

Patterns and processes of recently settled and juvenile American lobster (*Homarus americanus*) in the lower Bay of Fundy

by

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ABSTRACT

In this thesis I quantified, over 4 years, spatial patterns of early life phases of American lobsters (*Homarus americanus*) at multiple spatial scales in the lower Bay of Fundy, ranging from 0.55 m² cobble-filled collectors to large regions 127-674 km², and I conducted a field experiment and a modeling exercise to investigate which environmental (biological and physical) factors are responsible for the dominant patterns I observed. Benthic recruits and the following two juvenile phases (emergent and vagile lobsters) showed similar spatial patterns at the scales investigated (most patchiness at the “area” scale), but these differed markedly from the pattern (no patchiness at any of the scales investigated) displayed by the fourth life-history phase (adolescents). The number of stage IV larvae (i.e., postlarvae) caught in the plankton by light traps was significantly related to spatial variability in benthic recruitment at the area scale, but the number of stage I larvae was not. The modelling exercise identified four variables that were related to benthic recruitment patterns: North Atlantic Oscillation Index (NAO) over the larval period, fetch of the study area, juvenile abundance, and sea surface temperature over the larval period. Whereas some of these associations appear to be spurious, others suggest, as did the light trap study, that factors affecting postlarval supply are determinants of the spatial patterns observed. Also, the NAO index showed promise in predicting inter-annual variation in benthic recruitment patterns. This work highlights the importance of sparsely distributed nursery grounds to benthic recruitment of this species. As rapid climate change is affecting the distribution of the species and conditions for larval development, continuing monitoring of recruitment is of high and increasing importance. Such monitoring will also

allow testing of the predictive ability of the model developed in chapter three, which is an important next step for this work.

DEDICATION

I would like to dedicate this thesis to the memory of my good friend and fellow biologist Ingibjörn Guðjónsson who passed away way too soon.

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Preface

It is in human nature to seek and perceive patterns in our environment, and that trait was most likely helpful when the first *Homo sapiens* roamed the plains of Africa 200,000 years ago. Temporal and spatial patterns in the distribution of prey and edible plants were crucial for survival of those early hunters and gatherers. When humans settled down and started the agricultural revolution, knowing temporal and spatial patterns of plants was crucial for agricultural planning and maximizing of crops. These observations of patterns were the applied grounds for ecology as we know it today.

The first written records of what we call ecology can probably be attributed to natural history observations of ancient Greeks such as Aristotle and Theophrastus, who observed patterns in nature and described them in classics such as *History of Animals* and *History of Plants*. However, the word ecology was not “invented” until the 1880s, by Ernst Haeckel who defined ecology as “the whole science of the relations of the organism to the environment including, in the broad sense, all the conditions of existence”, and was later redefined by many notable scientists of the modern era such as Charles Darwin, Charles Elton, and G. Evelyn Hutchinson.

Most fundamentally I see ecology as being the use of patterns that we observe to make (hopefully) useful inferences and hypotheses concerning processes that underlie these patterns.

One thing that is important to keep in mind when looking at ecological patterns in nature, is that unlike patterns and processes in the classical natural sciences such as physics or chemistry, patterns and processes involving living organisms are highly scale dependent; this is an important truism about life, and it is also important procedurally because inferences can be influenced by the spatial and/or temporal scale at which observations are made.

The majority of this thesis focuses on patterns observed in nature, and how we can use those patterns to gain valuable insight into the ecology of the juvenile stages of Canada's most commercially important species, the American lobster. In my general introduction I will start by discussing the importance of spatial scale in ecology, and how we can come to different conclusions on processes underlying patterns depending on the spatial scale at which observations are made. I will then go over the ecology and life history characteristics of the focal species of this thesis, the American lobster, before giving a brief outline of the four chapters of the thesis. My first data chapter describes spatial patterns and patchiness in the abundance of young-of-year lobsters at a hierarchy of spatial scales in the lower Bay of Fundy. The second chapter describes a new tool to catch pelagic larvae, and it presents results on pelagic-benthic coupling suggesting that spatial variation in young-of-year strength is mostly due to patchy larval supply. The third chapter uses simple ecological modelling techniques to elucidate which processes (physical and biological) are likely the most important in explaining the patterns of young-of-year lobsters in the lower Bay of Fundy. The fourth chapter describes the spatial patterns and patchiness in the abundance

of older lobsters at the same spatial scales that I investigated for young-of-year lobsters in chapter 1, with special focus on how the patterns change among ontogenetic stages of sub-adult lobsters. At the end of the thesis, I summarize the major findings into general conclusions, and suggest what future work should be carried out as a direct continuation of my Doctoral thesis work.

General introduction

Ecology can be defined as the study of patterns in nature and the processes that underlie these patterns (Fortin and Dale 2005). As Urban and Keitt (2001) wrote:

“Ecological processes generate patterns, and by studying the patterns we can make useful inferences about the underlying process.”

Finding processes responsible for patterns has been the objective of ecologists everywhere since the early days of the field. But unlike in physics, where the same laws can describe the behavior of small atoms up to the movement of planets, the last 30 years of ecological research has shown that ecology is highly “scale dependent”, in that the scale at which observations are made can influence conclusions pertaining to processes at play (McGill 2010). For example, in the world of avian ecology, the quest for explanation of species richness patterns spawned more than 100 different hypotheses, depending in part on the spatial and/or temporal scale that was being considered, where some processes were good predictors at certain scales and not at others (Rahbek and Graves 2001). These findings highlight the importance for studies to be explicit about the scale(s) of their study, and for discussions concerning the importance of different processes to be scale dependent. Importantly, they also illustrate the need for multi-scale studies, to obtain a complete understanding of processes operating in nature (Rahbek and Graves 2001). In a classic study involving two species of songbirds in New England (least flycatcher and American redstart), different conclusions are reached concerning the dynamics between the two species depending on the spatial scale at which their distribution is studied (Sherry and

Holmes 1988). At the forest stand scale (0.04 to 0.1 km²), the two species' abundances are negatively correlated, due to competition and aggression, which normally leads to only one of the two species being found within a particular forest stand. However, at a larger regional scale (over 1 km²), abundances of these species are positively correlated as they both nest in similar forests (Sherry and Holmes 1988). In another classic example, Orians and Wittenberger (1991) showed how two processes operating at two different spatial scales affect habitat selection of yellow-headed blackbirds. At larger scales, the abundance of these birds is positively correlated with the distribution of marshes, as they forage in marshes with healthy insect communities. However, the birds only utilize the marshes to forage, and if their distribution is studied at smaller spatial scales when they are not foraging these birds are mostly found in trees and shrubs that offer cover, in proximity of marshes. These two examples show that inferences concerning processes in ecology can be dependent upon the scale at which a study is conducted.

Considering the importance of spatial scale in ecology, studies that compare spatial patterns in the abundance of a particular species at different scales have arguably not received the attention that they deserve, and that especially holds true for the marine realm. Studies addressing this question in the marine environment have primarily been done on sessile or moderately mobile species, which are relatively easy to quantify with transects and quadrats (e.g., Caffey 1985; Thrush 1999; Thrush et al. 2000), or zooplankton or fish, which are relatively easy to sample with nets (review by Folt and Burns 1999; Drew and Eggleston 2008; Grober-Dunsmore et al. 2008). These studies have shown marked

variation in the abundance of different species or functional groups at different spatial scales. For example, “patches” of high abundance have been documented at small scales (0.5-10 m up to 200 m) in marine zooplankton (Folt and Burns 1999), at three out of four spatial scales (0.0025 km², 50 km² and 555 km², but not 3 m²) in sessile intertidal barnacles (Caffey, 1985), and at the smallest (1-2 meters) and second largest scale (100-200 meters) scales sampled in the moderately mobile intertidal gastropod *Nerita atramentosa* (Underwood and Chapman 1996). Few similar studies have been conducted on highly mobile subtidal benthic species, and only one has investigated distribution patterns of the American lobster in a similar manner.

The American lobster (*Homarus americanus*)

This thesis is focused on the early life history phases of the American lobster (*Homarus americanus*), and this section provides some background information on the species. The American lobster supports the most important fishery, in terms of landed value, in both Canada (DFO 2014) and eastern North America as a whole (Wahle et al. 2004). It is a cultural icon of the Canadian Maritime provinces (New Brunswick, Nova Scotia and Prince Edward Island) and New England in the United States of America. Its distribution is along the North Eastern continental shelf of North America, from the Strait of Belle Isle, off the coasts of Newfoundland and Labrador, to Cape Hatteras, North Carolina (Lawton and Lavalli 1995). The American lobster was traditionally fished by native peoples of the east coast of North America well before settlement of Europeans in the region, but commercial fishing started in the 1800s (Fogarty 1995). Lobster landings in the late 1800s were high

(e.g., over 10,000 metric tonnes in the United States in 1880 and 40,000 tonnes in Canada in 1895), but landings decreased to less than half of that over the two world wars and the worldwide recession between them. After that downturn, landings have increased steadily, and they are currently at an all-time high (Miller 1995, DFO 2020). The main fishing effort takes place in New England and the Maritime Provinces of Canada, almost exclusively by baited traps, although bottom trawls are used in some rare cases (Fogarty 1995). Management of the fishery differs between the United States and Canada, where entry to the fishery is heavily regulated in Canada via number of licenses issued, while effort is less restricted in the United States. Fishing effort in both countries is also regulated in most regions by the number of traps allowed and seasonal closures, the use of minimum legal sizes to increase the likelihood that lobsters reproduce before being captured and similarly the release of reproductive females is encouraged or mandatory (Miller 1995).

One of the most recent life history revisions for American lobster, which was done by Lawton and Lavalli (1995), suggests that the species' life history should be divided into seven stages on the basis of different morphological, physiological, behavioural, and ecological considerations. These seven stages are: larvae, postlarvae, shelter-restricted juveniles, emergent juveniles, vagile juveniles, adolescents, and adults (Lawton and Lavalli 1995). This life history scheme will be used throughout this thesis, which will mostly focus on the three juvenile stages and the adolescent stage.

