LARVAL SUPPLY, SETTLEMENT, AND RECRUITMENT OF AMERICAN LOBSTER, HOMARUS AMERICANUS

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by

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ABSTRACT

This thesis contains three studies on the American lobster, *Homarus americanus*. Two took place in Bonne Bay, Newfoundland and a third used a long-term young-of-year (YoY) recruitment index from New England, USA. In the first study, planktonic larval and benthic suction sampling along the Bonne Bay estuary indicated larval concentrations were consistently highest at the mouth of the bay, with a more dramatic drop in density from early to late stages than reported elsewhere. The second study evaluated the spatial scale of correlations between YoY recruitment and older juvenile densities at some 70 sampling sites in New England. Strong correlations at even the finest scale (metre's), along with behavioural experiments, suggest postlarvae preferentially settle among resident conspecifics. The third study compared fishers' local knowledge of lobster hatching and nursery locations in Bonne Bay against ground-truth data collected by fishery-dependent and -independent surveys. Fishers accurately identified hatching but not nursery locations in the bay.

Keywords: *Homarus americanus*, larvae, advection, juvenile, recruitment, mortality, Local Environmental Knowledge.

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LIST OF ABBREVIATIONS

ADCP: Acoustic Doppler Current Profiler
SST: Sea Surface Temperature
AVHRR: Advanced Very High Resolution Radiometre
Z_{CM}: Mean Centre of Mass within the column
MLW: Mean Low Water
SCUBA: Self Contained Underwater Breathing Apparatus
GPS: Global Positioning System
CD: Calendar Day
YoY: Young-of-Year
Juv: Older Juvenile
CL: Carapace Length
MLS: Minimum Legal Size
LFA: Lobster Fishery Areas
LEK: Local Environmental Knowledge
FFAW: Fish, Food, and Allied Workers Union
CPUE: Catch Per Unit Effort
DFO: Department of Fisheries and Oceans Canada
ICEHR: Interdisciplinary Committee on Ethics in Human Research

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CO AUTHORSHIP STATEMENT

The author of this thesis designed the field and laboratory sampling methodologies, processed, collected, and analyzed all the data, and wrote this thesis. Dr. Paul Snelgrove and Dr. Richard Wahle made significant contributions to the experimental design, analysis of the data, and provided editorial comments of all chapters.

CHAPTER 1 GENERAL INTRODUCTION AND OVERVIEW

Introduction

Many marine benthic invertebrates have complex life cycles with planktonic larval stages capable of long distance dispersal (Thorson 1950). Our understanding of the influence of physical and biotic processes on larval transport and patterns of settlement has improved considerably in recent decades (Connell 1985; Gaines and Roughgarden 1985; Underwood 1989), but the spatial scales at which these processes operate continues to be debated (see Pineda et al. 2009 for a review). Knowledge of these processes could have important implications for population recruitment and connectivity, issues vital to the study of marine communities, fisheries management, and the design of marine protected areas (Cowan et al. 2001; Baskett et al. 2007; Cowan et al. 2007; Metaxas and Saunders 2009).

Abundance and fecundity of reproductive females are the first potential limiting factors for regional larval supply. Physical factors then influence larval transport and retention, through circulation, coastal topography, and water column stratification (Alldredge and Hamner 1980; Lobel and Robinson 1986; Connolly and Roughgarden 1999). Larval behaviour can also influence transport, although larval swimming distances are generally small relative to hydrodynamic transport (Thorson 1950; Scheltema 1986). Vertical migration is common in marine planktonic invertebrates, often in response to food availability, predator avoidance, and horizontal displacement (Webley and Connolly 2007; Cohen and Forward 2009). A few metres of vertical displacement can dramatically affect horizontal transport (Kimmerer and McKinnon 1987; Hinckley et al. 2001; Metaxas 2001; Vikebø et al. 2005). Numerous field and laboratory studies show increased larval concentrations near physical discontinuities such as pycnoclines, convergences, fronts and interval waves that are believed to result from a combination of physical and behavioural interactions (see Metaxas 2001 for a review).

The American lobster (*Homarus americanus*) exhibits a complex life history typical of most marine decapods. Larvae develop through three stages into a postlarval stage which settles to the seafloor (Ennis 1986; Charmantier et al. 1991; Lawton and Lavalli 1995). Postlarval lobsters are relatively strong swimmers with an average swimming speed of 13.2 cm/s (Cobb et al. 1989) and exhibit active habitat selection for structurally-complex habitats such as cobble-boulder, which results in the non-random distribution of juvenile stages (Scarratt 1973; Cooper and Uzmann ; Cobb et al. 1983; Wahle and Steneck 1992).

Settlement patterns of marine benthic invertebrates are influenced by larval supply, behaviour, availability of suitable habitat and hydrodynamic forces at both oceanic and benthic boundary layer scales (Woodin 1986; Butman 1987; Snelgrove et al. 1993; Abelson and Denny 1998; Sponaugle et al. 2002). Settling larvae can respond to chemical and tactile cues associated with the seabed including chemical signals emitted by sediments, fauna, flora, and conspecifics (O'Connor and Richardson 1998; Head et al. 2004). Although most laboratory studies have focused on single cues, larvae likely respond to multiple cues that may operate simultaneously and hierarchically (Kingsford et al. 2002; Ettinger-Epstein et al. 2008).

For commercially important marine species in particular, incorporating the knowledge of resource users is fundamental to effective management of fisheries. Fisher knowledge includes anecdotal observations while they are on the water as well as catch data. This information can help to assess the health of stocks, migratory routes of animals, and to estimate animal abundances (Neis et al. 1999; Anadon et al. 2009). In addition to the knowledge that fishers can contribute, working with them can help integrate stakeholders in the scientific process and build community understanding of a fishery. This collaboration creates greater involvement and stewardship that moves fishing beyond a political or capital endeavour.

American lobster has been commercially fished on the coastal and shelf waters of the Northeast US and Atlantic Canada since the late 1800s, where it is currently one of the most economically important single-species fisheries. As other fisheries decline, many fishers are increasingly dependent on this fishery for their livelihood. Lobster landings are now at historic highs through much of its range, despite exploitation rates sometimes exceeding 90% (FRCC 2007). The mechanisms responsible for the resilience of this species to high exploitation rates is largely unknown (Fogarty 1998), although the fishery has sustained decades of harvesting at very high exploitation rates.

The Bonne Bay ecosystem is at the northern geographic limit for American lobster, but nonetheless produces sufficient recruitment to support a commercial fishery. Bonne Bay (Fig. 2.1) is a subarctic fjord on the west coast of Newfoundland that is divided into two arms. The relatively sheltered, linear shape of Bonne Bay, combined with comparatively simple wind-driven and tidal flow (Richards and deYoung 2004), creates the potential for a self-seeding population. The Bonne Bay ecosystem therefore provides a unique natural laboratory in which to examine connectivity between physics and recruitment in cold-water environments.

The overall objective of this thesis was to use American lobster (*Homarus americanus*) as a model organism of benthic crustaceans to study recruitment dynamics during the larval, juvenile, and egg bearing female stages to understand the interaction of bio-physical processes that determine recruitment success. Recruitment of benthic invertebrates with planktonic larvae can be defined as survival to a post-settlement stage, and is influenced by processes that operate both before and after settlement (Connell 1961; Caley et al. 1996; Hunt and Scheibling 1997). Successful recruitment is controlled by three major components; larval supply, larval behaviour at the time of settlement, and survival of settlers to the time of census (Keough and Downes 1982; Eggleston and Armstrong 1995). Temporal and spatial variation in rates of larval recruitment has long been recognized as a major driver of marine population dynamics (Doherty and Williams 1988; Caley et al. 1996).

This thesis consists of an introductory chapter, three core data chapters, and a concluding chapter. Two chapters focus on Bonne Bay, Newfoundland and one examines a long-term recruitment index from New England, USA. Chapter 2 is the first study of patterns in the abundance and distribution of larval and young-of-year (YoY) lobsters in Bonne Bay, Newfoundland. The objective was to investigate the spatial and temporal distributions of American lobster larvae in the Bonne Bay ecosystem to understand how larval dispersal may contribute to lobster population dynamics. Specifically, I set out to examine how spawning location, inferred from abundances of stage I larvae, and seasonal timing were related to the subsequent distribution and abundance of late stage larvae and

YoY settlers. I then considered how these patterns could be used to draw inferences on population connectivity within and outside the Bonne Bay system.

Chapter 3 presents long-term recruitment data from New England and pairs field observations with behavioural experiments to test hypotheses on the spatial association between newly settled YoY lobsters and older conspecifics in shallow cobble nurseries. A fundamental question in marine ecology is how to differentiate the effects of passive mechanisms of larval dispersal from behavioural effects on spatial patterns of recruitment. Recruitment and settlement of YoY and early juvenile lobsters are strongly associated with structurally complex nursery habitats such as cobbles and boulders (Scarratt 1973; Cooper and Uzmann 1980; Wahle and Steneck 1992). I examined the hypothesis that YoY may be associated with older juveniles because postlarvae may be attracted to older conspecifics during settlement. Toward this end, the aims of this chapter were to evaluate the relationship between YoY and juvenile lobsters using eight years (2001-2008) of long-term recruitment data analyzed at three spatial scales (regional, site, quadrat) of data aggregation and to investigate the behavioural responses of post-larvae to the presence of older juveniles.

Chapter 4 summarizes results of interviews and at-sea sampling with fishermen to identify lobster spawning areas, and the collection of data on lobster fecundity to examine reproductive output from different geographic areas. The objective of this chapter was to collaborate with local fishers to discuss and record their knowledge of different stages of the life cycle of American lobster. Additionally, I accompanied them in their daily fishing routines in order to determine the size frequency distribution of lobster and the distribution of egg-bearing females. Collaborations with fishers also provide a mutually beneficial learning experience.

Determining recruitment dynamics of American lobster is important because it represents a lucrative fishery on the east coast of North America. Bonne Bay represents one of the coldest environments that lobsters experience and yet supports a commercial fishery. This study represents the first investigation of recruitment in Bonne Bay and thus the incorporation of FEK can help guide scientific studies where background scientific data does not exist. The utilization of a long-term recruitment index provides the opportunity to examine patterns and processes at a variety of spatial scales and provides a powerful resource to evaluate patterns and suggest mechanisms that influence recruitment dynamics

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CHAPTER 2 : DISTRIBUTION AND ABUNDANCE OF EARLY LIFE STAGES OF AMERICAN LOBSTER IN THE COASTAL WATERS OF NEWFOUNDLAND. PASSIVE AND ACTIVE PROCESSES.

Abstract

Planktonic stages of American lobster, *Homarus americanus*, were sampled in Bonne Bay on Newfoundland's west coast from 2006 to 2008 with neuston tows. These are the first systematic surveys of early life stages of American lobster at the northern limit of its distribution. Forty-minute tows were made at fixed stations at approximately ten-day intervals spanning the summer months of 2006 and 2007. Information from these tows guided an intensive two-week survey in 2008 at two-day intervals. Larval hatching began in mid-June in both 2006 and 2007 when surface water temperatures reached 12 °C. There were two distinct hatching peaks in mid to late July. Stage I larvae largely disappeared from surface waters by mid-August. The concentration of larvae during peak hatching increased from 28.6 larvae $\cdot 10^3 m^{-3}$ 2006 to 75.0 larvae $\cdot 10^3 m^{-3}$ in 2007 and to 250.1 larvae $\cdot 10^3 m^{-3}$ in 2008. Spatial patterns of stage I larvae were consistent among and within seasons with areas of high abundance in the Outer Bay in all three years. Late stages were rare in 2006 and 2007 but comparatively numerous in 2008 in the Outer Bay. The highest larval concentrations were generally during downwelling produced by predominant southwest winds. The rarity of later stage larvae in these samples suggests early stages are flushed from Bonne Bay prior to moulting or that larval mortality is high.

Benthic recruitment surveys in 2007 and 2008 revealed correspondingly low recruitment of young-of-year (YoY) lobsters.

Laboratory behavioural experiments to determine the response of different larval stages to light and salinity showed that stage I larvae are positively phototactic, although the effect dissipates in later stages. In halocline experiments that tested four different salinity gradients (21-30, 24-30, 28-30, 30-30), stage I lobsters avoided surface layers with salinities < 24 psu. Results for other stages were non-significant.

Together these results comprise one of the first investigations of larval and postlarval distributions in one the northernmost distributions of American lobster and provide interesting insight into recruitment dynamics of this species at fringe of its biogeographic rang. A better understanding of lobster connectivity in coastal Newfoundland hinges on determining larval supply and recruitment patterns, which may be particularly important for a species at its northern limit and in a region with the potential for a long-term warming trend.

Introduction

For decades, marine ecologists have studied larval dispersal, settlement, and benthic recruitment (e.g. Wilbur 1980). For those benthic taxa with complex life cycles, the planktonic phase has the greatest potential for dispersal, and thus often determines connectivity between subpopulations (Scheltema 1986; Sponaugle et al. 2002; Cowen et al. 2007). However, several studies have shown that this concept may be overly simplistic (Shanks 2009). Recruitment is conventionally defined as survival through settlement to the juvenile or adult benthic stage (Gaines and Roughgarden 1985; Harding et al. 2005; Gaines et al. 2007; Xue et al. 2008; Cowen and Sponaugle 2009). The study of larval connectivity evaluates the exchange of individuals among local populations, from larval hatching to benthic settlement areas (Caley et al. 1996; Todd 1998; Kinlan and Gaines 2003; Cowen et al. 2007). In effect, connectivity encompasses the spatial footprint of a population, including pelagic and benthic environments through all stages of ontogeny.

The processes that determine connectivity span multiple spatial scales that are influenced by a variety of biological and physical variables (Pineda 2000; Pineda et al. 2007; Cowen and Sponaugle 2009; Metaxas and Saunders 2009). Larval dispersal is influenced primarily by hydrodynamics, which is important at all spatial scales from large ocean gyres, to meso-scale factors such as the interaction of water masses with topography, and micro-hydrodynamic processes at the time of settlement (Scheltema 1986; Snelgrove et al. 1993; Kinlan and Gaines 2003). Determining the extent to which recruitment is derived locally or from multiple, linked populations is an ongoing challenge that can be clarified with methodologies such as genetics (see review in Hedgecock et al. 2007)

Swimming speeds of marine invertebrate larvae are typically modest relative to ocean currents (Butman 1987), and larvae have therefore been considered largely passive in their dispersal capabilities. Nonetheless, active vertical migration may contribute to dispersal and survival through horizontal displacement (Queiroga et al. 2002), predator avoidance (Metaxas and Burdett-Coutts 2006), and the pursuit of food (Burdett-Coutts and Metaxas 2004). Although vertical migration typically covers smaller spatial scales than horizontal transport, vertical movement can affect dispersal over considerable distances (Kimmerer and McKinnon 1987; Metaxas 2001). Vertical migration is often in response to gradients in environmental factors such as light and salinity (Metaxas et al. 2009).

In American lobster, *Homarus americanus*, eggs are extruded onto the female abdomen (spawning) where they incubate for nine to 11 months (Templeman 1940; Helluy and Beltz 1991) before larvae are released from mid-May through early September (hatching), beginning earlier in the more southerly distributions. Larvae subsequently develop through three larval stages (I-III) and metamorphose to a postlarval stage (IV) which makes the transition from the water column to a benthic habitat (Ennis 1986; Charmantier et al. 1991; Eggleston et al. 1998b). Larval duration in the water column is three to six weeks (Templeman 1936; Lawton and Lavalli 1995; Lam et al. 2003), depending on water temperature (MacKenzie 1988), creating potential for geographic differences in dispersal and thus potential connectivity (Harding et al. 1987;

Incze et al. 2000; Harding et al. 2005; Xue et al. 2008). Larval development times lengthen dramatically below 12 °C. This temperature is therefore considered a minimum critical threshold for development and survival (MacKenzie 1988).

Although lobster larvae are known to migrate vertically, they are generally restricted to surface waters and their distribution is therefore governed by surface circulation, including wind, on-shore propagating tidal waves and bores, and associated upwelling events (Harding et al. 1982; Harding et al. 1987; Hudon and Fradette 1993). Larval studies in the Gulf of Maine and the Gulf of St Lawrence over the past 40 years suggest a strong contribution from wind-induced transport (Harding et al. 1982; Hudon and Fradette 1993; Katz et al. 1994; Incze and Naimie 2000).

Postlarval settlement is influenced by behaviour (Cobb et al. 1989b; Kingsford et al. 2002), near-bottom flow (Lillis and Snelgrove 2010), and the availability of suitable habitat (Wahle and Steneck 1991). Lobsters settle in water < 25 m deep (Incze et al. 1997) and select cobble-boulder habitat that confers a survival advantage (Barshaw 1994). Settlement locations and patterns of postlarvae at depths beyond the reach of divers are unresolved and are currently under investigation (Wahle unpub. data). Postlarval distributions are indicative of YoY settlement patterns (Wahle and Incze 1997; Incze et al. 2006) because juveniles are sedentary (Lawton and Lavalli 1995; Wahle and Incze 1997) and juvenile mortality is generally relatively low (Wahle 2003).

The aims of this study were to: (1) investigate the spatial and temporal distributions of early life history stages of American lobster in Bonne Bay, Newfoundland, in order to understand how larval dispersal and settlement contribute to lobster population dynamics, and (2) evaluate how light and salinity gradients influence the vertical distribution of larval and postlarval stages in the water column.

Bonne Bay is a subarctic fjord on the west coast of Newfoundland. Although it supports a commercial lobster fishery, it is near the northern geographic limit of American lobster. Larval supply likely limits lobster recruitment in coastal Newfoundland given the larval minimum temperature requirement of 12° C (Templeman 1936; MacKenzie 1988). Nonetheless, the relatively sheltered, linear shape of Bonne Bay, combined with comparatively simple wind-driven and tidal flow (Richards and deYoung 2004) typical of many coastal fjords (Klinck et al. 1981), creates the potential for a self-seeding population. Larval retention may also depend on freshwater export from the estuary. Freshwater flow into the estuary can also set up strong vertical salinity gradients and this stratification can, in turn, affect larval vertical distributions. The Bonne Bay ecosystem therefore provides a unique natural laboratory in which to examine larval distribution patterns in cold water environments. Quantifying spatial and temporal patterns of early life stages in the area is a first step in that direction. Specifically, I set out to examine how the location and seasonal timing of the spatial variability in the distribution and abundance of larvae, postlarvae, and YoY recruits, and how these patterns could be used to draw inferences on population connectivity.

Materials and Methods

Study site

Bonne Bay is located on the west coast of Newfoundland and is divided into two main arms and an outer bay (Fig. 2.1). The relatively deep (~ 250 m maximum) and protected East Arm is separated from the rest of Bonne Bay by a shallow sill (~ 20 m). The East Arm has several sources of freshwater input. Surface temperatures vary from a summer maximum of 18 °C to sub-zero temperatures in winter, when Bonne Bay often freezes over. The absence of a sill in the relatively shallow (~150 m maximum) South Arm allows open exchange with the outer bay and greater exposure to the Gulf of St Lawrence, although sea ice can isolate the bay in the spring.

Larval sampling

Plankton samples were collected over a three-year period (2006 - 2008) during the summer months when larvae are normally present. A 500-µm, 6-m long neuston net mounted on a rectangular 2-m x 1-m frame was equipped with flotation to maintain the top of the net at the air-sea interface while towing to an effective depth of approximately 0.75 m. Tows were conducted for 40 min at ~ 2.5 knot (4.6 $km \cdot h^{-1}$). The water volume sampled at each station was determined using a mechanical flow metre (General Oceanics) affixed to the centre of the net. The net was towed 20 m behind the boat in a circular pattern to ensure it remained in undisturbed water clear of the boat's wake. The tow path was monitored with a handheld GPS unit to avoid resampling the same volume. Surface temperature and weather conditions were recorded for all tows. Typically, tows occurred between 0600 and 1800 h. Plankton samples were preserved in a 5% buffered formalin solution and lobster larvae were later sorted, staged (Herrick 1911), and counted. Larval concentrations were standardized to the number of larvae per 10^3 m^3.

The number of sampling stations and seasonal timing of sampling changed over the three years as information accumulated on where and when larvae were most abundant (Fig. 2.1). Initially, sampling stations for 2006 were chosen to cover as much of

Bonne Bay as possible, and most sites were re-sampled again in 2007. Plankton sampling occurred from June to September in 2006 (Calendar Day, hereafter CD 167 – 251) and 2007 (CD 164 – 248) at approximately biweekly intervals. In 2008, I focused the sampling on a 2-week period in late July and early August when, based on the previous two years sampling, larvae were expected to be most abundant, and all stages were expected to be in the water column (CD 210-216).

Statistical analysis

Spatial and temporal patterns are presented for all larval stages in Bonne Bay, however, statistical analysis of patterns were only possible for stage I larvae, because later stages were too rare in the first two years to permit a rigorous analysis. Larval abundance was compared among sites nested within different regions of Bonne Bay. Sites are defined as a towing location and regions as pooled sites that divided the Bay into five major sections (Outer Bay, Outer Sill, South Arm, Inner Sill, and East Arm) (Fig. 1). I utilized a Generalized Linear Model approach to evaluate spatial and temporal effects on stage I larval concentrations, however, because the sampling strategy in 2008 was fundamentally different than 2006 and 2007, the 2008 data were analyzed separately. Specifically, for the 2006 and 2007 data I used a mixed-effects analysis of variance model (ANOVA) in which Year (2006, 2007) and Month (June, July, August) were fixed factors with Month nested within Year. Site and Region were random factors with Site nested within Region. Region and Site were treated as random effects because the regions and sites were only a small subset of the possible regions and sites I could have considered, and because I want to generalize over a broader geographic area from those locations.

Although sampling was conducted in September of both years, larvae were absent from all samples and that month was not included in the analysis.

Because larval abundance peaked during July of 2006 and 2007, sampling in 2008 focused on sampling on four occasions during July of 2008 to examine spatial patterns more closely. In this case, I compared Region and Site nested within Region using a one-way ANOVA.

Environmental Data

Temperature was recorded in 2007 and 2008 using thermistors deployed 1 m and 9 m below the surface from early July (CD 183/184) to late October (CD 274/275). Temperature measurements were recorded hourly and averaged to produce a daily mean temperature. Temperature at 17 m in 2006, 2007 and 2008 was obtained from an Acoustic Doppler Current Profiler (ADCP) located at the sill (Fig. 2.1, OS1). Sea Surface Temperature (SST) distributions were obtained for all years from May to Oct from Advanced Very High Resolution Radiometer (AVHRR) satellite data (St Lawrence Observatory - http://www.osl.gc.ca/en/index.html).

Wind speed and direction data were obtained from Environment Canada, Meteorological Service of Canada, and were recorded in Daniels Harbour (50.24° N, -57.58° W), which is ~ 80 km north of Bonne Bay. All wind data were recorded hourly and daily averages were calculated for May through October of 2006 (CD 121-304), 2007 (CD 121-304), and 2008 (CD 122-305). To examine the relationship between winds and larval concentrations I converted hourly wind observations to wind stress (force applied to the sea surface) using the formulas from Banks and Herrera (1977):

$$\tau = \rho_a * C_d * U_w^2 \qquad \text{Equation 2.1}$$

where p_a (air density) = 1.25 kg·m^{-3}, C_d (drag coefficient) = 1 x 10^{-3} (0.63 + 0.066 U) and U_w (velocity) = wind speed in m·s^{-1}.

Wind data were also converted to an along-shore component. The coastline referred to as 'along-shore' essentially follows a N-S (5 ° true north) direction (Banks and Herrera 1977). In short, southerly winds generate an Ekman flux with onshore flow in the near-surface layer generating downwelling conditions that deepen the pycnocline. Conversely, northerly winds favour upwelling conditions whereby compensating return flow of deep water erode and thin the pycnocline near the coast. Wind data are conventionally reported in the direction from which they are coming, whereas currents are reported in the direction they are going. However, wind data needed to be converted to surface transport direction to utilize the following equations.

$$Along = S * \cos(CO - dir) \qquad \text{Equation 2.2}$$

where S (velocity) = speed m · s^{-1}, CO (coast orientation) = 5° dir (direction toward) = wind direction. The across-shore component was not included in the analyses because there was no clear linkage with larval distributions in preliminary investigations.

Temperature-dependent larval stage durations were obtained from MacKenzie (1988) for stage I-III, Incze and Naime (2000) for postlarvae, and modified by multiplying by 0.4 to correct for field development times (Xue et al. 2008) that are shorter than previously reported (Annis et al. 2007).

$$D_I = (851(T - 0.84)^{-1.91}) * 0.4 \qquad \text{Equation 2.3}$$

$$D_{II} = (200(T - 4.88)^{-1.47}) * 0.4 \qquad \text{Equation 2.4}$$

$$D_{III} = (252(T - 5.3)^{-1.54}) * 0.4 \qquad \text{Equation 2.5}$$

$$D_{IV} = (0.5 * (0.3588833\,T^2 - 14.316\,T + 156.895) * 0.4 \qquad \text{Equation 2.6}$$

Where D is days, the subscripted symbol next to D denotes larval stage, and T is temperature (°C). These equations were used in conjunction (MacKenzie 1988) with surface temperatures for Bonne Bay to determine estimated development rates throughout the season when larvae are known to be present. These estimated development rates were then used along with known physical (surface circulation) and behavioural (vertical migration) variables to estimate potential dispersal distances.

Benthic sampling

Suction sampling

I assessed benthic recruitment at five sites in mid- to late October and early November in 2007, and at 3 sites in 2008 (Fig. 2.1). Sampling targeted sub-littoral, cobble-boulder habitats from 3-6 m below Mean Low Water (MLW) because previous studies have shown that lobsters prefer this type of habitat (Wahle and Steneck 1991). In 2007, I chose sites to provide broad coverage of Bonne Bay, but modified these sites in 2008 based on knowledge gained from plankton sampling and interviews with local fishers (see Chapter 4).

Diver-based suction sampling has been used extensively to monitor recruitment success and habitat use in American lobster (Wahle and Incze 1997). Within each sampling area, SCUBA divers haphazardly dropped a 0.5 m^2 quadrat onto the cobble bottom. They then estimated percent cover of rock, sand, and seaweed within the quadrat in order to assess habitat quality. Each quadrat was then sampled for lobster by removing the cobble by hand while operating a suction sampler, which excavated the underlying sediment to a depth of ~ 7 cm.

A mesh apron on the sides of the quadrat prevented lateral escape of lobsters while suctioning. The suction sampler consisted of a 180-cm length of 7.6-cm diameter PVC tube with a 1.5-cm, removable mesh bag (30 cm x 20 cm) affixed to the upper end of the tube. A SCUBA tank supplied air a few centimetres above the lower mouth of the tube, suctioning sediments and fauna into the bag until the sample was complete and the bag was removed, sealed, and replaced with a new one prior to collection of the next sample. To sample a quadrat, one member of the dive team removed the rocks and macroalgae while a second diver operated the airlift. As many as ten quadrats were sampled in a given dive, after which all sample bags were transported to the surface and live sorted on the boat. All lobsters were enumerated and measured prior to returning them to the water. Eight quadrats were assessed at each sampling site in 2007 and 12 in 2008 (Fig. 2.1).

Postlarval collectors

Passive postlarval collectors described by Wahle et al. (2009) were deployed in Bonne Bay in 2007 (five sites) and 2008 (seven sites) (Fig. 2.1). Collectors were constructed of rigid 10-gauge, vinyl-coated 3.6-cm wire (1 m x 0.5 m x 0.015 m), providing a 0.55 m^2 surface area for settlement. The bottoms of the collectors were fitted with wood runners for durability and ease of stacking. The bottoms and sides of the collectors were double lined with a 5 mm Vexar® mesh and a 1.5 mm plastic-coated window screening to prevent newly settled organisms from escaping into the adjacent seafloor. The top cover was constructed from the same rigid wire mesh as the rest of the trap in order to retain the cobble substrate without interfering with postlarval settlement.

In 2007, I deployed a temperature logger at each site to record bottom temperature, and in 2008 I expanded this sampling to include a surface and bottom temperature logger. The location of each tray was recorded using GPS at the time of deployment. Collectors were deployed in mid- to late June, preceding expected larval settlement in this area by approximately one month. This was done to condition the trays with naturally occurring microbial fouling and other organisms. Collectors were retrieved in late October – early November of each year once postlarvae were no longer found in the water column. Upon retrieval, all trays were live processed on site, with lobsters, crabs, and fish enumerated prior to release. Crabs and fish were enumerated in order to determined potential competitors or predators. In 2007 and 2008, I deployed 12 and 10 collectors at each site, respectively.

Visual surveys

Lobster abundances were assessed in 2008 with visual surveys of quadrats at seven sites (Fig. 2.1). Divers swam approximately three metres apart and parallel to the shore until they located cobble-boulder substrate. They then dropped a 1-m^2 quadrat haphazardly on the bottom and recorded the percent rock cover before removing cobble and rocks to an approximate depth of 25 cm. All lobsters in the quadrats were sexed and enumerated. This methodology was repeated for 12 quadrats at each site. No statistical analysis of lobster abundance was possible for any of the benthic sampling methodologies because numbers were too low.

Larval behaviour

Larval rearing

During summer 2007, fifteen berried females were captured in Bonne Bay and maintained at the Bonne Bay Marine Station, Norris Point Newfoundland in 120 litre tanks with a continuous flow of seawater. A berried female is egg bearing, and thus has embryos on her ventral side of the abdomen. Females were fed frozen squid every second day and observed three times daily to record water temperature and to document larval presence until all larvae had hatched. Typically, a female would hatch her embryos over a four to seven day period (pers. obs.). Females were subsequently V-notched (a V shaped notch on the inner right uropod used to mark breeding females) and returned to Bonne Bay. To ensure females were close to hatching, only females in stage III-IV of embryonic development were retained (Appendix 4.1, Chapter 4).

Hatching occurred in two periods, with six females hatching between June 21–26 and seven females from July 17-30. Two of the 15 females lost their brood and were returned to the ocean. Larval escape from the holding tanks was prevented by attaching a funnel with 1-mm mesh on its sides to the outflow pipe. Following hatching, larvae were gently removed from the females' tank with a small net and placed into a 120-litre holding tank within 15-litre buckets where the sides had been partially cut away and replaced with 1-mm mesh. Larvae were held in unfiltered seawater with a salinity of 30 psu, at a concentration less than 100 larvae$\cdot$ml^{-1}. Larvae were fed a diet of frozen CYCLOP-EEZE®, a nutrient-enriched copepod, three times daily. Adults and larvae were held at ambient Bonne Bay shallow water (30 m) temperature, which fluctuated between 6-10 °C in mid June and increased to 10-14 °C in late July.

Experimental design

Laboratory experiments were designed to work in tandem with the field studies to assist in understanding vertical migration behaviours of American lobster larvae. Field sampling focused on neuston layer sampling, and an understanding of the degree to which this sampling methodology biases estimates of lobster abundance and distribution is therefore important. Separate experiments were designed to determine how different larval lobster stages (I, II, III, IV) respond to a salinity gradient and to the presence or absence of light. Treatments included the presence or absence of light from an overhead source, the presence of different strengths of halocline, and the absence of a halocline. Experiments were conducted in plexiglass columns (50 x 10 x 10 cm) marked at 2-cm vertical increments and capped with opaque styrofoam. Each column was surrounded by a larger black column that prevented light penetration or reflection. One face had 2-cm bands of magnetic strips that could be quickly removed to observe the water column within that depth band and minimize light disturbance to larvae during observation of the response of different stages of larvae to the different treatments. Starting at the base, each band was removed, larvae were counted, and the band quickly replaced. Each treatment combination of the light and salinity experiments was repeated for each of the first three larval stages (described below). However, insufficient individuals survived to stage IV to conduct the light / dark experiments. For each treatment and developmental stage the centre of mass within the column (Z_{CM}) was calculated as:

$$Z_{CM} = \sum P_i * Z_i \qquad \text{Equation 2.7}$$

where P_i = proportion of larvae in the 2-cm increment *i* and Z_i = the associated column height *i*.

Response to salinity

Larval response to a salinity gradient was measured by creating haloclines of different intensity within the plexiglass columns. I established haloclines by first filling the columns to a height of 30 cm with 1- micron filtered, lower salinity water (see below). Ambient (higher) salinity water was gravity fed to the bottom of the container through a small 2-mm tube that penetrated the styrofoam cap at the middle of the column and extended to the base of the column. This higher salinity water was added until the lower layer was ~15 cm deep. Lobster larvae were then added to the lower layer through a 1-cm tube at the side that extended to ~2 cm above the base of the column. Additional ambient water was added to the bottom layer until the total water column height was 50 cm. Water samples were gently removed with a pipette every cm and salinity determined with a temperature-compensated refractometer. Numbers of larvae were measured within each 2-cm depth increment after 15 minutes. All experiments were conducted under fluorescent light at 15 °C between dawn and dusk to avoid complications of light variation and circadian rhythms.

Four contrasting halocline treatments were established, each with a bottom (ambient) salinity of 30 psu and top layer salinities of either 21 psu (hereafter 21/30 treatments), 24 psu (hereafter 24/30 treatments), 27 psu (hereafter 27/30 treatments), or 30 psu (hereafter 30/30 treatments). Four replicates of each treatment were completed for each larval developmental stage (I, II, III, IV). Fewer larvae were used in later experiments because cannibalism reduced available larvae (stage I n = 20-50 individuals, stage II n = 15–20, stage III n =10 – 15, stage IV n = 3-4). For illustrative purposes, I plotted the proportion of larvae counted in each of the 12 depth increments at 15 minutes post release in the experimental tank. To statistically evaluate the null hypothesis that the distribution of larvae in the top and bottom halves of the tank were independent of the salinity treatment (21/30, 24/30, 27/30, 30/30), I used a chi-square 2 x 4 contingency table analysis. Counts from the replicate trials were pooled prior to this analysis.

Response to light dark

Larval response to light was observed under 40-watt fluorescent lights enclosed in an opaque waterproof case. Using the methodologies described above, I added larvae above the bottom of the column and recorded their vertical distribution after 15-minutes. Four replicates of each of two treatments (presence | absence of light) were completed for the first three larval stages (I, II, III), again with differing numbers as a result of cannibalism that limited larval availability (stage I n = 75-110 individuals, stage II n = 30–60, stage III n =12 – 15, stage IV = none available). Again, I used proportions rather than counts to correct for differences in numbers of larvae added. I summed the percent distribution of larvae in the upper and lower half of the experimental column for each of the light treatments. I then created a 2 x 2 contingency table to evaluate the vertical distribution of lobster larvae in the presence and absence of light and tested the statistical null hypothesis that the vertical distribution (above/below halocline) was independent of light treatment (light, dark).

Results

Larval sampling

The abundance of larval lobsters in Bonne Bay was highly variable in space and time during 2006-2008 surveys, both within and among years. In 2006, only stage I lobsters were sampled in appreciable numbers and stages II to IV were relatively rare (Fig. 2.2). Larval hatching had begun by Calendar Day (CD) 166 (mid-June) in 2006, peaking initially on CD 191 (mid-July) and tapered off to small numbers a few weeks later on CD 207 (late July). Concentrations then continued to diminish and larvae were absent by CD 236 (mid-August). No stage II or III larvae were sampled and stage IV lobsters were rare and limited to the entrance to the bay in mid- to late August (Fig. 2.2).

