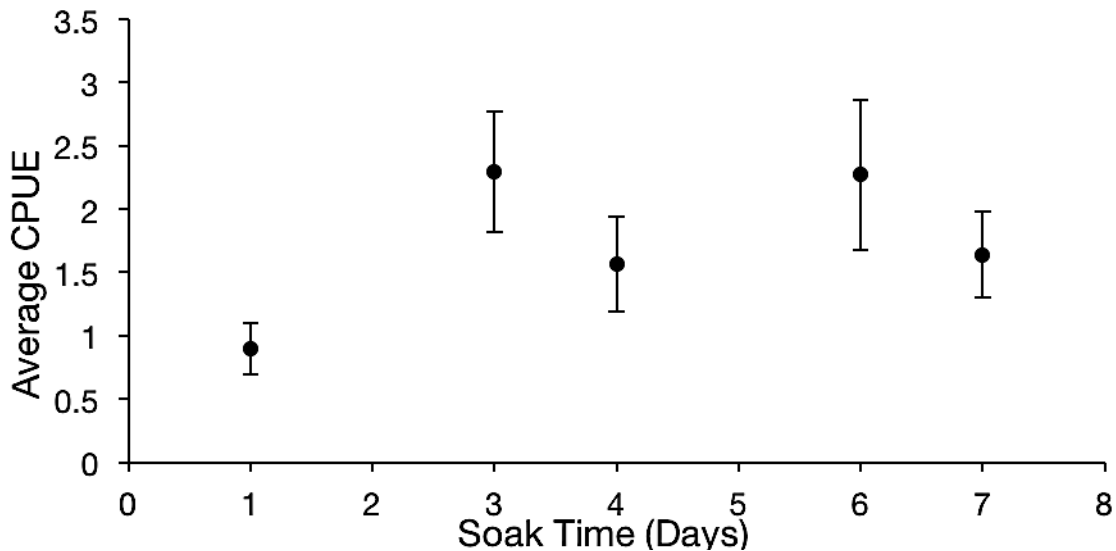
Figure 2.13 Soak time had little effect on catch ($p = 0.48$, $df = 4$) when combining all six study sites.

The small-mesh standard trap captured the highest number of lobsters, followed by the standard trap and then the juvenile collectors (Figure 2.14). The small-mesh standard trap primarily captured sublegal sized lobster (61-80mm in CL), which was the most abundant size class overall (Figure 2.14). Juvenile collectors captured fewer lobsters, due to the fact that their entrances (heads) were modified to restrict the entry of sublegal and legal lobsters, however they did appear to be more selective for small lobsters, as expected (Figure 2.15). In fact, both juvenile collectors trap types captured fewer lobsters ($n = 95$) than standard traps, but were more selectively to smaller sized lobsters, targeting a higher percentage of juvenile lobsters (cumulatively 64% of the catch). Overall, juvenile lobster (<60mm) were captured in similar

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numbers in the four trap types (p = 0.128), but both juvenile collectors excluded the captured of