The life cycle of the American lobster is comparable to that of other benthic crustaceans with a pelagic larval stage. It starts with mature females releasing larvae, which develop

inside eggs kept under the females' abdomen; the larvae are released as stage 0 (i.e., prezoa), but they molt to stage I almost immediately after hatching (Lawton and Lavalli 1995). Stage I larvae then go through another three molts in the water column, where they grow from ~1.7 mm carapace length (CL) to ~3.9 mm CL when "physiologically competent" and ready to settle on the sea floor (Lawton and Lavalli 1995). Lab studies indicate that the three first larval stages of the pelagic phase likely last \approx 11-54 days, depending mainly on temperature, and that the stage IV postlarva spends an additional 14 days in the plankton before it is ready to make the transition from the pelagos to the benthos (Phillips 2006). When the postlarva is competent to settle on the bottom it starts to display vertical swimming, or diving to find suitable habitat to settle on; failure to find suitable habitat can prolong the planktonic life of the postlarva (Botero and Atema 1982). In the laboratory, settling postlarvae show strong preference for cobble, over sand or mud habitat (Botero and Atema 1982), and field studies have only been able to find recently settled postlarvae in complex habitats such as cobble and eelgrass beds (Wahle 1993). After the postlarva settles on the bottom it molts and enters a phase called shelter-restricted juvenile (~4-14 mm CL), which rarely ventures outside its shelter, possibly due to vulnerability to predators. Wahle and Steneck (1992) showed that tethered juveniles slightly above that size suffered significantly lower mortality if they had access to cobble shelters than if they did not have access to shelter. When the juvenile has grown to ~15-25 mm carapace length it starts to emerge from its shelter, and that phase is called the emergent juvenile phase. When the animal reaches ~25 mm carapace length it enters the vagile juvenile phase, which is thought to make longer and more frequent foraging excursions. With further increased

size (~ 40 mm CL), the lobster enters the adolescent phase, which is characterized by the development of sexual organs (i.e. physiological maturity), and then it enters the adult phase (>50 mm CL), which is functionally mature.

As is the case for many commercially important species, the biology and ecology of the American lobster have been studied extensively (e.g., Factor 1995, Phillips 2006). Due to its size, abundance and occurrence within depths that are easily accessible, it has received more research effort than other commercial clawed lobsters such as the European lobster (*Homarus gammarus*) and the Norwegian lobster (*Nephrops norvegicus*) (Butler et al. 2006). Four extensive reviews are available on all aspects of the American lobster's biology: the first one "The American lobster; a study of its habits and development", by Herrick published in 1895; "The biology and management of Lobsters", edited by Cobb and Phillips published in 1980; "Biology of the Lobster *Homarus americanus*", edited by Factor published in 1995; and the most recent one "Lobsters: Biology, Management, Aquaculture and Fisheries" edited by Phillips published in 2006 and revised in 2013. Even though the adult stage has been extensively studied and is rather well known, there are still important knowledge gaps, such as the understanding of stock structure, recruitment- and metapopulation dynamics of the species. These questions have brought the attention of researchers to the larval and postlarval stages, including to the question of whether a functional relationship could be described between successful settlement on the benthos and recruitment to the fishery (i.e. growth up to legal size) (Incze et al. 2003). That intriguing question led to the emergence of the Atlantic lobster settlement index (ALSI), a

collaborative monitoring program led by academics, government scientists and lobster harvesters that measures the annual abundance of newly settled lobster in a number of locations in New England US and Atlantic Canada using both SCUBA-assisted suction sampling and vessel-deployed “bio-collectors”. Data have been collected for over 20 years in select locations in New England and one in the Bay of Fundy, and for shorter time periods in other regions, such as Nova Scotia, Prince Edward Island, and many locations in New Brunswick. These data are now considered in management of the lobster stock in Maine (Wahle et al. 2013), and recent study shows how such indices can be used to predict fisheries recruitment (Oppenheim et al. 2019). Such indices have been used for stock assessment and management of rock lobsters in Australia for couple of decades (Caputi et al. 1995) and will surely be part of stock assessment for the American lobster throughout its range in the future.

Far less is known about the ecology of lobster larvae than that of adults, mainly due to difficulties in sampling these early life stages in the field, since they are fast and competent swimmers and are also believed to be nocturnal (Cobb et al. 1989). Most of our knowledge of these pelagic stages therefore comes from laboratory studies, often conducted in relation to aquaculture. These studies have shown that the three pelagic larval stages make up a short period in the life cycle of the lobster, and the developmental time for each larval stage depends on various factors, but most importantly on temperature (Butler et al. 2006). The planktonic stages are considered the main dispersal mechanism for the species (Chasse and Miller 2010, Incze et al. 2010), although movement of adults may be important in some

areas (Krouse 1980, Stasko 1980, Ennis 1984, Campbell and Stasko 1986, Morse et al. 2018). To get at the extent of larval transport, studies using plankton tows have been conducted (Miller 1997), but in recent years the main focus has been on using oceanographic models to predict larval drift by currents (Katz et al. 1994, Incze and Naime 2000, Xue et al. 2007, Chasse and Miller 2010, Incze et al. 2010). These models typically use estimated egg production by berried females based on field sampling, as well as currents, temperature, winds, freshwater input and larval developmental time at each stage to predict where they reach stage IV and are ready to settle (Chasse and Miller 2010, Incze et al. 2010). Such models have been created for the Gulf of Maine (Incze et al. 2010) and the southern Gulf of St. Lawrence (Chasse and Miller 2010) and the Gulf of St. Lawrence, the Scotian shelf and the Bay of Fundy (Quinn et al. 2017). One important limitation of these models is that they do not incorporate behavioural decisions made by the postlarva at time of settlement, such as how these might be affected by substrate characteristics (e.g., cobble versus mud bottom).

There is also relatively little known about the ecology of young benthic recruits, in large part due to sampling difficulties; it was not until SCUBA assisted “suction sampling” was invented in the late 1980’s that small recently-settled postlarvae could be sampled effectively in the field. The postlarva makes the switch from the pelagic habitat to the bottom and is one of the most critical stages for recruitment of *Homarus americanus*, as mortality is thought to be high during that stage but to decline markedly and gradually in the following juvenile stages (Lawton and Lavalli 1995, Butler et al. 2006). Both laboratory

experiments and sampling in nature have shown that postlarvae prefer settling in cobble habitat (Botero and Atema 1982, Wahle and Steneck 1991, Wahle and Incze 1997, Palma et al. 1999), and it has actually been suggested that the lack of suitable cobble habitat (i.e. where post-settlement mortality is low) is one of the most important limiting factors for settlement and early survival (Wahle and Steneck 1992, Incze et al. 2003). Another important factor is supply of competent larvae (Butler et al. 2006), as seeding experiments in the field have shown that some nursery areas could potentially sustain higher numbers than are normally observed (Wahle and Incze 1997). Successful settlement is also affected by water temperature (Butler et al. 2006), as postlarvae observed in the field seem to stop displaying diving behaviour in water around 12°C and lower, and it has also been shown that larvae do not pass thermoclines where the difference is more than 6°C (Boudreau et al. 1991).

Sampling of recently settled American lobster postlarvae started in the late 1980s through the pioneering work of Wahle and Steneck (1991). Their work off the coasts of Rhode Island and Maine, in the United States, showed that the abundance of young-of-year lobsters was limited to rocky habitat and was very patchy at the scale they sampled (3-13 km) (Wahle, 1993). Two studies have specifically looked at patchiness in benthic recruitment of American lobster. Wahle and Incze (1997) found high and low extremes on two sides of a small island in the Gulf of Maine and suggested that differences in larval supply were responsible for these patterns, most likely because of wind-driven surface currents, since they found no difference in habitat characteristics or post-settlement

mortality between the two sites (Wahle and Incze 1997). In another study, Palma et al. (1999) looked at patchiness in benthic recruitment of American lobster, rock crab and Jonah crab. This study was done at a much larger scale and involved suction sampling and PVC collectors on at least 3 different substrates and at spatial scales ranging from a few centimeters to hundreds of kilometers in the Gulf of Maine. This study did not look at within-substrate patchiness, nor did it look at the inter-annual consistency of the patterns observed. In addition, no study has looked at how spatial patterns established at settlement are modified during the species' early life history.

In the first chapter of my Doctoral thesis, I assessed spatial patterns in benthic recruitment (density of young-of-year within a few months post-settlement) of American lobster in the lower Bay of Fundy. These analyses indicated that the area scale (0.4-4 km²) was most important to patchiness in benthic recruitment, with a significant but smaller amount of variation in recruitment at the region scale (127 and 674 km²), and virtually no significant variation at the smaller spatial scales. Despite inter-annual variability in benthic recruitment, these spatial patterns and scales of patchiness were largely consistent across years, indicating that some areas were consistently more important than others to lobster benthic recruitment. The objective of the second chapter was to develop and test a new device to catch pelagic stages of lobster. This work was mostly successful as we built and tested a trap that use a light source as a lure, and which caught larval stages of American lobster in nature. The spatial pattern of patchiness of postlarvae (stage IV) in the light traps was consistent with that of young juvenile lobsters in the bio-collectors, suggesting the

importance of postlarval supply to spatial patterns in benthic recruitment. In the third chapter I used an ecological modelling approach to identify processes responsible for the settlement patterns identified in the first chapter, by looking at which biological and physical variables explained variance in these spatial patterns of settlement. Of the 11 variables considered, three physical and one biological variable were present in the best model: the North Atlantic Oscillation index, sea surface temperature, juvenile lobster presence, and fetch. Whereas some of these associations appear to be spurious, others such as the NAO index and juvenile abundance could potentially drive patterns of benthic recruitment in the region. In the fourth chapter I quantified spatial and temporal patterns of different life phases of juvenile lobsters at the same scales and locations that the abundance of young-of-year lobsters was quantified, and I used those patterns to test published life history models for these juvenile lobsters. The first three life history phases of lobsters showed similar spatial patterns as benthic recruits, but the fourth phase did not; results suggest that patterns established at settlement are retained until the onset of adolescence, when increased activity and movements disrupt those patterns and result in a more uniform distribution.

Chapter 1: Patchiness in American lobster benthic recruitment at a hierarchy of spatial scales

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Original Article

Patchiness in American lobster benthic recruitment at a hierarchy of spatial scales[†]

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Abstract

The overarching goal of ecology is to uncover natural patterns and the processes that underlie them. Importantly, both patterns and processes are dependent upon scale. In this study we assessed spatial patterns in benthic recruitment (density of young-of-year within a few months post-settlement) of American lobster in the Canadian Gulf of Maine by deploying, over three consecutive years, between 413-505 cobble-filled collectors in a spatially nested design: regions (127 and 674 km²), areas within regions (0.4-4 km²), sites within areas (0.003-0.23 km²) and “sub-sites” within sites (0.00004-0.06 km²). We quantified spatial patterns of benthic recruitment using a nested ANOVA, variance component analysis and a randomization approach developed for this study. These analyses indicated that the area scale (0.4-4 km²) was most important to patchiness in benthic recruitment, with a significant but smaller amount of variation in recruitment at the region scale (127 and 674 km²), and virtually no significant variation at the smaller spatial scales. Despite inter-annual variability in benthic recruitment, these spatial patterns and scales of patchiness were largely consistent across years. Of the 11 study areas surveyed, three were identified as recruitment “hotspots” and four as recruitment “coldspots”, based on density frequency distributions. The location of these different recruitment “hotspots” and “coldspots” suggests that patchiness at the area scale may be related to the effect of local currents and topographical features on larval retention. The lack of significant patchiness at the smallest scale of the collector is at first surprising, given previous work on substrate selection by competent postlarvae, but likely arose because our sampling tool offered a

standard and high-quality substrate, indirectly confirming the importance of substrate to small-scale patterns of benthic recruitment.