The 2007 hatching season began approximately on CD 176 (late-June), peaked on CD 186 and 207 (mid- and late July), and was over by CD 248 (early September) (Fig. 2.2). In 2008, sampling only focused on time of year peaks found in 2006-2007, CD 210 to 216 (late July and early August). During that two-week period the highest numbers of all stages occurred on CD 212 (July 30) (Fig. 2.2).

Spatial patterns of stage I larvae were consistent among and within seasons with regular 'hot spots' of abundance in the outer bay during 2006, 2007, and 2008 (Fig. 2.3), although highest values varied among the three outer bay sites in different years. Differences between outer and inner bay sites were less pronounced in 2008, with high concentrations of all larval stages near OS2 and SA1 sites that often exceeded those at the outermost OB3 site (south side of entrance) but not at OB2 (north side of entrance) (Fig. 2.3). Stage I larvae were most abundant in the South Arm ($2 \cdot 10^{-3}$ m^{-3}) in 2006, in the Outer Bay ($7 \cdot 10^{-3}$ m^{-3}) in 2007, and in the Outer Sill ($3 \cdot 10^{-3}$ m^{-3}) in 2008 (Fig. 2.3).

Annual maximum concentrations for 2006, 2007, and 2008 coincided with these regions (15, 38, and 196 larvae · 10^3 m^{-3} respectively).

Statistical analysis of spatial and temporal effects for the 2006 and 2007 surveys indicate a non-significant effect of month and year although the seasonal pattern of greatest peak stage I abundance in July was consistent from year to year (Table 2.1). The regional effect, taken in the context of variability among sites, was significant, suggesting a tendency of stage I larval concentrations to be greater in the Outer Bay. There was no significant interaction effect between Region and Year. In many instances, differences in larval concentrations were evident for sites less than 0.5 km apart for a given sampling period (Fig. 2.3). Despite the absence of a significant Year effect in the statistical analysis, peak concentrations of stage I larvae increased each year so that 2008 peaks were 3 times those of 2007 and 19 times those of 2006.

In 2006, stage II and III larvae were absent, and stage IV larvae were found only in the Outer Bay and in low concentrations (seasonal average 0.01 larvae · 10^3 m^{-3}, maximum concentration 0.05 larvae · 10^3 m^{-3}). In 2007, late stage larvae were again found only in the Outer Bay, with average concentrations of stage II, III larvae, and IV postlarvae of 0.01, 0.01, and 0.03 larvae · 10^3 m^{-3} respectively. Maximum concentrations of stage II, III larvae, and IVpostlarvae were 0.10, 0.06, and 0.12 larvae · 10^3 m^{-3} respectively.

Spatial patterns in 2008 were markedly different from the same period of July-August in the two preceding years, in that all stages were present at all sites and regions sampled. As a result, there was no statistical Region effect observed for stage I larvae for this two-week period in 2008 (Table 2.2). During this period the spatial pattern of later stages mirrored that of stage I larvae (Fig. 2.4), although later stage larvae were abundant for the first two days of sampling and then largely disappeared.

Over 24-h cycles, repeated tows at two sites in Bonne Bay in 2006 indicated lowest larval concentrations from noon to 14:00 h, peak numbers between midnight and 06:00 at the Inner Bay site, and again from 06:00 to 11:00 and 16:00 to 19:00 at the Outer Bay site (Fig. 2.5).

Environmental Data

Satellite data (SST) showed that surface temperatures had warmed to 12 °C by CD 158, 168, and 172 in 2006, 2007, and 2008 respectively (Fig. 2.6A). Peak SST from satellite data were similar for all years, reaching 17.1 °C by CD 212 in 2006, 17.6 °C by CD 207 in 2007, and 17.8 °C by CD 208 in 2008. Average surface temperatures remained above the critical 12 °C threshold for larval development for different periods in 2006 (100 days, CD 160 – 260), 2007 (45 days, CD 190-235), and 2008 (80 days, CD 175-255) (Fig. 2.6A). In 2007, temperatures at 9 m in Bonne Bay were 12 °C by CD 189 (July 7, Fig. 2.6D), and peak hatching at this depth occurred at 16 °C. Continuous temperature data confirm that except for short spikes of 17 °C from CD 200 – 220, temperatures at 9 m in 2007 were 14 °C or less (Fig. 2.6B). In 2008, average surface temperature was already 12 °C when temperature recording began on CD 183 (Fig. 2.6C) and had peaked at 19 °C by July 28-30 (CD 210-212, Fig. 2.6C). In 2008, surface temperatures were above 12 °C for approximately 3 months (CD 185 – 280), and above 15 °C for approximately 2 months (CD 195 – 265), peaking at 19 °C on CD 208 (Fig. 2.6C).

Larval development times vary with temperature regimes in that potential development time to settlement may decrease from 21 days at 12 °C to 8 days at 18 °C (Fig. 2.7). Average temperature during the 2-month Bonne Bay hatching season was 15 °C in 2006 and 2008 but only 12 °C in 2007. Temperature consistently peaked from late July to early August. Steady unidirectional surface flows of ~ 5 $\text{cm}\cdot\text{s}^{-1}$ could transport larvae from 36 to 160 km, depending on larval duration (Fig. 2.7).

In 2006, 2007, and 2008 strong southwesterly winds were generally positive along-shore (Fig. 2.8). In 2006, high concentrations of larvae were generally preceded by downwelling-favourable winds early in the season (Fig. 2.9). Of particular note is a generally sustained event (CD 167-CD 192) beginning with a larval concentration of 0.8 larvae $\cdot$ 10^3 m^{-3} and increasing steadily to 3.9 larvae $\cdot$ 10^3 m^{-3}; however, this pattern was less evident in 2007 (Fig. 2.10). The 2008 sampling series occurred during a wind reversal event, where relatively high concentrations of late-stage larvae and postlarvae were present on the first two sampling days after a seven day period of southwest wind. The wind reversal resulted in a drop in surface temperature, from 18 °C to 14 °C (Fig. 2.11). Subsequently, concentrations of later stage larvae dropped off dramatically. The onshore Ekman flux during the CD 167-CD 192, 2006 event illustrates the transport potential within Bonne Bay. A representative wind stress during this period was 0.13 N m^{-2}, giving rise to an onshore Ekman flux ($=\tau/\rho f$, where τ is the alongshore stress, ρ the water density taken as 1022 kg $\cdot$ m^{-3}, and f the Coriolis parametre, $1.1*10^{-4}$ s^{-1}) of ~1.1 $\text{m}^2 \cdot \text{s}^{-1}$. The width of the mouth of the Bay is about 2.5 km, resulting in total flux of about 2800 $\text{m}^3 \cdot \text{s}^{-1}$. The volume of the upper 25 m of the Bay is approximately $7*10^8$ m^3; therefore the onshore Ekman flux is sufficient to displace the upper 25 m of Bonne Bay approximately 9 times ($2800\ m^3\ s^{-1}*25\ days*86400\ s\ d^{-1}/7*10^8\ m^3$) during just this 25 day period. Clearly sustained events of this magnitude could greatly affect the larval concentrations in the Bay.

Benthic sampling

Settled YoY lobsters were sampled in 2007 and 2008 but not 2006 (Fig. 2.12). In both sampling years, densities of YoY lobsters were low compared to more southerly locations (Wahle unpub. data). These densities suggest low rates of recruitment, perhaps commensurate with the low numbers of stage IV postlarvae observed in the bay. Densities of rock crab were high in suction samples and collectors compared with other locations, however, cunner densities were considerably higher in collectors than in suction samples (Fig. 2.12). Unfortunately, in 2008 most collectors were lost from one of the outer bay sites (OB3), and logistics precluded suction sampling in the outer bay or outer sill.

Larval behaviour experiments

The magnitude of response to light varied among stages. Stage I larvae responded to light by moving to the bottom of experimental tanks, whereas stage II and III larvae did not (Fig. 2.13, Table 2.3). Stage IV postlarvae were not available for these experiements

The response to salinity gradients was also stage dependent. Stage I larvae and stage IV postlarvae responded to salinity gradients by moving away from the most dilute strata, whereas the stage II and III larvae concentrated in the lower strata regardless of the presence of a halocline (Fig. 2.14, Table 2.4).

Discussion

This study marks the first quantitative analysis of early life stages of American lobster in Newfoundland, near the northern extreme of the species' geographic range. The larval hatching season is approximately two months in Bonne Bay, as has been found in other regions (Harding et al. 1983), although cooler surface water temperatures suggest prolonged development. Protracted development can significantly impact dispersal and survival, particularly in light of previous work that shows changing wind patterns can influence surface circulation and larval lobster distributions (Cowen et al. 2007; Incze et al. 2010).

A literature survey of 21 independent larval lobster surveys at locations between Cape Cod and Newfoundland shows that larval hatching season varies from 8 to 12 weeks. Temperature of first larval occurrence averaged 12 °C (±0.5°C SE) and peaked at 15° C (±0.6 °C SE). Maximum larval concentrations in Bonne Bay were higher than most other areas sampled except for Buzzards Bay, Massachusetts (Appendix 2.1). Maximum larval concentrations in 2006 (28.6 larvae per 10^3 m^3) and 2007 (75.5 larvae per 10^3 m^3) were also similar to these other areas where the maximum concentration was 62.5 10^{-3} m^3 (± 22.0 SE) (Appendix 2.1). As in Bonne Bay, areas of coastal Massachusetts (Lux et al. 1983; Mattiessen and Scherer 1983) were extremely variable among years. One striking difference in Bonne Bay was that stage I lobsters consistently exceeded 95% of the larval lobster total. The average for other areas was 49 % (±6.7 SE), though it varied from 23-80% in one study (Appendix 2.1) from Rhode Island (Bibb et al. 1983).

Earlier work conducted in 1938 on Newfoundland's west coast shows that stage I larval concentrations at sites south of Bonne Bay comprised 14 to 46 % of total larval lobsters (Templeman and Tibbo 1945). Although direct comparisons of concentrations are difficult because of differences in methodologies, the highest concentrations of stage I lobsters from St. George's Bay were 118 stage I larvae in 718 minutes of towing (0.16 larvae/min), and from Bay of Islands were 100 stage I larvae in 435 minutes of towing (0.23 larvae/min). For Bonne Bay, when considering only 2008 surveys, using the same methods as above, and during the same late July and early August time period, I collected 235 stage I larvae in 520 minutes of towing in 2006 (0.45 larvae $\cdot \text{min}^{-1}$). In 2007 I collected 1244 stage I lobsters in 360 minutes of towing (3.46 larvae $\cdot$ min^{-1}), and in 2008 there were 5591 stage I larvae in 800 minutes of towing (6.98 larvae $\cdot \text{min}^{-1}$). Thus, concentrations in Bonne Bay were substantially greater than those reported by Templeman and Tibbo (1945).

Concentrations of stage I larvae are comparable to those reported elsewhere, however, the dramatic decline in concentrations by stage II relative to stage I results in comparatively low concentrations of later stage larvae. Thus, I conclude it is likely that lobster mortality and/or larval export from Bonne Bay is high.

As has been observed elsewhere, larval lobsters appear when surface temperatures exceed 12 °C in early summer (Harding et al. 1983), coinciding with a time when zooplanktonic prey are abundant (Hargrave et al. 1985). Surface temperatures in Bonne Bay exceeded 12 °C for 2 – 3 months during the summers of 2006 to 2008, and were reached by CD 152 (June 1) in 2006 and 2007, and CD 172 (June 21) in 2008. Templeman and Tibbo (1945) noted little hatching in Newfoundland before July, but the presence of abundant larvae in June 2006 and 2007 suggests that hatching may occur earlier now than previously observed. Peak hatching typically occurs one month after initial hatch, and appears closely coupled with peak summer temperature in Bonne Bay, as previously shown in southwest Nova Scotia (Harding and Trites 1988). In Bonne Bay, berried females are found in water as shallow as 1 m (pers. comm. Keith Reid), where favourable hatching temperatures are more likely.

The timing and location of hatching locations can significantly impact dispersal distances and thus larval connectivity among lobster populations (Harding et al. 2005; Xue et al. 2008; Kenchington et al. 2009). Although berried females aggregate in inshore regions elsewhere (Campbell 1990), no specific aggregations were identified in Bonne Bay (Chapter 4). Regional comparisons of berried female aggregations and distributions need to account for the depth restrictions experienced by lobsters in each region. Precise knowledge of timing and location of migratory patterns of reproductive female lobsters in Bonne Bay would help improve assessment of likely larval sources.

'Hot spots' of stage I larvae were consistently seen in outer Bonne Bay from 2006 to 2008, where the highest larval concentrations for a given survey were always found at one of the three outer bay sites. However, regional differences were not statistically significant given the high site-to-site variability within each region. Sporadically high concentrations of stage I lobsters at the Inner Sill (IS1) suggest either hatching pulses from the East Arm or pulses of stage I larvae brought in on a flood tide and swept away on ebb flow. The latter seems less likely given that there was no noticeable link between surface flow direction over the sill and larval concentration at stations adjacent to the sill. Nor were there any consistent patterns in that region during a time-intensive sampling series conducted over a 24 h period in 2006. The potential role of tides in sill exchange merits additional study, noting previous work on the importance of fjord sills for hydrodynamic exchange in Bonne Bay (Richards and deYoung 2004), and elsewhere (Berntsen et al. 2009). For example, larvae may be flushed from the nearshore prior to moulting to a later stage, as reported elsewhere in Newfoundland (Templeman and Tibbo 1945).

The geographic locations of larval ‘hot spots’, when present, were consistent among years, although the absolute abundances varied greatly. The source of the dramatic increases in concentrations of different larval stages in 2008 compared with the previous two years is unclear. Larval supply is influenced by the number of larvae hatched, advection (winds, tides, currents), and variation in mortality (biological, environmental variables). However, the higher abundances of stage I larvae in 2008 suggests increased larval supply, or hydrodynamic features that concentrated larvae in Bonne Bay. Inter-annual variation in larval abundance is common for a wide range of species (Siegel et al. 2008), including lobster postlarvae (Incze and Naimie 2000). However, local fishers have reported increasing densities of berried females every year since about 2003 (Chapter 4), suggesting increasing levels of larval production in the bay.

Bonne Bay surface circulation is driven primarily by southwesterly summer winds that produce an onshore surface flow in a northeast direction along Newfoundland’s west coast (Gilbert and Pettigrew 1993). Wind data for 2006-2008 were consistent with this pattern. Predominant southwesterlies in 2007 were expected to produce higher larval concentrations than the other years sampled, however, 2008 concentrations were the highest. Rapid wind reversals can quickly advect water offshore (Daly and Konar 2008). In 2008, larval concentrations were highest during onshore winds favourable to downwelling that produced a warm surface layer in the first two sampling days. Temporary reversal to offshore winds produced rapid coastal upwelling (e.g. Asplin 1999) that decreased surface temperatures at all sites.

Invertebrate larval transport has been linked to shoreward transport in surface convergences above internal waves (Shanks and Wright 1987; Pineda 1991), sometimes producing visible surface slicks (for review see Ermakov et al. 1992) that may indicate the presence of larval lobster (Harding et al. 1982), and other species (Kokita and Omori 1998; Vandendriessche et al. 2006). Downwelling-favourable winds concentrate lobster and other crustacean larvae (Templeman and Tibbo 1945), enhancing settlement (Hudon and Fradette 1993; Wahle and Incze 1997; Eggleston et al. 1998a; Dudas et al. 2009). Flotsam trapped in these surface slicks may protect neustonic organisms from predators, and provide potential food and shading (Kingsford and Choat 1985). Langmuir circulation cells also concentrate seaweed and flotsam in windrows under which lobster larvae are more likely to occur (Harding et al. 1982). Another predominant circulation pattern in Newfoundland is persistent eddies in the lee of headlands. Not only might these eddies act to retain plankton at the mouth of bays in the lee of headlands, but these eddies are also often accompanied by upwelling of nutrients, causing persistent phytoplankton hot spots (pers. comm. Don Deibel).

Although the fjord may represent a favourable environment for larval growth and development, export and mortality may pose risks to early planktonic life stages. Winds, tides, and freshwater input strongly influence the advection and retention regime of a fjord (Aksnes et al. 1989). While enhanced plankton productivity in fjord systems may create an ideal larval habitat, predators such as jellyfish may concentrate in fjords and augment larval mortality (Sornes et al. 2007). Video Plankton Recorder (VPR) observations from the sill in Bonne Bay show dominance of ctenophores and hydromedusae, both potentially predators of larval lobsters (Deibel unpub. data).

The potential for export from the Bonne Bay system and along shore transport is considerable. Estimated coastal surface currents of 6-10 $cm \cdot s^{-1}$ (Gilbert and Pettigrew 1993) could disperse larvae as much as 8 $km \cdot day^{-1}$. At ~ 14° C, larval development through stage I would require 1 – 2 days and produce a net transport distance of 7 to 17 km for water temperatures of 18 °C or 12 °C respectively. Because stage I larval duration is brief, concentrations of this stage may reflect brood stock locations, however, even with the 1-3 d duration of stage I larvae, individuals could be flushed from a small system such as Bonne Bay before moulting to stage II. Thus, it is reasonable that much of the attrition in larval abundance observed from stage I to II may be explained by advection alone.

The potential dispersal distance from hatching through stage IV is estimated to be160 km. This calculation does not account for poorly-understood behaviours such as vertical migrations or hydrodynamic complexity, which is influenced by coastline configuration, wind reversals, and tides. If various stages of American lobster larvae migrate vertically, this behaviour may contribute to lower than predicted distances of net transport if currents are baroclinic in velocity and/or direction. Studies in the Gulf of Maine that consider shoreline configuration and larval mortality suggest that dispersal potential diminishes dramatically with proximity to the coast (Incze et al. 2010). In Bonne Bay, a small embayment adjacent to an open coastline, larvae may be more likely to be dispersed and flushed from the bay in the absence of vertical migration or other behaviours.

Clearly, larval mortality and/or flushing from Bonne Bay is high given that surveys only a few days apart showed dramatically different larval concentrations and large decreases in abundances of stage I versus II lobsters. Mortality rates in the field are notoriously difficult to estimate and likely vary regionally, however, plankton mortality is generally assumed to be very high (Pechenik and Levine 2007). Scarratt (1968; 1973) estimated that survival of larval lobster from stage I to settlement in Northumberland Strait varied from 0.11 to 2.49 %, based on a 15-year time series of lobster larval surveys. His estimates assume surface tows adequately sampled all larval stages. St. Georges Bay, NS has comparable survival to settlement of 1.9 % (Harding et al. 1982). A lower survival rate should be expected for Bonne Bay given its location at the northern limit for lobster, and from 2008 estimates is lower than 1 % survival.

Rivers and melt water supply significant fresh water influx to Bonne Bay, particularly in the East Arm. Outflow of surface freshwater not only represents a mechanism to explain variable larval export, but low salinities in a surface freshwater layer could be physiologically stressful for larval lobsters. Survival is low in lobster larvae raised in salinities < 21 psu (Scarratt 1968; see Charmantier et al. 2001 for general review), and earlier studies found larvae raised in salinities < 18 psu did not survive to settlement (Templeman 1936). My experiments showed that in the presence of a halocline, larvae responded with an immediate 'stall and flair' response in both 21 and 24 psu, and yet readily crossed a halocline from 27 to 31 psu. These results suggest that lobster larvae may descend from fresh surface layers to avoid physiologically stressful salinities. Throughout the sampling season, larval numbers were considerably lower in tows collected during rainfall (pers. obs.).

This study cannot fully separate salinity from density effects. It is possible that larvae responded to density differences rather than to salinity differences. For example, densities at 15 °C are 1015.3, 1017.6, 1019.9 and 1022.2 $kg \cdot m^{-3}$ for salinities of 21, 24, 27, 30 psu respectively. Depending on larval density, sharper density gradients may represent a significant change in buoyancy where, for example, a larva may be neutrally buoyant in at a salinity of 30 psu but would sink at 21 psu, thus having to exert effort to maintain its position in the water column.

My laboratory experiments also indicate that stage I larvae were more responsive to light than stages II and III. Unfortunately low survivorship of larvae did not allow light-dark trials to be conducted for stage IV postlarvae, however, earlier studies show that stage IVs respond positively to light (Harding et al. 1987). In culture tanks stage II and III larvae were inactive and negatively buoyant, and without aeration they sank to the bottom (pers. obs.). Unlike stage I larvae and stage IV postlarvae (pers. obs.), they also did not respond to food. Whether this behaviour was an artefact of laboratory rearing requires verification through field observations of larval swimming behaviour.

Multiple types of invertebrate larvae are positively phototactic (Jekely et al. 2008; Cohen and Forward 2009). Stage I and IV lobsters are thought to concentrate in the surface metre (Harding et al. 1982), in response to light (Templeman 1936; Harding et al. 1987; Annis et al. 2007) and temperature, respectively (Boudreau et al. 1991). Twentyfour hour larval surveys in Bonne Bay did not reveal day-night differences in vertical distribution. However, this inference is based on one tow series and more work is necessary to understand the diurnal patterns exhibited by larval stages of American lobster. Over Browns Bank, Nova Scotia, however, stage I lobsters were limited to the upper mixed layer, and migrated daily from 20 m depth in day to surface waters at night (Harding et al. 1987). Experimental studies show that lobster larvae prefer to remain above the thermocline (Boudreau et al. 1991). Stage II and III vertical distribution remain poorly understood (pers. comm. Gareth Harding, Stephen Nolan), and these stages are rare in surface tows. The factors that influence vertical migration may be specific to local environmental conditions. Two years of benthic sampling in Bonne Bay with visual surveys, quadrat suction sampling and benthic collectors all suggest very low densities of YoY lobsters relative to comparable collections further south in the species range. It is unlikely that sampling methodology inadequately sampled later larval stages. Neuston tows for lobster larvae sampling have been an accepted tool for determining their distribution. Lower abundance could be related to limited larval supply given the high rates of larval attrition observed in the larval surveys. Habitat is not likely limiting in Bonne Bay, given that divers found a considerable proportion of cobble habitat seafloor comparable to that in Maine (Chapter 3), and lobster densities well below estimated carrying capacities for cobble boulder habitat (Cobb et al. 1989a; Wahle and Incze 1997).

Studies in the Gulf of Maine show that consistent circulation delivers larvae to predictable settlement areas (Wahle and Incze 1997). Conditions that favour the delivery, retention, and survival of planktonic larvae must be at play, but post-settlement mortality could also be a factor. Abundant cunner and rock crab likely prey on and compete with settling and post-settled lobster. Given the northerly location of Bonne Bay and the limited fishery relative to areas such as the Gulf of Maine, the significantly lower densities of adult lobsters alone might explain the low larval and YoY numbers, though comparable numbers of stage I larvae to southern areas suggest mortality and/or export are likely factors.

Low densities of late larval stage and benthic lobsters in Bonne Bay do not diminish the importance of lobster recruitment studies at northern distribution limits, where climate change impacts are more likely than in the middle of their distribution. This first survey of lobster larval and early benthic life stages in Bonne Bay sets an important baseline from which to evaluate future changes in the population. This data will be especially interesting in the context of predicted range expansions that may result from climate change. Improved understanding of lobster recruitment in western Newfoundland can also lead to better understanding of the connectivity of lobster populations at the northern edge of its geographic range that may also apply to associated benthic species with complex life histories.

Tables

Table 2.1: Four-way nested ANOVA to determine annual and spatial differences in stage I lobster larval concentrations in Bonne Bay from 2006 to 2007.

Factor	**SS**	**df**	**MS**	**F**	**P**
Year	43.68	1	43.68	0.50	0.50
Region	296.96	4	74.24	4.86	0.03
Month (Year)	351.70	4	87.93	87.93	0.13
Site (Region)	106.84	7	15.26	15.26	0.94
Region*Month	338.98	8	42.37	42.37	0.50
Error	6160.66	129			

Table 2.2: Two-way ANOVA to determine annual and spatial differences in stage I lobster larval concentrations in Bonne Bay during the time of peak abundance in July-August 2008.

Factor	**SS**	**df**	**MS**	**F**	**P**
Region	4803.56	3	1601.19	0.35	0.75
Site (Region)	5367.84	4	5367.84	2.27	0.3
Error	68802.3	15	4586.82		

Table 2.3: Chi-square analysis of light dark experiment to determine the difference between the vertical distribution of lobster larvae in the upper and lower side of the experimental column.

stage	**n**	**χ**	**p value**
I	75-100	143.56	<<0.0001
II	30-60	0.01	0.92
III	12-15	0.00	0.97

Table 2.4: Chi-square analysis of the salinity experiment to determine the difference between the vertical distribution of lobster larvae above and below the halocline in the experimental column.

stage	n	χ	p value
I	20-50	93.8	<<0.0001
II	15-20		
III	10-15	6.3	0.10
IV	3-4	59.43	<<0.0001

Table 2.5: Daily proportional distribution of American lobster larval stages for 2008 neuston tows in Bonne Bay.

CD	I	II	III	IV
210	0.78	0.07	0.06	0.07
212	0.92	0.03	0.03	0.01
214	0.99	0	0	0.01
216	0.98	0.01	0	0.01

Figures

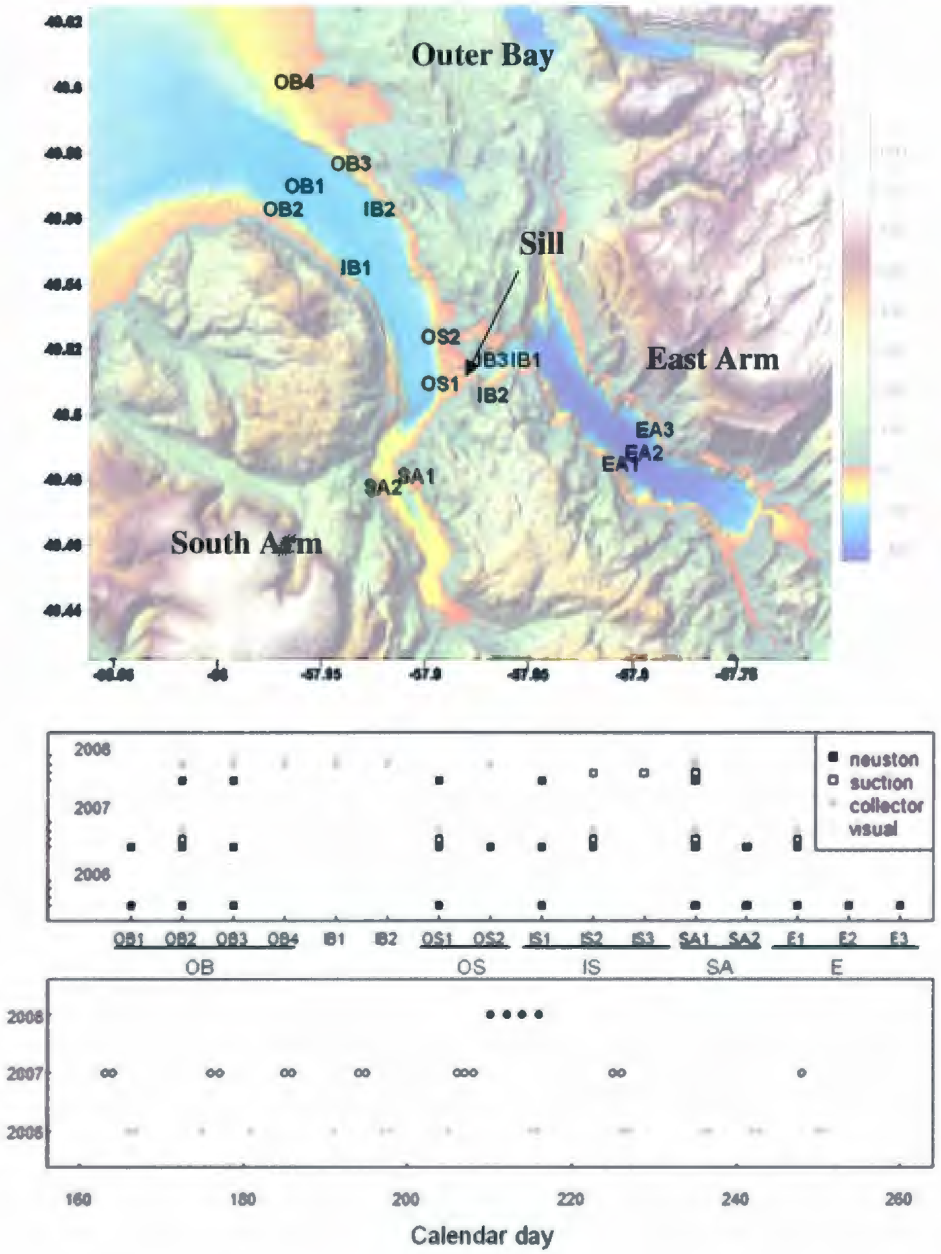


Figure 2.1: Sites and regions in Bonne Bay, Newfoundland sampled using different methodologies in 2006 – 2008. Lower panel shows sampling frequency of neuston tows. ADCP located at OS1 site.

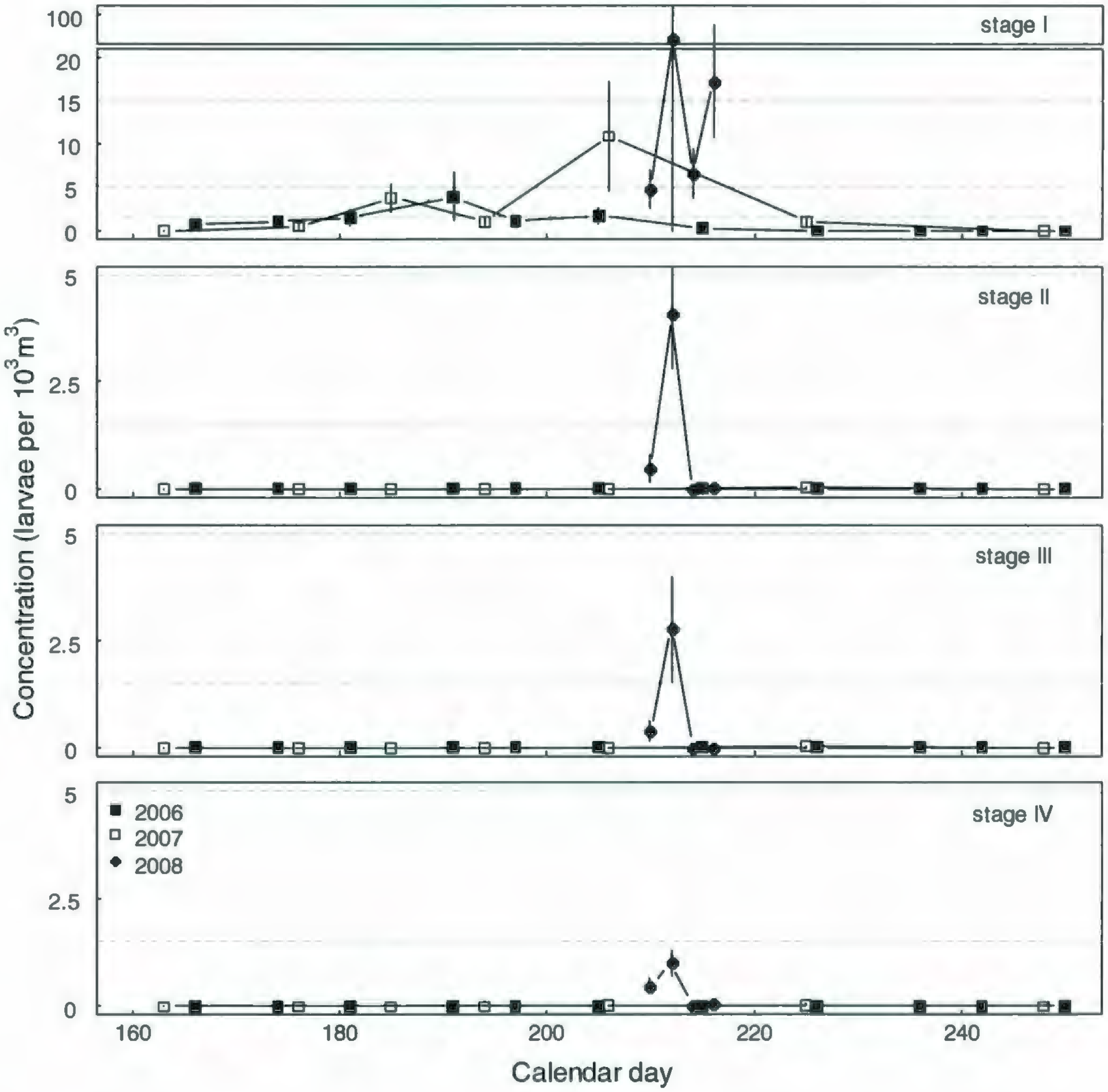


Figure 2.2: Temporal variability of the site average concentrations of lobster larval stages for Bonne Bay determined from neuston tows. Vertical lines denote error bars (SE). Y axis is different on top panel, and horizontal grey reference lines identify same values (1.5, 5, 15) among panels.