larger lobsters. Overall, trawls captured a large size range of lobsters.
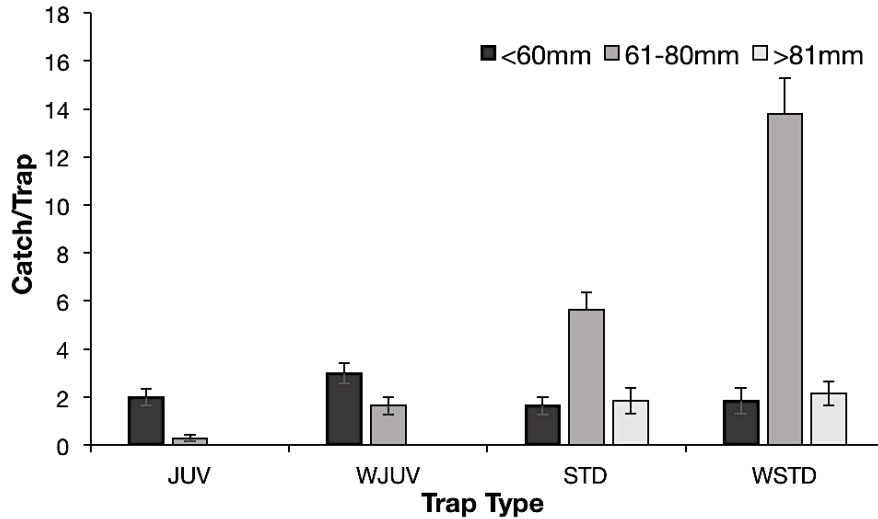
Figure 2.14 Comparison of size composition of three size classes (approximately juvenile, sublegal and legal) by trap type where JUV = juvenile collectors, STD = ventless traps and W = wrapped in small mesh. Only catch data from the River, LB1, LB2 were used as these areas had similar relative abundances and size structures of lobsters.
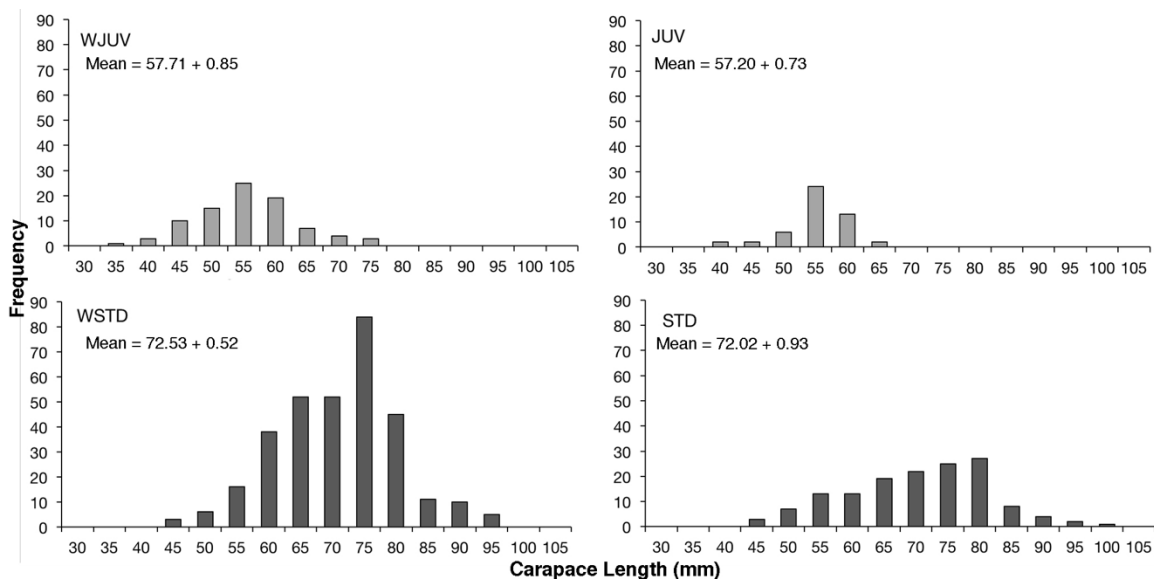
Figure 2.15 Size frequency distribution of lobster catch by trap type. The size structure of catch was similar within pairs of traps, and juvenile collectors both captured roughly the same range of small-sized lobster (unpaired t-test, p = 0.99), whereas standard traps targeted roughly the same composition of larger lobsters (unpaired t-test, p = 0.95). When comparing both juvenile collectors to both standard traps, overall catch structure differed, and juvenile collectors targeted only smaller lobsters (one-way ANOVA p < 0.001).

Catch Data

Trap trawls were pulled 13-15 times (333 total traps were hauled) during the summer of 2014 at six sites in the estuary. A total of 602 lobsters were captured and of this total, 149 (approximately 25%) were juveniles (<60mm). Lobsters ranged from 38 - 102 mm carapace length (CL) in size, with an average size of size 69.02 ± 0.45 mm CL. The smallest lobster (38 mm) was captured in the river, and in general, the average size of lobsters increased at sites furthest up into the estuary, while the abundance of lobsters decreased (Figure 2.16). The CPUE of juvenile lobsters was similar in the river, lower Little Bay and upper Little Bay (p = 0.66, df = 3), but none were captured in Great Bay (Figure 2.17). Adult abundance was not as restricted, and lobsters were captured at all sites. Overall, fewer lobsters were captured at the two sites furthest into the estuary than all other sites (p <0.001, df = 5).