Key words

American lobster, benthic recruitment, spatial patterns, patchiness, spatial scale

Introduction

Ecology can be defined as the study of patterns in nature and the processes that underlie these patterns (Fortin and Dale 2005). As Urban and Keitt (2001) wrote “ecological processes generate patterns, and by studying the patterns we can make useful inferences about the underlying process”. However, processes behind patterns are scale dependent. In general, physical factors are thought to play a relatively larger role at larger spatial and temporal scales and animal behaviour is thought to play a relatively larger role at smaller scales (Turner et al. 1989). For example, large-scale (e.g., kilometer scale) patchiness in abundance of marine invertebrates has often been attributed to oceanographic processes affecting larval supply while larval behaviour has frequently been attributed with patchiness at smaller scales (e.g., meter scale) (Underwood and Chapman 1998).

At least three broad mechanisms can lead to patchiness in abundance of organisms (Roughgarden 1977). First, large-scale physical processes, such as wind or ocean currents, can affect the dispersal of propagules, which in turn can lead to patchiness in the distribution and abundance of juveniles and adults (Roughgarden 1997). Second, habitat preference can affect the distribution of a species; if a species has special habitat requirements that vary at a particular “patch size”, then this species will display a “patchy” (i.e., clumped, or aggregated) distribution at that same scale. Third, if individuals of a species display aggregative behavior, as is common with larvae and juveniles of corals, hydrozoans, spiny lobsters, and barnacles (Knight-Jones and Stevenson 1950; Williams 1976; Anderson and Behringer 2013), then this species’ distribution will be patchy as a

result of, and at a scale relevant to, those behavioural aggregations. McGill (2010) recently considered the distribution of species in relation to four potential drivers: climate, species interactions, habitat, and dispersal. He suggested that climate and dispersal play a role at very small scales (microclimate/microhabitat selection, 10s of meters) as well as at very large scales (physical tolerance/seasonal migrations, 1000s of kilometers), that species interactions are mostly relevant at small scales (100s to 1000s of meters, but see Gotelli et al. 2010), and that habitat is most important at intermediate scales (1 - 1000 km). Identifying the scale(s) at which differences in abundance occur is important for two related reasons, first to identify the scale at which important processes are occurring and second to identify what these important processes may be.

Sampling of patchy, or aggregated, populations at different scales can lead to very different conclusions concerning the ecological processes that affect the distribution of these populations. A classic example concerns two species of songbirds in New England, least flycatcher and American redstart, where different conclusions are reached concerning the dynamics between the two species depending on the spatial scale at which their distribution is studied (Sherry and Holmes 1988). If the two species are studied at forest stand scale (4 to 10 hectares), their abundances are negatively correlated, likely due to interspecific competition and aggression, which normally leads to only one of the two species being found within a particular forest stand. However, at a larger regional scale (over 100 hectares), abundances of these species are positively correlated as they both seek the same type of nesting habitat (Sherry and Holmes 1988). In another classic example, Orians and

Wittenberger (1991) showed how two processes operating at two different spatial scales affect habitat selection of yellow-headed blackbirds. At larger scales, the abundance of these birds is positively correlated with the distribution of marshes, as they forage in marshes with healthy insect communities. However, the birds only utilize the marshes to forage, and if their distribution is studied at smaller spatial scales when they are not foraging these birds are mostly found in trees and shrubs that offer cover, in proximity of marshes. These two examples show that inferences concerning processes in ecology can be dependent upon the scale at which a study is conducted.

Considering the importance of spatial scale in ecology, studies that compare spatial patterns in the abundance of a particular species at different scales are relatively rare. Most such studies have been conducted in the terrestrial realm (reviewed by Kotliar and Wiens 1990), and fewer in freshwater (e.g., Li et al. 2001; Allan et al. 1997; Yannarell and Triplett 2004), and marine (Underwood and Chapman 1996; Underwood and Chapman 2013) environments. Studies that have been conducted in the marine environment have been primarily on sessile or moderately mobile species, which are relatively easy to quantify with transects and quadrats (e.g., Caffey 1985; Thrush 1999; Thrush et al. 2000), or zooplankton or fish, which are relatively easy to sample with nets (review by Folt and Burns 1999; Drew and Eggleston 2008; Grober-Dunsmore et al. 2008). These studies have shown that abundance varies at different spatial scales in different species or functional groups. For example, patches have been documented at small scales (0.5-10 m up to 200 m) in marine zooplankton (Folt and Burns 1999), at three out of four spatial scales (0.0025

km², 50 km² and 555 km², but not 3 m²) in sessile intertidal barnacles (Caffey 1986) and at the smallest (1-2 meters) and second largest scale (100-200 meters) scales sampled in the moderately mobile intertidal gastropod *Nerita atramentosa* (Underwood and Chapman 1996). Few similar studies have been conducted on highly mobile subtidal benthic species, such as lobsters (but see below).

The life cycle of the American lobster *Homarus americanus* is similar to that of other benthic invertebrates with a pelagic larval phase. Mating usually occurs after a female moults, following a complex courtship ritual. Eggs are fertilized externally as they are extruded by the female (Atema and Voight 1995), who carries the embryos under her abdomen for 9-11 months. After the prezoa larva hatches it moults and is released/swims into the water column (Talbot and Helluy 1995). Once in the water column the larva undergoes an additional three moults over a period of 1-12 weeks, depending on temperature and potentially larval origin (Ennis 1995; Quinn et al. 2013), before metamorphosing into the postlarval stage, which superficially resembles the adult and will make the transition to the benthos. When the postlarvae are competent to settle on the benthos, they start to periodically dive to the bottom to find suitable shelter to settle. Laboratory trials have shown that failure to find suitable shelter can prolong the postlarval stage up to 2 weeks (Botero and Atema 1982; Boudreau et al. 1990), which can be costly since this last pelagic stage is energetically demanding (Capuzzo and Lancaster, 1979) and delayed settlement can lead to smaller size later on in the juvenile's life (K. Dinning, personal communication). In the laboratory, settling postlarvae have shown strong

preference for cobble over other substrates such as sand or mud (Botero and Atema 1982), and in the field, recent settlers have mainly been found in shallow cobble habitat (Wahle and Steneck 1991; Wahle and Incze 1997; Palma et al. 1999). Efforts to find recently settled postlarvae in other habitats have resulted in very few animals found (MacKay 1926; Wahle 1993).

Wahle and Steneck (1991) were pioneers in sampling American lobster postlarvae in nature. Their work off the coasts of Rhode Island and Maine, United States, showed that the abundance of young-of-year (YOY) lobsters was limited to rocky habitat and very patchy at the scale they sampled (3-13 km) (Wahle 1993). These findings were the basis for a study by Wahle and Incze (1997) in Maine, United States, which sought to explain a sharp contrast in the density of YOY lobsters on two sides of a small island. Based on differences in catches of postlarvae in larval tows on both sides of the island, the authors concluded that this difference in YOY density was mainly due to differences in larval supply, due to the island's topography (Wahle and Incze 1997); incidentally, this finding also suggests that YOY abundance measured at the end of the settlement period is likely a good indicator of larval supply to an area in this species. On a larger geographic scale, Palma *et al.* (1999) looked at YOY abundance patterns in the American lobster, Jonah crab (*Cancer borealis*) and Atlantic rock crab (*Cancer irroratus*) on at least 3 different substrates and at spatial scales ranging from a few centimeters to hundreds of kilometers in the Gulf of Maine. For American lobster, patchiness in YOY abundance was mainly observed at small scale, between cobble bottom and other substrates that are not as suitable

for lobster settlement (i.e. sand and other fine sediment), while YOY abundance of the two crab species was similar among substrates, presumably due to a lack of habitat selection by the larvae of these species. However, for all three species patchiness in YOY abundance was also observed at the large “regional scale” (hundreds of kilometers), presumably due to large-scale variability in egg production or oceanographic control of larval delivery.

The overarching goal of this study is to enhance our understanding of patterns and scales of patchiness in “benthic recruitment” of American lobster postlarvae. We define benthic recruitment as the density of lobsters measured weeks to a few months (1-14 weeks) after settlement. As such, benthic recruitment is certainly somewhat lower than settlement densities. However, the two are likely more similar in American lobster than in most other marine species with pelagic larvae, given that post settlement mortality and movement of recently settled lobsters are relatively low (Lawton and Lavalli 1995; Palma et al. 1999). We intend to advance our understanding of patchiness in American lobster benthic recruitment by i) identifying recruitment “hot spots” and “cold spots” (based on density frequency distributions) within a new geographic domain, shallow cobble habitats in the Canadian Gulf of Maine, ii) using standardized settlement substrates in a fully-nested sampling design to identify the spatial scale(s) of patchiness in benthic recruitment, iii) investigating inter-annual consistency in spatial patterns of benthic recruitment.

Methods

We quantified lobster benthic recruitment at a hierarchy of spatial scales (Figure 1.1.1) using passive “settlement collectors” designed to mimic optimal habitat for lobster postlarvae and juveniles (Wahle et al. 2009; Wahle et al. 2013). The settlement collectors resemble a flattened lobster trap, made out of wire mesh, with the following dimensions: 91.4 cm long, 61 cm wide and 15.2 cm high. Each collector was filled with cobble (round quarry rocks 10-25 cm in diameter), to mimic optimal settlement substrate for lobster postlarvae. These collectors have been shown to collect comparable numbers of postlarvae on quality cobble bottom as suction sampling by SCUBA divers (Wahle et al. 2009, Wahle et al. 2013). During this study the collectors were always deployed in cobble habitat considered good for settlement and were in the shallow sub-tidal in less than 12 metres of water at low tide. The bottom substrate in the sampling sites was confirmed using a combination of SCUBA diving, bottom grabs, ROV videos, and traditional ecological knowledge from fishermen and scientists that have worked in these regions for decades. They were deployed in late June-early July and recovered in late October-early November in 2010 (n = 413 collectors total), 2011 (n = 553) and 2012 (n = 452), which is expected to cover most if not all of the settlement period of lobster postlarvae in the study region.

Upon recovery the collectors were carefully inspected, and all lobsters found were measured for carapace length (CL) from the eye socket to the back of the thorax. Individuals measuring ≤ 13 mm CL were assumed to have settled in the year of sampling, based on inspection of size frequency distributions during a pilot study conducted in Beaver

Harbour (one of the areas sampled in this study), New Brunswick, in 2008 and 2009. These lobsters will be referred to as young-of-year (or YOY) and are the only individuals included in the analyses presented in this paper. It is expected that this cut off (13 mm) is not entirely accurate for all individuals and in all years, given variation in settlement date and growth, but it provides an appropriate reference point for the current analyses and inferences derived here hold when we reduce this cut-off to 12 or 11 mm CL.