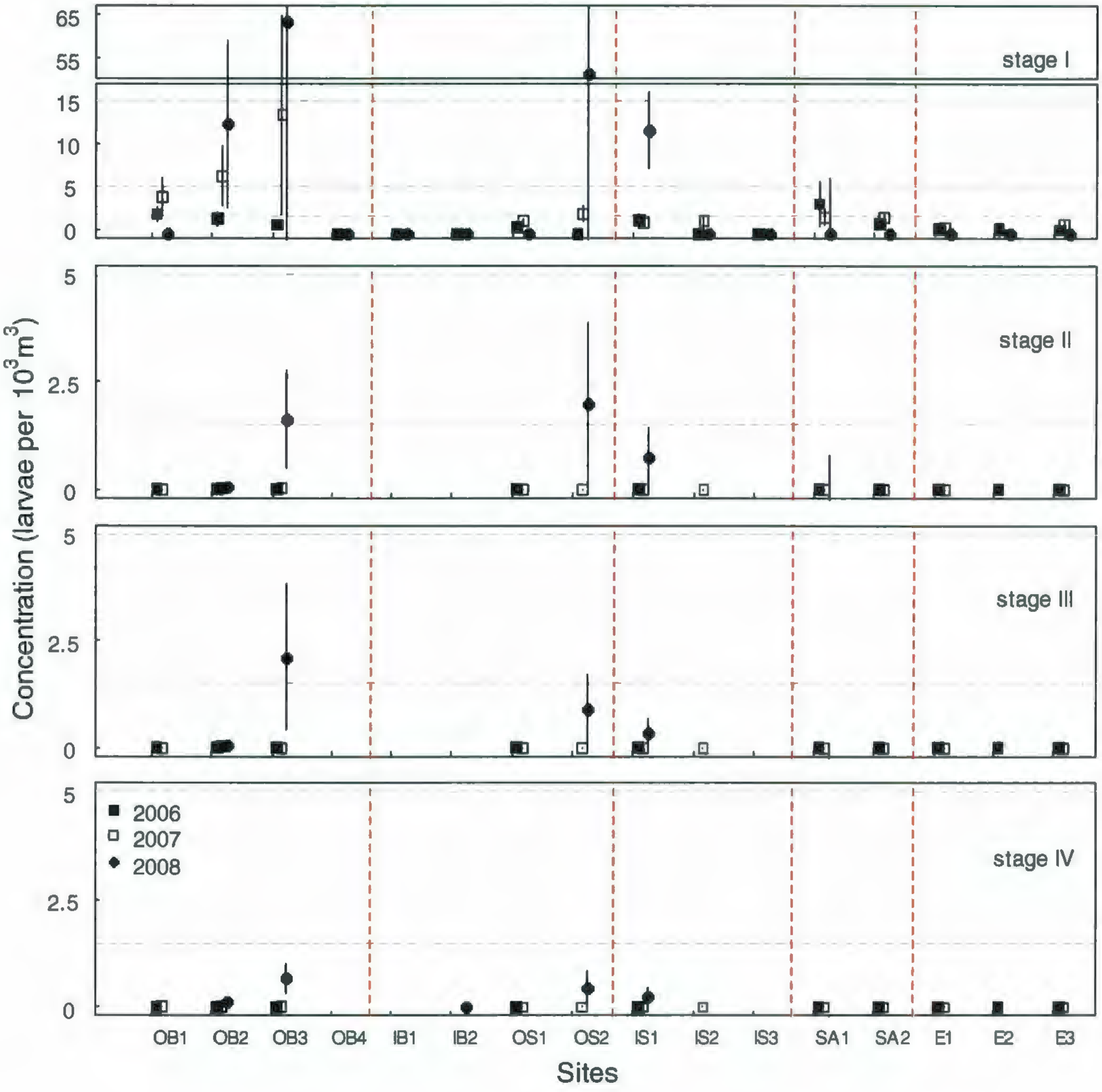


Figure 2.3: **Spatial concentration of different larval stages determined from neuston tows at each sampling site averaged over all sampling periods. Vertical lines denote error bars (SE). Vertical axis is different on top panel, and horizontal grey reference lines identify same values (1.5, 5, 15) among panels. Vertical dashed red lines separate regions.**

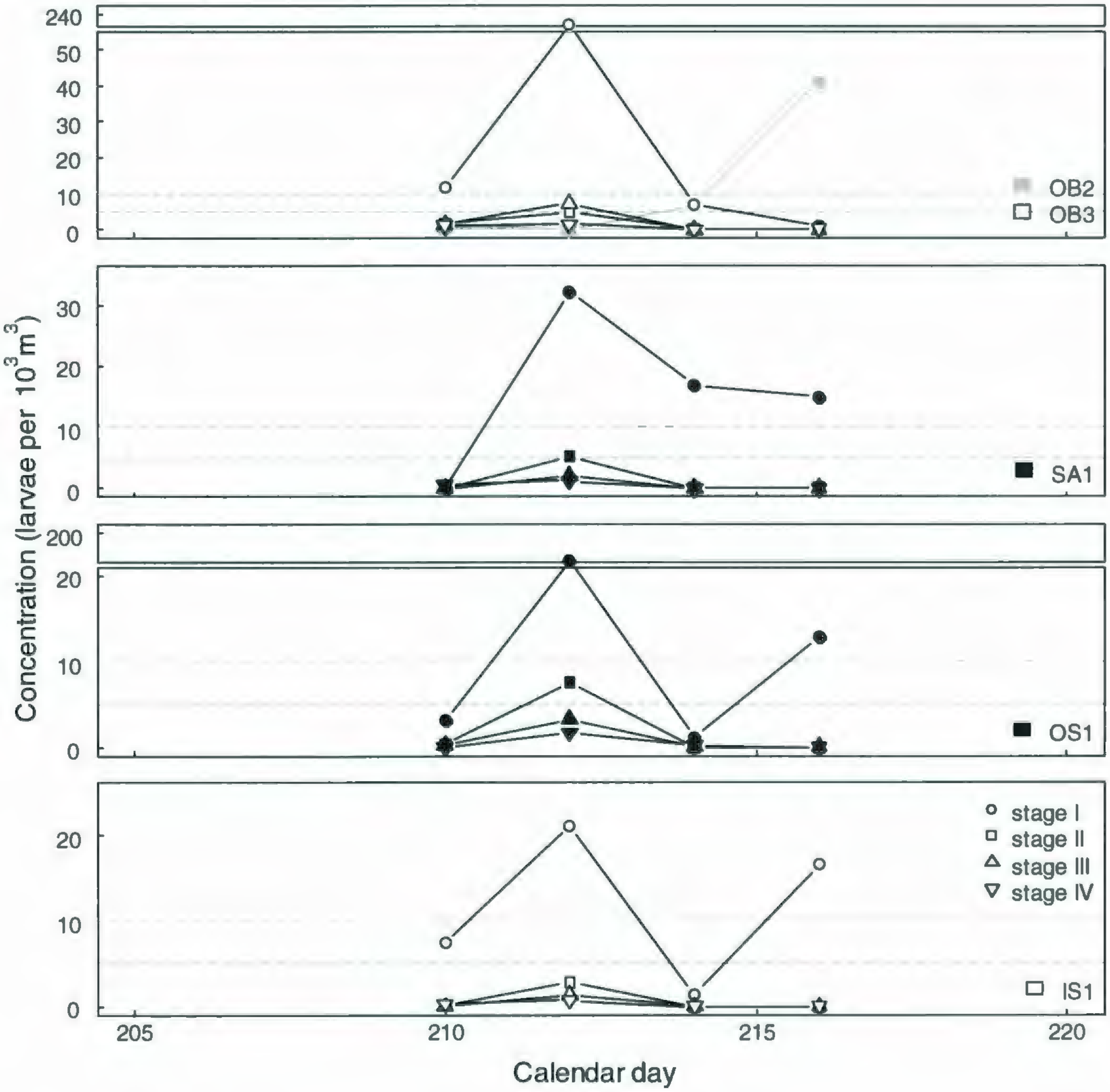


Figure 2.4: Temporal distribution of different larval stages determined from neuston tows in different regions in 2008. Y axis scale is different on panels, and horizontal grey reference lines identify same values (5, 10) among panels.

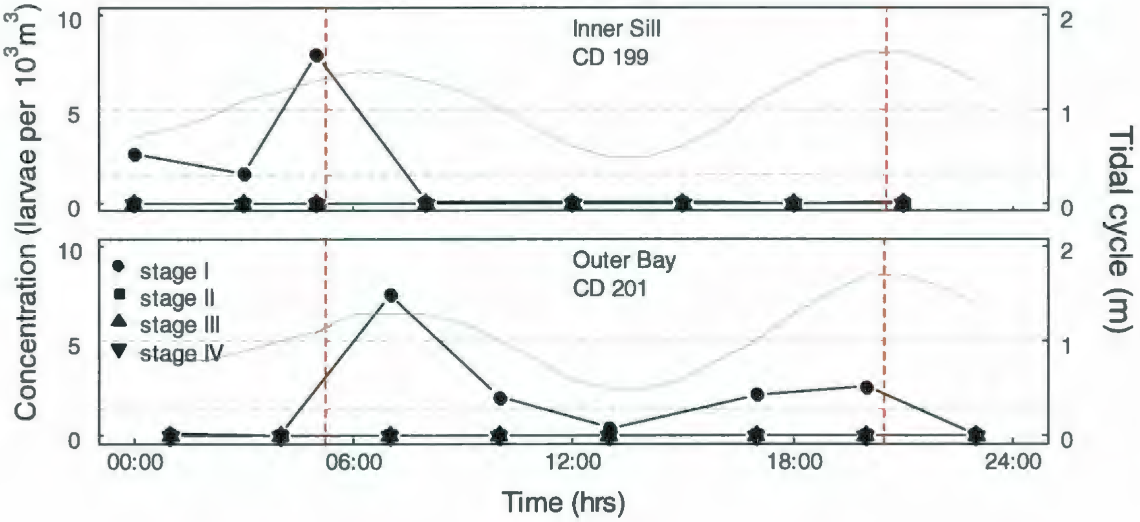


Figure 2.5: Concentration of stage I to stage IV lobsters in neuston tows taken over a 24-hour period in two different locations in Bonne Bay. Newfoundland. Grey line denotes tidal cycle. Horizontal grey reference lines identify same values (1, 5) among panels. Vertical red lines denote sunrise and sunset.

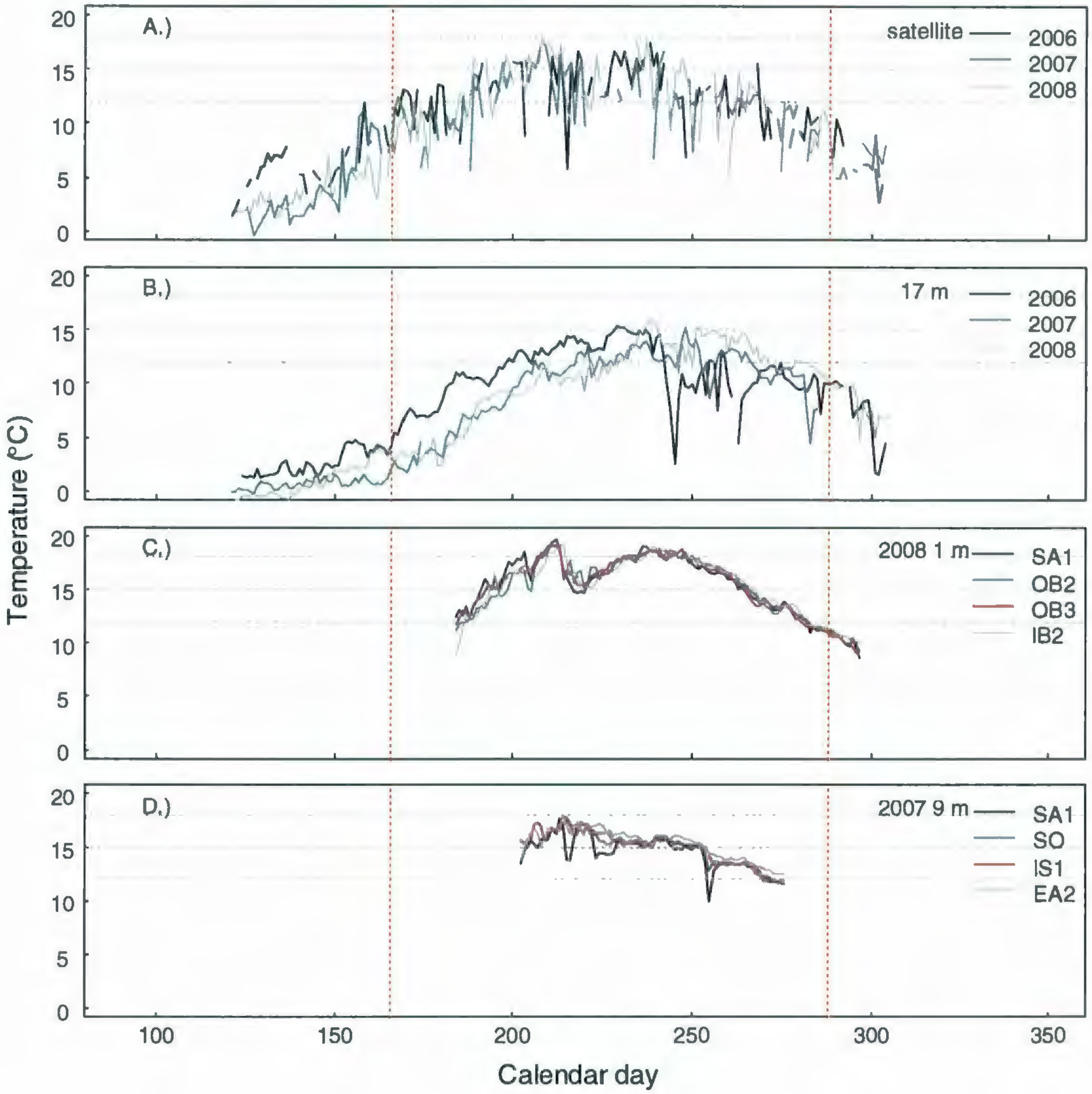


Figure 2.6: Temperature profiles for Bonne Bay from 2006 to 2008 (sea surface temperature, 17 m) and within 2007 and 2008 at different sites in Bonne Bay. Dashed grey line represents 12°, 15°, and 18 ° C temperature. Vertical dashed red lines represents larval hatching season.

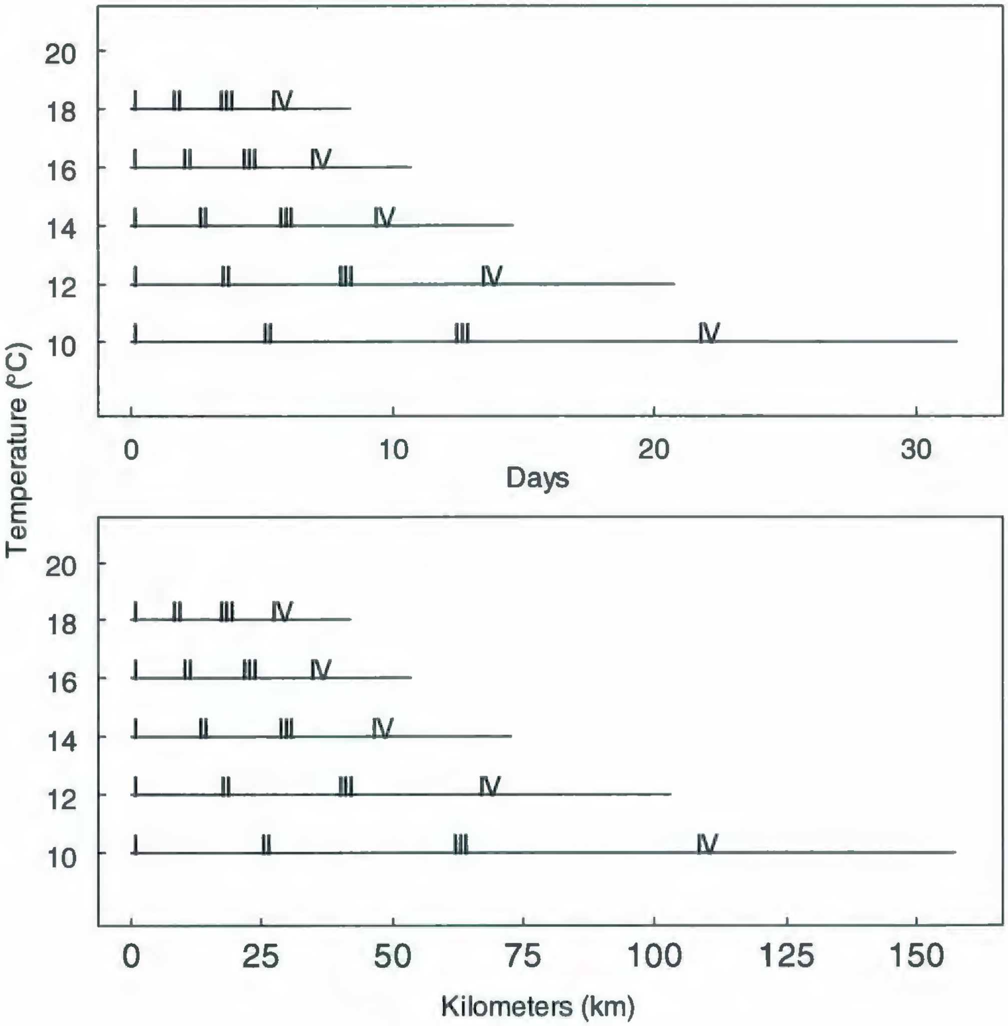


Figure 2.7: Larval development times (upper, Annis et al, 2007), and potential dispersal distances (lower) for west coast Newfoundland current (Gilbert and Pettigrew, 1993). Points mark the beginning of each larval stage (I, II, III, IV). Dispersal distance is max possible from passive dispersal at 5 cm · s^{-1} and assumes larvae remain for the entire time in the neuston and does not account for tidal influence, wind reversals, or larval behaviour.

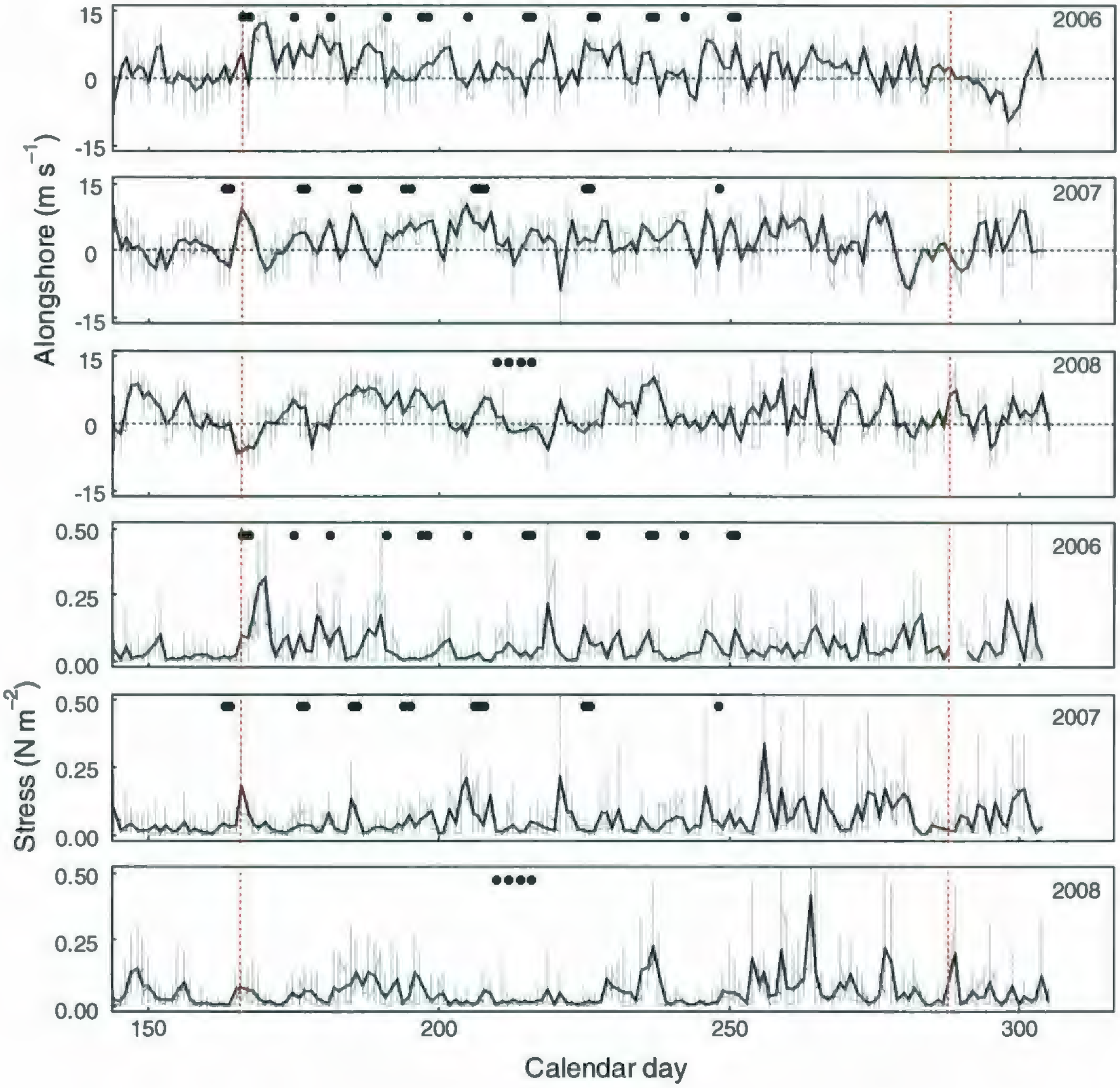


Figure 2.8: Daniels Harbour wind stress (lower, N m^{-2}) and along shore wind velocity (upper) shown in hourly measurements (grey) and daily averages (black) from May to October in 2006, 2007, and 2008. Dashed vertical red lines are larval hatching season. Circles are sampling days.

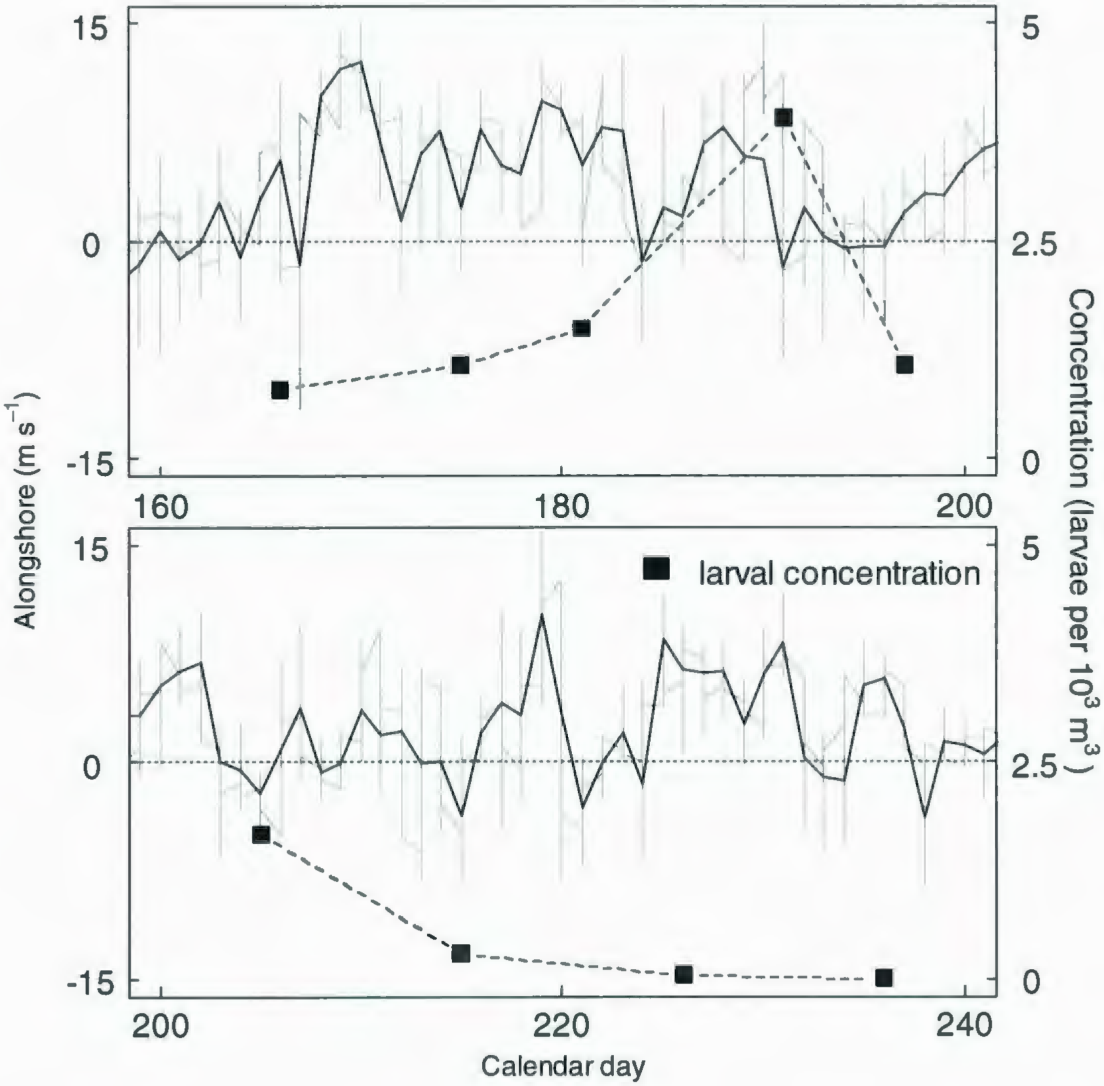


Figure 2.9: **Daniels Harbour along-shore wind velocity shown in hourly measurements (grey) and daily averages (black) in 20 day increments for the duration of the larval period in 2006. Dashed line shows larval concentration averaged over all sites in Bonne Bay.**

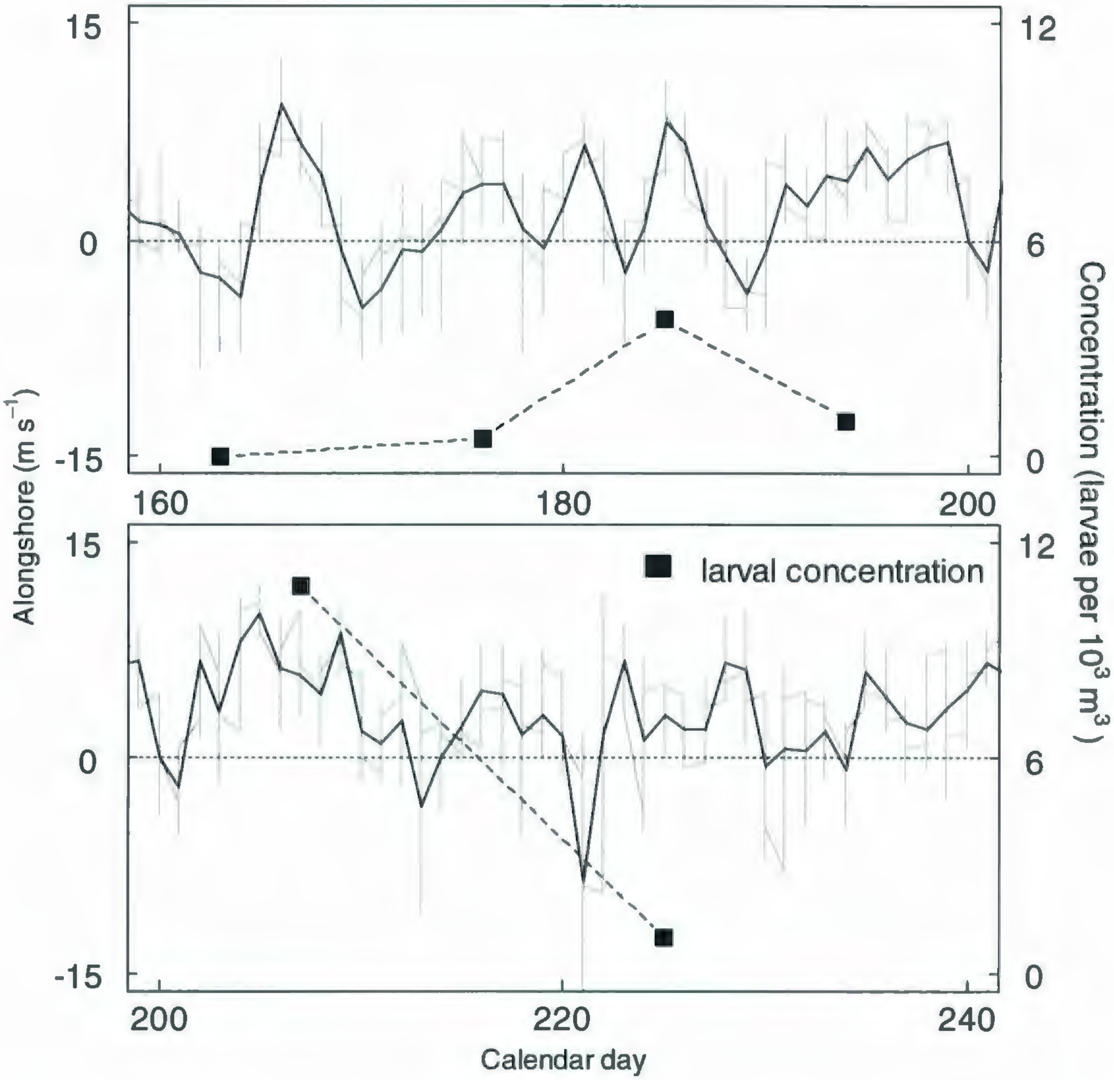


Figure 2.10: Daniels Harbour along-shore wind velocity shown in hourly measurements (grey) and daily averages (black) in 20-day increments for the duration of the larval period in 2007. Dashed line shows larval concentrations averaged over all sites in Bonne Bay.

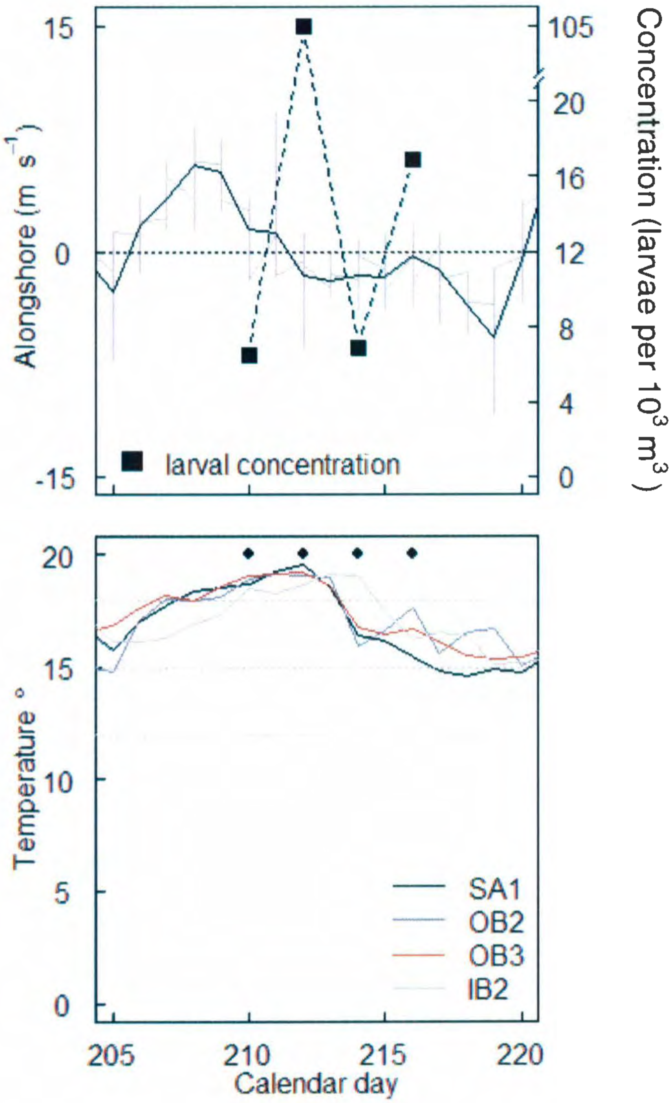


Figure 2.11: Daniels Harbour along-shore wind velocity shown in hourly measurements (grey) and daily averages (black) for the duration of the larval period in 2008. Dashed line shows larval concentration averaged over all sites in Bonne Bay. Table 2.7 shows percent distribution of larval stages for each sampling day.

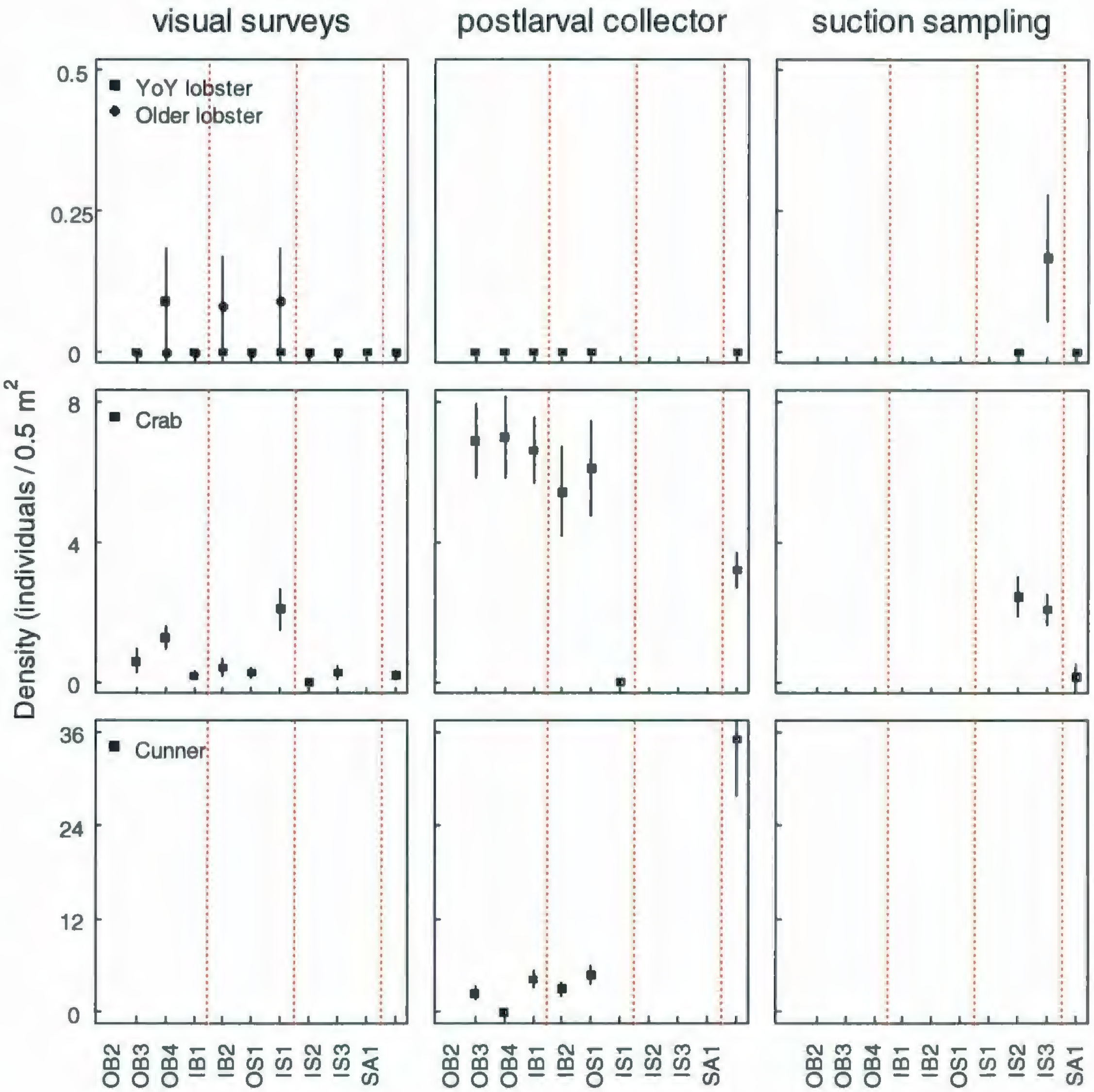


Figure 2.12: 2008 Benthic sampling densities of lobster, crab, and cunner from visual surveys, postlarval collectors, and suction sampling. Vertical lines denote error bars (SE). Dashed vertical red lines separate regions.