Previous studies have demonstrated that the sex ratio of lobsters in GBE is more and more skewed towards males as one moves further away from the coast (Howell et al., 1999; Munro and Therriault 1983). The data from this study were consistent with that report. Male to female ratios ranged from 1.4:1 at the river to 2.7:1 in upper Little Bay (Figure 2.18). Only adult male lobsters were captured at the two sites beyond upper Little Bay and therefore no ratios were calculated for these sites. When comparing the observed sex ratios to the expected and even 1:1 male to female ratio, the adults demonstrated a significant male skew at all but the river site (Figure 2.19, Fisher's Exact Test, p = 0.027). Although captured in smaller numbers, juvenile lobsters maintained even sex ratios at the four sites where they were captured (Fisher's Exact Test, p = 0.995).
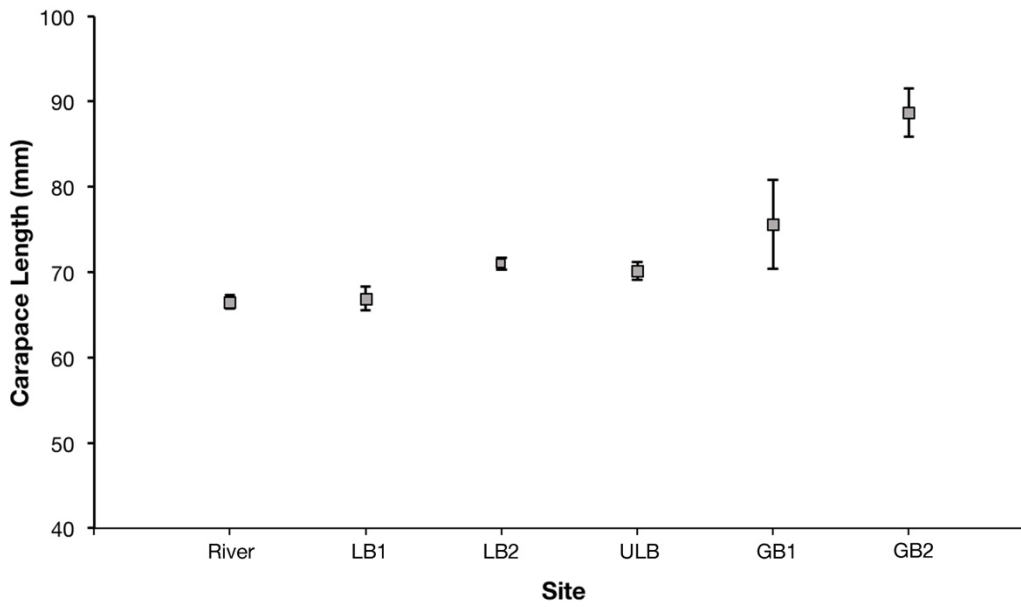
Figure 2.16 The mean carapace length of lobsters captured at six study sites on an estuarine gradient. The smallest sizes lobsters were captured in the river (n = 185) and the largest lobsters were captured at the site furthest into Great Bay (GB2, n = 6).
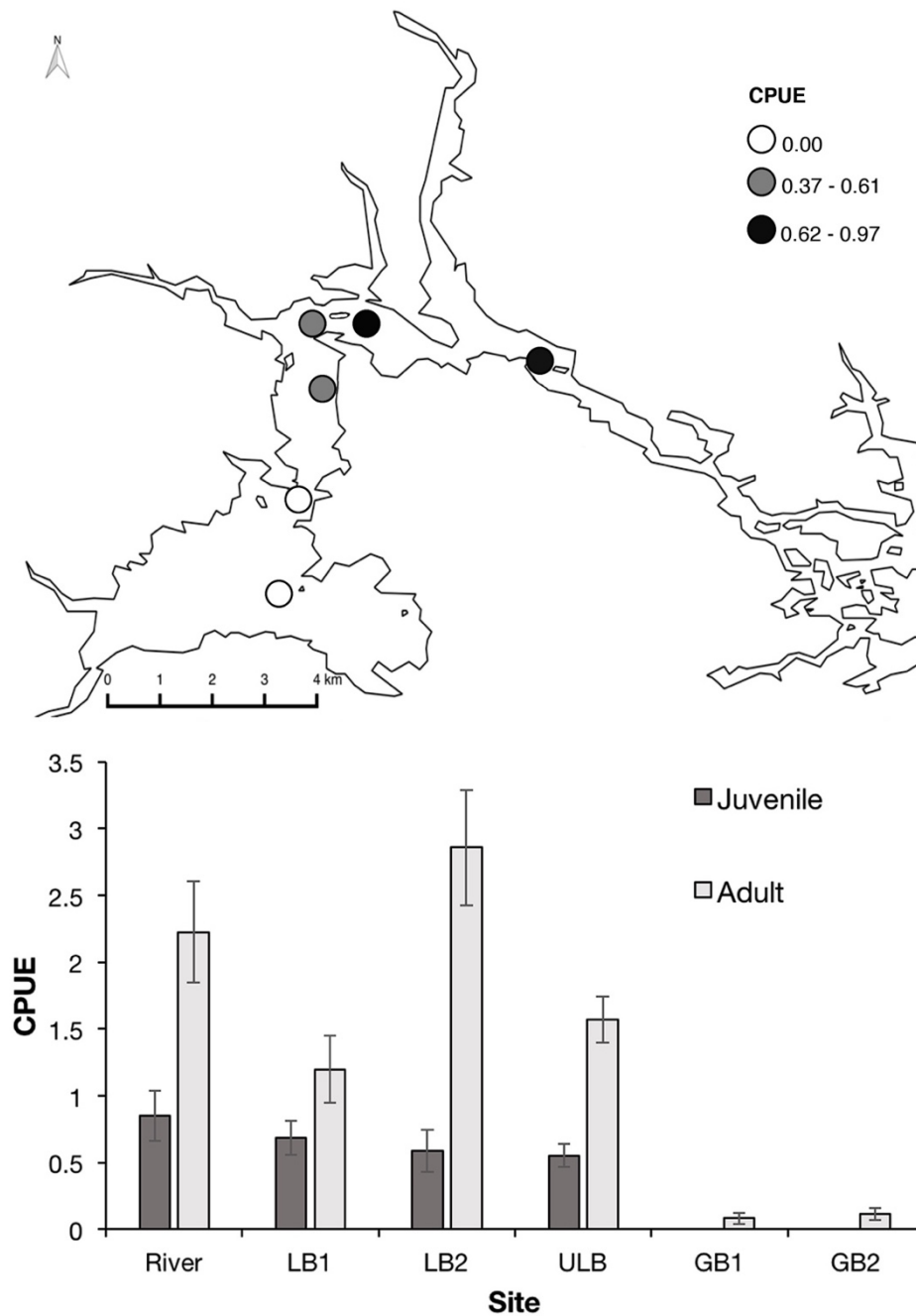