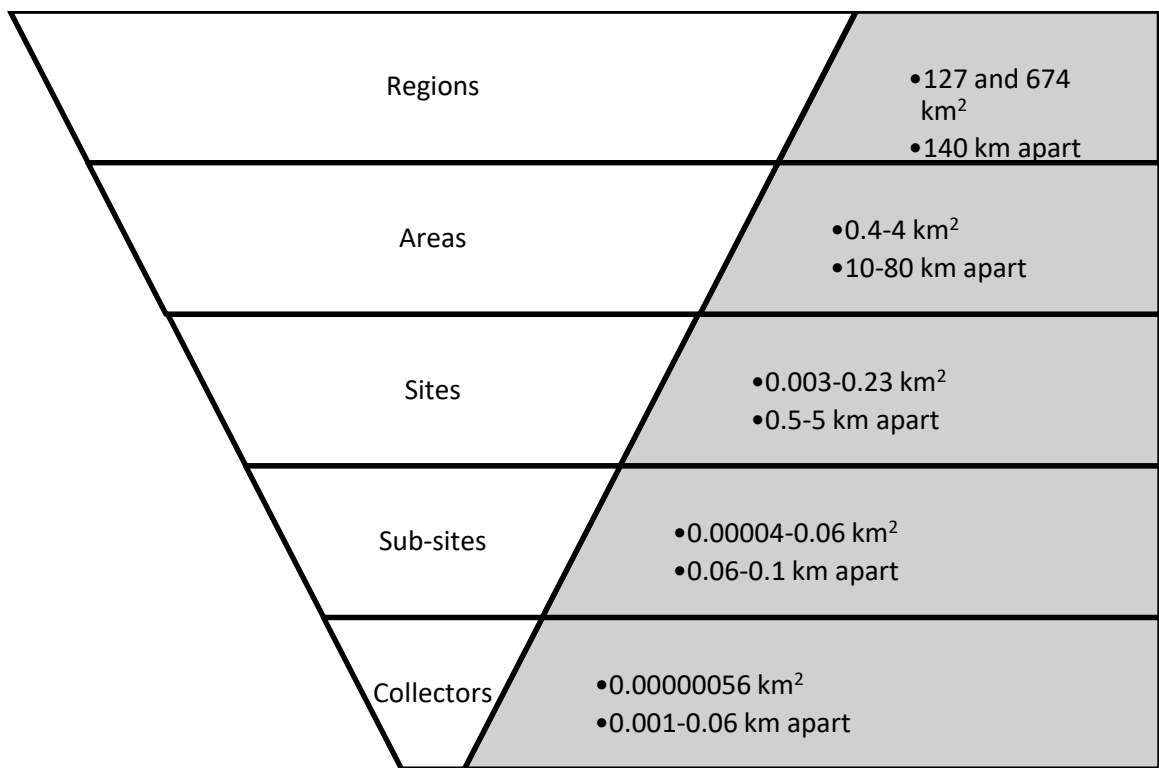


Figure 1.1.1. - Hierarchy of spatial scales sampled in this study, showing minimal convex polygon of the area of seabed covered by replicates at each scale and the distance between the centre of replicates within each of these scales.

Spatial scale hierarchy

Regions

Our sampling design consisted of two large regions in Atlantic Canada, south New Brunswick (SNB) and southwest Nova Scotia (SWNS). The straight-line distance between the centres of the two regions is 143 km (Figures 1.1.1 and 1.2.2), and the minimum convex polygon made from the different sampling areas of the SNB region covers ca. 127 km² of seabed while that for the SWNS region covers ca. 674 km². The main reason for this difference in area covered is that the two regions were originally defined by different sampling programs, one to evaluate scale of patchiness in benthic recruitment (SNB) and one to develop index sites for benthic recruitment monitoring (SWNS). Although it would have been desirable to have these be more comparable, they are actually not very different from one another considering the range of scales covered by the study (0.00000056-674 km²).

Areas

We selected 11 sampling areas within these regions, six within SNB and five within SWNS. The seabed area of the minimum convex polygons made up from the different sites of a given area ranged from 0.4-4 km² and the areas within the regions were 10-80 km apart middle to middle.

Sites

We used 2-3 sampling sites within each area. The seabed area of the sites' minimum convex polygon made from the different collectors within each site ranged from 0.003-0.23 km² and the sites within each area were 0.5-5 km apart.

Sub-site

To bridge the large gap in spatial scale between our smallest scale (collector) and our second smallest scale (site), we divided all our sites post-hoc into sub-sites. In dividing each site into two sub-sites effort was made to keep the number and coverage of collectors in each sub-site as similar as possible. Coverage of each sub-site was 0.0004-0.15 km² of seabed and distance between sub-sites of a same site was 0.06-0.1 km.

Collectors

We deployed 15-25 collectors (0.56 m²) depending on how many we could fit on the cobble patch in each site, while preventing line entanglement. The different collectors within each site were 0.001-0.06 km apart.

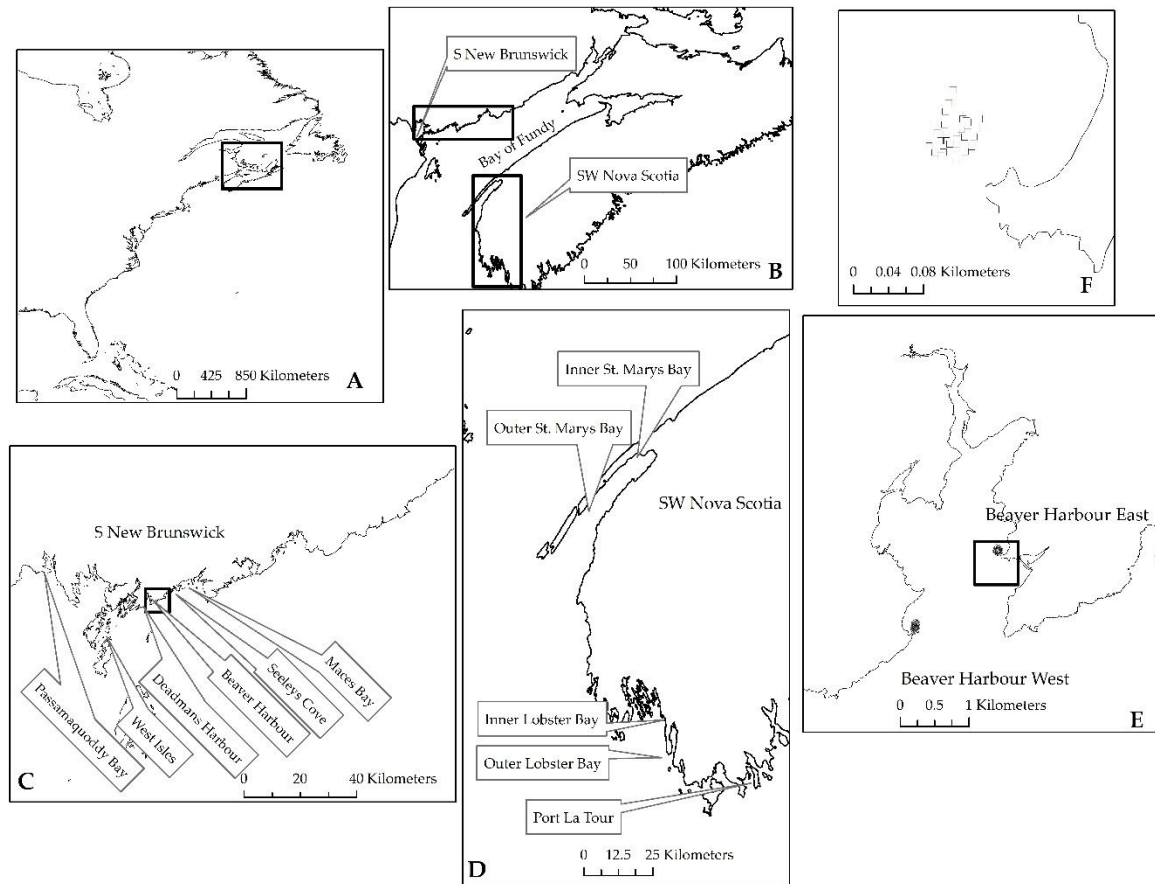


Figure 1.2.2. Maps showing the hierarchy of spatial scales sampled in this study. Map A highlights the Canadian Gulf of Maine (Bay of Fundy and southern Nova Scotia) on the east coast of North America. Map B shows the two study “regions”, South New Brunswick (SNB) and South-West Nova Scotia (SWNS). Maps C and D show study “areas” within the SNB and SWNS study regions, respectively. Map E shows groups of collectors at two study “sites” within the Beaver Harbour study area, and map F shows “collectors” that make up the eastern site within the Beaver Harbour study area.

Statistical analysis

The data was analyzed separately for each of the three study years using four-level nested ANOVAs with unequal sample sizes (Sokal and Rohlf, 1995); collectors (n = 15-25) were nested within sites, sites (n = 2-3) were nested within areas, and areas (n = 5-6) were nested within study regions (n = 2). Years were analyzed separately due to significant interactions

that arose when year was included as a factor in the model. Due to violation of normality, generalized linear models using a zero-inflated Poisson distribution were also run, and these were used to confirm the interpretation of ANOVA model results; i.e., whether the p-value associated with a particular model term was significant ($\alpha = 0.05$). The two models agreed in 11 of 12 comparisons (three years x four spatial terms/year), with the exception being significant variation at the site scale in 2012 in the ANOVA model ($p = 0.04$), but not in the generalized linear model ($p = 0.10$). The ANOVAs were then followed by variance component analyses (VCAs) to estimate the variation in YOY abundance at each spatial scale as a percentage of the total variation in YOY abundance (Caffey 1985; Sokal and Rohlf 1995).

Since the spatial categories (regions, areas, sites etc.) overlap to some extent in area coverage, patchiness was further investigated, again for each year separately, by calculating indices of patchiness for each replicate of each spatial scale (e.g., different collectors of a same site, for all sites) and relating these to the actual area occupied by each replicate on a continuous scale. Two common indices were used, the variance/mean ratio and Green's coefficient (see Krebs 2014 for descriptions). However, given that the variance/mean ratio can erroneously suggest randomness when applied to data with certain patterns (Krebs 2014), and that it is difficult to assign confidence limits to Green's coefficient (Krebs 2014), we developed an additional approach, which was based on variance as a metric for patchiness and randomization of the data to assess the likelihood of observed results. More specifically, observed variance in YOY abundance among

replicates of each “spatial unit” (e.g., among sites of a particular study area) was compared to the distribution of variances obtained from randomization of the data at the appropriate spatial scale. For example, to estimate patchiness at the site scale of a particular study area, the observed numbers of YOY lobsters in each collector of the study area were randomly allocated 10,000 times to the different collectors of the study area, and variance in YOY abundance among sites was calculated after each randomization. This randomization process created a frequency distribution of variance estimates for the spatial unit (the particular study area) in question, which was used to calculate a probability (p-value) of obtaining a variance in YOY abundance among sites as great or greater than that observed under the null hypothesis that YOY abundance was random within that particular spatial unit. The p-values obtained through this exercise were correlated with both the variance/mean ($r = 0.71$, $p < 0.0001$) and Green’s ($r = 0.74$, $p < 0.0001$) indices. For simplicity, we only report here the p-values obtained by the randomization approach.