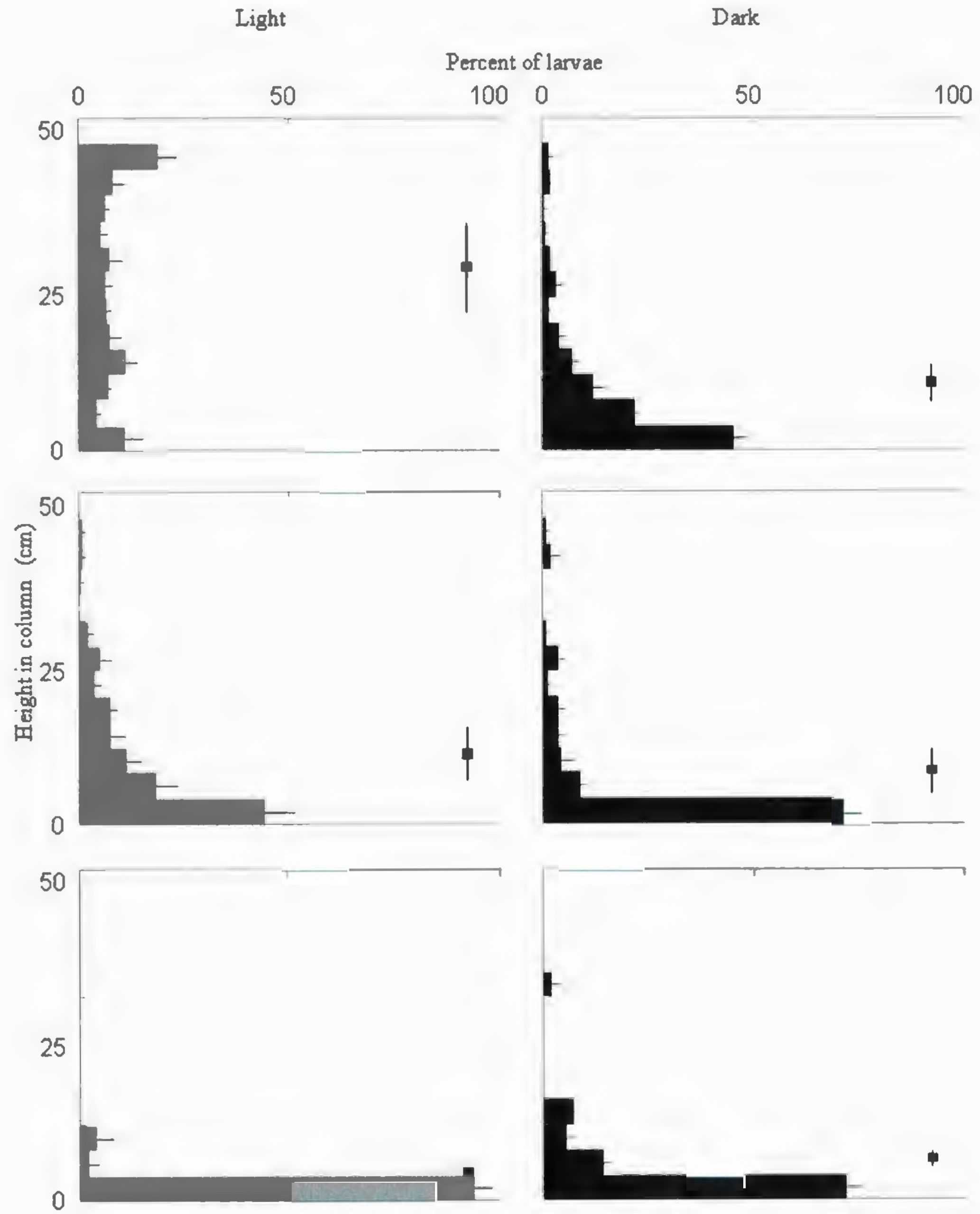


Figure 2.13: Percentages of stage I, II, and III larvae in the light and in the dark after 15 minutes. Dots represent mean larval depth (ZCM). Horizontal lines denote error bars (SE). See Table 2.3 for Chi-square analysis.

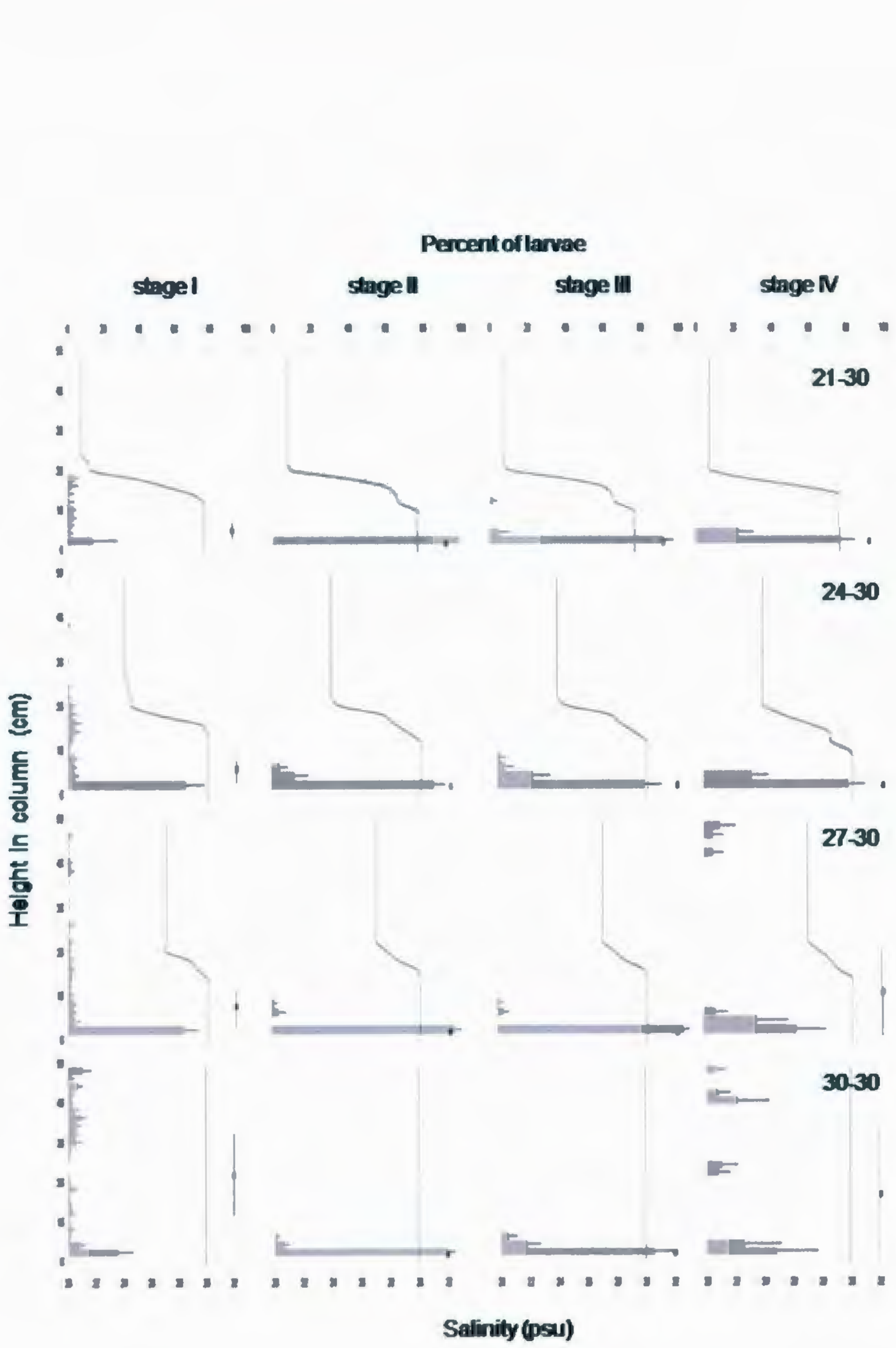
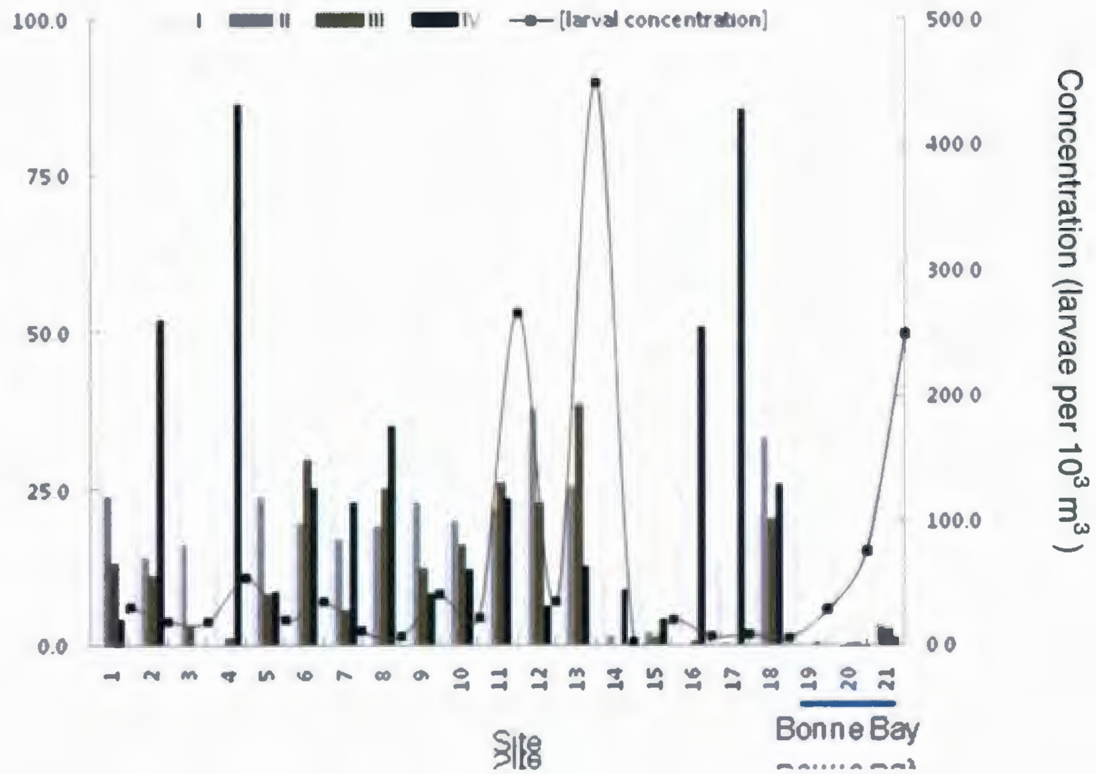


Figure 2.14: Percentages of stage I, II, and III larvae and stage IV postlarvae in different salinity treatments (21-30, 24-30, 27-30,30-30) after 15 minutes. Line represents column salinity profile. Dots represent mean larval depth (ZCM). Horizontal lines denote error bars (SE). See Table. 2.4 for Chi-square analysis.

Appendix



Appendix 2.1: Percent stage distribution of lobster larvae and postlarvae from various other lobster studies. Bars represent percent stage distribution, line represents maximum larval concentration. See Appendix 2.2 for sites and references.

Appendix 2.2: Sites and references for regional comparison of larval and postlarval distributions.

ID	state/prov	region	year	authors
1	RI	Block Island Sound	1977	Bib et al 1983
2	RI	Block Island Sound	1978	Bib et al 1983
3	RI	Block Island Sound	1979	Bib et al 1983
4	NH	Hampton - Seabrook	1978	Grabe et al. (1983)
5	MA	Cape Cod Bay	1975	Lawton et al. (1983)
6	MA	Cape Cod Bay	1976	Lawton et al. (1983)
7	MA	Cape Cod Bay	1977	Lawton et al. (1983)
8	MA	Cape Cod Bay	1974	Matthiessen and Scherer (1983)
9	MA	Cape Cod Bay	1975	Matthiessen and Scherer (1983)
10	MA	Cape Cod Bay	1976	Matthiessen and Scherer (1983)
11	MA	Upper Buzzards Bay	1977	Collings et al (1983)
12	MA	Lower Buzzards Bay	1976	Lux et al. (1983)
13	MA	Lower Buzzards Bay	1979	Lux et al. (1983)
14	ME	Penobscott Bay	1976	Greenstein et al (1983)
15	NS	Lobster Bay	1983	Tremblay and Sharp (1989)
16	NS	south west nova	1977	Stasko and Gordon (1983)
17	NS	south west nova	1978	Stasko and Gordon (1983)
18	QC	Iles de la Madeleine	1980	Hudon and Fradette (1993)
19	NL	Bonne Bay	2006	Burdett-Coutts et al. (thesis)
20	NL	Bonne Bay	2007	Burdett-Coutts et al. (thesis)
21	NL	Bonne Bay	2008	Burdett-Coutts et al. (thesis)

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CHAPTER 3 DO SETTING LOBSTERS SEEK CONSPECIFICS? SPATIAL LINKGAGES BETWEEN YOUNG-OF-YEAR AND OLDER JUVENILES.

Abstract

I examined the spatial association between young-of-year (YoY) and older juvenile American lobsters (*Homarus americanus*) across multiple spatial scales using a long-term recruitment index time series collected in New England, USA. I complemented this analysis with laboratory experiments to determine behavioural responses of settling postlarvae to the presence of conspecifics. Data aggregated at the regional scale (10s to 100s of kilometres) showed that YoY recruitment was significantly associated with older juvenile densities for all eight years of the analysis. Positive correlations at this scale support previous research showing the importance of circulation-driven patterns of larval supply in generating positive relationships between newly settled YoY and established juvenile lobsters. At the quadrat-level (0.5 m^2), for all eight years analyzed, there was a highly significant association between the frequency of quadrats containing YoY and the density of older juveniles. In contrast, above a minimum threshold of cobble habitat cover, there was less evidence of an association between cobble percent cover and the frequency of quadrats containing YoY lobsters. I hypothesize that settlement behaviour contributes to the association with conspecifics.

Although it is well established that early benthic phase juvenile lobsters (~0 – 2 years old) are strongly associated with structurally complex habitats, little is known of variables other than habitat complexity that may enhance successful recruitment. I suggest that resident conspecifics may serve as a habitat quality proxy for postlarval lobsters, as is true for other benthic taxa, despite potential post-settlement risks such as competition and predation. Short-term (4 min) laboratory behavioural experiments showed that postlarvae spend significantly more time on the bottom in the presence of conspecific juveniles. In longer-term (24 h) experiments, postlarvae initially settled more rapidly in the presence of conspecific juveniles, however, this effect dissipated with time. The absence of suitable habitat in the experimental chambers may have inhibited a longer-term response. While conspecifics may serve as an initial attractant to postlarvae, additional habitat cues such as the presence of cobble may be necessary to encourage settlement.

Introduction

Larval settlement of many marine benthic invertebrates is a critical stage that marks the transition from a pelagic to a benthic habitat, as well as a dramatic shift in the scale of dispersal (Connell 1961; Paine and Levin 1981). Spatial patterns of recruitment to benthic habitats are determined by the interaction of biological and physical processes that operate over a broad spectrum of spatial scales (Scheltema 1986; Roughgarden et al. 1988; Etherington and Eggleston 2000; Pineda et al. 2009). Because interpretation of patterns and processes that are evident at one scale may change when viewed from another, a comprehensive evaluation of the mechanisms of recruitment requires integration across multiple spatial scales (Hewitt et al. 1997; Thrush et al. 1997).

Benthic recruitment is typically defined as survival to a post-settlement stage (Connell 1985; Menge 1992). Survival to that point is influenced by processes that operate both before and after settlement (Caley et al. 1996). Pre-settlement processes operate for the duration of the planktonic stage and result from a combination of larval supply, transport and mortality, availability of suitable habitat, and behaviour (Butman 1987; Pineda 2000). Post-settlement processes can operate for the duration of benthic life and encompass a variety of physical and biological factors (Keough and Downes 1982; Wahle and Incze). Examination of quantitative linkages between life stages can lend insight into fundamental mechanisms of recruitment.

Passive larval transport by ocean currents can influence dispersal and recruitment dynamics at multiple spatial scales, from those as large as ocean basins and as fine as grains of sand (Scheltema 1986; Snelgrove et al. 1993; see Pineda 2000; Pineda et al. 2009 for reviews). Meso-scale eddies generated by complex coastlines and bottom topography can enhance or reduce settlement at scales of tens to hundreds of kilometres (Kinlan and Gaines 2003), whereas micro-hydrodynamic effects on near-bottom turbulence and eddies can influence larval settlement at scales of centimetres and millimetres (Snelgrove et al. 1993). Although larval vertical movements in the water column in the water column can have large scale consequences by influencing the extent of passive horizontal transport (Kimmerer and McKinnon 1987; Metaxas 2001; Vikebø et al. 2005), larval behaviour in general is typically believed to influence distribution patterns over smaller spatial scales (Butman 1987). For example, habitat selection can influence fine-scale choices related to shelter and substrate quality (Seed and Wood 1994; Hunt and Scheibling 1997). Indeed, some species demonstrate a clear ability to discriminate between different habitats during larval settlement (Butman et al. 1988; Krug and Zimmer 2004).

Post-settlement processes, such as competition, mortality, and movements are also important because they can decouple a settlement signal from subsequent recruitment patterns, typically over small spatial scales (Pile et al. 1996; Pardo et al. 2007). The extent to which variable recruitment mirrors the variability in larval settlement may vary between regions depending on whether or not populations are resource-limited (Doherty 1982; Hughes 1984).

The American lobster, *Homarus americanus*, is one of the most important commercial species on the east coast of North America. It exhibits a complex life history typical of most marine decapods. Larvae are released over a three-month period that ranges from a start time of May towards its southern geographic limit to August at its northern limit (Aiken and Waddy 1980). Larvae develop through three larval stages and a postlarval stage, the last of which settles to the seafloor (Lawton and Lavalli 1995). Unlike the larvae, postlarval lobsters are relatively strong swimmers and actively seek pre-existing shelter, resulting in a strong association of juvenile stages with structurally complex habitats such as cobbles and boulders (Scarratt 1973; Cooper and Uzmann 1980; Wahle and Steneck 1992). Early benthic phase lobsters strongly associate with shelter-providing habitat during their first year or two of life, likely because of susceptibility to predation (Wahle and Incze 1997), and are therefore behaviourally and ecologically distinct from larger, less vulnerable lobsters. The use of structurally-complex habitats as refuge by juvenile crustaceans is common because they provide survival advantages that include protection from predation, from adverse hydrographic conditions, and from other physiological stressors (Howard and Nunny 1983; Lavalli and Barshaw 1986; Wahle and Steneck 1991).

To the extent that consistent annual differences in larval supply establish local and regional differences in settlement, and given limited early juvenile movement, recent settlers are expected to associate with older conspecifics less than 3 years old. Given the dependence on cobble-boulder habitat for the first few years of life, settlement strength is a major determinant of the abundance of older juveniles in cobble nurseries (Wahle et al. 2004). After several years, however, juveniles outgrow this habitat dependence and emerge from nurseries. Nevertheless, the degree to which resident conspecifics promote or deter settlement of new cohorts remains unknown.

Larval behaviour at the time of settlement is a widespread mechanism of optimizing survival probability (Keough and Downes 1982; Zimmer and Butman 2000; Kingsford et al. 2002), where larvae utilize settlement cues that include odour, substrate type and complexity, as well as the presence of conspecifics (Pawlik 1992; O'Connor and Richardson 1998; Head et al. 2004; Dwornanyn and Pirozzi 2008). Many benthic taxa are attracted to conspecifics at the time of larval settlement, including echinoderms (Burke 1986; Pearce and Scheibing 1990), polychaetes (Jensen and Morse 1984; Pawlik et al. 1991), molluscs (Tamburri et al. 2007), barnacles (Raidmoni 1991) and ascidians (Young 1988). Positive responses to conspecifics can result in large mono-specific aggregations (reviewed in Burke 1986). Studies of aggregation during early recruitment in mobile marine species, however, are scarce (see Jensen 1989 for crabs). Pelagic postlarval lobsters have been observed to orient swimming toward the odour of adults (Boudreau et al. 1993), but conspecific attraction in American lobster has otherwise received little attention. As a rule, clawed lobsters are typically asocial and generally do not share shelters (Childress and Herrnkind 2001). On the one hand, it is reasonable to expect that settling postlarval lobster could benefit from the use of cues from conspecifics to guide them to favourable habitat. However, settlement among conspecifics could negatively impact new recruit survival by enhancing intra-specific competition or cannibalism (Pechenik 1999; Moksnes 2004).

The American lobster settlement index is a long-term time series of YoY lobster recruitment to coastal nurseries. The index has been collected over a broad spatial scale in New England, USA, and provides a powerful resource to evaluate patterns and suggest mechanisms that may influence recruitment dynamics in this species. Although strictly speaking, these data measure recruitment rather than settlement, the difference between recruitment and cumulative settlement has been shown to be negligible because post-settlement mortality rates in American lobster are relatively low (Wahle and Incze 1997; Palma et al. 1998). Additionally, whereas young juveniles of motile species may redistribute between habitats after settlement (Etherington and Eggleston 2000; Moksnes 2002), post-settlement migrations of young lobster are believed to be minimal, at least during the first year (Incze and Wahle 1991). Thus, the YoY recruitment index provides a useful tool to identify trends which, in combination with finer-scale laboratory experiments, can provide useful insights into the mechanisms that influence lobster survival and the scale at which they are important. I use these data to determine whether YoY density depends on the resident population of older conspecifics, and how this relationship is influenced by intra-specific effects within the same year.

The aims of this study are therefore to (1) evaluate the relationship between YoY and older juvenile (Juv) lobsters using eight years (2001-2008) of the American lobster settlement index time series, analyzed at three spatial scales of data aggregation, and (2) conduct laboratory experiments to investigate the behavioural responses of postlarval stages IV and V lobsters to the presence of older juvenile conspecifics.

Materials and Methods

Recruitment Time Series

Suction sampling

To evaluate the relationship between YoY density and older juvenile (Juv) density and cobble-boulder cover, I used data from the American lobster settlement index, a long-term, diver-based survey of lobster recruitment collected in New England and Atlantic Canada (Fig. 3.1). SCUBA-based suction sampling surveys have been conducted annually since 1989 in cobble-boulder nursery habitat <10 m below Mean Low Water (MLW) at the end of the settlement season, spanning late-August in the southern regions to late October in the north (Incze and Wahle 1991; Wahle and Incze 1997). Sampling sites were arranged in a nested design, in which there were 12-18 quadrats within 3-15 sites within 11 regions. Quadrat samples were separated by a few metres, whereas sites were separated by 1-10 km and regions by > 100 km. Sampling times at each location were late enough in the season to ensure that no significant additional settlement was likely. All lobsters enumerated in quadrats were measured (carapace length to the nearest 0.1 mm). The recruitment index was defined as the density of YoY lobsters in the population at the time samples were collected (Wahle et al. 2004). Whereas precise aging of lobsters is an area of continuing research (Wahle et al. 1996; Sheehy et al. 1999), YoY are distinguishable as a mode in the size-frequency distribution that is well established from long-term sampling for each region (Incze and Wahle 1991; Incze et al. 1997; Wahle et al. 2001; Wahle et al. 2004). Based on these size parameters, lobsters were defined as either 'YoY' or older juveniles 'Juv' (Table 3.1).

Evaluating YoY association with older conspecifics at different scales

I investigated the relationship between YoY density (individuals · 0.5 m^{-2}) and Juv density (individuals · 0.5 m^{-2}) at three spatial scales (region, site, quadrat) over an eight-year segment of the 20-year time series (2001 – 2008). Regions that were not consistently sampled during this time period or that had fewer than five replicate sites were not included, although the number of sites sampled within each region varied annually in some cases. Prior to analysis, raw count data per quadrat was square-root transformed to normalize the data and stabilize the variance.

As an initial assessment of the relative importance of conspecific effects on YoY recruitment in the context of spatial and temporal variability, I used a Generalized Linear Model approach. Specifically, I employed a nested mixed-model ANCOVA in which sites were nested within 11 regions (both random effects) and Year was a fixed effect with eight levels spanning 2001-2008. Older juvenile density (Juv) and cobble percent cover were included as co-variates in the analysis. Region and Site were treated as random effects because the regions and sites are only a small subset of the possible regions and sites I could have considered, and because I want to generalize about the larger geographic areas from those locations. Year was treated as a fixed effect because it included all years within the time frame of interest.

I used regression analysis to evaluate the YoY to Juv relationship among sites within individual regions. Because error terms were associated with both the dependent and independent variables, I used a Type II regression.

To evaluate the association between YoY and Juv at the quadrat scale I conducted a contingency table analysis because the large number of zero values precluded a regression analysis (Table 3.2). I created a 2 x 6 contingency table to evaluate the frequencies of quadrats with and without YoY at specified juvenile density categories (0, 1, 2, 3, 4, >4). I tested the statistical null hypothesis that the frequency of quadrats with YoY present was independent of older juvenile density. Separate analyses were conducted for each year, as in the larger-scale analyses, and the number of quadrats in each category is displayed in Table 3.3.

One drawback of the contingency table approach was that there were too few quadrats to conduct the analysis for any given site and year, thereby compromising my ability to detect whether a YoY-Juv association existed at that scale. I therefore devised an index of association as a measure of the degree to which YoY were associated with older juveniles within each site, relative to what would be expected if they settled independently of juveniles. I reasoned that this index may provide a useful indication of postlarval choice, rather than supply because larval supply is much less likely to vary at the level of quadrats within sites than it is across sites. For each site, I first assumed that if YoY settlement was independent of the presence of older juveniles, I would expect the percent of YoY in quadrats with older juveniles on average to be equal to the percent of quadrats with older juveniles. The difference between the observed and expected percent of YoY associated with older juveniles (Observed - Expected) was calculated as the site's index of association (IA), varying from -100 to +100. Sites with no YoY, no juveniles, as well as those where all quadrats were occupied by juveniles were excluded from the analysis because it was impossible to contrast observed and expect proportions of YoY. That criteria left 339 of the 498 sites, or approximately 40 sites sampled per year between 2001 and 2008, that could be used for this analysis. I used a one-sample t-test to evaluate the statistical null hypothesis that the mean IA each year differed from 0 at the 95% level of significance

Evaluating habitat effects

I also analyzed a subset of the data for which habitat information was available to determine whether Juv and YoY densities were related to the percent cover of prime cobble-boulder nursery habitat (diameters ranging from 10-50 cm). Although the settlement index survey is conducted in cobble-boulder-dominated habitat, there is some variability in the percent cover of the target habitat among quadrats, generally ranging from 50 to 100%. In a subset of regions, habitat cover has consistently been quantified by divers prior to sampling quadrats. For these locations I investigated the dependence of YoY and Juv density on cobble-boulder percent cover at the site and quadrat scales, as described above using a combination of ANCOVA and regression analysis for the region and site scale, and contingency table analysis for the quadrat scale. For the ANCOVA I added cobble cover as a covariate, allowing me to test effects of continuous (Juv density, cobble cover) and categorical (Year, Region, Site nested within Region) independent variables on the response variable (YoY density). A second, similarly-structured ANCOVA used Juv as the response variable to evaluate the role of cobble cover in determining densities of older juveniles in the context of spatial and temporal variability.

To evaluate the correlation between cobble cover and YoY density within each region, I conducted separate type II regressions among sites within a region for each year of the time series. For the quadrat scale analysis, I created a 2 x 4 contingency table to evaluate the frequencies of quadrats with and without YoY or Juv for different percent cover categories of cobble-boulder (0-40, 40-60, 60-80, 80-100) as a proportion of the total number of quadrats. For each year of the time series I tested the statistical null hypothesis that the frequency of quadrats with YoY present was independent of cobble-boulder cover. Table 3.4 shows the number of quadrats in each category.

Laboratory Experiments

Juvenile lobster (20 – 30 mm) were collected in mid-coast Maine by SCUBA divers and held in flow-through aquaria at the University of Maine's Darling Marine Centre, Walpole, Maine. Lobsters were fed a diet of frozen shrimp every other day. Postlarval lobsters were obtained from the Zone C lobster hatchery in Stonington, Maine and transported to the Darling Marine Centre. Postlarvae were maintained individually in 5 x 10 cm cylindrical containers in flow-through aquaria with filtered (20 µm) ambient seawater. Water temperature and salinity were recorded daily and fluctuated between 16 – 18 ° C and 28 – 30 psu, respectively. Postlarvae were fed frozen brine shrimp once a day.

To evaluate the settlement response of postlarvae to the presence of juveniles, I conducted two sets of experiments, termed 'short term' and 'long term'. Settlement was defined as the time at which an individual postlarva moved to the bottom of the aquarium. Settlement and metamorphosis in American lobster are separate events because metamorphosis occurs when stage III larval lobster moult into stage IV postlarval lobster, whereas a stage IV postlarva is only competent to settle approximately half way through that stage. In each case I observed the settlement response of individual postlarvae in the presence or absence of juveniles. In short-term experiments I evaluated the settlement response continuously over a 4-min period immediately after introduction, whereas in long-term experiments I observed settlement for a 2-min period every 6 h over a 24-h period. Experiments were completed between August and September 2008.

In total, I completed 47 replicates of the treatment with juveniles present and 48 control trials in which they were absent. Postlarvae were obtained from the hatchery by combining a mixture of several mothers' broods, which were distributed haphazardly into experimental treatments. Thus, postlarvae from all broods were distributed relatively evenly among treatments. Temperature ranged from 18-20 °C as recorded at the beginning and end of each trial.

For statistical analysis, trials and batches were analyzed together in order to increase replication. A trial is defined as a set of experiments occurring on one particular day, whereas a batch is defined as the group of postlarvae obtained from the hatchery at the same time. The proportion of postlarvae that settled in the presence of older conspecifics was tabulated by dividing the number of settled postlarvae by the total number of trials for each treatment. For short-term experiments I conducted separate analyses for each of these variables using a t-test with equal variance. For long-term experiments I examined the effect of the presence of conspecific juveniles on postlarval settlement using a binary logistic regression with Treatment (2 levels: Juv presence/absence), Time (5 levels: 0, 6, 12, 18, 24 h), and their interaction (Treatment * Time) as factors.

Juvenile Scent Experiments

A horizontal choice chamber (Fig. 3.2) was set up after the design of Goldstein and Butler (2009) to determine the effect of juveniles on stage V lobsters. A stage V lobster is the first benthic stage. A 90-cm segment of transparent 10-cm diameter plastic pipe was oriented horizontally and sealed on both ends with rubber caps. Two funnels were affixed within the tube, each one 15 cm from the end, with the funnel's mouth facing inward. The funnels served to baffle the flow of water entering the tube at the ends, and as an entry to the end chambers for lobsters moving from the centre of the tube.

Gravity-fed water entered the chamber at opposite ends from separate 20-L buckets through 0.6 cm diametre tubing at a flow rate of 100 ml / min. Flow was made equal at each end by check valves. One bucket was filled with 'juvenile scented' seawater while the other contained filtered, unscented seawater. Juvenile-scented water was prepared by placing five juveniles (20 – 30 mm) in a 20-L bucket of constantly aerated, 20-µm filtered seawater at 18° C for 24 h. Water overflowed from the choice chamber at a T-junction at the centre of the tube. The chamber was marked in 15-cm increments along the concentration gradient, labelled 1 – 6 (Fig. 3.2). Preliminary trials with food colouring confirmed the symmetry of flow and the presence of a concentration gradient. Choice chambers were entirely submerged in a large tank of 20-µm filtered seawater which reduced the distortion effect of the cylinder and facilitated lobster observation. Black plastic covered the top and two sides of the experimental tank to reduce light penetration to the experimental area. I established a scent gradient in the choice tube by simultaneously initiating water flow at each end of the choice chamber 30 min prior to the introduction of the stage V lobster. I also alternated the side that received juvenile-scented water between successive trials. Lobsters were placed into the choice chamber and kept in an 'acclimation' chamber for 5 min (15 x 2.5 cm piece of plastic tubing). Lobsters were released by lifting the plastic tube. Upon release, lobsters were observed continuously for 10 min, during which their location was recorded every 15 sec. Subsequently, lobster position was recorded every 5 min for a total observation period of 30 min. The trial was terminated when the lobster passed through the funnel on either end of the chamber or after 30 min. If the lobster passed through the funnel this was considered a 'decision' for the treatment to which it had migrated. A total of 40 individual lobsters were subjected to experimental trials in 2- choice chambers that were run simultaneously. Lobsters were not used more than once in each experiment and no food was provided during the experiments.

In order to determine the effect of juvenile-scented water on stage V lobsters, data were analyzed in two ways. In the first analysis, I tabulated the total number of trials where lobsters had entered either the control or juvenile-scented end chambers of the choice tube. Trials in which lobsters did not enter the end chambers within 30 min were eliminated. For the second analysis, I tabulated the proportion of time individuals spent in each half (juvenile/control) of the choice tube. In both cases, differences between treatments were determined with a paired t-test. All statistical analyses were conducted using $R^{®}$ statistical software with an alpha significance level of 0.05.

Results

Evaluating YoY association with conspecifics at different scales

As might be expected, the factors Year, Region, and Site nested within Region all explained a significant amount of variability ($p<0.001$) in YoY density (Table 3.5). However, the large F-ratio for the Juv factor indicates that juvenile density explained a large proportion of this variability. The fact that the density of established juveniles is such a strong predictor of YoY density in the same year justifies further examination of this association at different scales and developing an approach to distinguish conspecific effects from other drivers of YoY variability. Although a strong association between YoY density and older juvenile density might be expected if the spatial pattern of postlarval settlement was consistent from year to year, the role of behavioural attraction to conspecifics remains unclear. The following analyses therefore examined the spatial scale of the association in greater detail.

When aggregating data by region with regression analysis, YoY recruitment was consistently and strongly associated with older juvenile densities for all eight years of the analysis (Fig. 3.3). Regional averages of YoY density ranged from 0 to 1.1 individuals · 0.5 m^{-2} while that of older juveniles ranged from 0.02 to 2.8 individuals · 0.5 m^{-2}. The mid-coast Maine region consistently had high densities of both YoY and Juv whereas Buzzards Bay consistently had among the lowest densities (Wahle unpub. data).

Disaggregating the data to reveal among-site variability resulted in a similarly strong positive association between YoY and Juv, although the relationship was less consistent when examined among the sites within any given region (Fig. 3.4, Table 3.6). For example, in Mid-coast Maine, there was a consistent, significant association between YoY and Juv lobsters in all years except 2006. For the Casco Bay region, which neighbours the Mid-coast region, the association was significant for six of eight years. For more southerly regions such as York, however, only the 2007 association was significant, and the Buzzards Bay association was significant in only two out of eight years.

Further disaggregation of the data to evaluate quadrat-level patterns revealed a highly significant association between the presence of YoY and the density of juveniles for all eight years analyzed (Fig. 3.5). Quadrats containing Juv were more likely to contain YoY than those without Juv, and the proportion containing YoY increased with increasing juvenile density.

Analysis of the site-specific index of association (IA) indicated that the mean IA was greater than 0, suggesting YoY were positively associated with older juvenile lobsters at the quadrat scale within sites. The mean IA was significantly greater than 0 in six out of eight years (Fig. 3.6, Table 3.7), suggesting that for the most part the association between YoY and older juveniles was greater than would be expected by chance.