Figure 2.17 The distribution of juvenile and adult lobsters based catch. A) Abundance of juvenile lobsters /trawl haul) overlaid on a map of the estuary. Every km that was sampled is indicated, regardless of whether there was catch or not. B) The distribution of juvenile and adult lobsters at six sites in the GBE. The relative abundance of juveniles is lower than the abundance of adult lobsters, but remained consistent at each site (p = 0.66, df = 3) from the river up to upper Little Bay. No juveniles were captured at the upper Great Bay sites.
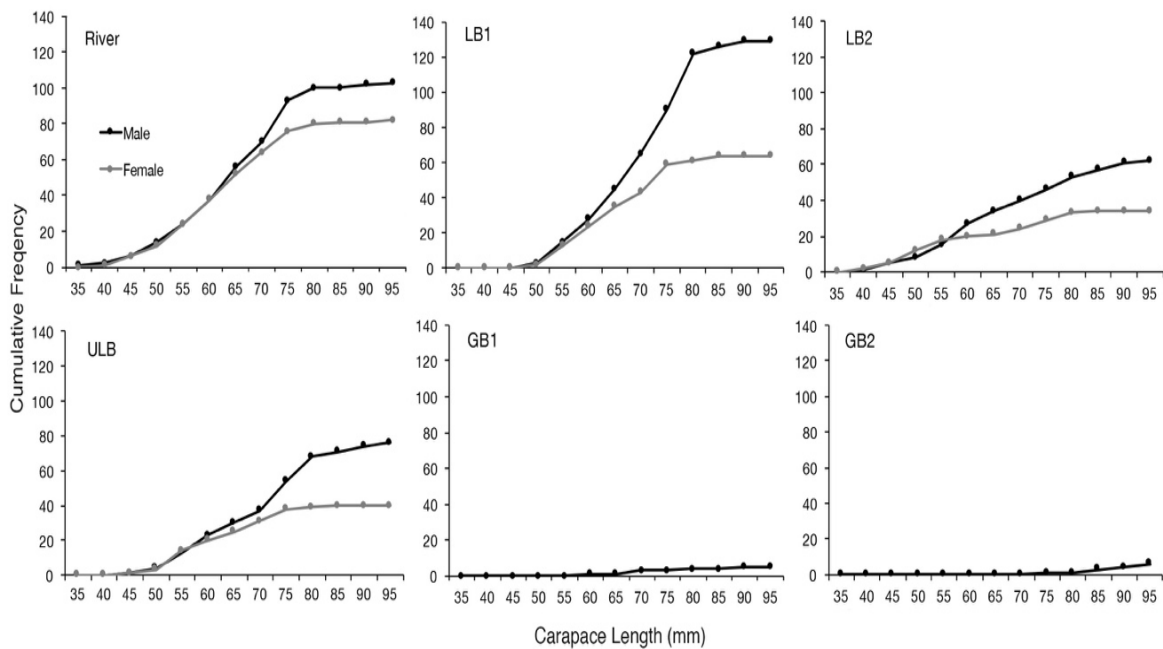
Figure 2.18 Sex ratio vs size class based on catch from all six sites. At sites where fewer lobsters were captured, there was also a male dominated sex ratio. At sites where there were more lobsters (towards the coast), the sex ratio was closer to 50:50. At all locations, the sex ratio was 50:50 at in the smaller size classes and then became more male dominated in the larger size classes. The largest lobster captured (102 mm) was excluded from this figure.
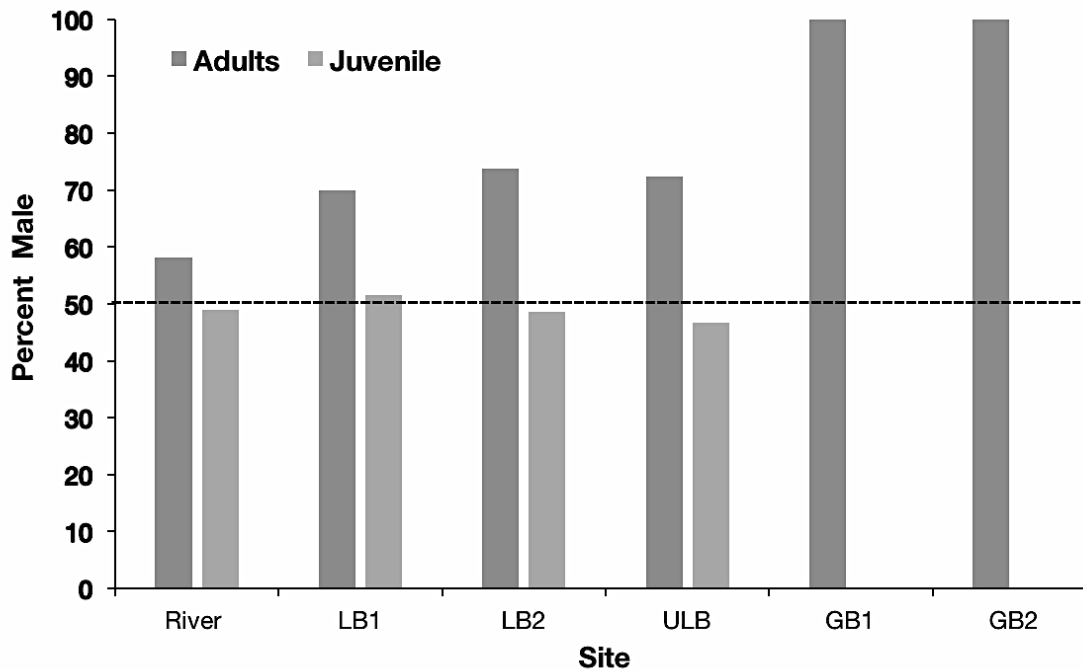
Figure 2.19 The percent of adult (>60mm CL) and juvenile (<60mm CL) male lobster captured at each site. The dashed line represents an even sex ratio, where there are 50% males and females.