All statistical models and tests were run in R (R Development Core Team 2013) and an alpha level of 0.05 was used in all inferential tests.

Animal ethics and welfare

This study was approved by the University of New Brunswick (Saint John) Animal Care Committee (protocol # 2010-EA-13).

Results

Nested analysis of variance

Results of the nested ANOVAs were generally consistent across years. At the largest spatial scale of the region, young-of-year density (YOY/m²) was greater in SNB than in SWNS (Figure 1.3.3). This difference was not significant in 2010 ($p = 0.341$), but it was significant in both 2011 ($p = 0.049$) and 2012 ($p = 0.013$) (Table 1.1.1). In SWNS average YOY densities remained between ca. 0.1 and 0.3 YOY/m² between 2010-2012, whereas in SNB they increased from ca. 0.4, to 0.8 and finally 1.1 YOY/m² over the three years of the study (Figure 1.3.3).

Variance in YOY density at the area scale was significant in all three years of the study and highly significant in two of these (2010: $p = 0.003$; 2011: $p = 0.0005$; 2012: $p = 0.018$) (Table 1.1.1). Several areas stand out for particularly high or low densities (Figure 1.3.3). This is especially true within the SNB region, where high densities of YOY (>0.6 lobsters/m², upper 25th percentile) were consistently (all 3 years) observed in three of the six areas, Beaver Harbour, Deadmans Harbour and Maces Bay. In contrast, densities of YOY were consistently very low (<0.09 lobsters/m², lower 25th percentile) at two of the five areas within the SWNS region, Inner Lobster Bay and Port LaTour, and at two of the areas within the SNB region, West Isles and Passamaquoddy Bay (Figure 1.3.3). There were, however, two exceptions to this general pattern, one in each study region; in SNB, Seeleys Cove showed very low densities of YOY in 2010 (0.03 lobsters/m²), but average densities in 2011 (0.33 lobsters/m²) and 2012 (0.30 lobsters/m²), and in SWNS, Outer St.

Marys Bay had high densities in 2010 (>0.6 lobsters/m²) but average densities (~ 0.40 lobsters/m²) in the following years.

YOY densities did not vary significantly between sites of a same area in 2010 ($p = 0.32$) or in 2011 ($p = 0.14$), but did marginally so in 2012 ($p = 0.042$) (Table 1.1.1). This significant result is the only instance where the nested ANOVA and the generalized linear model (GLM) did not agree, and the p-value obtained with the GLM for the site spatial scale was 0.1.

There was no significant variation in densities among sub-sites of a same site in any of the three years (all $p > 0.05$) (Table 1.1.1).

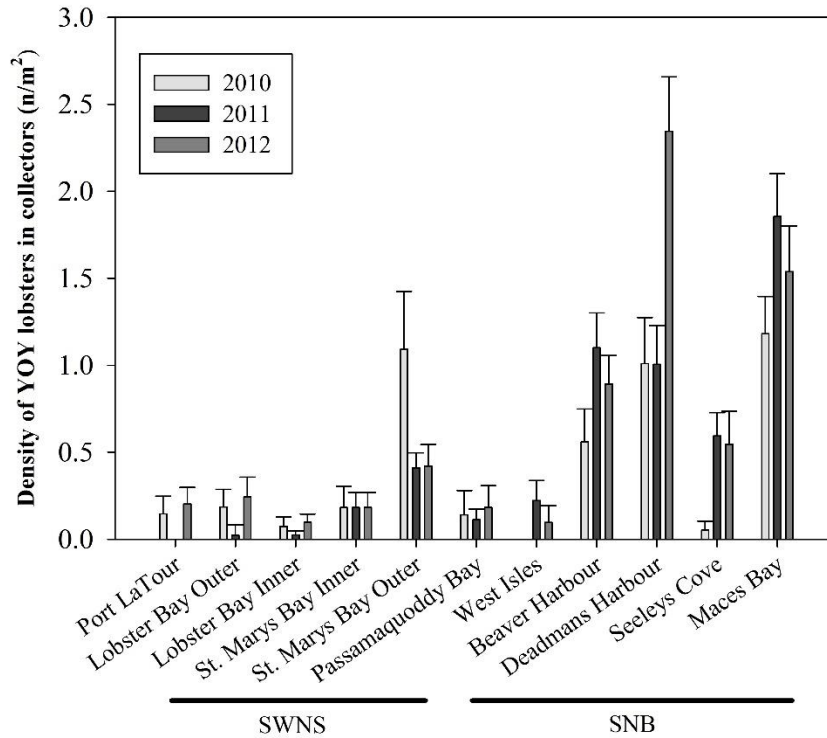


Figure 1.3.3. Mean (+SE) density of young of year lobsters (YOY, < 13 mm CL) in 11 areas of two regions (South West Nova Scotia [SWNS] and South New Brunswick [SNB]) over the three years (2010-2012) of the study.

Table 1.1.1. Results of four-level nested analyses of variance (ANOVA) of YOY density (lobsters/m²) at a hierarchy of spatial scales in 2010, 2011 and 2012. The F ratio for a particular scale and year was computed using the MS of the next smallest spatial scale as error term (e.g., $F_{\text{Region}} = \text{MS}_{\text{Region}}/\text{MS}_{\text{Area}}$).

Source of variation	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Among regions				
2010	1	2.23	1.01	0.341
2011	1	17.63	4.95	0.053
2012	1	3.20	9.48	0.013
Among areas within regions				
2010	9	2.20	6.75	0.003
2011	9	3.56	11.63	0.0005
2012	9	3.19	3.94	0.018
Among sites within areas				
2010	10	0.30	1.25	0.32
2011	12	0.31	1.66	0.142
2012	11	0.81	2.33	0.042
Among sub-sites within sites				
2010	21	0.24	1.44	0.096
2011	23	0.18	0.73	0.812
2012	23	0.35	1.31	0.158
Among collectors within sub-sites				
2010	379	0.17		
2011	459	0.25		
2012	428	0.27		
Total				
2010	413			
2011	505			
2012	472			

Variance component analysis

The variance component analysis largely agreed with the results of the nested ANOVAs, although it also suggested an important scale of variability that could not be discerned from the latter. More specifically, most of the observed variation in YOY density was attributed

to the smallest spatial scale sampled, i.e., the collector level (equivalent to the ANOVA error term), which explained 76% of the spatial variation in YOY density in 2010, 64% in 2011 and 58% in 2012. The area spatial scale, which was significant in all three years, was the second most important scale in the variance component analysis, explaining 19-21% of the spatial variation in YOY density in the three years of the study. The largest spatial scale, i.e., the region, explained no variation (0%) in YOY density in 2010, but 15-16% in 2011 and 2012, which was also consistent with results of the nested ANOVAs (the region term was not significant in 2010, but was significant in 2011 and 2012). Very little of the variation in YOY density was observed among sites of a same area ($\leq 6\%$) or sub-sites of a same site ($\leq 2\%$), which also is in good agreement with the results of the nested ANOVAs, as no significant variation in YOY density was observed at either of these spatial scales in any of the three study years (Table 1.2.2).

Table 1.2.2. Partitioning of total variation in lobster YOY density across the hierarchy of spatial scales used in the study in 2010, 2011 and 2012.

Scale	% observed variation		
	2010	2011	2012
Region	0.0	16.4	14.7
Area	20.0	19.1	20.7
Site	3.7	0.3	5.4
Sub-site	0.8	0.0	1.7
Collector	75.5	64.1	57.5

Patchiness indices

When the percentage of significant patchiness (% of units statistically significant at a particular scale) obtained via our randomization approach was plotted as a function of spatial scale (km), two clear patterns arose (Figure 1.4.4). First, there were relatively few instances of significant ($\alpha = 0.05$) patchiness in YOY density, only 9% overall, and second the incidence of significant patchiness was clearly dependent on scale. Only 0-5% of randomizations among collectors of a same site (0.001-0.06 km) showed significant patchiness in the three years of the study, which is not more than would be expected under a null hypothesis of no patchiness at an alpha level of 0.05. Similarly, few instances of significant patchiness were observed at the sub-site (3% across the three years; 0.06-0.1 km) and the site (15%; 0.5-5 km) scales across the three study years, while significant patchiness was quite consistently observed at the area scale (83%, or 5 out of 6; 10-80 km) and the regional scale (66%, or 2 years out of 3; 140 km) (Figure 1.4.4).

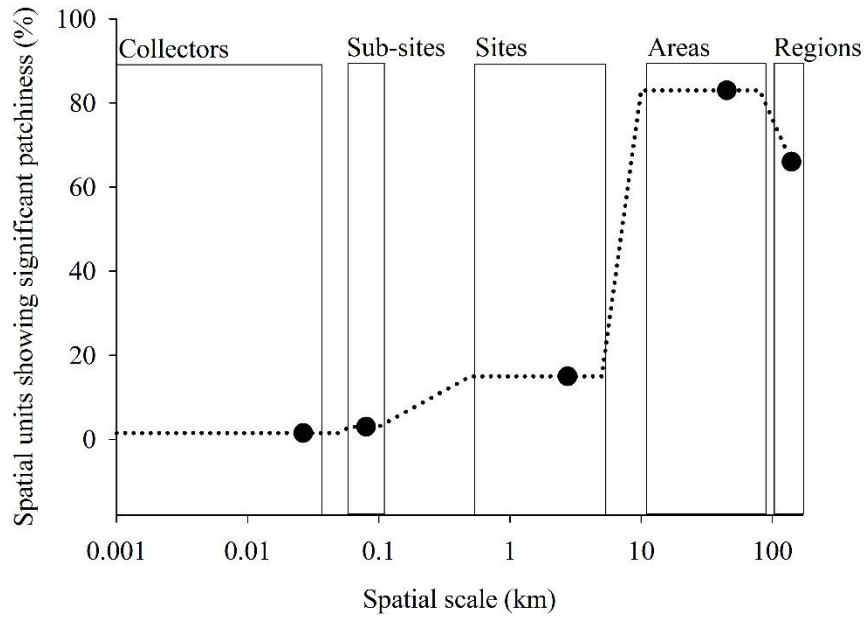


Figure 1.4.4. Percentage of units showing significant ($\alpha = 0.05$) patchiness in YOY (lobsters < 13 mm) density over the three years of the study (2010-2012) and at each of the five spatial scales of the study (i.e., collectors, sub-sites, sites, areas and regions); percent patchiness was determined by our index of patchiness and randomization of the YOY data, and spatial scale is depicted in terms of the distance between sampling units in kilometers. The boxes show the range of scale values for each scale category, while the black circles show the average of these values. Within any given year, $n = 413-559$ for the collector scale, 22-48 for the sub-site scale, 22-24 for the site scale, 11 for the area scale and 2 for the region scale.