Habitat Effects

The analysis of the subset of locations for which habitat data were also available indicated significant Region, Site, Year and Juv effects on variability in YoY density, but no significant effect of Cobble cover (Table 3.8). This result, taken together with previous evidence of a strong association with shelter-providing habitat (Wahle and Steneck 1991), suggests that once cobble cover is greater than about 30-40%, as is the case with the suction sample surveys, additional cover makes little difference to YoY densities. In contrast, I found the variability in cobble cover explained a significant amount of variability in Juv density (Table 3.9). It is likely that shelter availability becomes increasingly limiting to population densities with increasing body size (Wahle and Incze 1997; Wahle 2003).

Subsequent regression analysis further indicate that as long as a minimum amount of cobble-boulder was present, the YoY density-to-cobble cover relationship accounted for less of the variability than it did for Juv density-to-cobble relationship. Regression analyses were not possible among regions because of insufficient number of sites. Disaggregating the data to reveal among-site variability in cobble cover resulted in a significantly positive relationship between YoY density and cobble percent cover in only one out of eight years (Fig. 3.7), whereas the relationship between Juv density and cobble percent cover was positively significant in six out of eight years (Fig. 3.8).

Further disaggregating the data to evaluate quadrat–level patterns showed a significant association between the presence of YoY and quadrats with increasing cobble cover in four of the eight years examined (Fig. 3.9). As suggested by the regression analysis, the Juv-cobble cover association was somewhat stronger than that for YoY, with a significant association in five out of the eight years (Fig. 3.10).

Behavioural experiments

Short-term settlement experiment

During the 4-min observations of the short-term experiment, postlarvae spent significantly more time on the bottom of the aquarium in the presence of conspecific juveniles ($t_{94} = 2.36$, $P = 0.01$, Fig. 3.11). However, there was no statistically significant difference between the control and Juv treatment in either the total number of postlarval dives to the bottom ($t_{95} = 0.23$, $P = 0.41$, Fig. 3.11) or in the time until the initial dive ($t_{95} = 0.1049$, $P = 0.46$, Fig. 3.11).

Long-term 24-h settlement experiment

In the long-term experiment, postlarvae exhibited a significant time effect during the first two min ($p<0.001$), although the treatment effect was not significant (Fig. 3.12). There was no significant interaction between Juv treatment and time ($p=0.18$) (Table 3.12)

Juvenile scent experiments

In the choice experiments, there was no statistically significant difference in the movement of stage V lobsters either toward the control (unscented) or juvenile scented water (t_{34}=0.17, $p > 0.5$). Nor was there a significant difference in the amount of time stage V lobsters spent on either control (unscented) or juvenile scented water halves of the choice tube (t_{34}=0.50, $p > 0.3$).

Discussion

The long-term recruitment index demonstrates strong positive relationships between YoY and Juv densities at scales of metres (quadrats) to hundreds of kilometres (among regions). Mechanisms that could account for high correlations between YoY recruitment and established benthic conspecifics vary from consistent interannual spatial patterns of recruitment most likely driven by currents (Incze and Naimie 2000; Xue et al. 2008), as well as active behavioural selection for suitable habitat (Butman 1987), and attraction to conspecifics (Burke 1986). The limited swimming capacity of larvae and postlarvae would suggest, however, that large-scale patterns of recruitment are likely dominated by physical transport processes, whereas behavioural mechanisms are more likely to dominate at small scales. The importance of oceanography as a driver of recruitment patterns has been well documented over the last century in that environmental factors such as offshore advection can significantly impact recruitment patterns (Bailey 1981; Roughgarden et al. 1988). At large spatial scales, positive relationships between YoY and juveniles are most likely to arise from physical processes such as consistent circulation-driven differences in larval supply (Incze and Wahle 1991; Incze et al. 1997; Wahle and Incze 1997; Incze and Naimie 2000; Xue et al. 2008).

Multi-scale assessment of recruitment patterns can be a powerful tool in understanding the processes that influence those patterns. My initial ANCOVA indicated that juvenile density explains a large proportion of variability in YoY density, and justifies subsequent analyses at progressively finer scales. Persistent ocean circulation features such as coastal gyres and currents driven by prevailing winds can result in consistent spatial differences in larval settlement, which translate to consistent spatial patterns of benthic recruitment from year-to-year (Incze et al. 1997; Palma et al. 1998; Steneck and Wilson 2001; Wahle et al. 2004). This process alone could produce the strong correlation in spatial patterns observed between YoY and older year classes.

Although also positive in most cases, YoY-Juv correlations among-sites within a region were generally less consistent. Patterns of variation at meso-scales of 1-10 km, can be influenced by topographically-mediated ocean processes (Ebert and Russel 1988; Archambault and Bourget 1999; Palma et al. 2006) (e.g. upwelling, onshore/offshore winds), as well as the suitability of benthic habitat (Moksnes et al. 1997). These factors influence larval supply and successful settlement respectively (Pile et al. 1996; Pineda et al. 2009). For example, Wahle and Incze (1997) demonstrated that consistent annual differences in lobster recruitment on two sides of a small island (4 km long) were related to wind-driven circulation. As cohorts were followed through time, the differences disappeared, presumably because as cohorts aged, lobsters became increasingly mobile, in effect decoupling the settler-to-recruit spatial relationship. In the present study, there was a significant association between YoY and Juv for the Mid-coast region for all years except 2006, but non-significant results for the Buzzards Bay region for all years except 2001 and 2006. Demonstrating a relationship depends on having sufficient among site or region contrast in the data. For example, typically, the Mid-coast region had strong lobster recruitment (highest regional average in 6 out of 8 years), whereas Buzzards Bay had relatively low recruitment (lowest regional average in all years) (Wahle, unpubl. data). The one year in which the mid-coast result was non-significant (2006) was a poor-recruitment year for that region (~50% less than its 8-year average). Average annual recruitment between these sites fluctuated between 0.38 – 1.12 individuals / $0.5m^2$ and 0 - 0.06 individuals / $0.5m^2$, respectively.

If larger-scale factors influence larval supply inter-annually or among regions, they can dampen any signal of association between YoY and Juv. stages. Thus, broad-scale recruitment variation can significantly impact any signal related to behavioural interactions (Connolly and Roughgarden 1999). Additional studies that incorporate pelage-benthic coupling at this meso-scale are important to determine recruitment drivers (i.e., coastline configuration, habitat availability) that may favour strong recruitment. The importance of larval supply in determining settlement variation among sites has been widely documented, but our ability to evaluate the significance of small-scale mechanisms, and particularly behavioural effects, may be confounded by large-scale environmental effects (Bertness et al. 1992). Furthermore, the significance of density-dependent interactions (i.e., cannibalism, competition) are likely more prevalent in areas with a greater larval supply (Roughgarden et al. 1988).

American lobster is a useful model organism to examine the influence of conspecifics on postlarval settlement because benthic juveniles remain within cryptic nurseries for the first few years of life (Incze and Wahle 1991; Cowan et al. 2001; Wahle 2003). Approximately 90% of lobsters sampled at each site in each year were under 40 mm carapace length, and therefore represented a demographically distinct early benthic phase (Wahle and Steneck 1992).

My analysis of habitat effects suggests the percent cover of cobble-boulder is a better predictor of density of older juveniles than of YoY. Previous studies have also suggested that older, larger juveniles are more subject to shelter limitation than smaller ones (Wahle and Incze 1997). Natural densities of YoY rarely reach saturation densities as estimated by previous saturation seeding experiments (Wahle and Incze 1997). Acquisition of suitable shelter is essential for survival of early juvenile American lobster because of their vulnerability to predation at that size (Wahle and Steneck 1992). Although shelter-to-body size scaling relationships have been determined for several species of lobster (Spanier and Almog-Shtayer 1992; Wahle and Steneck 1992; Wahle and Incze 1997; Gristina et al. 2009), cobble size *per se* has not been shown to influence larval settlement decisions for the American lobster (Lillis and Snelgrove 2010).

Other lobster species have been shown to respond positively to the presence of conspecifics at the time of settlement. Conspecific density has been shown to influence postlarval recruitment of gregarious spiny lobster *Panulirus argus* (Zito-Livingston and Childress 2009), either as a result of reduced planktonic exposure where postlarvae use conspecific odours to quickly locate a shelter or as a result of higher survival probability of aggregations of juveniles that may be less vulnerable to predation (Childress and Herrnkind 1997; Briones-Fourzán and Lozano-Alvarez 2008). The finding that postlarval *Homarus americanus* may also respond positively to conspecifics is surprising given that clawed lobsters as a group are not generally gregarious, and tend to occupy and compete for individual shelters (Karnofsky et al. 1989). Consequently, there may be may be a carrying capacity determined by available shelters (Wahle and Incze 1997; Steneck 2006). It is likely that recruitment densities of YoY as determined by natural settlement do not approach that carrying capacity, although they may become crowded as individuals from a settlement cohort grow in body size (Wahle and Incze 1997; Wahle 2003). Laboratory studies of recently-settled American lobsters maintained at high density conditions suggest agonistic interactions in shelter-limited conditions (Paille et al. 2002). More work is necessary to understand the habitat requirements and density-dependent interactions of YoY lobsters.

The quadrat-scale analysis of the YoY-to-Juv relationship indicated that there is a potentially important association between juvenile and YoY lobster at very small spatial scales that cannot be as easily explained by hydrodynamic processes as it is at larger scales. For all years studied, the lowest proportion of YoY lobsters occurred in quadrats where juveniles were absent, and the frequency of quadrats that contained YoY lobsters increased steadily with increasing densities of juvenile lobsters. The index of association developed here provides a means to assess whether the association between YoY and Juv is greater than would be expected by chance.

The benefits of responding positively to and settling near conspecifics could be a mechanism to find suitable habitat (sea urchins: Tegner and Dayton 1977; barnacles: Crisp 1985; Jeffrey 2000; crab: Gebauer et al. 2002; Vadas and Elner 2003). My short-term laboratory experiments showed that postlarvae spent significantly more time on the bottom of the aquarium in the presence of juveniles. The long-term experiments were consistent with the short-term experiments in that at time 0, postlarvae showed an initial propensity to settle in the presence of juveniles. However, this effect dissipated over time. It is possible that other aspects of the habitat in the experimental tanks were not suitable for the postlarvae to remain on the bottom. In natural situations, determining a suitable settlement location depends on a variety of other sensory cues. It is likely that there is a hierarchy of cues necessary for settlement and final establishment in nursery habitat (Kingsford et al. 2002; Ettinger-Epstein et al. 2008). An interpretation of my results that is consistent with the cue hierarchy hypothesis is that the presence of juveniles may induce postlarval searching behaviour, but if suitable habitat is absent, the settlement process is delayed. In the crab *Chasmagnathus granulata,* Gebauer and Anger (1998) found that late stage megalopae accelerated metamorphosis significantly when simultaneously exposed to natural mud and conspecific odour than when exposed to either cue in isolation. In the American lobster, the decision to settle among conspecifics may carry the risk of cannibalism or being crowded from shelter, but this risk may be lower than the risk of settling in an unfavourable habitat. Field enclosure experiments with densities representative of the high end of the naturally-observed range suggest that older conspecifics have a negligible impact on YoY growth or survival (Wahle et al. 2001). Moreover, if settlement even in the highest density regions is not initially saturating (Wahle and Incze 1997), the survival advantages of settling among conspecifics may outweigh the disadvantages.

Response to conspecifics at the time of settlement is common among sessile species (barnacles: Jeffrey 2000; ascidians: Manríquez and Castilla 2007),as well as mobile (porcelain crabs: Jensen 1989; fiddler crabs: O'Connor 1991; hermit crabs: Harvey 1996) organisms. The attraction to conspecifics is consistent with laboratory findings that swimming postlarvae orient toward odour plumes from conspecifics (Boudreau et al. 1993). That the ability to detect and respond to the presence of older conspecifics is prevalent among a diverse array of taxa suggests it is an important mechanism of habitat selection during settlement.

Given the patchy and emphemeral nature of suitable habitat, conspecifics represent a potential indicator of suitable habitat. Thus, the net benefits of settling near conspecifices, once balanced with potential costs, may be species dependent. Reducing search time at the time of settlement may provide a post-settlement fitness benefit (Fletcher 2006). For species that are susceptible to cannibalism or increased competition, these risks must outweigh the risk of arriving in unfavourable habitat (Donahue 2006). Thus, behavioural experiments that offer conspecifics and suitable cobble habitat might yield a more persistent settlement response. Additionally, it is possible that the small spaces that recent settlers would occupy among older conspecifics may provide a predation refuge from other predators. While cannibalism is known to occur in laboratory conditions for American lobster, the extent to which it has a significant impact on recruitment dynamics is still poorly understood for this species (Wahle et al. 2001; Wahle 2003).

The costs and benefits of settling among conspecifics warrants further investigation in order to determine the degree to which habitat selection choices may be based on a combination of positive and negative interactions, the degree to which these interactions are density dependent (Hunt and Scheibling 1997), and how these cues might be influenced by patch size effects (Fletcher 2006). Whereas for mobile species, this decision is potentially reversible, the extent of post-settlement movement to “correct” for settlement mistakes is unknown for most species.

The present study uses a multi-scale approach to investigate the interaction of processes that function at different spatial scales and the degree to which these processes are reflected through recruitment. It is likely that hydrographic conditions set larval supply at large spatial scales, however, the results presented here suggest that behavioural responses to conspecifics may operate at the finest scales. The behavioural experiments reported here, in combination with the quadrat-scale results from the long-term data set, suggest that the presence of juveniles may help to explain spatial variability in recruitment of American lobster, despite the potentially negative effect that lobsters may have on each other after settlement. An understanding of how organisms interpret and respond to multiple, sometimes conflicting cues, such as conspecific effects in combination with variable sheltering quality, may provide more insight into the detailed behavioural mechanisms by which postlarvae search for and select suitable habitat.

Tables

Table 3.1: Size range definitions (mm CL) of YoY and Juv lobster in the various regions. Number of sites sampled within each region from 2001 to 2008. Shaded boxes show subset of regions used for the YoY- and Juv-cobble regression analysis.

			2001	2002	2003	2004	2005	2006	2007	2008
Mt. Desert Is.	≤13	>13	3	4	5	5	5	5	5	5
Penobscot Bay	≤13	>13	9	9	8	9	11	11	11	11
Mid-coast	≤10.5	>10.5	10	10	10	10	10	10	10	10
Casco Bay	≤10.5	>10.5	5	5	5	5	5	5	5	5
York	≤10.5	>10.5	5	5	5	5	5	5	5	5
Boston Hbr.	≤12	>12	7	7	7	6	7	7	7	6
Buzzards Bay	≤12	>12	5	5	5	5	5	5	5	5
Rhode Island	≤13	>13	6	6	6	6	6	6	6	6

Table 3.2: Number of quadrats with different densities of YoY.

	number of YoY lobsters			
year	0	1	>1	Total
2001	544	112	64	720
2002	557	122	45	724
2003	591	139	55	785
2004	575	130	53	758
2005	526	168	103	797
2006	608	132	56	796
2007	490	205	103	798
2008	617	121	50	788

Table 3.3: Number of quadrats with different densities of juvenile lobsters.

year	number of juvenile lobsters					
	0	1	2	3	4	>4
2001	385	188	84	41	13	9
2002	408	162	70	43	24	17
2003	440	175	81	37	35	17
2004	414	184	89	39	18	13
2005	391	194	102	54	30	26
2006	341	165	118	71	45	56
2007	344	216	138	52	30	18
2008	281	197	139	89	40	42

Table 3.4: Number of quadrats with different cobble percent cover.

year	**cobble boulder percent cover**				
	0-20	**21-40**	**41-60**	**61-80**	**81-100**
2001	3	17	66	134	91
2002	9	14	52	88	146
2003	2	9	72	137	89
2004	0	7	50	122	132
2005	41	40	120	217	148
2006	17	22	66	200	260
2007	26	55	77	158	288
2008	12	46	57	154	344

Table 3.5: ANCOVA to determine the effect of categorical variables (Year, Region, Site) and covariate (Juv density) on the dependent variable YoY density.

Factor	SS	df	MS	F	P
Region	12.42	7	1.77	3.86	<0.005
Year	6.71	7	0.96	16.33	<0.001
Juv	14.60	1	14.60	248.68	<0.001
Sites(regions)	22.09	48	0.46	7.84	<0.001
Error	296.50	5051	0.06		

Table 3.6: Coefficient of determination (R^2) values from type II regression analyses on the relationship between YoY and older Juv lobsters at the eight regions sampled from 2001 – 2008. Level of significance is described with * symbol (*=<0.05,=<0.01,***=<0.001). YoY=0 means that YoY densities were zero and analysis could not be conducted. Refer to Figure 3.4.**

year	Mt. Desert Is.	Penobscot Bay	Mid-coast	Casco Bay	York	Boston Hbr.	Buzzards Bay	Rhode Island
2001		0.16	**0.55	*0.65	0.24	0.03	***1	0.39
2002		**0.64	***0.69	*0.66	0.12	**0.86	0.39	0.24
2003	**0.93	0.03	***0.7	**0.9	0.2	**0.64	0.06	*0.54
2004	0.04	**0.59	*0.43	**0.83	0.1	0.35	0.15	0.42
2005	*0.77	0.16	**0.67	**0.9	0.45	***0.88	0.02	0.07
2006	0.39	0.25	0.08	0.31	0.01	0.23	***0.99	***0.95
2007	0.31	0.01	*0.36	0.17	0.74	*0.57	0.59	0.02
2008	0.45	0.17	*0.45	*0.7	0.01	0.33	YoY= 0	0.54*

Table 3.7: One sample T-test to determine whether the observed mean index of association is significantly different from 0 given the observed variability among sites. Refer to Figure 3.6.

year	n	mean	t	df	p	95_CI	95_CI
all	339	8.75	5.68	338	0.000	5.722	11.784
2001	38	7.58	1.47	37	0.149	-2.845	17.996
2002	40	11.89	2.52	39	0.016	2.337	21.445
2003	38	10.01	2.08	37	0.044	0.275	19.755
2004	46	11.28	2.18	45	0.034	0.867	21.697
2005	48	8.45	2.34	47	0.024	1.178	15.719
2006	40	12.53	2.74	39	0.009	3.263	21.789
2007	53	8.66	2.89	52	0.006	2.648	14.675
2008	36	-1.70	-0.43	35	0.671	-9.782	6.374

Table 3.8: Type II regression analyses (R^2) of the relationship between YoY lobsters and cobble-boulder percent cover at six of the eight regions sampled from 2001 – 2008. Level of significance: *p<0.05, **p<0.01, ***p<0.001. Refer to Figure 3.7.

year	Mt. Desert Is.	Penobscot Bay	Mid-coast	Casco Bay	York	Rhode Island
2001			0.2	0.11	0.29	0.02
2002			0.1	0.13	0.02	0.06
2003			0	0.05	**0.84	0.16
2004			0.02	0.09	0.31	*0.67
2005	0.01	0.07	0	0.25	*0.69	0.3
2006	0.02	0.05	0.05	*0.73	0.13	**0.83
2007	0.28	0.26	0.17	0.02	0	0.46
2008	0.61	0.04	0	0.04	0	0.47

Table 3.9: **Type II regression analyses (R^2) of the relationship between Juv lobsters and cobble-boulder percent cover at six of the eight regions sampled from 2001 – 2008. Level of significance: *p<0.05,**p<0.01,***p<0.001. Refer to Figure 3.8.**

year	Mt. Desert Is.	Penobscot Bay	Mid-coast	Casco Bay	York	Rhode Island
2001			***0.58	0.24	*0.76	0.12
2002			0	0.41	*0.69	0.34
2003			0.08	0	0.32	0.16
2004			0	0.02	0.17	0.33
2005	0	***0.63	0.09	0.2	0.16	0.07
2006	0.03	0.05	***0.55	*0.78	0.09	**0.9
2007	0.28	0.18	0.22	**0.94	0	0.34
2008	0.32	0	0.05	0.61	0.14	*0.6

Table 3.10: **ANCOVA to determine the effect of categorical variables (Year, Region, Site) and covariates (Cobble cover, Juv density) on the dependent variable YoY density.**

Factor	SS	df	MS	F	P
Year	6.45	7	0.92	12.11	<0.001
Region	3.92	4	0.98	1.94	0.25
Cobble	0.01	1	0.01	0.08	0.77
Juv	6.53	1	6.53	85.87	<0.001
Sites (regions)	12.15	24	0.51	6.66	<0.001
Error	144.57	1901	0.08		

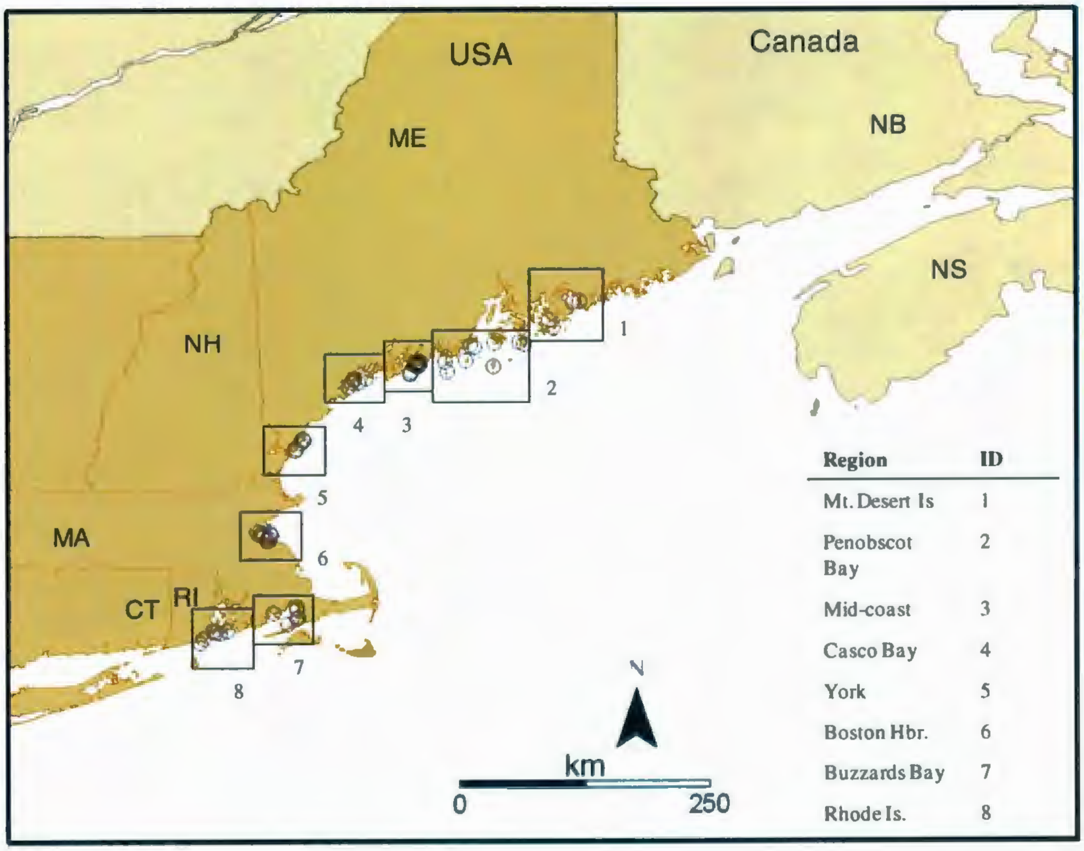
Table 3.11: **ANCOVA to determine the effect of categorical variables (Year, Region, Site) on the dependent variable Juv density.**

Factor	SS	df	MS	F	P
Year	6.45	7	0.92	6.35	<0.001
Region	68.07	4	17.02	11.69	<0.001
Cobble	1.74	1	1.74	11.96	0.001
Sites (regions)	34.95	24	1.46	10.02	<0.001
Error	276.42	1902	0.15		

Table 3.12: Logistic regression from long term experiment to determine the effect of the presence of juveniles on postlarval settlement. Refer to Figure 3.12.

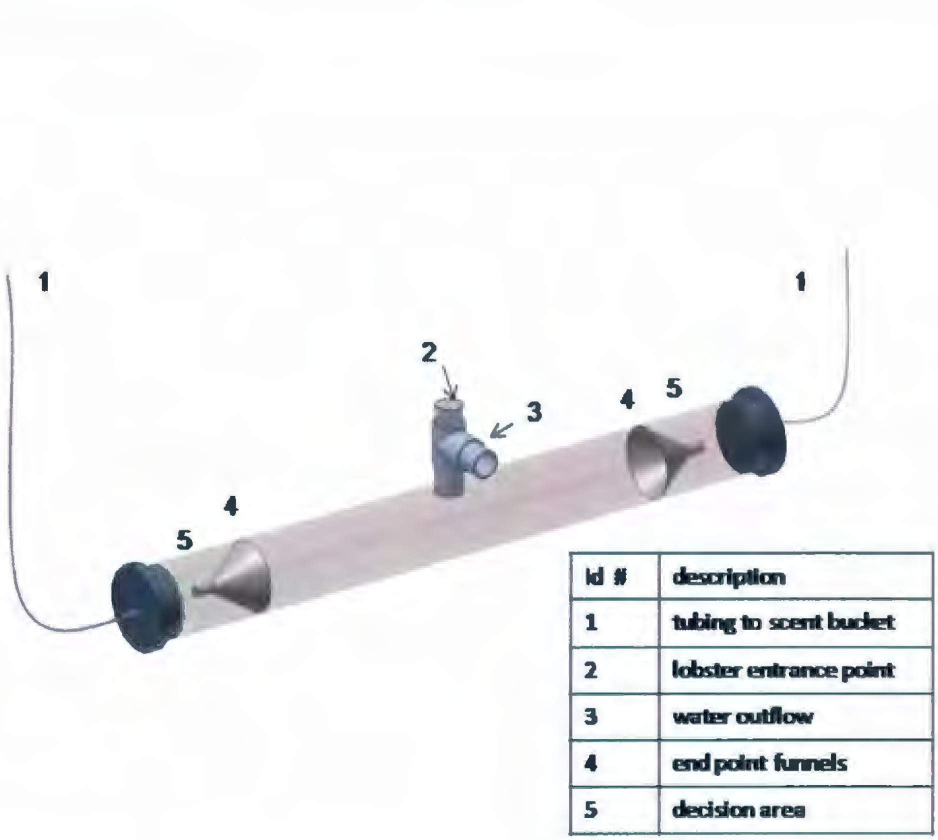
	estimate	SE	Z	P
intercept	-0.85	0.24	-3.58	<0.001
treatment	0.28	0.34	0.83	0.41
time	0.08	0.02	4.7	<0.001
interaction	-0.03	0.02	-1.33	0.18

Figures



Region	ID
Mt. Desert Is	1
Penobscot Bay	2
Mid-coast	3
Casco Bay	4
York	5
Boston Hbr.	6
Buzzards Bay	7
Rhode Is.	8

Figure 3.1: Regions used for annual recruitment survey index in New England for the years 2001 to 2008. Circles within regions represent sites sampled.



Id #	description
1	tubing to scent bucket
2	lobster entrance point
3	water outflow
4	end point funnels
5	decision area

Figure 3.2: Diagram of the horizontal choice chamber used for the stage V lobster behavioural experiments.

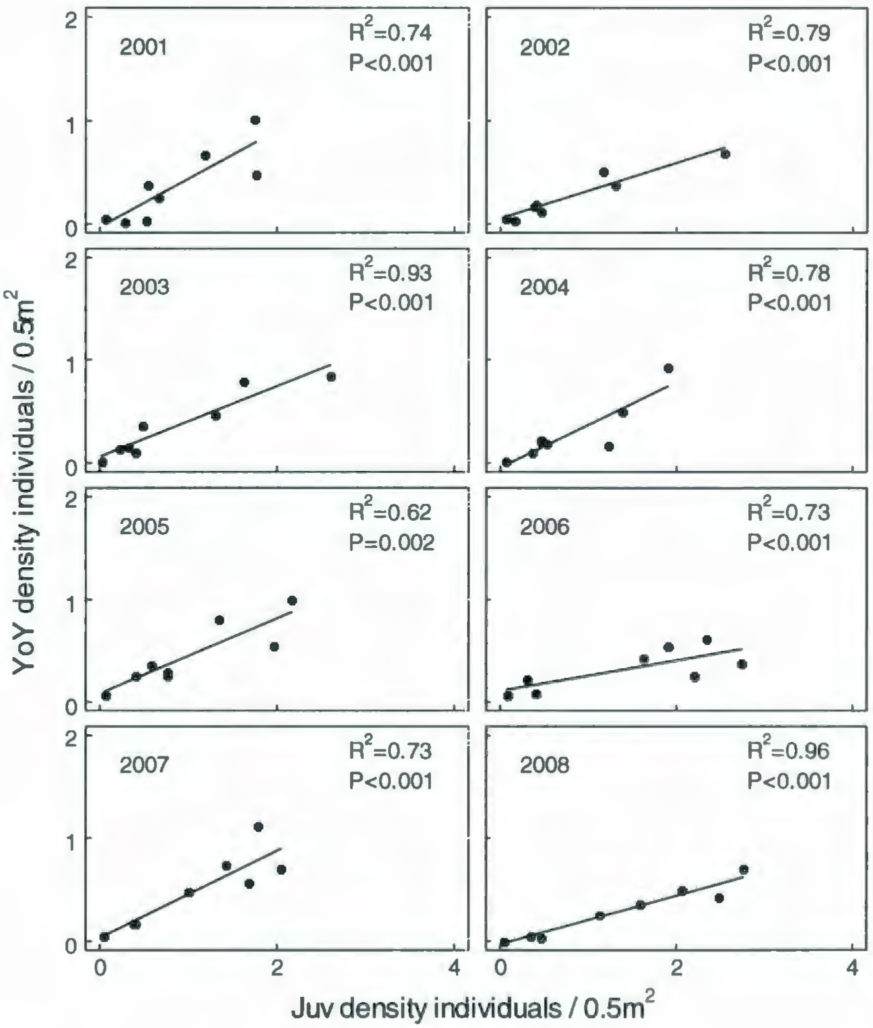


Figure 3.3: **Scatterplots and regression analyses for the relationship between the regional mean density of YoY and Juv lobsters at eight regions sampled from 2001-2008. Data were aggregated by region and square root transformed prior to analysis. Plotted data are untransformed.**

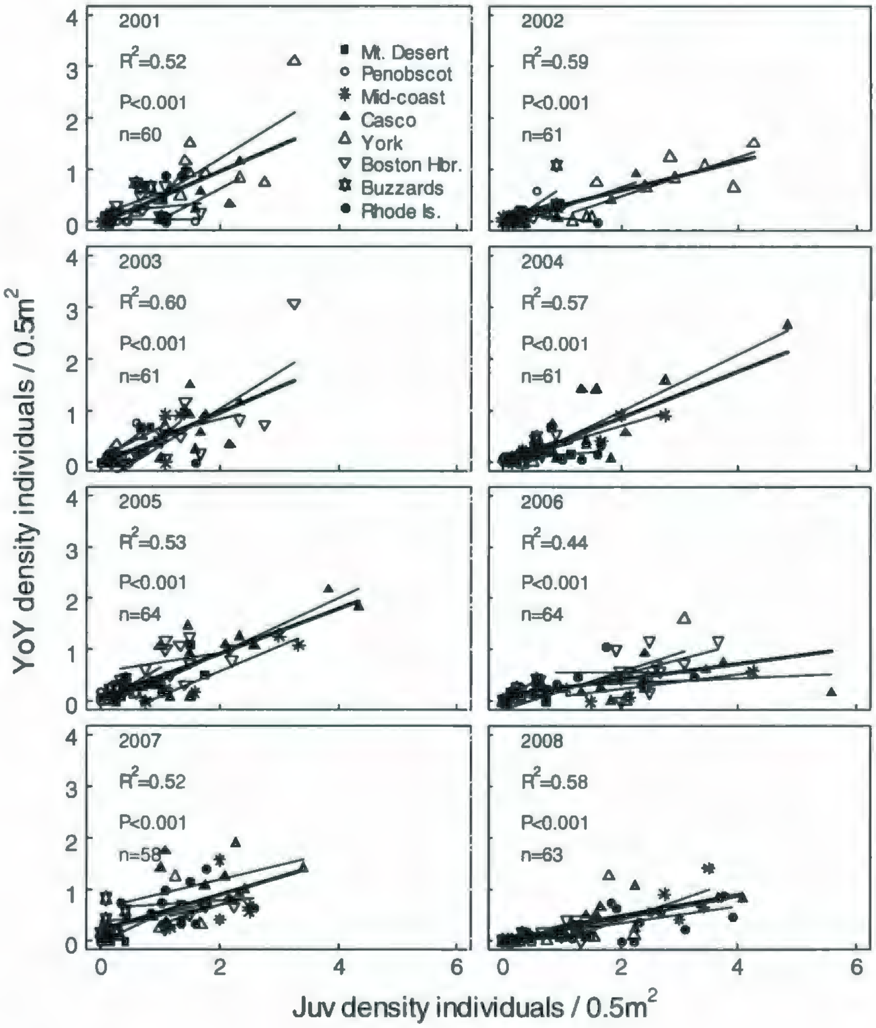


Figure 3.4: **Scatterplots and regression statistics for the relationship between YoY and Juv lobsters for the pooled 58 – 61 sites sampled among the eight regions from 2001 – 2008. Lighter weight regression lines plotted among sites within each region. (See Table 3.6 for regression statistics). Sites within regions denoted by different symbols (see legend). Data were aggregated by site and square root transformed prior to regression analysis. Plotted data are untransformed.**

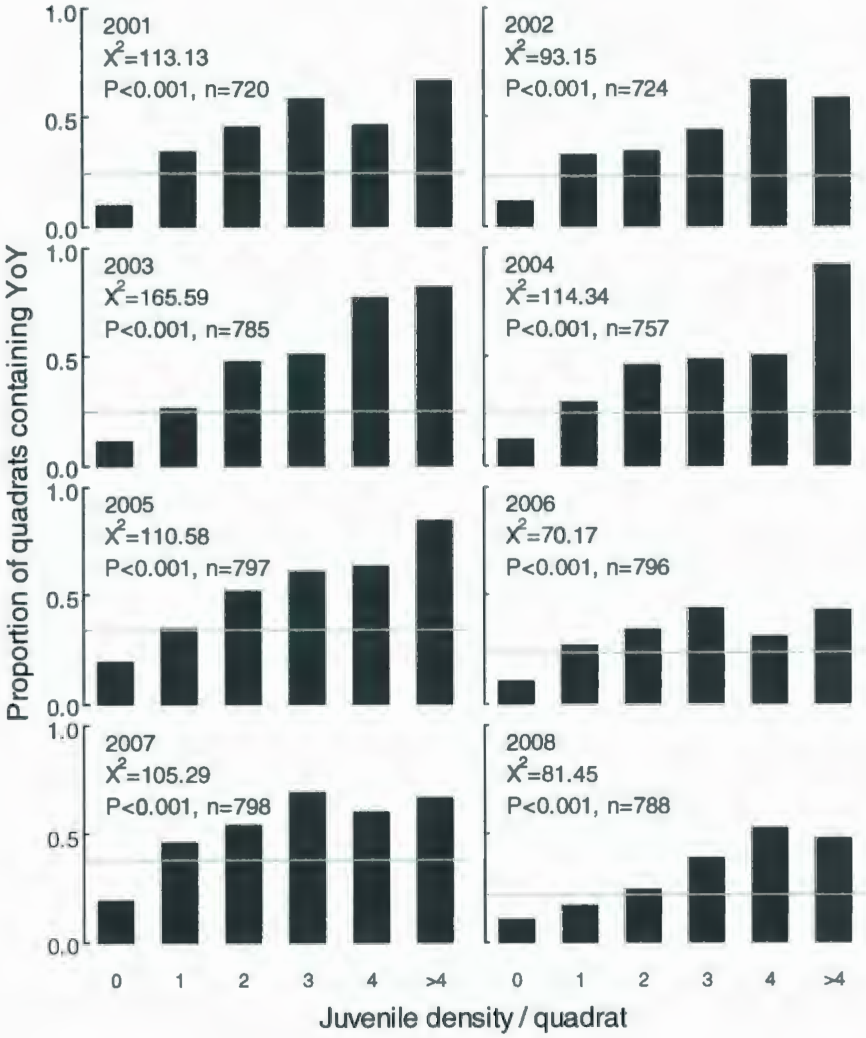


Figure 3.5: Observed frequency of quadrats containing YoY as a proportion of the number of quadrats in categories of increasing Juv lobster density. Grey horizontal bar denotes expected frequency if quadrats containing YoY were randomly distributed among the Juv density categories. N=number of quadrats sampled. (See Table 3.3 for number of quadrats for each size class of juvenile lobster).