Discussion

The characterization of the currents in the GBE, and the presence of juvenile lobsters in these areas support the hypothesis that lobsters that hatch in the GBE are likely retained and settle there. Late-stage ovigerous lobsters in GBE hatch their eggs in the estuary (Chapter I), and these larvae are retained in the system, settling and surviving through the subsequent juvenile stage. Moreover, there is some evidence from both the drifter and current studies that larvae hatched on the coast may be carried up the river, which is consistent with the data from Chapter 1. Thus, there is strong evidence that lobsters in the GBE originated from both a resident estuarine lobster population, and coastal lobsters.

Larval Retention

The movement of early and late stage (I and IV) larvae are largely determined by surface conditions (Matthiessen and Scherer 1983; Katz et al. 1994; Palma et al. 1999; Xue et al. 2008; Burdett-Coutts 2010; Incze et al. 2010), and characterizing them provides a better understanding of larval dispersal and subsequent settlement (Incze and Naimie, 2000), especially in estuarine systems. The GBE is a highly tidal system, ranging from a surface area of approximately 23 km^2 at high tide to 11 km^2 at low tide (reviewed in Short 1992). Therefore, it was expected that larval trajectories should be dynamic, and might exhibit large movements into and out of the estuary. Data collected during the 2007 NOAA study suggest that currents originating from all regions of GBE and river have the capability of moving water to the coast over a short amount of time, and therefore would export larvae. For example, when using current predictions to estimate the

location of larvae over the 8-16 day time frame, results did not show retention, and instead water was brought to the coast quickly and over a regular time frame (Figure 2.12). However, it was apparent that drifters slowly moved up into the estuary, generally remaining between kilometers 15 -20 in lower Little Bay after 24 hours. Previous, but limited, drifter data also showed retention in the estuary after 30 tide cycles (Goldstein 2012a, Figure 2.12).

The differences between the drifter data and predictions and the current predictions can be explained in several ways. First, in the NOAA study current profilers were placed in channels where water moves the fastest. In contrast, drifters were not restricted, and often moved out of channels. Second, the water current speeds differ by region in the estuary, and are faster in the river and lower Little Bay due to the land geography and channel width, but are much slower in upper Little Bay due to shallow areas (Figure 2.10, Nelson 1981). So, once drifters enter the estuary, they travel more slowly and were more likely to be retained. Third, there are two areas in the estuary where tidal flow restrictions occur; Dover Point in lower Little Bay, and Fox Point, in upper Little Bay (Short et al. 1992). The effect of these bottlenecks might be to retain objects on the surface. Lastly, although previous studies have broadly examined currents in the GBE (Brown and Arellano 1980; Ertürk et al. 2002; Bilgili et al. 2005; Kammerer 2007), there are a paucity of studies detailing the microclimates that have the potential to influence larval behavior (i.e., eddies might help facilitate vertical migration) and thus could lead to their retention in certain areas of the estuary. This is important for two reasons: First, eddy-diffusion greatly impacts larval drift (Langier 2003), and second larval lobsters do not swim well (Cobb et al. 1989), do not settle out in fast moving water, and probably need to seek out slower moving water before they can settle (Chassé and Miller 2010). Drifters may, in a sense, mimic lobster larvae by spending more time out of the stronger currents that exist in the channels, and this might

explain why both empirical evidence and extrapolations made over two weeks indicate that drifters move slower as they leave the channel. As a result, drifters carried into Little Bay on incoming tides moved less due to slower moving currents in upper Little Bay (Figure 2.10). Additionally, while the directionality of drifters and currents was often similar, the magnitude of movement was not (Figure 2.12), indicating the influence by unmeasured surface conditions.