Discussion

This study demonstrates that benthic recruitment of American lobster in the Canadian Gulf of Maine varies at a hierarchy of spatial scales, and it provides insight into processes that may underlie some of these patterns.

Patterns

The three quantitative approaches we used to analyze our data revealed patchiness in benthic recruitment at certain spatial scales. Our analysis revealed significant evidence of patchiness in only 14 of the 163 tests (8.6%) done at different spatial scales and years of the study, which seems to suggest that benthic recruitment of American lobster is rarely if ever “patchy” (i.e., clumped, or aggregated), given the alpha level used in these analyses (5%). However, those instances of significant patchiness were clearly not independent of scale, and there was strong and consistent evidence of patchiness at certain scales. More specifically, whereas only 1.6% of tests at the collector scale (1/64), 4.7% at the sub-site scale (3/64) and 11.5% at the site scale (3/26) were significant, as many as 83.3% and 67.7% were significant at the area (5/6) and region (2/3) scales, respectively. The single instance of non-significant patchiness at the area scale may have been due to very low overall YOY abundance in the SWNS region in 2012. Results of the nested ANOVAs were consistent with those of randomization analyses, revealing statistically significant patchiness in benthic recruitment in 3/3 years at the area scale, 2/3 at the region scale, 1/3 at the site scale and 0/3 at the sub-site scale. These results were also largely consistent with the variance component analysis (VCA), which revealed that 20, 19 and 21% of the

variation in benthic recruitment occurred between areas of a same region over the three years of the study, respectively, 0, 16 and 15% between regions, $\leq 5\%$ between sites of an area and $<2\%$ between sub-sites of a same site. There was, however, one marked difference in the outcome of the VCA and the randomization analyses, which occurred at the collector scale. More specifically, the VCA revealed that most of the variability in YOY density was observed among collectors of a same site, with 76, 64, and 58% of the variance observed at this scale in the three years of the study, respectively. However, our randomization of the YOY density data clearly showed that the high variance observed at this scale was the unavoidable quantitative outcome of a relatively small number of YOY found among a relatively large number of collectors, and therefore likely not the result of any particular physical or biological process. We believe that such randomization approaches represent a useful tool to study spatial patterns of patchiness, and in particular to distinguish between patterns that arise “by chance” and those that may be predicted based on understanding of particular processes.

Our findings concerning the spatial scale of patchiness in lobster benthic recruitment are in general agreement with the small number of studies that provide comparable information. First, Wahle and Incze (1997) observed striking difference in benthic recruitment on two sides of an island in the Gulf of Maine, and the spatial scale of these two patches (ca. 1 km²) is roughly equivalent to the area scale of our study (0.4-4 km²), which is the scale that contributed most to process-driven patchiness in benthic recruitment. Similarly, Palma *et al.* (1999) reported low variation in settlement at a scale that roughly

corresponds with our site scale (ca. 1-10 km, versus 0.5-5 km in this study), moderate variation at a scale similar to our region scale (ca. 120 km, versus 140 km in this study), and markedly more variation at a scale similar to our area scale (ca. 10-100 km, versus 10-80 km in this study). Finally, a more recent study with greater spatial coverage revealed variation in benthic recruitment between Rhode Island, mid coast Maine, New Brunswick and Nova Scotia at scales similar to our region scale (ca. 200 km, versus 140 km in this study) (Wahle et al. 2013). It is noteworthy that these congruent results were observed even though scale was represented in two different ways in these studies, first as area of the patches surveyed (Wahle and Incze 1997; this study) and second as the distance between these patches (Palma *et al.*, 1999; Wahle et al. 2013; this study).

What is perhaps more surprising than the consistency in the occurrence (or not) of patchiness at particular scales is that it was largely consistently the same areas (and to some extent the same regions) that showed high or low levels of benthic recruitment in different years. In particular, 3 sampling areas (out of 11), all in the SNB region (Maces Bay, Deadmans Harbour, and Beaver Harbour), consistently had a disproportionate number of the young-of-year and can be considered benthic recruitment “hotspots” (upper 25th density percentile). These areas had between 58-71% of all YOY sampled over the three years of the study, while comprising only 27% of the areas surveyed. Similarly, 6 of the 11 areas (55%) consistently had fewer than 5% of the annual abundance of YOY, and can therefore be considered benthic recruitment “coldspots” (lower 25th density percentile). This consistency was observed despite the fact that mean benthic recruitment varied to some

extent between the three years of the study. We found some evidence of similar consistency at the regional scale, with benthic recruitment being significantly greater in SNB than in SWNS in both 2011 and 2012; in 2010 benthic recruitment was very similar in the two regions. Benthic recruitment did, however, increase markedly from 2010 to 2012 in the SNB region, while it decreased moderately between 2010 and 2011-2012 in SWNS. These results therefore indicate some consistency in spatial patterns in benthic recruitment at the region scale over the three years of the study, while at the same time showing that benthic recruitment also fluctuates independently in our two study regions from year to year. Our ability to investigate patchiness at the region scale is somewhat limited since we only had two regions in our study. Therefore our inferences are more relevant to the two regions we studied than to the “regional scale” in general.

Environmental processes affecting spatial patterns

Our randomizations indicated that the high variance in benthic recruitment at the collector scale (0.55 m^2) was not greater than would be expected if YOY that were found in a particular site were randomly allocated to the different collectors of that site, which indicates that high variance at the collectors scale was likely not the result of any particular physical or biological process, but rather was probably the outcome of a relatively small number of YOY inhabiting a relatively large number of collectors. At first, this result suggests that small-scale habitat selection by postlarvae did not affect their recruitment to the benthos in our study, which is inconsistent with results of several laboratory experiments (Botero and Atema 1982; Boudreau et al. 1990). This result is likely due to

the fact that we used a “standardized habitat” to sample young of year lobsters, in the form of collectors filled with cobble, which eliminated the opportunity for postlarvae to select amongst small patches of varying quality. Consistent with this interpretation is the fact that a recent field study (Burdett-Coutts et al. 2014) found significant variation in American lobster YOY abundance among quadrats haphazardly deployed on heterogeneous cobble beds.

We believe that the strong and consistent patchiness at the area scale (0.4-4 km²) is related to small-scale topographical features and coastal currents and their role in the delivery and retention of larvae to these areas. For example, there are strong tidal currents around one of the lowest benthic recruitment areas (West Isles), which may prevent larval settlement given the strength of the current (time and depth-averaged tidal currents ca. 3 m/s) relative to the swimming capabilities of postlarvae, which have been recorded swimming at a maximum of 0.18 m/s in the field and 0.14 m/s in the laboratory (Cobb et al. 1989; Rooney and Cobb 1991; Karsten et al. 2008). In contrast, the embayments characterizing our three highest benthic recruitment areas (Maces Bay, Deadmans Harbour, and Beaver Harbour) may encourage larval retention.

Variation in benthic recruitment at the “region” scale (127 and 674 km²) might be explained by large-scale oceanic currents and perhaps also differences in larval production between the two study regions. Palma et al. (1999) and Wahle et al. (2013) similarly attributed spatial variability in benthic recruitment among regions in New England and

Atlantic Canada to the modulation of larval transport and delivery by large-scale oceanographic currents.

Future work should more explicitly investigate physical and biological processes potentially underlying variability in benthic recruitment at different spatial scales, with the “area scale” (0.4-4 km²) being of particular interest given the high variability in benthic recruitment observed at this scale in this study. We recommend in particular quantifying the relationship between variability in benthic recruitment and the following biotic and abiotic factors: bottom and surface temperatures, wind, wind driven fetch, presence of juvenile lobsters, rainfall, Atlantic oscillation index (NAO), geopotential height and surface temperature anomalies.

Importance of monitoring benthic recruitment

The development of tools to predict trends in the abundance of commercially fished species represents one of the main goals of fisheries science. In the case of lobsters and crabs, larval settlement indices, which quantify the abundance of the life stage that makes the transition from the pelagos to the benthos, have proven markedly more useful than indices based on egg production or larval stages sampled with larval tows. For example, Miller (1997) found no spatial correlation between egg production or early larval stages (I-III) and fishery recruitment of American lobster (at the scale of 190 km in eastern Nova Scotia) but found significant correlation between postlarvae (stage IV) in the water column and fishery recruitment. In Australia and New Zealand, settlement indices are now being used to forecast two lobster fisheries, the western rock lobster (*Panulirus cygnus*) and the southern

rock lobster (*Jasus edwardsii*) (Phillips, 1986; Caputi *et al.*, 1995; Booth and McKenzie, 2009). Similarly, in the Caribbean spiny lobster (*Panulirus argus*), postlarval settlement indices have been developed with the future goal of fisheries forecasting (Acosta *et al.* 1997; Eggleston *et al.* 1998). In an effort to establish a similar predictive tool for the American lobster, lobster benthic recruitment data has been collected for over 20 years in select locations in New England and one in the Bay of Fundy. This data is now considered in management of the lobster stock in Maine (Wahle *et al.* 2013), which led to the development of the American Lobster Settlement Index (ALSI), a collaborative monitoring program led by academics, government scientists and lobster harvesters that measures annual abundance of newly settled lobster in a number of locations in New England and Atlantic Canada using both SCUBA-assisted suction sampling and vessel-deployed collectors. In addition to its forecasting role, the ALSI database could also be used to support analyses similar to those conducted in this study, to further assess scale of patchiness in lobster benthic recruitment; the database would be particularly useful to assess patchiness at larger spatial scales, which were poorly replicated in this study. This unique database could also be used to improve future sampling designs. In particular, more explicit recognition of scale of benthic recruitment patchiness may lead to a reduction of redundant information by reduced sampling at scales where there is low variability in settlement and increase in useful information by increased sampling at scales where benthic recruitment varies more.

Summary

In summary, we identified several “hotspots” and “coldspots” of American lobster benthic recruitment in the Canadian Gulf of Maine, where patchiness in benthic recruitment occurred mainly at the “area scale” of 0.4-4 km² and to a lesser extent at the “regional scale” of 127-624 km², but not at smaller spatial scales. The high variance in young-of-year abundance at the scale of 0.4-4 km² may have been related to the role of small-scale coastal currents and topographical features in the retention and flushing of larvae from high- and low-recruitment areas, respectively. This high variance points to the need to increase the resolution of bio-physical larval dispersal models to be able to predict small-scale patches of high and low settlement of American lobster, which in turn will require improved understanding of smaller-scale coastal flow patterns (Chasse and Miller 2010 Incze et al. 2010).