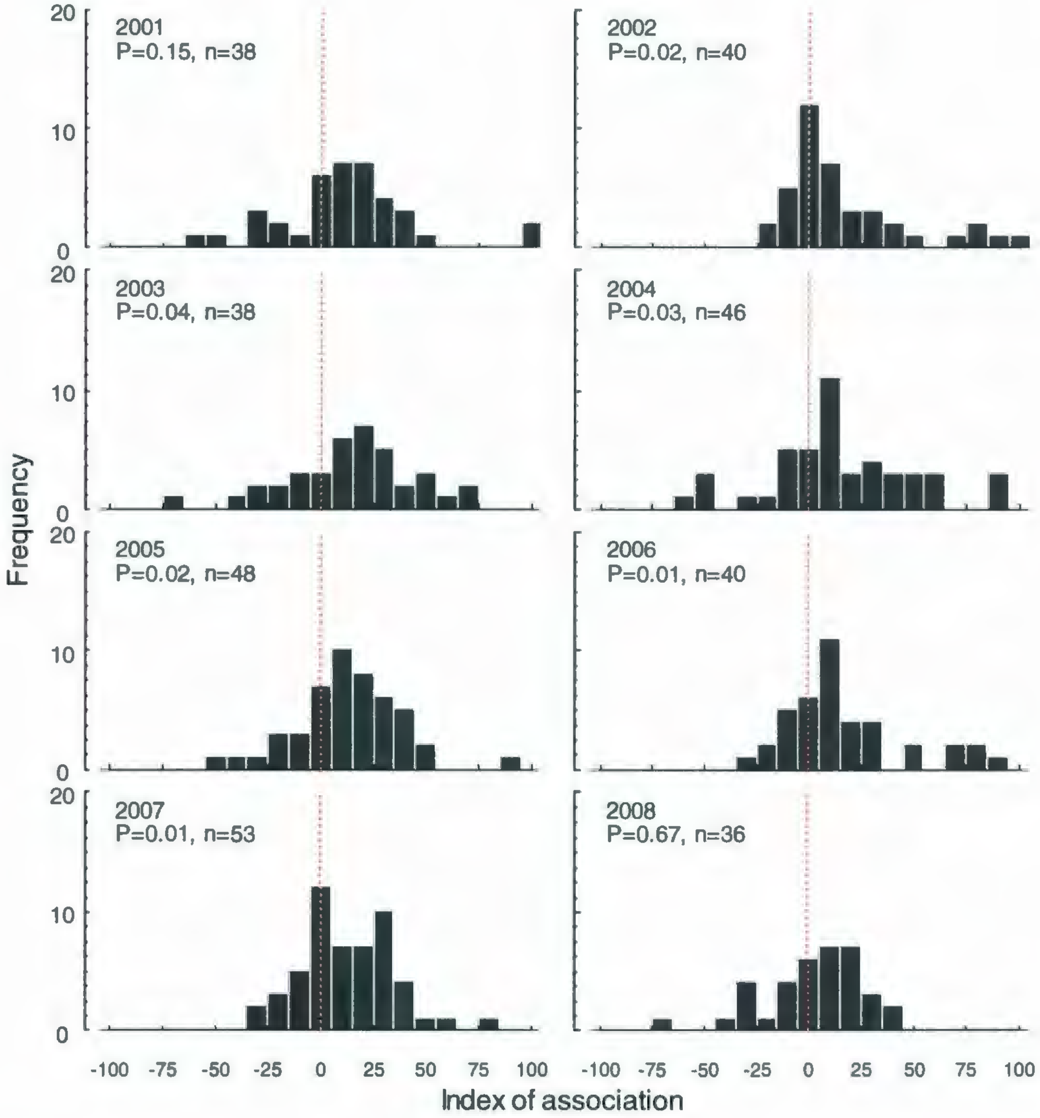


Figure 3.6: Index of association describing the level of association between YoY and older juvenile American lobsters. Horizontal red line denotes hypothesized mean. (See Table 3.7 for statistical summaries).

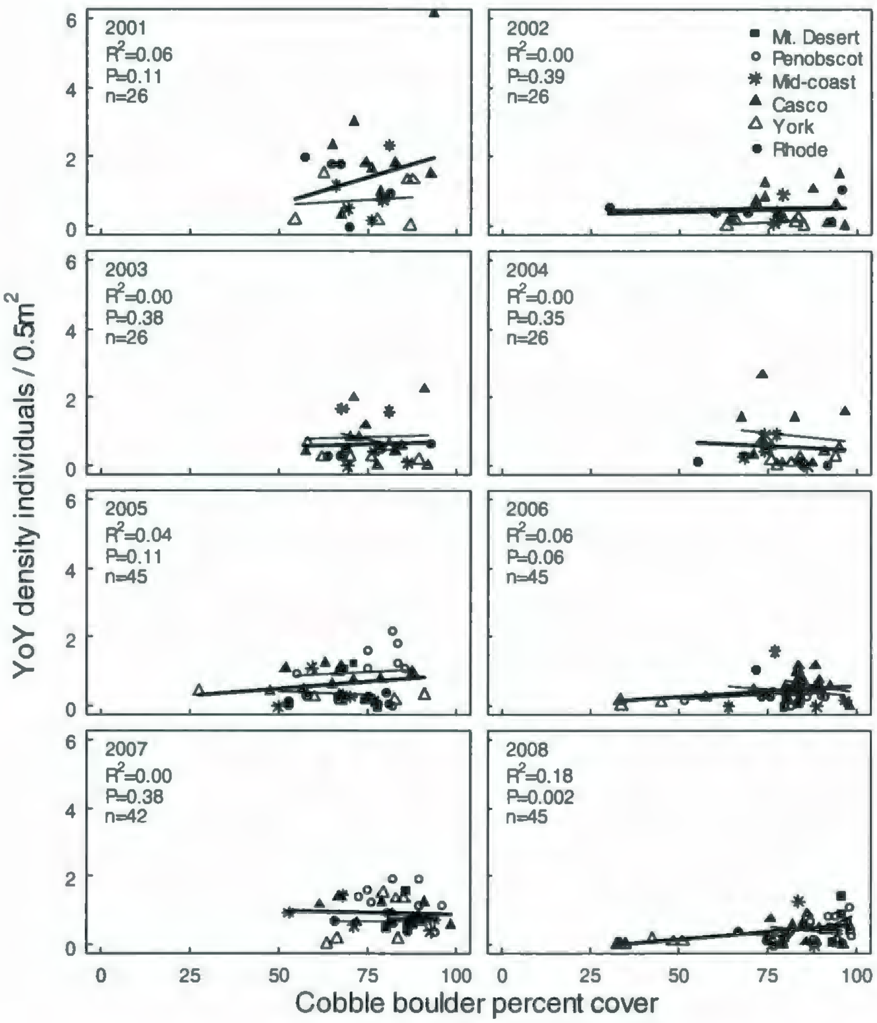


Figure 3.7: Scatterplot and regression analysis for the relationship between YoY lobster density and cobble-boulder percent cover. Cobble cover data were available for 26 to 46 sites sampled among the four to seven regions from 2001 to 2008. Regression lines also plotted among sites within each region (See Table 3.8 for regression statistics). Sites within regions denoted by different symbols (see legend). Data were aggregated by site and are untransformed. Thick black line represents the among-region regression, while lighter black line represents regression among sites within each region.

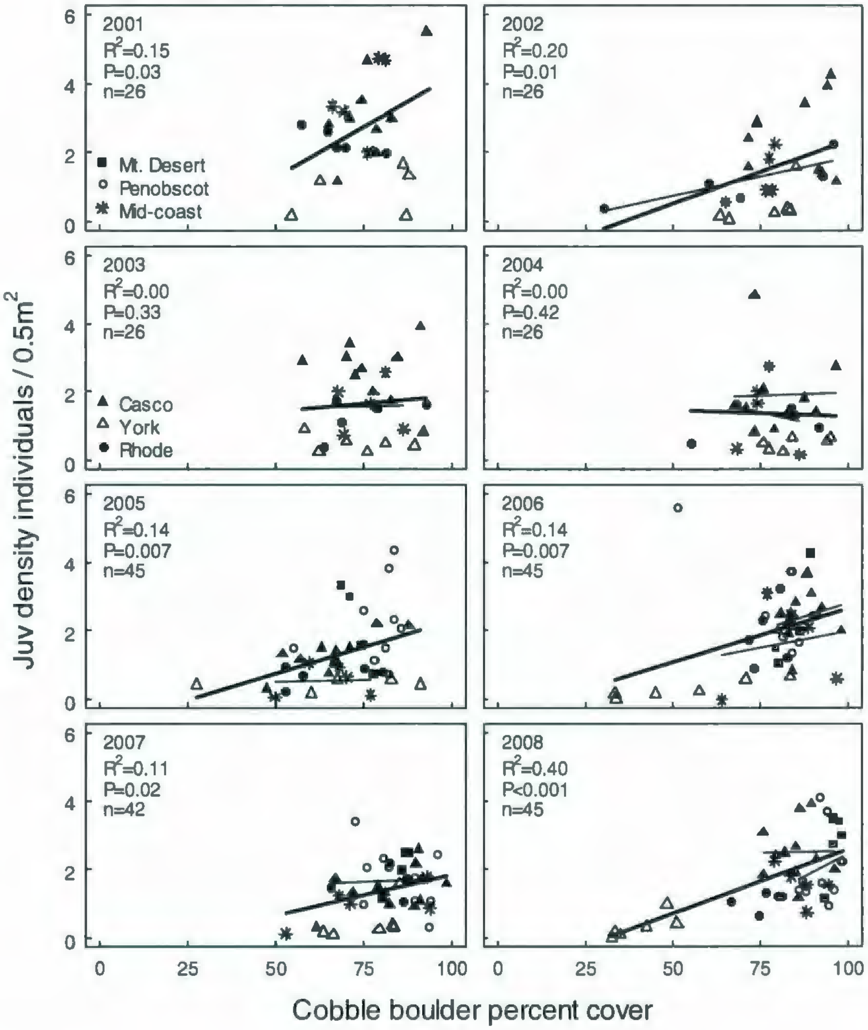


Figure 3.8: **Scatterplot and regression analysis for the relationship between juvenile lobster density and cobble-boulder percent cover. Cobble cover data were available for 26 to 46 sites sampled among the four to seven regions from 2001 to 2008. Regression lines also plotted among sites within each region (See Table 3.9 for regression statistics). Sites within regions denoted by different symbols (see legend). Data were aggregated by site and are untransformed. Thick black line represents the among-region regression, while lighter black line represents regression among sites within each region.**

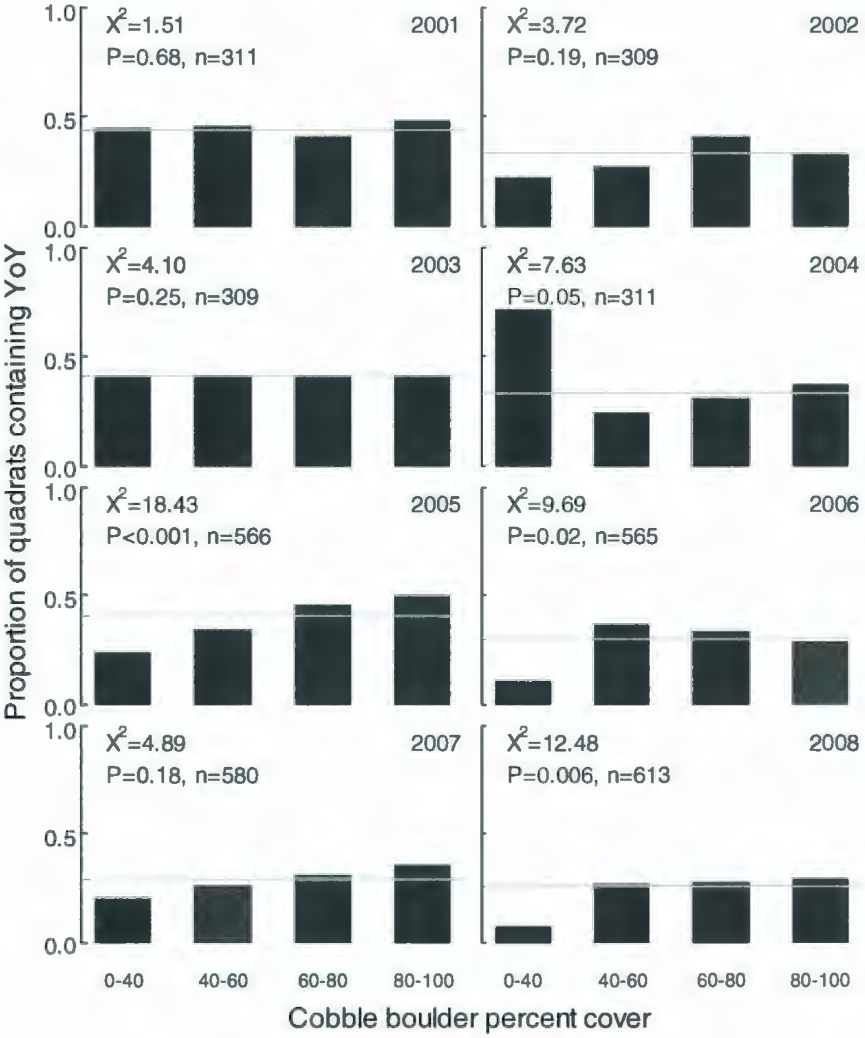


Figure 3.9: **Observed frequency of quadrats containing YoY as a proportion of the number of quadrats in categories of increasing cobble boulder percent cover. Grey horizontal bar denotes expected frequency if quadrats containing YoY were randomly distributed among the cobble boulder percent cover categories. N=number of quadrats sampled. (See Table 3.4 for number of quadrats for each cobble boulder percent cover).**

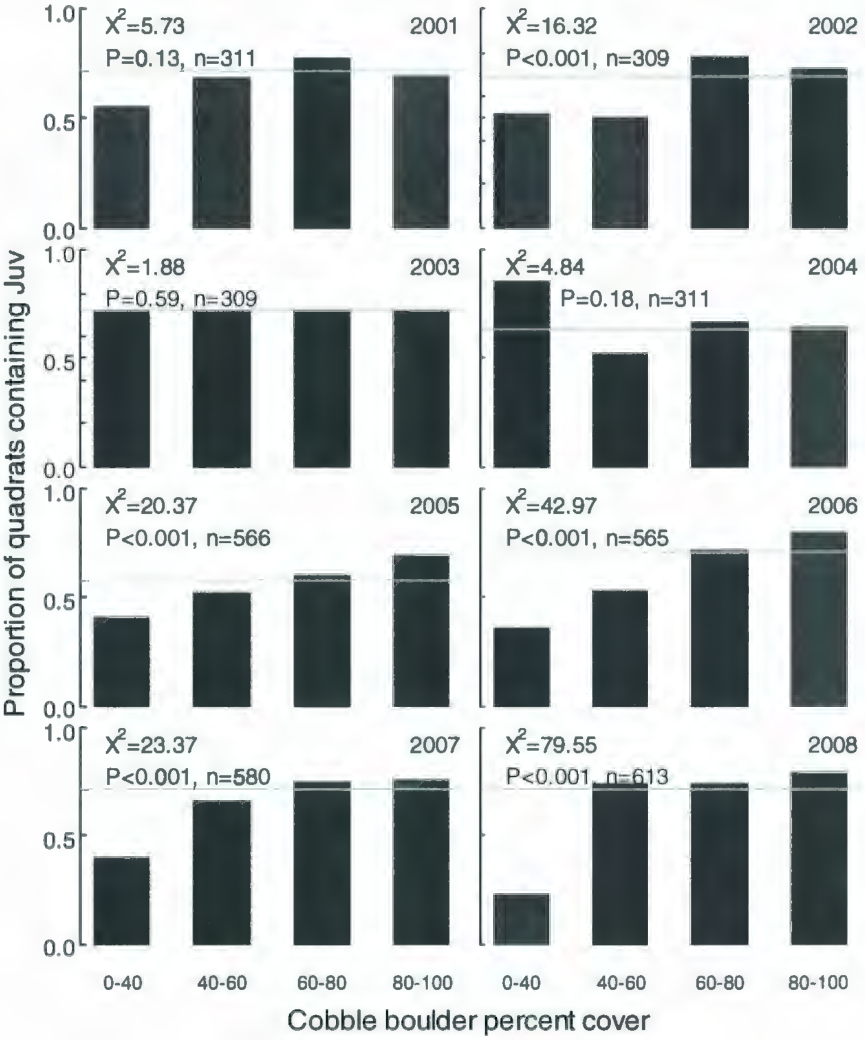


Figure 3.10: Observed frequency of quadrats containing Juv as a proportion of the number of quadrats in categories of increasing cobble boulder percent cover. Grey horizontal bar denotes expected frequency if quadrats containing YoY were randomly distributed among the cobble-boulder percent cover categories. N=number of quadrats sampled. (See Table 3.4 for number of quadrats for each cobble boulder percent cover).

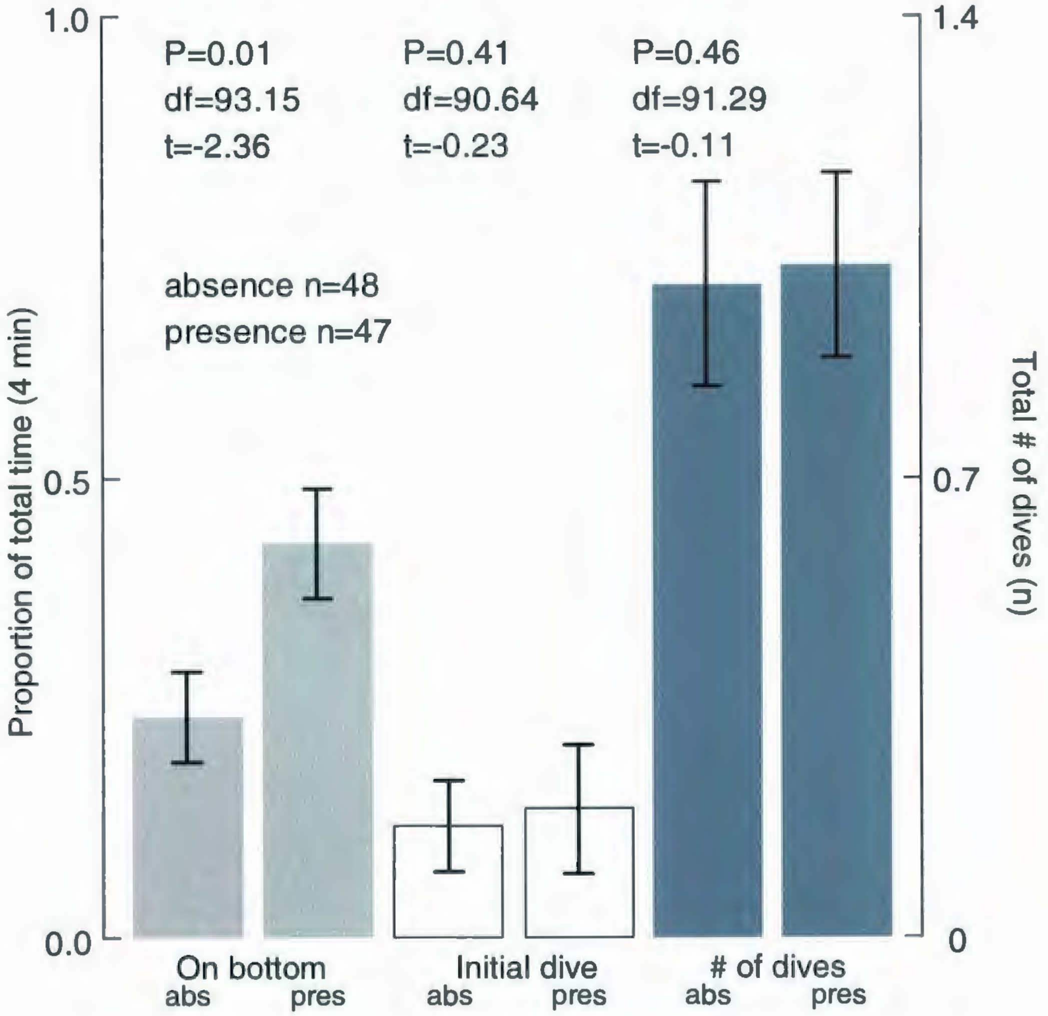


Figure 3.11: Response of YoY in short-term experiments to the juvenile (pres) and control (abs) treatments, as determined by the mean (± 1SE) proportion of time spent on the bottom of the aquarium, proportion of time until the initial dive (refer to left hand scale), and total number of dives (refers to right hand scale).

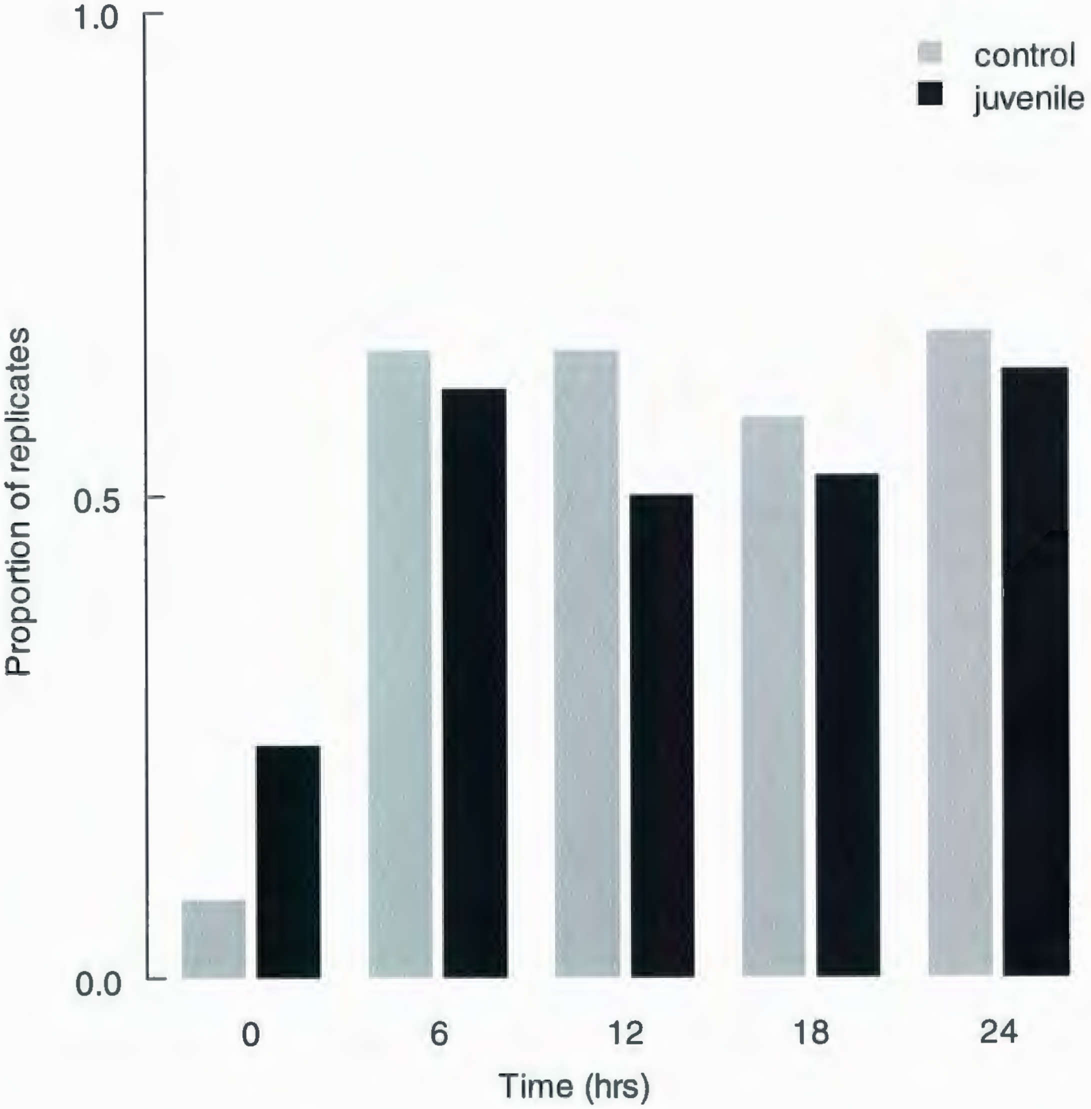


Figure 3.12: **Response of YoY in long-term experiments to the juvenile and control treatments as determined by determine the proportion of postlarvae that settled in each time increment over a 2-min observation period. See Table 3.12 for statistical analysis.**

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CHAPTER 4 : INTEGRATING LOCAL ENVIRONMENTAL KNOWLEDGE (LEK) INTO LOBSTER RECRUITMENT STUDIES IN BONNE BAY, NEWFOUNDLAND.

Abstract

The decline in groundfish quotas has created increasing dependence on American lobster, *Homarus americanus* in Newfoundland's coastal fisheries. Fishers in three communities in Bonne Bay are particularly dependent on lobster for their livelihood. This study aimed to integrate scientific and fish harvesters' local environmental knowledge (LEK) to identify potential lobster hatching and nursery habitats within Bonne Bay, and more specifically to identify hotspots of larval production where protection of adult lobsters might be particularly important. As in many other regions, the majority of lobsters harvested in Bonne Bay are at or close to the Minimum Size Limit (MSL). Fishers provided valuable input on potential 'source' habitats for larval lobster based on their knowledge of 'hot spots' for berried female lobsters. This information was supplemented with trap survey data and fecundity measurements that largely confirmed their belief that females in Bonne Bay's East Arm hatched large numbers of larvae. However, larval sampling (Chapter 2) suggests that substantial numbers of berried females may also occur in the Outer Bay where a large amount of lobster harvesting occurs. Efforts to obtain LEK on the location of juvenile lobster nurseries were largely unsuccessful because recently-settled young-of-year (YoY) lobsters are so small that most

fishers were unaware of their location and distribution. Nonetheless, previous studies have established that YoY lobsters prefer structurally complex habitats such as cobble, and it may be possible in the future to use LEK to support research on juvenile lobsters by focusing on their knowledge of bottom habitat as a proxy for juvenile lobster locations.

Introduction

American lobster (*Homarus americanus*) has been fished commercially on the eastern seaboard of North America since the late 1800s, and currently represents one of the most important fisheries in Atlantic Canada and the United States. Recent declines in other fisheries have increased dependence on this species in many coastal communities. Lobster exploitation rates in many areas are in excess of 90%, and populations are now dominated by new, mostly immature recruits, close to the Minimum Size Limit (MSL) (FRCC 2007). The status of this resource and its economic importance must be considered in relation to the collapse of Atlantic cod, which had devastating economic, ecological, and social repercussions in Newfoundland (Hutchings and Myers 1994; Hutchings 2000)

The Canadian fishery is divided into 47 Lobster Fishery Areas (LFA) and is largely inshore (Fig. 4.1, Appendix 4.1). Management is based on control of effort by limiting the number of licenses, types of gear, and length of season. Biological protection measures include a MLS (Minimum Legal Size), protection of berried females, and lath spacing on traps to permit escape of sub-legal sized lobsters. These are the minimum and required management strategies. Management strategies are determined separately for each LFA whose small size provides opportunity for fisher involvement in decision making.

Local Environmental Knowledge (LEK) is the knowledge acquired by resource users and/or their families through their day-to-day activities (Smith and Berkes 1993;

Alcock et al. 2003). "Local knowledge of coastal marine systems is based on long-term empirical observation, is practical and behaviour-oriented, structured, and is a dynamic system capable of incorporating the awareness of ecological perturbations" (Ruddle 2000). Fishers accumulate a wealth of information about their fishery, their environment, and fishing during their careers, through personal experience, conversations, and other social interactions (Murray 2006). There is increasing interest in collaboration with local fishers to bring that knowledge to the science, management, and policy of fisheries resources (Neis et al. 1999a; Murray 2006; Comeau and Smith 2009). Knowledge obtained from fishers differs from scientific knowledge in its method, terminology, and scope (Freire and Garcia-Allut 1999). Personal interviews with fishers can provide extensive information on resources (Neis et al. 1999a) that can benefit scientific investigations (Davis et al. 2004). Because fishers work on the water, collaborating with them also offers an opportunity to sample lobster while actively engaging them in the research process. Despite significant benefits to other stakeholders (de Freitas and Tagliani 2009), the use of LEK has been limited in fisheries scientific studies (Neis et al. 1999b).

Bonne Bay, a fjord on the west coast of Newfoundland, represents an ideal opportunity to pair fisher and scientific knowledge through researchers at the Bonne Bay Marine Station and an active lobster fishery (LFA 14A). Fishers in three communities (Rocky Harbour, Norris Point, Woody Point, Fig. 4.2) are actively involved in a lobster fishery that extends 9 weeks from early May to early July of each year. During this period the MLS is 82.5 mm and there is also a maximum legal size of 133 mm. Between the three communities there are approximately 27 lobster fishers, and 300 traps are permitted per license.

The objective of this study was to collaborate with local fishers to incorporate their knowledge of American lobster into scientific sampling of different life history stages. A second objective was to work with fishers at sea to obtain berried females for fecundity estimates and larval rearing (Chapter 2) and to collect at-sea sampling data about the lobster population. A third objective was to analyse at-sea lobster data for Bonne Bay collected between 2005 and 2007 contained in a database provided by the Fish, Food, and Allied Workers (FFAW) and Fisheries and Oceans Canada. Finally, I identify research interests for lobster-related topics of lobster fishers in western Newfoundland, which may provide direction for future research.

Materials and Methods

I evaluated the spatial distribution of adult lobsters by accompanying fishers on their boats during the commercial fishing season from May 4 to July 4, 2007. Lobster were measured, enumerated, and sexed. I observed female condition (berried/non-berried) and, for those bearing eggs, the stage of embryo development (Appendix 4.2). Embryo colour develops from black (stage I), green (stage II), brown-orange (stage III), to orange-eyed (stage IV) and colour is thus broadly indicative of embryonic developmental stage. GPS positions were recorded for each string of pots, as were number of pots and lobsters per string.

I divided Bonne Bay into Gulf, Outer Bay, Inner Bay, and East Arm for regional analysis (Fig. 4.2), noting that sampling was not possible in the South Arm because interested fishers could not be found. Lobster abundances were standardized by calculating the Catch Per Unit Effort (CPUE) for the season. Specifically, I divided the total number of lobsters measured in each length increment and category (gender, reproductive status) by the total number of traps sampled. An index of abundance was assessed by examining the size frequency distribution of lobsters, mean CPUE by region, temporal changes in CPUE through the season, and average size of lobsters.

Prior to analysis, raw CPUE data were log transformed to normalize the data and stabilize the variance. A three-way ANOVA was used to test for spatial differences in CPUE with Region (4 levels: Gulf, Outer Bay, Inner Bay, East Arm), Size Group (2 levels: legal, sublegal) and Reproductive Category (3 levels: male, female, berried) as main effects. Within this model, I tested for interactions between Region x Reproductive Category and Region x Size Group. This is a mixed effects model because it includes both fixed and random factors. Region is treated as a random effect because the regions are a subset of the possible regions I could have considered. Size group is considered fixed because it is constrained by the sublegal and legal size range of lobster. Reproductive status is a fixed effect because it includes all possible categories for lobster gender.

At-sea DFO / FFAW hiistorical data

At-sea sampling data for Bonne Bay were provided by the Fish, Food and Allied Workers (FFAW) Union and the Department of Fisheries and Oceans Canada (DFO). Each year between May and July, at-sea observers accompanied fishers to determine the size frequency distribution of the population. Observers recorded gender and female condition, but not embryonic development.

Prior to analysis, raw CPUE data were log transformed to normalize the data and stabilize the variance. I used a four-way ANOVA to test for spatial differences in CPUE for Region (2 levels: Rocky Harbour, Norris Point), Size Group (2 levels: legal, sublegal), Reproductive Category (3 levels: male, female, berried) and Year (3 levels: 2005, 2006, 2007) as main effects and mean size as the dependent variable. Within this model, I also tested the interactions Region x Reproductive Category and Region x Size Group. Unfortunately, data cannot be aggregated into fishing regions because counts are identified by the port where lobsters were landed and by an anonymous fisher ID number. Sampling in Rocky Harbour spanned 14 days between May 5 and June 14, 2005, 11 days between May 8 and June 22 in 2006, and 14 days between May 7 and June 30, 2007. Norris Point was sampled over 7 days between May 16 and June 18, 2005, over 6 sampling days between May 10 and June 19, 2006, and over 7 sampling days from May 11 to June 21, 2007.

Fecundity

I defined fecundity as the number of embryos on the pleopods at the time of capture. A total of 45 berried lobsters (15 in 2006, 30 in 2007) were held alive for no longer than three days, at which time they were hand stripped of eggs. Care was taken not to harm the lobsters, which were regularly submerged in clean seawater during stripping to reduce physiological stress. Carapace Length (CL) was measured from the posterior edge of the eye socket to the posterior edge of the carapace at the mid-line to the nearest millimetre. From the stripped egg mass, I counted all eggs in 2006. In 2007, I collected three subsamples of 2000 eggs per female and placed them each in tin foil containers separate from the remainder of the egg mass. Excess water was removed with a pipette prior to recording wet weight. Eggs were then oven dried for 24 hours prior to reweighing. I then calculated the total numbers of embryos for each female lobster sampled based on the average dry weight of subsamples. Regression analysis for each year determined the relationship between carapace length and number of eggs. I also compared my fecundity measurements with those generated by previous studies in Newfoundland.