A complete picture of lobster larval transport in the GBE requires both an understanding of these hydrographic dynamics and larval lobster behavior. While the earliest and latest stage (I and IV) larvae are positively phototaxic (Ennis 1995), and are found in shallow water, less information is known about the in situ behavior of intermediate stages (II and III); but it is suspected that they remain at deeper depths (Harding et al. 1987). In the GBE, currents moved faster at depth (approximately 5 m) than the surface (Wengrove 2012), and there is the possibility that intermediate stage larvae are transported from the estuary in these currents. However, many early stage larvae were captured in a protected cove in the estuary during another study (field observation), which indicates that some larvae may be retained by certain aspects of their behavior which might bring them into contact with slower moving water.

Overall, the current data predicts several possible outcomes for larval trajectories. Larvae could be: 1) exported from the GBE; 2) coastal larvae could be imported into the estuary; and 3) larvae originating in the estuary could be retained within the system. However, the overall trend obtained from the drifter data is that most estuarine larvae are probably retained in the estuary. Specifically, it appears as if they might accumulate in the lower Little Bay area. This is also where I found the most ovigerous females with late stage eggs in the spring, a high concentration of larvae in plankton tows, and a high abundance of juvenile lobsters.

Another factor that might favor the retention of larvae is rapid larval development due to warmer waters (Templeman 1936; Hughes and Matthiessen 1962; Sastry and Vargo 1977; Mackenzie 1988) in GBE. The summer water temperatures in the GBE were within the range that lead to the fastest larval development (Harding et al. 1987; Mackenzie 1988), and as a result, larvae were more likely to settle closer to their origin because they spent less time in the water column (Miller 1997; Chasse´ and Miller 2010; Incze et al. 2010; Quinn and Rochette 2015). In fact, recent studies suggest that larvae might even develop faster in situ, which would further increase the likelihood that they would be retained in the estuary and have a high abundance in the area around Little Bay and the upper reaches of the river (Annis et al. 2007)

Juvenile Recruitment

The distribution and abundance of juvenile lobsters (<60mm), which are non-migratory, and native, provide evidence for successful settlement. A number of small lobsters were captured (n=129), encompassing several size classes of juveniles, with the highest numbers in the upper river. The further traps moved up into the estuary from this point, the fewer juveniles we caught. This pattern validates the results of other studies that reported the presence of recently settled lobsters in Little Bay, including new recruits in the size range of 10-30 mm CL (NHFG 1989, 1990, 2008; Becker 1994). It has been proposed that larvae concentrate and settle out in these areas because cobble bottom is prevalent, supporting the habitat requirements for survival (Wahle et al. 1991; Wahle 1992; Becker 1994; Grizzle et al. 2008). Interestingly, because drifter trajectories encompass areas in both Little and Great Bay when larvae should be settling, larvae were either passively exported to these areas and survived because of good habitat, or larvae 'choose' these areas, and may have employed active behavioral mechanisms such as swimming

(Ennis 1986; Cobb et al. 1989). Juvenile lobsters were not found in the sites furthest into GBE, which is likely a result of unfavorable conditions for settlement and survival, including high water temperatures and low salinity (Templeman 1936), soft substrate (Wahle 1993; Tang et al. 2015), and a higher prevalence of benthic predators (Barshaw et al. 1994). The distribution of juvenile lobsters also follows an interesting trend; larval growth rates are maximized at 15-18°C (Mackenzie 1988) and lobsters settled out in areas experiencing a similar bottom temperature regime (see temperature figure in Chapter I).

At sites where juvenile lobsters were found in the highest abundance, the sex ratio was very close to the 1:1 male to female ratio normally seen in coastal populations (Krouse 1973; Cooper et al. 1975; Carlberg et al. 1978; Moriyasu et al. 1999, Figure 2.19). In comparison, the adult sex ratio was male dominated, and increased in the areas furthest up the estuary, as has been reported previously (Munro and Therriault 1983; Howell et al. 1999) . This difference is likely due to the movement of adult lobsters, whereas juvenile lobsters are able to maintain a 1:1 ratio as a result of moving less.

While fewer juveniles were captured (Figure 2.17) than adults, this difference may be a result of differences in catchability, due to either to behavioral differences or trap design, or both (Miller 1990). For example, lobsters in the 5-40 mm CL range are shelter restricted, and are typically not captured with traps. However, I was somewhat successful in targeting juvenile lobsters by using small-mesh juvenile collectors, which both prevented the escape of smaller, sub-legal sized lobsters by using a reduced mesh size, and prohibited the entry of larger lobster through modified trap heads. Due to the selectivity of the modified small-mesh juvenile collectors, a greater number of juvenile lobsters were captured than non modified traps, and may in the future, serve

as a better survey tool to specifically target smaller lobsters.