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Chapter 2: Light traps as a tool to sample pelagic larvae of American lobster (*Homarus americanus*)

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LIGHT TRAPS AS A TOOL TO SAMPLE PELAGIC LARVAE OF AMERICAN LOBSTER (*HOMARUS AMERICANUS*)

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Addendum to the publication

During the examination of this thesis, it was pointed out that I may have assumed that postlarvae display positive phototaxis over a longer period than they do, and hence that the postlarvae caught during the study may not have accurately reflected differences in postlarval supply to my different study areas. In an older study that was pointed out to me by a member of the examining committee, stage IV postlarvae started displaying negative phototaxis approximately halfway through this phase (Hadley 1908). While I was aware that postlarvae become negatively phototactic during their development, and did acknowledge this in the paper, I did not explicitly address when this transition occurred and whether this could have affected the interpretation of my results, pertaining to different levels of supply of postlarvae to my different study areas. Based on development functions of stage IV postlarvae (Quinn and Rochette 2015) at temperatures they experienced during this study, I estimate their total development period to have been ca. 31-36 days, and hence that they may have showed negative phototaxis in the area for 15-18 days before settlement. This means that there is a certain time lag between when postlarvae were caught in the light traps and when they would have been ready to settle on the bottom, which could have led to further displacement of the postlarvae after they reached the light trap sampling sites. I acknowledge this source of uncertainty, and that this uncertainty does somewhat weaken the evidence for the argument developed in this paper. However, the facts remain that all postlarvae were found in areas where the recruitment of YOY to the sea floor was high, and that this distribution was significantly ($p = 0.0048$) skewed relative to the number of traps deployed in these different areas, suggesting that the light traps likely did provide an

accurate index of postlarval supply at the spatial scales considered in this study (10-80 km between areas), despite this uncertainty.

The external examiner also rightly pointed out that there was no proper control for the light treatments in the lab experiment, and that the larvae may have simply entered the traps by chance, and not because they were attracted to the light source. This was indeed not thoroughly addressed during the study, because of an insufficient number of postlarvae to include proper control trials. I did, nevertheless, set up one tank with seven (remaining) postlarvae and a light trap with no light source. None of these seven postlarvae were found inside the trap after the 24-hour study period, compared to an average of 57% and 53% in the “low” and “high” light intensity treatments, respectively, suggesting that the postlarvae in these latter treatments did indeed enter the traps because of the light, and not simply by “chance”. Importantly, however, my inferences concerning spatial variation in the supply of postlarvae would not be challenged if this was untrue. In fact, given the photosensitivity issue discussed above, the spatial patterns documented in the study would be expected to be an equivalent or potentially even a better indicator of postlarval supply if postlarvae entered the traps by chance, and not due to the light source.

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Abstract

We built a simple and relatively inexpensive light trap and tested its efficacy at catching pelagic larvae of the American lobster *Homarus americanus* in the field and the laboratory. We were particularly interested in assessing the potential of using these traps to support research on pelagic-benthic coupling, and therefore contrasted the abundance of postlarvae in the light traps to spatial variability in postlarval settlement. In laboratory experiments, 55% of postlarvae placed in 1 m diameter tanks were caught by the light traps, and 24% of postlarvae placed inside the light traps escaped, over a 24-hour period. In the field, the light traps caught lobster larval stages I and IV (i.e., the postlarva), but no stage II or III larvae. Catches of lobster postlarvae were lower than in previously published larval tow studies when standardizing for the amount of time the sampling devices spent in the water, but were roughly similar to these when standardized for the number of work hours required to obtain the samples. The light traps also caught a suite of other invertebrates, such as northern krill and all larval stages of green crabs and Atlantic rock crab, as well as some fishes, such as juvenile lumpfish. The abundance of stage IV lobster postlarvae was significantly related to spatial variability in settlement, but unsurprisingly that of stage I larvae was not. Our results suggest that light traps may eventually provide an additional tool to sample lobster larvae and postlarvae, which may be particularly useful to study pelagic-benthic coupling as this passive sampling device better lends itself to the simultaneous sampling of many areas than do larval tows. However, we believe further lab and field experiments investigating modified trap designs, optimal soak time, and effect of

depth, should be conducted to improve the efficacy of this new tool in American lobster research.

Introduction

Pelagic larval phases of marine invertebrates and fishes have traditionally been sampled with vertical or horizontal larval tows, which involve pulling or pushing nets with various size openings and mesh through the water (see McGurk 1992, for examples). Such larval tows work particularly well at sampling slow and abundant planktonic organisms, but they are somewhat less efficient at sampling strong-swimming and scarce organisms (Pineda et al. 2010). In addition, larval tows as they are currently designed are difficult to use in shallow water bordering irregular coastlines and they are weather dependent. For example, larvae that usually occupy the surface layers are thought to move to deeper waters when it is raining or when wave action is considerable (Wilder 1953; Øresland 2007). Larval tows also tend to be logistically involved and expensive, especially if multiple locations have to be sampled simultaneously. These limitations of larval tows have led to the emergence of various passive collectors as another tool to sample pelagic larvae (Pineda et al. 2010). These passive collectors are generally relatively easy and quick to operate from the shore or from a small boat, making it easier to sample many locations simultaneously. They can also be deployed for multiple days, which means they sample over longer time periods than tows and are thus less affected by conditions that might temporarily affect larval behaviour (e.g., diving to avoid waves or rain). Finally, these passive collectors can easily be deployed at different depths and often catch delicate organisms without harming them (Øresland 2007).

Going back to the late 1930s, larval tows have been the tool of choice in a number of studies to quantify the abundance of different larval stages of the American lobster *Homarus americanus* Milne Edwards, 1837 (Fogarty 1983). These tows have generally captured relatively high numbers of stage I larvae, but markedly lower numbers of stages II and III, and somewhat fewer stage IV (i.e., postlarvae), which are particularly strong swimmers and also presumably less abundant due to mortality (Scarratt 1973). The postlarva has been the focus of studies on stock structure and connectivity, as it is the larval stage that eventually makes the transition from the plankton to the benthos. Over 4 years of sampling and approximately 1,600 30-min tows in the Northumberland Strait, Canada, Wilder (1953) caught an average of 32.8, 6.9 and 3.2 larvae of stages I, II, and III per tow, respectively, but only 2.6 postlarvae (stage IV) per tow. In another 4-year study in southern New-England, Lund and Stewart (1969) concluded that lobster larvae were widely distributed in offshore waters, but only three 30-min tows out of 50 contained more than 10 larvae (max of 24), and these only comprised stage I and II individuals. A greater number of larvae were caught inshore, but the number of postlarvae remained low, fewer than 2 per tow (Lund and Stewart 1969). Similarly, in an attempt to link spatial variation in postlarval abundance to fisheries landings, Miller (1997) used multiple larval tows in seven coastal divisions along the eastern shore of Nova Scotia, Canada, and although study results were useful in revealing link between postlarval abundance and fisheries landings only 0.3 - 3.3 postlarvae/1000 m² were caught in the different divisions. Given the importance of lobster postlarvae to the study of source-sink dynamics and their relatively low numbers in larval tows, likely due to low natural densities and perhaps also gear

avoidance, we decided to test the efficacy of a passive sampling device to capture these larvae.

The passive larval sampling device that we choose to explore was a “light trap”, which was originally designed to catch larval stages of fish in lakes, and on the Great Barrier Reef in Australia (Gregory and Powles 1985; Doherty 1987). During Doherty’s (1987) first trials, the light trap sampled both fish larvae and invertebrate zooplankton, including crab larvae, euphausiids and caridean shrimp, which then led to their widespread use to monitor invertebrates and fishes on coral reefs (Choat et al. 1993; Reynolds and Sponaugle 1994; Meekan et al. 2001). Most of these studies were conducted in tropical waters, but Hickford and Schiel (1999) showed that light traps are also effective at catching fish larvae and invertebrates in the temperate waters south of New Zealand.

These light trap studies in tropical waters led to a recent study in Sweden where light traps were used to assess the vertical distribution of Norwegian (*Nephrops norvegicus*, Linnaeus, 1758) and European (*Homarus gammarus*, Linnaeus, 1758) lobster larvae (Øresland 2007). In this study, 75 traps deployed over a period of ≈ 8 days caught 102 *N. norvegicus* of larval stages I-III and 34 *H. gammarus* of larval stages I and II. Since these two European species are closely related to the American lobster *Homarus americanus*, we decided to build traps similar to these in design (Øresland 2007).

The overarching goal of our study was to assess the potential of using light traps to support research on American lobster larvae in nature, with particular interest in the final larval

stage (i.e., the postlarva). We were particularly interested in this larval stage because it: i- is generally captured in low numbers, ii- provides an indication of potential for settlement in an area, and iii- is most relevant to studies of connectivity and recruitment. The four objectives of this study were to: (1) build an inexpensive passive light trap based on Øresland's (2007) design; (2) assess in the laboratory the tendency of lobster postlarvae to enter and escape the light trap, the later being a problem reported in other light-trap studies (Meekan et al. 2000); (3) test the light trap's ability to catch pelagic larval stages of the American lobster in the field; (4) conduct a preliminary investigation of the potential of using light traps to study pelagic-benthic coupling, by linking spatial patterns of larval abundance and settlement.

Material and Methods

Light trap design

Our light trap design is a simplified version of the light trap used by Øresland (2007). The Øresland (2007) light trap has a modifiable trap opening and it is modular, which enables it to be customized easily for different applications. Our light trap is made of a single solid piece of white PVC pipe, 10 cm in diameter and 40 cm long, which reduced complexity and cost. We molded the top of a clear plastic 2L soda bottle over one end of the PVC tube, such that the 2.4 cm opening of the bottle was the entrance to the trap (Figure 2.1.5). On the other end of the PVC tube we placed a 10 cm rubber cap that was tightened on with a hose clamp. For deployment a rope was tied to each end of the trap, and a stainless-steel clip was placed in the middle of the rope so it could easily be clipped on to a mooring. As a lure, Fenix Tactical LD40 LED flashlights were used. According to the manufacturer these flashlights are shockproof and waterproof down to 2 m depth, although pressure testing done by us on a subsample of the flashlights revealed that they were waterproof to 10 m. The flashlights use four AA batteries, with a battery life of 10 days and 8 hours at the lowest brightness setting (4 lumens), which is what was used in the field study. Total cost of materials to build and operate (excluding boat rental) one trap over 10 days (flashlight included) was 80 Canadian dollars. Each additional 10-day deployment of one trap costs around 4 Canadian dollars, as batteries need to be replaced after each deployment.