Catch rate

Annual commercial live weight catch rates (kg) were acquired from DFO for LFA 14A and for the entire province to determine temporal fluctuations in lobster catches over the past eleven years.

Fisher interviews

I developed a standardized fisher interview schedule that was approved by the Interdisciplinary Committee on Ethics in Human Research (ICEHR) (Appendix 4.3). A list of potential fishers was created for each fishing community by contacting one fisher and asking "other than yourself, who would you say knows the most about the local fishing grounds?" In total eight fishers agreed to be interviewed, two from Woody Point, three from Rocky Harbour and three from Norris Point.

I conducted interviews in January of 2008 and November of 2009 by presenting a photocopy of the nautical chart of the fishing area and asking fishers to identify areas where they fished and areas they believe are utilized by different life history stages of American lobster.

Results

Size frequency distributions of males, females, and berried females sampled in commercial traps in 2007 all peaked near the MLS, and no lobsters exceeded the legal catch size window (Fig. 4.3). This peak was also reflected in mean lobster size for male and female lobsters (Table 4.1). A large proportion of undersized females were egg-bearing, although few females with or without eggs exceeded 100 mm CL (Fig. 4.3). Abundances of male lobster tapered off above 110 mm CL (Fig. 4.3). When the data are segregated into regions the trend is similar in that lobster size frequency distributions peak at the MLS, however, regional differences in CPUE become evident because East Arm has a relatively high proportion of MLS lobsters relative to other regions (Fig. 4.4).

Average catch rates of sublegal lobsters regardless of reproductive category (male, female, berried female) were highest in the Inner Bay and Gulf (Fig. 4.5). However, the variability for the Inner Bay was larger than for the Gulf. Regional differences in the average catch rates of legal-sized lobsters were less apparent (Fig. 4.5). The three-way ANOVA results detected significant differences in CPUE for Region but non significance for Size Group and Reproductive Category. The interaction Region x Reproductive Category was not significant, however the significant Region x Size Group term indicated that the number of individuals of different size groupings caught varied significantly with region (Table 4.2).

At-sea DFO / FFAW historical data

The FFAW lobster at-sea sampling data showed trends in size frequencies of lobsters in Rocky Harbour and Norris Point that were similar to my at-sea sampling data. Peak frequencies were at or close to the MLS of 82.5 mm in 2005, 2006, and 2007 (Fig.

4.8). Average size of lobsters between regions and years remained stable and, as with my at-sea sampling data, was close to the MLS (Table 4.3).

Similarly, very few lobsters exceeded the catchable size window. In 2005, the largest range of females (non-berried and berried) over the MLS were reported at Norris Point (Fig. 4.6). CPUE of all lobsters showed significant differences for Region but not for Size Group, Reproductive Category, or Year. The interaction terms Region x Reproductive Category and Region x Size Group were significant (Table 4.4, Fig. 4.9), indicating that the numbers of individuals of different size groupings and reproductive categories differed significantly among region. Although average CPUE for sublegal male and female lobsters was also higher in Rocky Harbour than Norris Point, these regional differences were less apparent for sublegal female lobsters (Fig. 4.9).

In 2005, Rocky Harbour CPUE of male and female lobsters were higher than elsewhere (Fig. 4.7), however, the CPUE of berried females were similar between Rocky Harbour and Norris Point (Fig. 4.7).

Temporal patterns in the overall live weight CPUE (kg) appear relatively stable (Fig. 4.10). Lobster catches generally increased from 1999 to 2009 in Newfoundland and in LFA 14A. Over a ten-year period, live weight in LFA 14A increased by ~100,000 kg (Fig. 4.10). Consistently LFA 14A contributed ~ 11 % of the total Newfoundland catch (Table 4.7).

Fecundity

There was a strong and significant relationship between carapace length and the total number of brooded embryos in 2006 ($F_{1,13} = 9.091$, $p = 0.01$) and 2007 ($F_{1,25} = 125.5$, $p < 0.001$) (Fig. 4.7). Comparative fecundity from other Newfoundland regions in earlier years confirm a strong relationship between CL and the number of brooded eggs, although the size frequency covered in those studies was broader than the Bonne Bay data (Fig. 4.7).

Fisher interviews

The lobster fishery

Only about 30 % of lobster fishers in Bonne Bay were interviewed, which is a relatively small proportion of fishermen in the Bay. Fishing experience of this group ranged from 20 – 30 years, and all of them had fished with their fathers as children, and always fished the same areas. While there are no specific regulations governing the areas fished in Bonne Bay, non-verbal agreements between fishers in different communities have divided the bay into territories (Fig. 4.2). Fishers in Rocky Harbour typically fish the areas around Rocky Harbour extending from Salmon Point to Green Point (Fig. 4.2). Woody Point fishers work South Arm and the north and south side of the Outer Bay. Norris Point fishers typically work along the northern side of the Outer Bay and East Arm. All three fisher areas converge on the north side of the entrance to the Bay, and there is overlap in the Outer Bay between harvesters from Woody Point and Norris Point (Fig. 4.2). The fishers in Woody Point share the south side of the Outer Bay with fishers from nearby Trout River, who also work the exposed coast northwest of Bonne Bay.

Lobster fishers in Bonne Bay are permitted to deploy 300 traps, which has been the legal limit since 1998, before which it was 450 traps. Fishers reported that they had seen no differences in catch rate since this change in the trap limit. Fishers deployed approximately the same number of pots per line within a community, but it may differ among communities. For example, in Norris Point and Rocky Harbour, five and ten traps are deployed per line respectively, while fishers in Woody Point set either fives or singles. When asked why the different communities fish different numbers of traps, they responded that number depended on bottom type, such as rocky or sandy bottom, and the angle of the slope. Fishers were asked to define a good seasonal catch and their responses varied from 5000 to 6500 lbs (2273 to 2955 kg). This catch corresponds to an approximate value of $20,000 to $26,000 at $4.00 per lb ($ 1.80 per kg). When asked if they thought that the average catch had changed in recent years, most agreed that the fishery had been stable for the past four or five years, despite price fluctuations from $4.00 to $6.00 lb ($1.80 to $2.70 per kg).

The current MLS of 82.5 mm was introduced in 1998, before which it was 81 mm. When asked how this change had affected them, fishers generally did not feel strongly about it, although catch rates stabilized the year following the size increase. The maximum size limit of 133 mm introduced in 1998 also produced no strong reaction, although several fishers felt that the limit should be standardized across the province because only the west coast has an enforced maximum legal size.

Although the lobster fishery is open for approximately two month, many fishers indicated that they do not fish the entire season. Fishers involved in other fisheries remove their traps about two weeks before the end of the lobster season in order to prepare for other fisheries such as turbot. A couple of fishers noted that there were too few harvestable lobsters remaining in the water to justify the effort, whereas others reduced their number of traps by half (~150) and checked their traps every second day rather than daily.

Fishers set their traps in 10 to 40 ft (3-to 12m) of water, in some cases extending out to a maximum of 60 ft (18 m). All fishermen said they move their traps in shallower as the season progresses and water warms. All fishermen noted that there are consistently fewer lobsters when winds blow from the northeast.

Berried female lobsters

When asked if they had observed different colours of the lobster spawn (embryos) all fishers had noticed that the embryos were different colours, although only two of them were aware this was because of different stages of embryo development. Although fishers observed changing colours during spawning, they did not identify differences in their migrations or locations. However, fishers were able to clearly identify areas were berried females aggregated. Fisher's clearly identified preferred locations of berried females (Fig. 4.2) at the outer headlands to the bay entrance on the north and south sides, as well as sites in the Inner Bay. Several fishers stated that larger females migrate into Bonne Bay because they were captured near the Gulf in the beginning of the season and well within the Bay later in the season. Harvesters also felt that densities of berried females had increased over the past four or five years, and the size of egg-bearing females had decreased. Fishers noted that females start to lose their spawn (hatch) around the second week of June when they are 'not as full' and have completed their hatching when they become 'slubby', meaning hatched out.

V-notch

A V-notch is a conservation measure to identify a female lobster as a known breeder. When breeding females are captured, they are notched on the inner right uropod, adjacent to the middle uropod of the telson, before they are released unharmed. Fishers are legally required to return notched and breeding females to the ocean. When asked if fishers V-notch lobsters there were very few fishermen interviewed that do V-notch. When asked why not, many of them felt that not enough other people in the community were V-notching so, "why should I put one back when the next guy is going to keep one?" In one instance a fisherman felt that V-notching would actually be detrimental to the lobsters survival. When asked if others in the community are V-notching the females, all fishermen said that there were very few. They don't find very many V- notched lobsters in the waters, however when they do find one, they will generally re-notch a lobster that appears to be outgrowing its initial V-notch.

Juvenile and small lobsters

In general, the same areas that fishers identified as hotspots for berried females were also sites with higher densities of undersized pre-recruit lobsters (Fig. 4.2). The smallest lobster that fishers reported ranged from approximately 30 – 55 mm carapace length; individuals in this size range were frequently caught. Fishers also felt that the proportion of lobsters under the MLS had increased in recent years. They estimated that they returned between 30 – 60 % of lobsters in the traps to the sea because they were berried females or were below the MLS size. Some fishers recalled seeing what they thought were very small lobsters in and around the beaches as small children.

Areas fishers identified as having complex habitat (rocks, etc.) were generally the same areas where they identified greater abundances of berried females and sub-legal lobsters. Fishers felt that lobsters prefer structurally complex habitat with abundant rock and kelp cover.

Predators

Fishers felt that the primary predators on small lobsters were wolffish, cunner, and sculpin. Wolffish were seen as predators of all size classes of lobsters because a wide size range of dead lobsters were found in traps that contained wolffish.

Discussion

The goal of this study was to work with fishers to determine likely hotspots within Bonne Bay for adult lobster, and more specifically for hotspots of larval production that might be priority locations where protection of females may be particularly important. This information complements field sampling for larval and juvenile stages described in Chapter 2. The initial approach of sampling with fishers as they hauled their traps showed that the average size of lobsters across sexes and regions is very similar. Due to the selectivity of the traps and lobster behaviour the smallest and largest lobsters were absent from the catch. The harvest is dominated by lobsters at or just above the size of fishery recruitment, and the sharp drop in the proportion of lobsters above legal size in the size distribution of the catch indicates that the majority of the fishery is largely dependent on recent recruits, and typical of other areas where very few individuals survive one moult group above the harvestable size (FRCC 2007; DF0 2009). There were no statistically significant spatial differences in size of lobsters based on gender and maturity (male, female, berried female). Although the proportion of berried females in the East Arm is greater than in other regions, the East Arm is fished later in the season when the proportion of berried females is likely greater as harvestable lobsters are removed. Patterns of berried females in Grand Manan, in the Bay of Fundy, suggest they aggregate in areas conducive to embryonic development and larval dispersal (Campbell 1990). However, there is no indication of similar behaviour in the Îles-de-la-Madeleine population (Gendron and Savard 2008).

A second, related approach depended on observer data collected by FFAW during 2005-2007. Direct comparisons are difficult because of differences in how the data were aggregated. Norris Point and Rocky Harbour landings show comparable densities of berried females, although fewer males and non-berried females were landed in Rocky Harbour. Given the established fishing territories noted earlier, these data suggest comparable densities of berried females in East Arm to other areas fished by Rocky Harbour fishers.

At-sea sampling data shows that CPUE of legal sized lobsters remained stable over the course of the fishing season in all areas except the Inner Bay and East Arm, where it increased. The CPUE of sublegal lobsters increased in all areas. This is intuitive because as harvestable lobsters are removed from the fishery a greater proportion of the catch will be comprised of the remaining undersized sublegal and berried lobsters. Many fishers stop fishing weeks before the season terminates because the legal lobster catch is so low.

Larval supply links not only to the abundance of berried females but also to the number and quality of eggs produced, which in turn may be influenced by water temperature. Water temperature is a major determinant of the size at which lobsters reach sexual maturity, and thus if temperatures in Bonne Bay are warmer than in previous years lobsters may become sexually mature at a smaller size. Fecundity, a measure of the number of eggs produced, increases with female size because larger lobsters have a greater surface area on which to carry eggs (Ennis 1981). Additionally, this scaling relationship is common in almost all invertebrates and is thought to be largely due to the available volume of ovary scaling to the second or third power of female body length (pers. comm. Don Deibel). Larger females produce heavier eggs in both *H. americanus* (Attard and Hudon 1987) and *H. gammarus* (Latrouite et al. 1984), which is thought to correlate with energy content, and thus healthier eggs. However, if larger females produce larger eggs, total mass of eggs might not be indicative of the number of eggs produced. Future work should investigate the differences in egg size variability within individual lobsters, and within and between size classes.

Fecundity in 2006 was considerably lower than in 2007, likely because the hatching season was already well underway. Thus, some females may have already released part of their brood. Hatching can span three to seven days (personal observation). Alternatively, there may have been higher egg mortality during that year. Mechanisms underlying natural egg loss over the course of the 11-month embryonic duration are unknown, although losses have been attributed to disease, nemertean infestations, predation, and commercial handling (Aiken and Waddy 1980; Campbell and Brattey 1986). Losses as high as 35% have been reported in other lobster species (Abello and Sarda 1982). If losses resulting from natural causes are high, fecundity is better estimated close to hatching time, however, if egg mortality varies regionally or seasonally a better estimate of fecundity maybe taken shortly after egg extrusion.

Fishers identified South Arm and the Outer Bay (OB3) as hotspots for berried females. While there were no significant spatial differences in densities of berried females, distinct patterns of stage I larval distributions were evident in neuston tows from 2006 through 2008 (Chapter 2). Concentrations of stage I larvae were consistently higher in the Outer Bay site, however, South Arm concentrations were more variable. They also identified waters adjacent to OS2 as another hotspot for berried females, and although habitat in this region was suitable and pristine, there were few larvae and YoY settlers. Given the rapid loss of stage I larvae from Bonne Bay (Chapter 2), either from advection or mortality, berried female distributions may not predict stage I larval distributions. Regular larval 'hot spots' occurred near the entrance of the Bay, however CPUE of berried females was no higher than elsewhere. If East Arm females contribute equally to the Bonne Bay larval pool, it is not reflected in the distribution of stage I lobsters.

Studies have used incidence of berried females in size frequency analyses to construct an index of functional maturity in both *H. americanus* (Ennis 1981; Aiken and Waddy 1986; Estrella and Cadrin 1995) and *H. gammarus* (Latrouite et al. 1984; Lizárraga-Cubedo et al. 2003). Size at maturity and the size-fecundity relationship is important in determining which size classes contribute most to egg production. Local fecundity estimates are necessary because the environment affects growth rates and size at sexual maturity (Campbell and Robinson 1983). A standardized protocol is needed to avoid sampling differences that affect regional comparisons, such as when during embryonic development females are collected, sample size, and sampling methodology (Aiken and Waddy 1980; Ennis 1981; Estrella and Cadrin 1995).

Egg-per-recruit is a standard measure used to estimate the theoretical reproductive potential of a population by estimating the number of eggs a female will spawn over her expected life time. The goal of fisheries regulations in implementing a MLS is to allow at least 50 % of females to reproduce before they are harvested. In Newfoundland, 50% functional maturity is estimated to occur at 81 mm (Ennis 1985), which was the MLS until it was increased to 82.5 in 1998 (DF0 2009). Although the benefit of this increase has not directly been determined, it has been shown that increased MLS can increase egg production (Ennis 1985). Size at sexual maturity complements fecundity estimates to produce more accurate models of egg production for Bonne Bay and potentially for the entire LFA.

Recruitment in the Bonne Bay lobster fishery, as is true elsewhere, depends heavily on eggs produced by small, undersized females. In Bonne Bay, peak densities of berried and non-berried females are very close to the MLS. Indeed, egg production by undersized females could account for up to 80% of the total egg production in Newfoundland (Ennis 1985), with similar size frequency ratios shown in other fishing areas (DFO 2009). Larger females are known to be more fecund (Aiken and Waddy 1980; Ennis 1981; Estrella and Cadrin 1995) with larger eggs (Attard and Hudon 1987), potentially indicative of healthier larvae with higher survival probability. But under current fishing practice they make a relatively small contribution to larval production, although the impacts of this are not known. A successful protective measure of female lobsters was mobilized by fishers in Maine in the early 1960s, where a berried female was identified as a known breeder with a V-notch in the right side of her telson. This V-notch would remain through several moults to identify an individual lobster as a known breeder.

These lobsters are required by law to be returned to the sea. This serves as a conservation strategy to protect female lobsters in the catchable size window and is practiced by fishers across most of the lobster biogeographic range. A very small proportion if at all of fishers in Bonne Bay support and believe in V-notching, and in some cases a few fishers felt that V-notching would cause lobster mortality.

Studies elsewhere suggest that protection of large females can increase egg production (MacMillan et al. 2009). Although the maximum legal size limit has been in effect since 1998 on the west coast of Newfoundland, few lobsters escape the catch window. The higher proportion of legal-sized berried females in East Arm warrants further investigation. Continued sampling to determine size frequency distribution, proportion of berried females, and pleopod maturity will contribute to better understanding of the high production rates of stage I lobsters in this bay (Chapter 2).

Bonne Bay fishers stated that lobsters are becoming sexually mature, and thus egg-bearing, at a significantly smaller size than in the past. Studies of various fish species (see Kjesbu and Witthames 2007 for review) indicate that sustained fishing pressure on the larger sizes can selectively favour individuals that reproduce before they are harvested, with the net effect of lowering the average size-at-maturity (Harris and McGovern 1997; Kuparinen et al. 2009). While the effect of this pressure on lobster has not been extensively studied, Estrella and Cadrin (1995) found no differences in fecundity or size-at-maturity measurements in southern Massachusetts, when compared to a study conducted in the same region 100 years earlier. Continued sampling by the FFAW will assist in the establishment of a long-term data set to monitor the variations in size-at-maturity estimates.

The Canadian fishery assessment depends entirely on landings to infer stock abundance, although landings are biased by fishing effort (FRCC 2007). Aspects of lobster biology such as size, sex, moult condition, intra-specific interactions, and female condition can influence lobster catch rates in traps (Miller 1990), as can temperature and wind patterns (Smith and Tremblay 2003; Drinkwater et al. 2006). An additional factor influencing catch rates in lobster traps is trap saturation and differential catchability due to differences in trap construction. Trap data are also considered an unreliable method to determine abundance and distribution of berried females as their behaviour changes during certain times of embryonic development (Miller 1990). Despite these biases, trap survey data are the most efficient means to obtain large-scale comparisons, and provide an excellent opportunity to engage local fishers in stock assessments (Claytor and Allard 2003). Standardized trap sampling methodology could decrease potential biases, including increased sampling frequency by collaborating with fish harvesters (Comeau and Smith 2009).

Local fishers have stated that catch rates have remained stable in recent years. While catch rates for Bonne Bay are unavailable, landings for LFA 14 A have been stable over the last 4 years, following prominent fluctuations. Continued monitoring of CPUE in LFA 14 is recommended, noting that despite stable landings in recent years, the long-term trend is downward (FRCC 2007).

Established fishing territories creates an opportunity for local participation in governance that can enhance communication between resource users and managers (Wilson et al. 1994). Understanding the needs and knowledge of resource users is important in the field of human-environment interactions (Dietz et al. 2003). Climate change may impact stakeholders if temperature changes shift lobster distributions or reduce local recruitment and create conflicts among fishers, and must be considered for future governance (McIlgorm et al. 2010).

This study illustrates how LEK can guide scientific studies in small coastal communities where scientific data are few. Local fishers assisted in determining sampling locations for YoY surveys, and could have assisted in designing locations for plankton sampling. Although fishers had little knowledge of planktonic stages and recently-settled lobsters, they had extensive knowledge of the distributions of spawning females and bottom type, which may be hotspots for stage I and YoY lobsters respectively, not withstanding the displacement of larvae and settling postlarvae from their place of origin. Stage IV postlarval lobsters are well known to search for and select cobble-boulder habitat at the time of settlement (Cobb et al. 1989), and fishers are very familiar with this bottom type on their fishing grounds. Consistently, fishers reported their most successful catches near rocks and boulders, with kelp cover. Thus, continued efforts to map the Bonne Bay seafloor are recommended by combining fisher interviews and scientific field surveys (SCUBA and transects, habitat models sensu Galparsoro et al. 2009). Preliminary surveys showed adequate habitat for YoY lobsters was probably not limiting (Chapter 3). The small sample size of fishers interviewed limits the ability of this study to effectively support or refute the relevance of LEK to this study. However, fishers were all very knowledgeable of lobsters and interested in research being conducted in their areas. Future studies should consider incorporating the use of LEK at the earliest stages of research so that collaborations and relationship with fish harvesters can be established prior to the initiation of research.

The use of fisher knowledge to identify spawning habitat is not new. Cod fishers in Norway knew of many more spawning sites than did scientists (Maurstad 2002). Fishers might also offer knowledge of the migratory potential of female lobsters and the extent to which they aggregate. Fisher knowledge on the locations and distributions of undersized pre-recruit lobsters can be validated by comparison with at sea sampling data. Deployment of ventless traps would more accurately define the locations and distributions of undersized lobsters.

In addition to adding knowledge to this thesis, LEK also raised interesting hypotheses for future studies. In particular, future studies might be focused on environmental effects on catch rates, female migrations, size at sexual maturity, and aggregative spawning behaviours. Communicating directly with stakeholders can also increase the trust and collaboration between local fishers and science (Hart and Calhoun 2010), and match science more precisely with societal need (Gendron et al. 2000; Sarewitz and Pielke 2007; Rochet et al. 2008). As an example, local fishers stated that lobster catches are lower on a NE wind, and higher on a SW wind. Catches may be linked to upwelling and downwelling events and associated temperature fluctuations, since lobster movements and catchability are temperature dependent (Drinkwater et al. 2006, pers. comm. Brian Petrie). Voluntary logs of catches could provide an easily implemented opportunity to test these hypotheses, and create an opportunity for collaboration.

Fishers have a wealth of knowledge that can be drawn on to stimulate ideas to guide future studies, and engaging fishers in data collection provides an opportunity for knowledge exchange. When scientists work closely with fishers, the social aspects of the fishery become much more evident. Because many lobster fisheries are coastal, they interact with land users, and are vulnerable not only to fishing impacts but other factors, such as pollution and shoreline development. American lobster may be particularly vulnerable to temperature changes that are predicted by climate change models (Tlusty et al. 2008), and fishers may be an 'early warning system' for ocean change.

Tables

Table 4.1: Average size (mm) of lobster in the Bonne Bay region from 2007 at-sea sampling survey.

	Bonne Bay			Gulf			Outer Bay		
Size	□	♀	♀B	□	♀	♀B	□	♀	♀B
sublegal	55	78	78	78	78	78	78	78	79
Legal	88	88	88	88	89	91	90	89	85
All	55	82	81	80	81	81	83	82	81

	Inner Bay			East Arm		
Size	□	♀	♀B	□	♀	♀B
sublegal	76	77	78	75	75	75
Legal	89	88	85	89	88	90
All	81	81	79	81	79	79

Table 4.2: Three-way ANOVA results on differences in average CPUE of American lobsters in Bonne Bay between Region, Reproductive Category, and Size Group as determined by 2007 at-sea sampling data.

Factor	df	SS	MS	F	P
Region	3	0.0001	0.0001	6.49	0.01
Reproductive Category	2	0.0002	0.0002	2.03	0.50
Size Group	1	0.0029	0.0029	13.91	0.25
Region * Size Group	1	0.0002	0.0002	13.29	<0.001
Region * Reproductive Category	1	0.0001	0.0001	1.21	0.27
Error	1324	0.0205	0.0001		

Table 4.3: Average size (mm) of lobsters from FFAW 2005-2007 at sea sampling survey in different regions of Bonne Bay.

	Rocky Harbour 05			Rocky Harbour 06			Rocky Harbour 07		
Size	☐	♀	♀B	☐	♀	♀B	☐	♀	♀B
Sublegal	75	75	77	76	75	78	77	76	77
Legal	89	90	91	89	89	92	90	89	92
All	79	79	80	81	80	80	82	80	80

	Norris Point 05			Norris Point 06			Norris Point 07		
Size	☐	♀	♀B	☐	♀	♀B	☐	♀	♀B
Sublegal	78	77	79	77	77	78	77	77	78
Legal	91	89	94	88	89	87	89	89	87
All	83	80	83	80	79	80	82	81	80

Table 4.4: Four-way ANOVA results on differences in CPUE (individuals per trap) between Region, Year, Size Group, Reproductive Category as determined by FFAW at-sea sampling data.

Factor	df	SS	MS	F	P
Region	1	0.0006	0.0006	47.05	<0.001
Reproductive Category	2	0.0008	0.0008	4.00	0.50
Size Group	1	0.0050	0.0050	16.67	0.25
Year	2	0.0000	0.0000	0.33	0.56
Region * Size Group	1	0.0003	0.0003	28.85	<0.001
Region * Reproductive Category	1	0.0002	0.0002	15.68	<0.001
Error	1989	0.0270	0.0001		

Table 4.5: Proportion of Newfoundland lobster landings contributed by LFA 14A.

Year	Proportion
98	
99	
0	0.1
1	0.13
2	0.11
3	0.11
4	0.09
5	0.11
6	0.11
7	0.11
8	0.11
9	

Figures

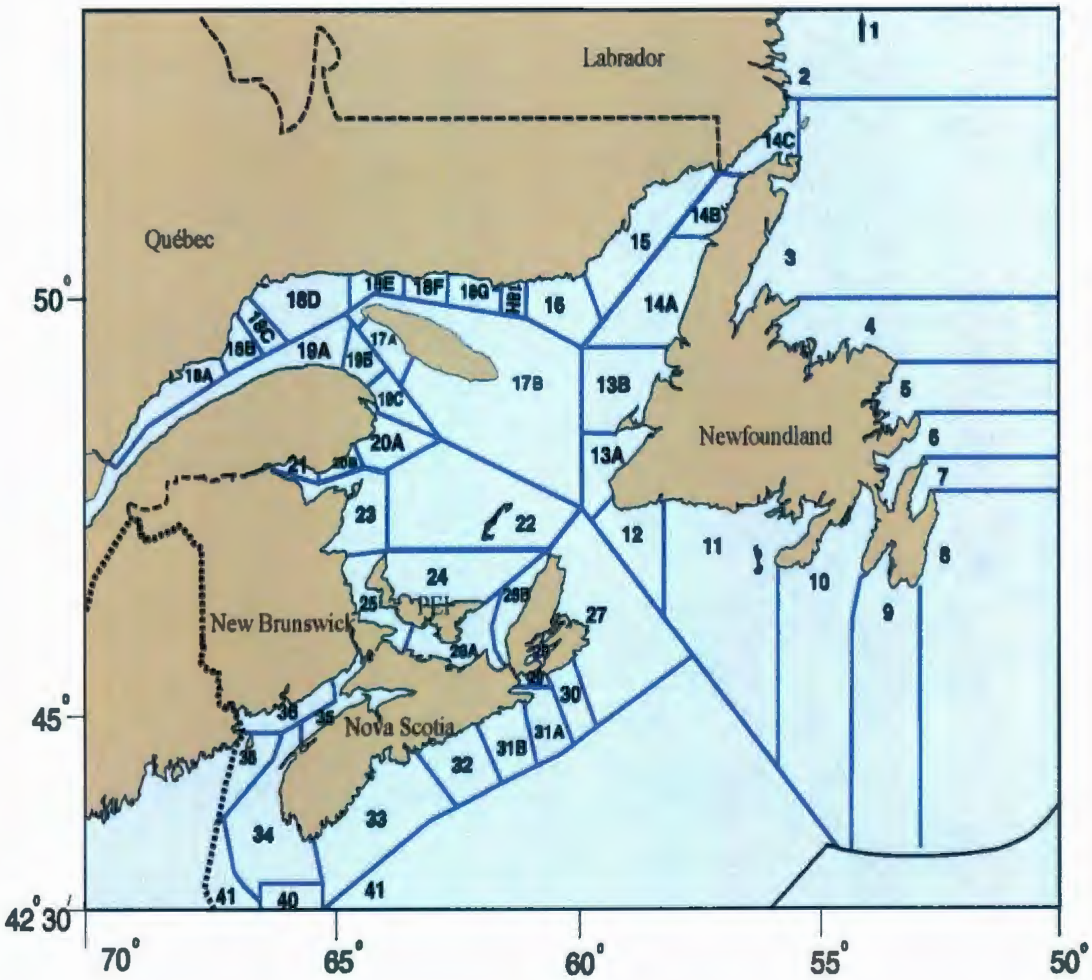


Figure 4.1: Lobster Fishing Areas (LFAs) in Canada.

http://www.gov.ns.ca/fish/marine/map/lobster_full.shtml (March 2010)

Figure 4.2: **Bathymetry and topography of Bonne Bay. White rectangles represent regions for lobster at-sea sampling. Yellow circles represent location of communities. Coloured lines represent fishing grounds of each community. Blue polygons represent areas idenentified by local fishers as hotspots of abundance for ovigerous females and juvenile lobsters. WP = Woody Point. NP = Norris Point, RH = Rocky Harbour, TR=Trout River.**

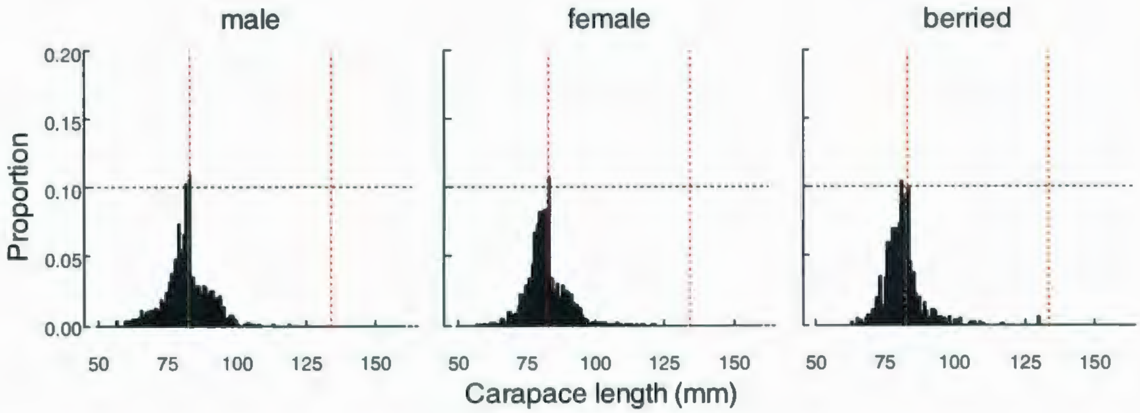


Figure 4.3: **Size frequency distribution of males, non-berried females and berried females in Bonne Bay in 2007 from at-sea sampling survey. Vertical red line denotes legal catch window. Horizontal dashed black line identifies same value (0.10) between panels for reference.**

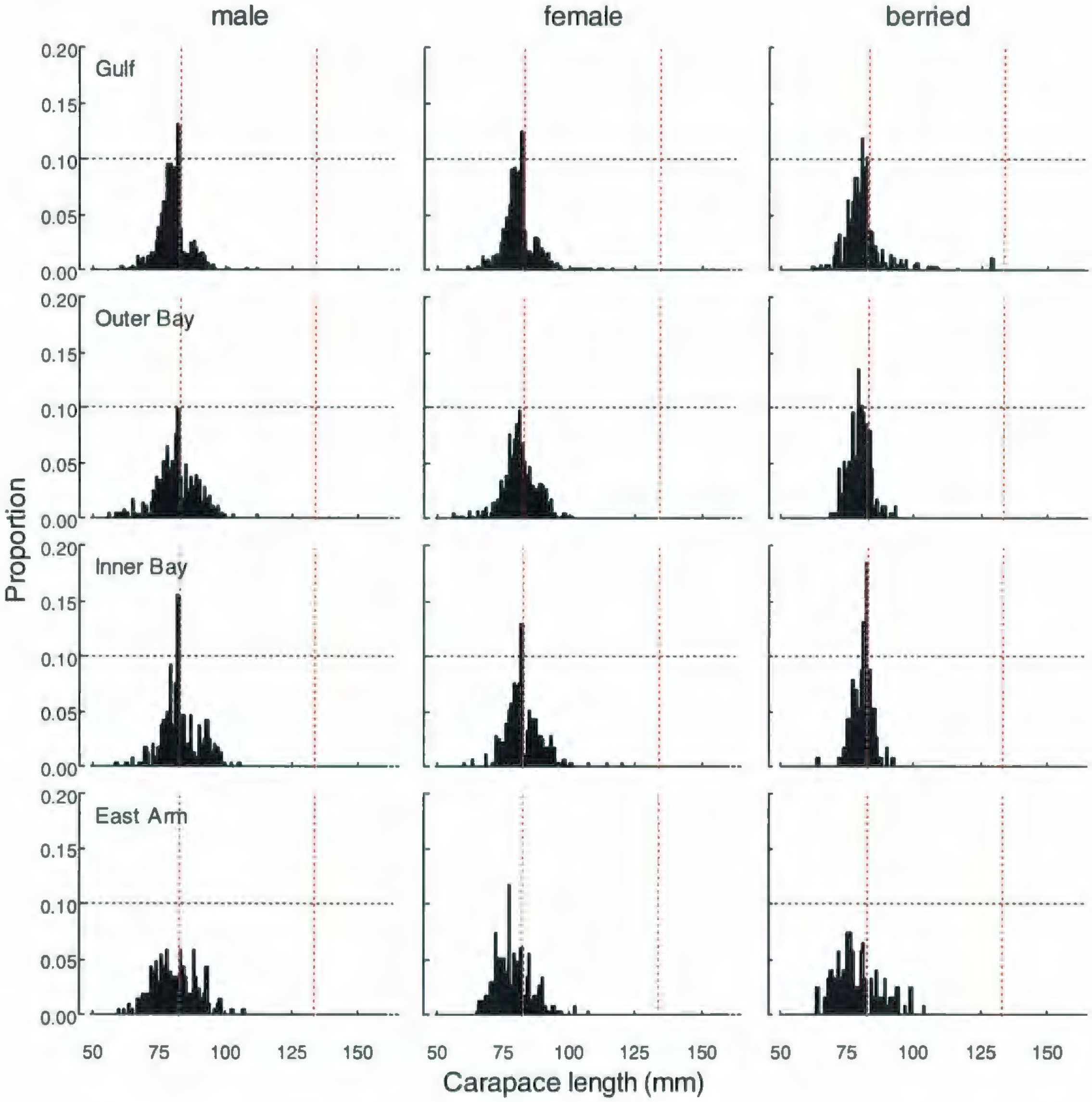


Figure 4.4: Size frequency distribution of different lobster categories (male, female, and berried) in different regions of Bonne Bay in 2007 at-sea sampling survey. Vertical red line denotes legal catch window. Horizontal dashed black line identifies same value (0.10) between panels for reference.