Juvenile recruitment is an important process to understand, as initial recruitment is used as an indicator for subsequent year classes (Burdette-Coutts et al. 2014; Wahle et al. 2004). Recruitment failure has already occurred in parts of Southern New England (ASMFC 2015) and several studies predict unfavorable shifts of larval retention in the inshore waters of the Gulf of Maine (Oppenheim et al. 2015). Therefore, it is increasingly important to characterize transport and identify areas where settlement occurs. While other, earlier studies sampled for larvae in GBE, the working assumption was that larvae originated exclusively from the coast, and settlement did not occur in the estuary at a sustainable level. However, this study provided evidence that larvae originate from, and settle in, select areas of GBE. The subsequent concentrations of juvenile lobsters are likely a result of density-dependent processes such as habitat choice (Botero and Atema 1982; Wahle and Steneck 1991; Wahle 1992), because most were found in areas in GBE where rock, cobble or eelgrass are prevalent (Nelson 1981; NHFG 1989, 1990; Short 2002). Generally, ovigerous lobsters employ strategies to maximize the survival of their offspring (Jarvis 1989; Goldstein 2012b; Goldstein and Watson 2015a), and their use of GBE indicates adequate conditions. Therefore, the self-recruiting population of American lobster in GBE may not be entirely supplemented by seasonal migrations of coastal lobster are previously believed (Watson et al. 1999).

CONCLUSIONS

Conclusions

Previous studies in Great Bay estuary and the New Hampshire coast have surveyed for ovigerous

females, as well as larval and early benthic phase lobsters (NHFG 1989, 1990, 2008; Goldstein

2012b; Langeley et al. 2014), but little had been done to examine the source-sink (connectivity)

relationships between the NH coast and GBE. It was generally assumed that the ovigerous

lobsters captured in the GBE during the summer migrated there from the coast (NHFG 1989,

1990; Watson et al. 1999), and that winter and early spring conditions in the estuary were unable

to support a resident lobster population. However, the findings from this thesis indicate that,

while there was some exchange of adult and larval lobsters with coastal lobsters, there was also

evidence for an independent group of resident lobsters that reproduce in the estuary.

The first hypothesis I tested, that lobsters reproduce in the GBE and their eggs hatch there, was

supported by the presence of ovigerous females carrying late-stage eggs in Little Bay and the

upper part of Piscataqua River. These eggs were further developed than those carried by coastal

lobsters during a similar time frame, and remained further developed throughout the hatching

season. The eggs carried by these ovigerous lobsters also hatched earlier in the estuary (May vs

June at the coast) and over a shorter amount of time (34 vs 42 days at the coast). Additionally,

early-stage larvae were captured in the estuary, during a time period that coincided with the time

that lobster eggs were hatching in the GBE.

The second hypothesis, that juvenile lobsters recruited to the estuary, was supported both by the

drifter data, that indicated larvae were likely retained within the estuary, and the catch data showing the presence of juvenile lobsters, as small as 38 mm CL, in the GBE. Additionally, the highest abundance of juvenile lobsters was in areas where larvae were predicted to settle. These are also areas where larvae that originate from the GBE and the coast likely overlap and were captured in slightly higher numbers. Early-stage larvae continued to be captured after ovigerous lobsters had finished hatching their eggs in the estuary, and there was evidence, from drifters, that larvae could be transported from the coast up into the GBE. The GBE is influenced by a large tidal prism (Bilgili et al. 2005), and as a result, areas like Little Bay and the river are more influenced by, and resemble, coastal conditions in terms of salinity and temperature. Therefore, conditions in certain areas of the estuarine system meet the requirements for the survival of all life-history stages of the lobster.

In conclusion, the data obtained during these studies revealed that lobster eggs hatch in the Great Bay Estuary, and some of these larvae are retained and settle in the estuary. These processes may aid in supporting a self-recruiting, residential lobster population in Great Bay Estuary, NH, and further rigorous work would solidify the complex recruitment dynamics associated with maintaining an estuarine lobster population.

Implications for the Lobster Fishery

Quantifying juvenile recruitment is an important process, and is used as an indicator for subsequent year classes (Miller 1997; Fogarty at el. 1998; Wahle et al. 2004; Burdett-Coutts et al. 2014) Recruitment failure has already occurred in parts of Southern New England (ASMFC 2015) and is predicted to continue into the southern range as waters warm above the thermal stress levels of the lobster (Wahle et al. 2009; Howell 2012; ASMFC 2015). Conversely, it is

predicted that there may be positive impacts of global warming on Gulf of Maine (GOM) lobsters as water temperatures warm to the range that maximizes larval growth (Drinkwater et al 1996; Fogarty et al. 2007; Quinn and Rochette, 2015; Hare et al. 2016). However, there is uncertainty in the future spatial patterns of recruitment and areas where settlement occurs are expected to shift in the GOM (Oppenheim et al. 2015). Therefore, it is essential to both continue monitoring areas where settlement occurs (Cowan 1999; Wahle et al. 2013), as well as identify sources of recruits to the fishery that may not be already accounted for (Ennis and Fogarty 1997). If estuaries are a viable source of new recruits to the American lobster fishery, future work should examine the degree that they serve as a nursery grounds, and their contribution to recruits to the fishery (Beck et al. 2001). In fact, because estuaries tend to be warmer than coastal waters, estuarine females mature at a smaller size and thus might have more opportunities to reproduce before being harvested; which indicates they are, in fact, a type of nursery ground for lobsters (Little and Watson 2003). Finally, it has been suggested that managing local, self-recruiting populations is more effective than at the meta-population level (Prodöhol et al. 2006). These smaller delineations allow managers to account for difference in biological, behavior and genetic characteristics of subpopulations that influence reproduction and recruitment.