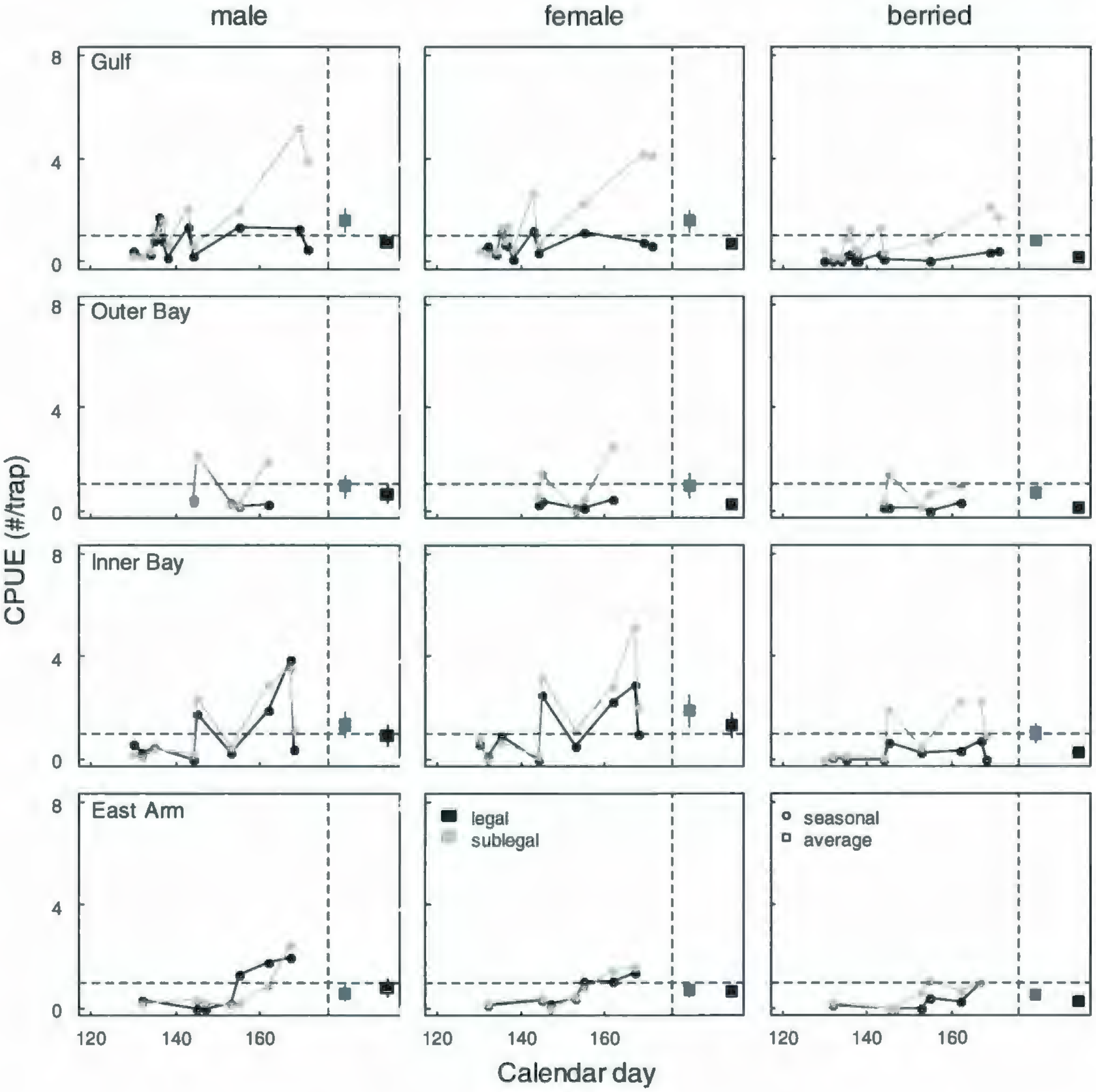


Figure 4.5: Seasonal and average CPUE of undersized (≤ 82.5 mm) and legal (>82.5 mm) lobster categories (male, female, and berried) in LFA 14A from 2007 at-sea sampling survey. Horizontal dashed black line identifies same value (1.0) between panels for reference. Vertical black line divides daily CPUE from average CPUE. Vertical lines denote error bars (SE).

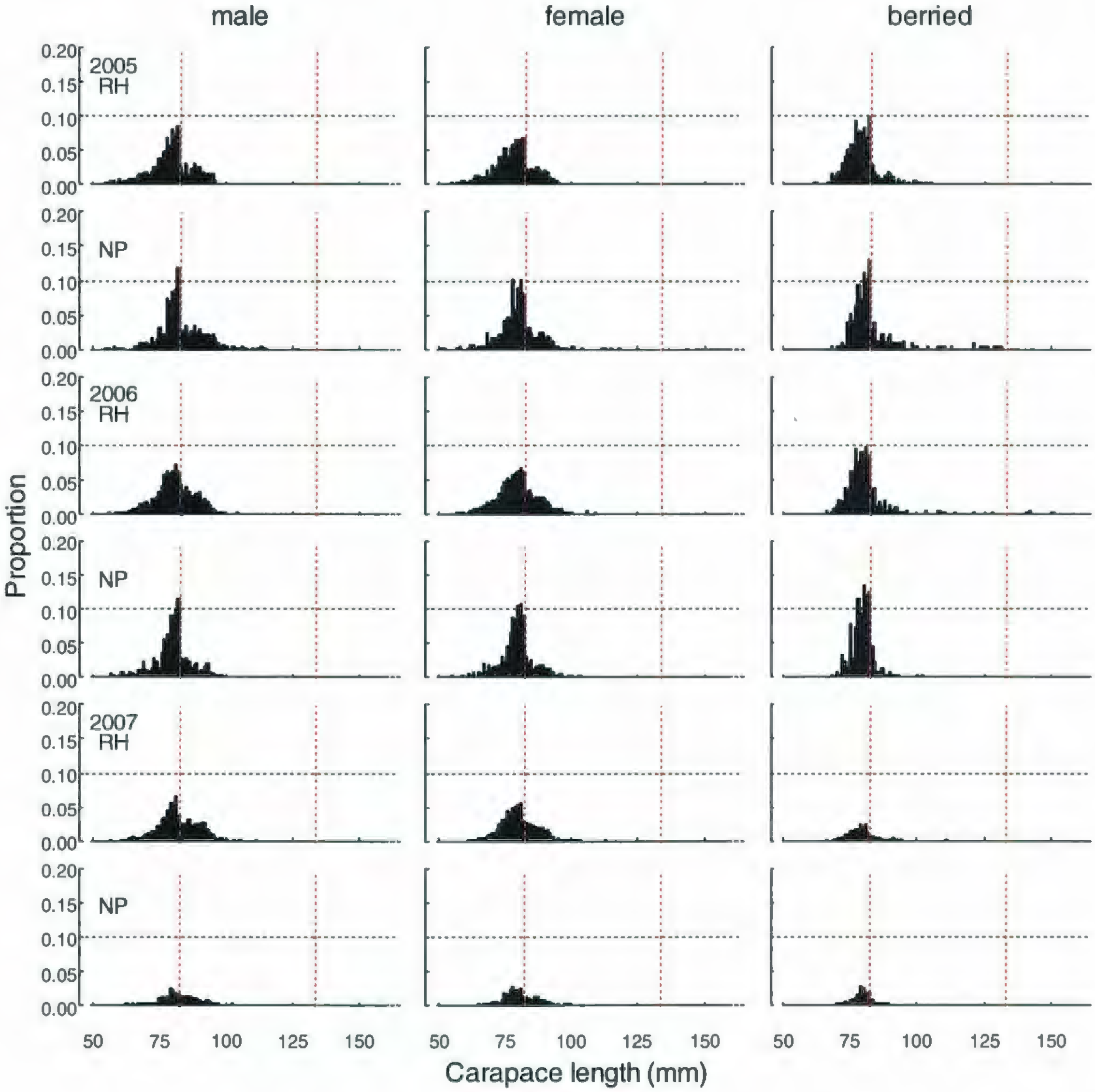


Figure 4.6: **Size frequency distribution of different lobster categories (male, female, and berried) in LFA 14A from FFAW/DFO data in 2005, 2006, and 2007 from at-sea sampling survey. RH = Rocky Harbour, NP = Norris Point. Vertical red line denotes legal catch window. Horizontal dashed black line identifies same value (0.10) between panels for reference.**

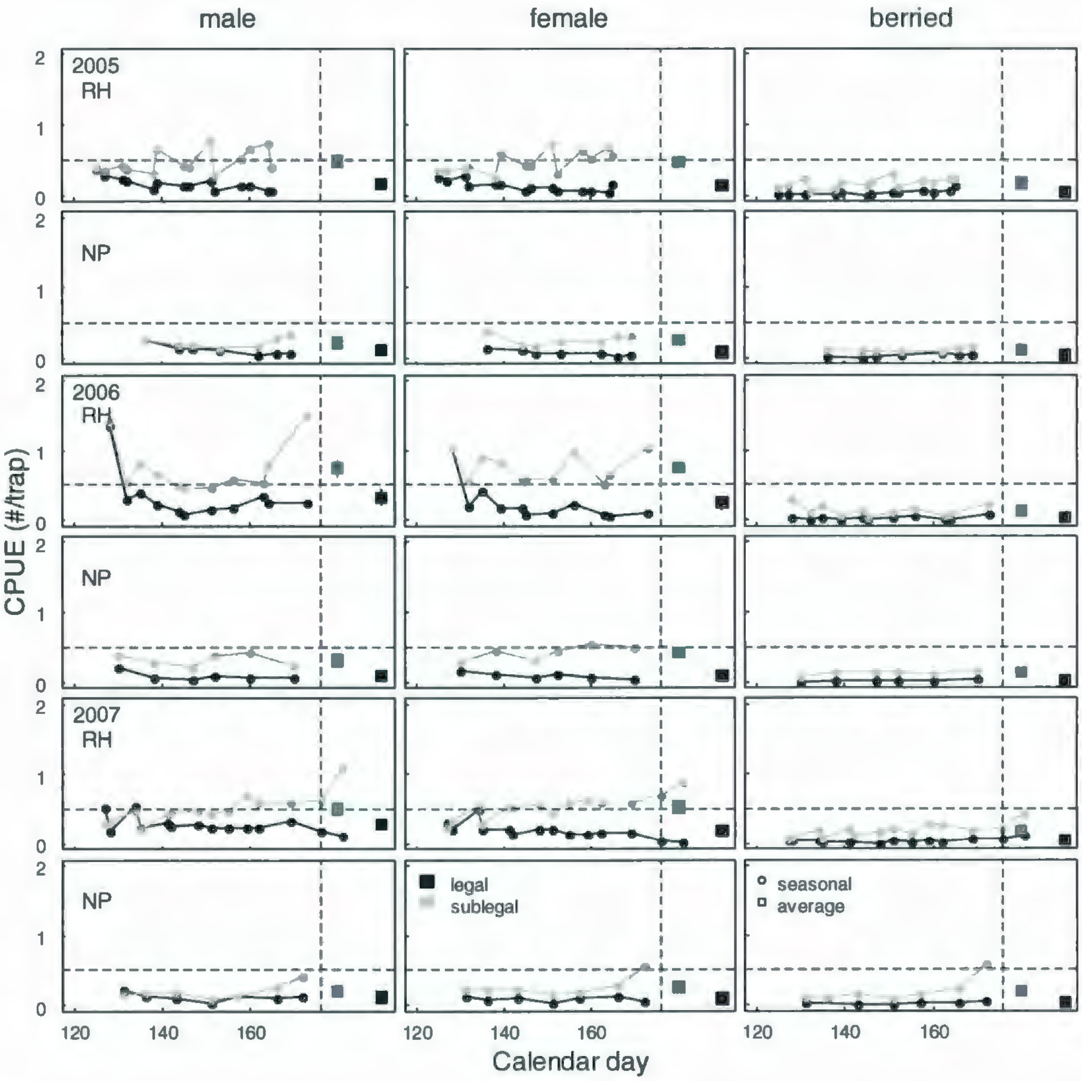


Figure 4.7: Seasonal and average CPUE of undersized ≤ 82.5 mm) and legal (>82.5 mm) lobster categories (male, female, and berried) in LFA 14A from FFAW/DFO data in 2005, 2006, and 2007 from at-sea sampling survey. RH = Rocky Harbour, NP = Norris Point. Horizontal dashed black line identifies same value (1.0) between panels for reference. Vertical black line divides daily CPUE from average CPUE. Vertical lines denote error bars (SE).

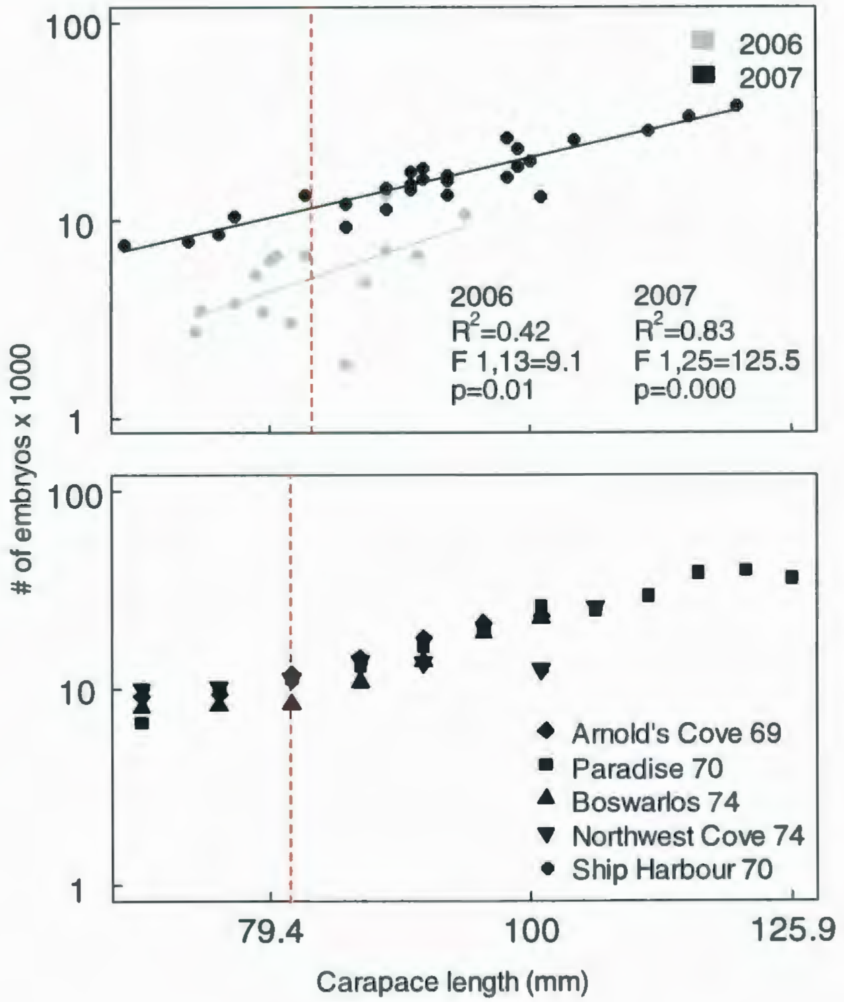


Figure 4.8: Fecundity in 2006 and 2007 analysis in Bonne Bay and comparison from Newfoundland literature (Ennis 1980). Red vertical line denotes MLS at time of sampling. Data are log transformed but normal scale shown for comparative purposes.

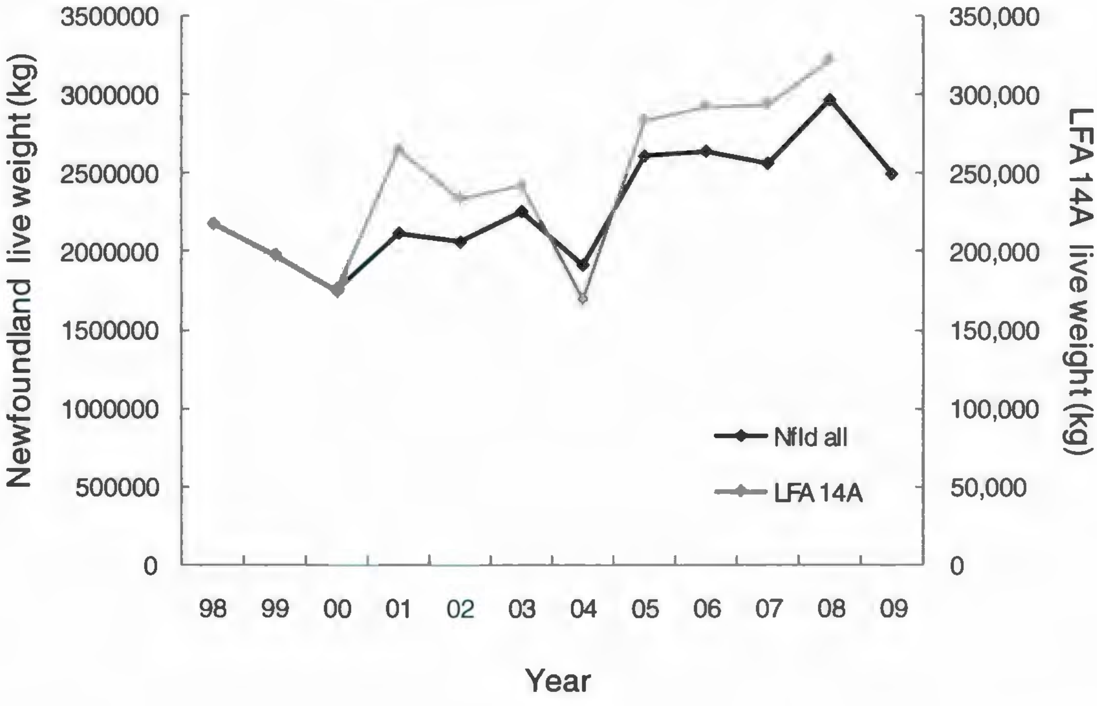
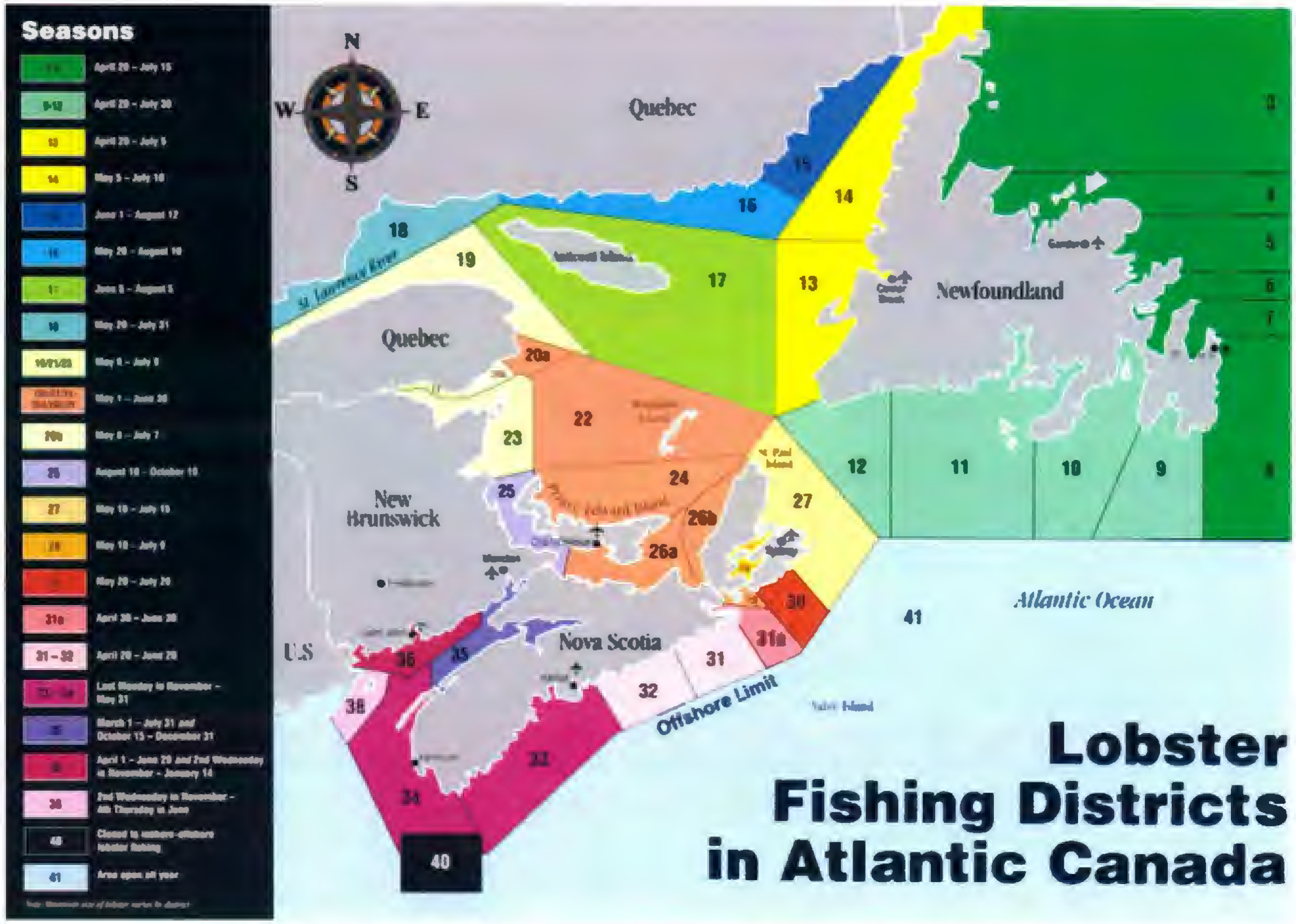


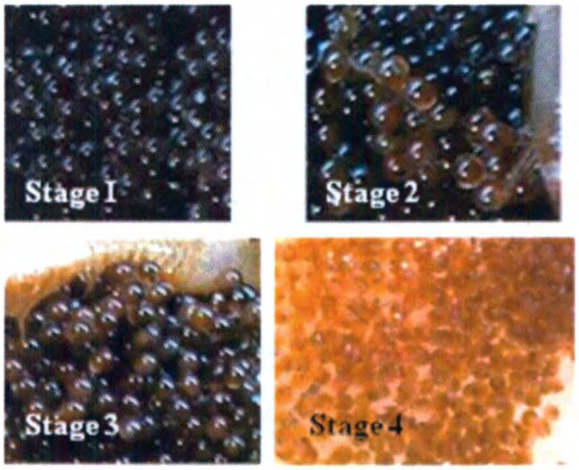
Figure 4.9: Annual commercial live weight of American lobster (*Homarus* americanus) landed in Newfoundland from 1998 to 2009 for the province of Newfoundland and LFA 14A. Source: DFO Data.



Lobster Fishing Districts in Atlantic Canada

Appendix 4.1: Lobster Fishing Areas (LFAs) and seasons in Canada.

http://www.gov.ns.ca/fish/marine/map/lobster_full.shtml (March 2010)



Appendix 4.2: Stages of Embryonic development of American lobster, *Homarus americanus*.

Appendix 4.3: Fisher Ecological Knowledge (LEK) Interviews conducted in Bonne Bay, Newfoundland. 2008-2009.

I'm going to start with some general questions about your lobster fishery

1. What year did you start fishing lobster? Have you always fished for lobster?
2. Did your father fish for lobster?
3. Have you always fished from this community?
4. Do you fish alone or with a partner?
5. If you fish with a partner- who and how many years have you been fishing together?
6. When you fish together, who empties the pots?
7. Are your pots metal or wood? Why do you have a preference?
8. How many pots do you fish? Have you always fished this many pots?
9. Have you always fished this many pots? What was it before? Have you noticed any changes?
10. Do you fish your pots on a line? How many on a string? Why?
11. What direction relative to the shoreline do you set your pots? Why?
12. Has your average catch changed over the years? Why do you think that might be?
13. On average, what would be a good seasonal catch? What would be a bad seasonal catch?
14. Has the minimum size always been what it is? Has the maximum size always been what it was?
15. What do you think of the changes?
16. Have you noticed any changes in the lobster catch over the past years? Why do you think this might be?

17. Do you fish for the whole lobster season? If not, why?

18. How deep do you think the lobsters go in this area?

19. What depth of water do you fish in? Does this change over the season?

20. Is there a particular type of bottom that lobsters like?

21. Are there any particular weather patterns that favour or deter lobsters from your pots?

22. Can you show me where you set your pots? Does where you set your pots change over the fishing season? Why?

23. Do other people set their pots around where you set yours? Who?

24. Are there particular areas around here where fishermen from this community normally fish? If yes- can you show me the area for your community fishery on the chart?

25. Do fishers from other communities fish in this area? Do you know where they fish?

26. Are there boundaries between communities for where people fish? Have these changed over the years?

Now I want to ask you some questions about spawny or berried lobster

27. The berried lobsters that you see in this area – what do they look like?

28. Have you noticed different coloured eggs or spawn on the lobsters? If yes, can you describe the differences you have observed?

29. Do you notice any differences in where the females with different coloured spawn are located?

30. On your grounds, is there a particular time in the season when the females start to have berries or eggs under their tails? If yes- when is that time? Has this changed over the years?

31. Around what point in the season do you think the females start to hatch? What makes you think that they are hatching?

32. Have you noticed any changes over the years in when lobsters start to hatch?

33. Is there a particular kind of bottom where they seem to like to hang out? To release their young?

34. Do you notice any areas where the spawney females tend to aggregate?

35. Have you noticed any parts of your lobster fishing area that are more likely to have berried (spawny) female lobsters than others – i.e. where they seem to cluster? If yes-would you mind showing me those areas?

36. If yes, has thing changed over the years? Why do you think that is?

37. Are there any areas that you avoid because there are too many berried females?

38. Do you always find more spawny lobsters in these areas or only at certain times of the season? If only at certain times of the season, When?

39. What is the biggest spawney female you have ever seen? What was the smallest? Has this changed over the years?

40. Do you notice any differences in where large or small spawney females are located?

41. What size range would you say most of the berried females you return are?

42. Have you noticed any changes in the size at which females are spawney?

43. What proportion of your catch would you say is berried females?

44. What type of bottom do you think that the spawney females like?

45. Do you think the berried lobsters move around a lot? What makes you think that?

46. What do you think that the spawney females are eating?

47. How often do female lobsters reproduce in this area?

48. Is there anything else about berried females that you have observed that I haven't asked you about?

49. Do you have any questions for me about spawny lobsters?

V-notch

50. Do you V-notch female lobsters? If yes/no why?

51. Do other people in this community V-notch lobsters?
52. Do you find V-notched females in the water?
53. What proportion of your catch is V-notched females?
54. Of these – do you see berried V-notched females?

This next part of the interview has some questions about lobsters after they have been released from the mothers. Here are some pictures of lobsters when they are at the larval stage and after they settle out on the bottom and start to look more like lobsters.

55. Are there any areas you fish that you have noticed a high proportion of small undersized lobsters?
56. Has this changed over the years?
57. What type of bottom do you think small lobsters like?
58. What part of the bay do you think might be nursery habitat for very small lobsters?
59. Why do you think this area has so many young lobsters?
60. Is there much shelter there?
61. What is the depth of water there? What is the bottom like? Which direction are the currents moving in? Why do you think there might be more small lobsters in that area?
62. Are small lobsters found in close proximity to larger lobsters?
63. Where do you think the small lobsters are coming from?
64. What is the smallest lobster you have ever had in your pot?
65. Is this the smallest lobster you have ever seen? If no then where was the smallest lobster you've ever seen?
66. What is the bottom like in that area?
67. What are these small lobsters eating? Where are they going? Are they taking the bait?

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68. Any idea what eats small lobsters? What makes you think that?

69. Are there any particular areas where you notice a lot of cunners and sculpin?

70. Have you ever found lobster parts in the guts of another organism?

71. Is there anything else you have observed about young lobster at each of these stages that I haven't asked you about?

72. Do you have any questions for me about these little guys?

Feed back loop – show my data to ask them what they think of what I got?

73. We think that lobsters might like bottom that is .... are there areas of the Bay that have lots of kelp? Or rocks? Or areas where young lobsters could hide?

That wraps up my questions for you.

74. Do you have any questions for me? Many thanks

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CHAPTER 5 : SUMMARY AND CONCLUSIONS

Successful recruitment in benthic populations is influenced by a variety of physical and biological variables that interact at a wide range of temporal and spatial scales and on different components of the life cycle. This thesis investigated recruitment patterns and processes relevant to recruitment during the larval and settlement stages in one of the most northerly populations of American lobster (*Homarus americanus).* Additionally, recruitment patterns were investigated utilizing a long term recruitment index in tandem with small scale behavioural experiments. Lastly, I incorporated LEK to aid in the direction that research could follow to determine factors relevant to recruitment in reference to the distribution and abundance of egg bearing females.

This study of the spatial and temporal distributions of early life stages of American lobster in Bonne Bay, Newfoundland represents the first attempt to examine lobster recruitment dynamics in this location and is one of few studies in Newfoundland, which is the northern distribution limit for this species. High concentrations of stage I larvae were consistently seen in outer Bonne Bay during summer sampling, however, sporadically high concentrations within the Bay suggest hatching pulses followed by rapid mortality or advection. The dramatic decline from stage I to stage II lobster in Bonne Bay further suggests high mortality or advection. Comparison with regional larval surveys for other areas in the geographic range of lobster shows that concentrations of stage 1 larvae in Bonne Bay are similar to other regions but concentrations of later stage larvae are comparatively low. Late stage lobsters were only present in appreciable numbers in 2008, suggesting strong interannual variability in abundance of late larval stages in Bonne Bay. A further examination of dispersal dynamics at the Outer Bay will likely provide useful insight into lobster dispersal in Bonne Bay. Freshwater input may be a key factor in larval export and mortality in Bonne Bay, given that laboratory behavioural experiments showed that larvae avoid salinities lower than 24 psu. Downwelling-favourable winds predominate in Bonne Bay during the summer months, which can favour larval transport toward the coast. Indeed, higher larval concentrations were positively related to the time since a wind reversal event which resulted in an offshore wind.

Chapter three examined the relationship between YoY and older juvenile lobsters and the extent to which this may be influenced by conspecific attraction. American lobster represents a useful organism to examine this relationship as lobsters are dependent on cobble-boulder habitat for their first few years of life. Settlement patterns are potentially influenced by larval acceptance or rejection of substrate specific cues. Settlement near conspecifics confers the potential advantage of indicating suitable habitat that provides protection from predators. Suitable settlement locations may create a hierarchy of cues necessary for settlement and final establishment in nursery habitat. The behavioural experiments presented here suggest such a hierarchy, where the presence of juveniles may induce postlarval searching behaviour, but if suitable habitat is absent larvae do not settle. An understanding of how larvae sense and respond to multiple cues may provide more insight into habitat selection.

YoY and early juvenile lobsters are strongly associated with structurally complex nursery habitats such as cobbles and boulders, and the role of conspecific attraction in creating this association is largely unknown. I analyzed eight years (2001-2008) of long-term recruitment data at three spatial scales (regional, site, quadrat) of data aggregation to show a strong positive relationships between YoY and Juvenile densities at wide range of spatial scales (metres/quadrat, tens of kilometres/site, hundreds of kilometres/regions). Persistent ocean circulation patterns such as ocean gyres and wind-driven currents create spatial differences in larval settlement, which translate to consistent year-to-year differences in benthic recruitment. This mechanism could produce the strong correlation in spatial patterns observed between YoY and older year classes at the local and regional scale, but it would be difficult to explain the co-occurrence of YoY and older conspecifics in the same quadrat simply on the basis of passive larval transport.

Quadrat-scale analysis of the YoY-to-Juv relationship revealed a strong association between juvenile and YoY lobster at very small spatial scales that cannot be explained by hydrodynamic processes. The lowest proportion of quadrats with YoY lobsters consistently occurred where juveniles were absent, and the frequency of quadrats that contained YoY lobsters increased steadily with increasing densities of juvenile lobsters. In contrast, increased cobble coverage above a minimum level made little difference to the presence of YoY in quadrats.

The final objective of this study, described in Chapter 4, was to collaborate with local fishers in order to discuss and record their knowledge of different stages of the life cycle of American lobster, and to determine the size frequency of the lobster population and the distribution of berried females by accompanying them in their daily fishing routines. The initial approach of sampling with fishers as they hauled their traps showed that the average size of lobsters across sexes is similar among regions. The low numbers of larval lobsters and absence of very large lobsters indicates that the majority of the fishery is largely dependent on recruits that migrate from outside Bonne Bay. Recruitment in the Bonne Bay lobster fishery, as is true elsewhere, likely depends heavily on eggs produced by small, undersized females. In Bonne Bay peak densities of berried and non-berried females are very close to the minimum legal size. Although larger females are known to be more fecund, the extent to which their eggs produce healthier larvae with a higher survival probability has not been clearly resolved.

Fishers identified hotspots for berried females and undersized pre-recruit lobsters, which need to be substantiated with more rigorous scientific support, such as tagging studies, underwater video and dive surveys to properly understand the migrations and behaviours of egg-bearing females. The incorporation of standardized traps in Newfoundland and elsewhere in Atlantic Canada will help resolve some of the associated biases, and contribute to a larger regional study.

This study illustrates how LEK can help to guide scientific studies in small coastal communities where scientific data is limited. Local fishers assisted in determining priority sampling locations for YoY surveys, and could have assisted in selecting locations for plankton sampling. Though fishers had little knowledge of planktonic stages and recently-settled lobsters, they had extensive knowledge of the distributions of spawning females and bottom type, which are potential hotspots for stage I and YoY lobsters, respectively. Stage IV postlarval lobsters are known to select cobble-boulder habitat at settlement, and fishers are very familiar with the bottom type on their fishing grounds. Behavioural experiments on settlement cues for American lobster may help to identify potential nursery habitats in areas such as Newfoundland where YoY lobsters are difficult to find.

Recruitment in marine invertebrates exhibiting complex life history strategies is governed by the interaction of physical, biological and chemical processes operating at numerous spatial scales. This study marked the first attempt at quantifying dispersal and recruitment processes of American lobster in Bonne Bay, one of the most northerly distributions of American lobster. Despite low abundance of larvae and YoY, there is significant value in understanding recruitment dynamics of lobster larvae at its northern limit. The environmental sensitivities of a species are most evident at the fringe of its distribution, and thus may serve as indicators of the impacts of climate change. Continued sampling of YoY lobsters would contribute to a large-scale collaboration to understand settlement patterns of American lobster across its biogeographic range. Furthermore, while recruitment is comparatively low, it is enough to sustain a viable lobster fishery along the west coast of Newfoundland. While the New England long term recruitment index supported previous research that shows consistent patterns of oceanographic circulation results in regular recruitment hotspots, the analysis of the relationship between YoY and older juveniles at all spatial scales indicates a potentially important settlement behaviour where postlarvae may respond positively to the presence of conspecifics. The extent to which this cue is important is unknown at this time, yet provides opportunity for future research directions. Finally, the incorporation of Local Environmental Knowledge into the research in Bonne Bay provides evidence of the importance of establishing collaborations with locals, particularly in small communities where there is little to no background scientific data. Building relationships to bridge the gap between resource users and science will assist in establishing a more cohesive communication mechanism where stakeholders can contribute to research directions. Determining the variables that influence lobster recruitment at local and regional spatial scales is important because American lobster is an incredibly valuable fishery along the east coast of Canada and the United States.