While estuaries like GBE might serve as sources of recruits, they are also valuable serving as a 'natural laboratory' (Goldstein 2012a), that might provide insight into how warming waters will influence hatching and the survival of lobsters. In particular, estuaries are warmer than adjacent coastal waters and the impact of warming water will be seen first in estuarine lobsters. These populations have already provided insight into the behavioral strategies that lobster employ when exposed to sub-optimal conditions (Jury et al. 1994a; Watson et al. 1999). However, since the GOM is warming at a rate faster than almost any other oceanic body of water (Pershing et al.

2015), future work should examine the GBE lobsters thoroughly to understand how temperature change will effect lobsters both at the individual level (i.e., genetics, physiology, behavior,) and at the population level (competition, connectivity, dispersal and recruitment (Harley et al. 2006; Madeira et al. 2012; Hare et al. 2016). Arguably, understanding these dynamics, in particular the link between dispersal (i.e., larval pathways) and subpopulations is crucial (Fogarty 1998), as it facilitates the long-term survival of populations, particular species experiencing environmental uncertainty.

Future works in GBE

While the drifter study provided support for retention and settlement, they did not provide a complete analysis. Both studies only provided data for surface waters, which influence only the movement of early and late stage larvae. The transport of mid stage larvae (II and III) in the estuary remains largely unknown, and these stages often sparse in plankton tows, only appearing when deeper water depths are sampled (Harding et al. 1987). However, the movement of late-stage larvae likely influence where settlement eventually occurs, and was not accounted for in this study. Recent studies used particle transport models at several depths, and might provide better estimates for settlement areas (Incze et al. 2010; Stanley et al. 2015). Also, drifters were only at large for a few hours to a few days, which did not encompass the time frame that larvae are in the water column. Longer drifter trials should be attempted to gather empirical data pertaining to this time frame. Additionally, the dynamics of water currents in the Piscataqua River should be probed in greater detail; drifters released in these areas ran aground quickly, and as a result, tracks were shorter in duration from this area. Lastly, the model took into account simple down or up estuarine movement and did not account for lateral movement, and thus the

movement component of the model could be improved. In particular, adding complex directionality to the model might help to predict the behavioral aspects of larvae (i.e., vertical migrations and swimming, (Cobb et al. 1989; Boudreau et al. 1991, Stanley et al. 2015), which was not accounted for in this study.

One major finding from the drifter study was that larvae should concentrate in areas of GBE (Little Bay) as a result of being retained by slower moving water. Therefore, future plankton tows should be conducted in areas of GBE where there are coves, eddies, or other microclimates, to validate findings from the drifter study. Preliminary plankton tows did capture a large number (15) of larvae in coves in Little Bay (field obs.). However, these were all also early-stage larvae. This is unsurprising, as early-stage larvae are the most commonly captured stage (Harding et al. 1987) because they are only found for a short time in warmer water temperatures and quickly pass through to later stages that seek deeper depths (Boudreau et al. 1991), which I did not sample. It has been suggested that when only stage I larvae are found that there is either high mortality of the subsequent stages, or export of larvae out of the system (Burdett-Coutts 2010). Some of the larvae captured during this study were intermediate to late stage I, indicating that export does not occur immediately, and that larvae were retained almost all the way through the initial stages. More importantly, the presence of stage I larvae is more likely to represent contributions from a local spawning population (Grabe et al. 1983). Overall, expanding the survey area, as well as sampling at deeper depths would help to identify whether or not late stage larvae are also found in the estuary, and would provide stronger evidence for settlement. Additional work should quantify the early benthic phase, or young-of-year lobster that bridge settling larvae to older juveniles in GBE. This is important in determining if larvae are able to establish a nursery (Cowan et al. 2001) and survive in a given area. While efforts to survey EBP

lobsters are difficult, initial findings show that they exist in GBE, and rigorously quantifying their presence would confirm successful settlement (NHFG 2008). Now that likely areas for settlement have been identified, suction sampling efforts can be focused on these habitats, which should make them more successful. Lastly, while lobsters exhibit little genetic variation (reviewed in Fogarty 1995), methods have been recently developed to differentiate populations (Benestan et al. 2015). Defining the genetic structure of juvenile, ovigerous and larval lobster found in GBE would answer the question whether these lobsters are part of an independent population.

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