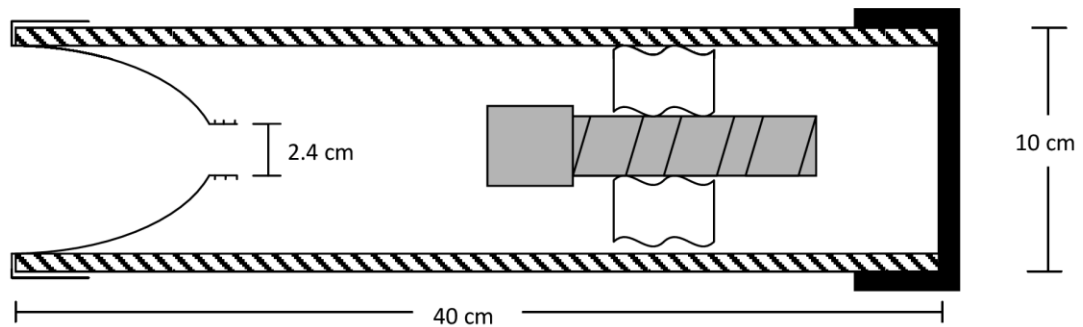


Figure 2.1.5 Diagram of the light trap used in this study. The main body of the trap (hatched area) was made of white PVC pipe, while its opening was made from the top of a clear 2-L plastic soda bottle. The other end of the trap was sealed with a rubber cap held down with a hose clamp. The flashlight was secured using the hard plastic ring from the bottom of the soda bottle such that the light source was close to the middle of the pipe.

Laboratory experiments

The tendency of lobster postlarvae to enter the light traps, under ideal conditions in the lab, was estimated by placing one light trap in each of eight tanks (1 m diameter, 0.8 m high) with running seawater at controlled temperature of 16°C and with a natural L:D cycle. Four of the tanks had the flashlights set at the high setting (110 lumens) while the other four had them set at the low setting (4 lumens), the latter being the setting used in the field study. We released 10 hatchery (*Homarus Inc*, Shippagan, New Brunswick) early-stage postlarvae in each tank, all of which were first confirmed to still be photo-positive, as postlarvae become photo-negative when they reach competency and are ready to settle (Cobb et al. 1989). The experiment was started at 10h00, and catchability was determined

by counting the proportion of postlarvae that were inside the trap when the experiment was ended 24 hours later.

The ability of postlarvae to escape the traps after being captured was estimated using the same eight tanks with the flashlights set again at high (110 lumens) and low (4 lumens) intensity. In this experiment, we put 10 lobster postlarvae into each trap before these were placed in the tanks. This experiment was started at 09h00 and ran for 24 hours.

Student's t-tests were used to compare the average proportion of postlarvae that were captured (experiment 1) and that escaped (experiment 2) in the two light intensity treatments.

Field sampling

We did the field component of our study in 6 geographical areas in the south-western Bay of Fundy, New Brunswick, Canada. The areas were selected because they had been monitored for American lobster settlement in 2009 - 2012, using cobble-filled settlement collectors (see Wahle et al. 2009). Three of those areas (Maces Bay, Beaver Harbour, and Deadmans Harbour) had high settlement densities while the other three areas (Seeleys Cove, West Isles, and Passamaquoddy Bay) had low or no settlement (Sigurdsson and Rochette, unpublished data). In each of the six areas, 8 light traps were deployed at 1 m depth on an anchored line, buoyed at the surface. The light traps were spread out so they were approximately 50 meters apart from each other. Settlement was also monitored in each of the areas with 50, cobble-filled, 0.5 m² settlement collectors (see Wahle et al. 2009).

The light traps were deployed on the 26th of July 2011, individually attached to the buoyed line of 8 collectors in each of the 6 study areas, and were attended every 6-10 days, depending on weather, until the 9th of October, which was expected to cover most of the period when lobster postlarvae were in the water column in the area. When the traps were attended, they were carefully pulled out of the water with the opening pointed up, to avoid loss of larvae. All contents of the trap were then poured through a 1 mm sieve and placed in a jar with seawater, which was brought back to laboratory facilities at the University of New Brunswick, Saint John, for later identification. The batteries of each flashlight were replaced, and the traps were redeployed. All lobster larvae found in the samples were identified in the laboratory to a stage (I, II, III or IV), decapod larvae were identified as zoea or megalope, and fishes and euphausiids were identified to species. All fish found in the traps were dissected to observe for evidence of consumption of lobster larvae.

In order to assess the sampling efficiency of the light traps relative to traditional larval tows, we compared catches of stage I, stage IV, and total number of larvae in our light traps to numbers obtained in larval tow studies from southern New England to Northumberland Strait between 1967 and 1982 and summarized in Fogarty (1983) that included information on number of tows and tow duration. Given that one is a passive and the other an active sampling device, we standardized and compared the number of larvae they caught both in relation to the i- amount of time the sampling gear was in the water and ii- hours of work required to acquire the samples.

The settlement collectors were deployed 7-13 July 2011 and retrieved 19-20 October 2011. Upon retrieval collectors were brought to the Huntsman Marine Sciences Centre, in Saint Andrews, NB, where they were carefully inspected for the presence of lobsters. All lobsters were measured for carapace length, and based on size frequency curves from this and previous years, all lobsters smaller than 13 mm carapace length were considered to have settled during the study period; mean density of settlers was estimated for each study area on the basis of the number of recently settled lobsters found in the collectors.

Results

Trap design

The traps held up well and were easy to attend to from a small inflatable boat with an outboard engine. Only three of the 48 traps were lost over the 76-day field experiment; one trap got washed up on the beach in hurricane Irene (late August 2011), another was likely stolen, while the third had its line to the surface buoy cut. In addition to the three lost traps, five flashlights flooded or broke and had to be replaced, three of those during hurricane Irene.

Laboratory experiments

Capture rates of lobster postlarvae over the 24-hour experimental period varied between 47-64% (Figure 2.2.6A), and did not differ significantly between the two light intensity treatments ($t_6 = 0.56$, $p = 0.60$). Percentage of postlarvae retained over 24 hours varied between 58-95% (Figure 2.2.6B), and also did not differ significantly between the two light intensity treatments ($t_6 = 0.65$, $p = 0.65$).

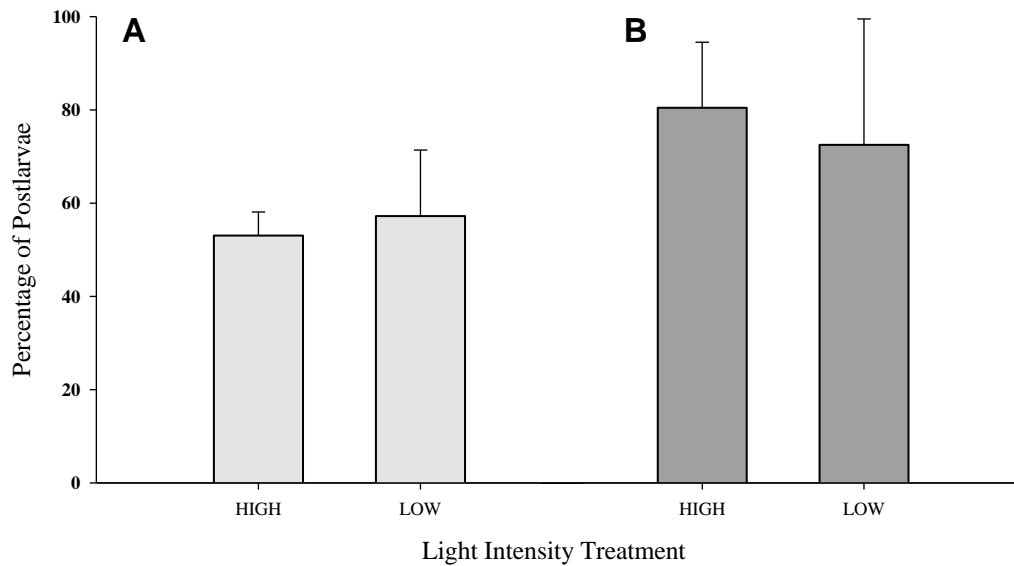


Figure 2.2.6. Mean percentage (+SE) of postlarvae captured (A) and retained (B) after 24 hours in the high (110 lumens) and low (4 lumens) light intensity treatments of two laboratory experiments testing the efficiency of the light trap.

Field sampling

A total of 8 stage IV postlarvae and 15 stage I larvae were caught in the field component of this study (Table 2.1.3). All of the postlarvae were caught in two of the three areas where settlement was high, and has been consistently high over the past 4 years (Beaver Harbour and Deadmans Harbour, NB), and none were captured in the three areas where settlement was low and has been consistently low over the same time period (Table 2.1.3). The probability of all 8 postlarvae being captured in the high-settlement areas under a null hypothesis of no spatial bias in the distribution of these postlarvae is 0.0048, accounting for the small difference in number of light traps used in high- and low-settlement areas. Stage I lobster larvae, in contrast, were split nearly evenly between high and low areas

(Table 2.1.3), 6 from one area where settlement was very high (Maces Bay), 1 from another area where settlement was high (Beaver Harbour) and 8 from one area where settlement was low (Passamaquoddy Bay). The 15 stage I larvae were caught in late July, whereas seven of the postlarvae were caught in middle of August and one was caught in late September (Figure 2.3.7). No lobster larvae were found in the stomachs of fish captured by the light traps.

The light traps in our study caught considerably fewer lobster larvae than previously published larval tows (Fogarty 1983), particularly when standardized for the amount of time the sampling gear spent in the water and less so when standardized for the number of work hours at sea required to obtain the samples (Table 2.2.4). For example, our light traps caught 0.00009 stage IV larvae per trap-hour of sampling compared to an average of 0.9 for the 7 larval tow studies published in Fogarty (1983). However, when the numbers of stage IV larvae caught were compared in terms of hours of work at sea, the capture rate of light traps was similar to some of the less successful tow studies, with around 0.18 postlarvae/working hour (Table 2.2.4). Similarly, only 0.0017 stage I larvae were caught per hour sampled by the light traps compared to an average of 19 per hour sampled in the larval tow studies. Differences in catches of stage I larvae were lower when standardized for working hours, but they were still considerable, with 0.34 stage I larvae caught per working hour by the light traps compared to 19 in the larval tow studies.

Table 2.1.3. Catches of the four larval stages of American lobster *Homarus americanus* in the light traps and densities of recently settled (young of year) lobster in cobble-filled settlement collectors. Light traps and settlement collectors were both deployed in 2011 in three areas where settlement has

been high in the last 4 years (0.8-2.5 settlers/m²) and three areas where it has been low (0-0.6 settlers/m²) (Sigurdsson and Rochette, unpublished data).

Areas	Average settlement (n/m ² ± SE)	Number of light trap hauls	Stage (n)				
			I	II	III	IV	Total
High settlement areas							
Deadmans Harbour 45.0476°N, 66.7812°W	1.00±0.22	50	0	0	0	4	5
Maces Bay 45.1080°N, 66.5718°W	1.85±0.25	50	6	0	0	0	6
Beaver Harbour 45.0683°N, 66.7252°W	1.10±0.20	44	1	0	0	4	4
All high areas	1.32 ±0.27	144	7	0	0	8	14
Low settlement areas							
Passamaquoddy Bay 45.1502°N, 67.0359°W	0.11±0.06	50	8	0	0	0	8
Seeleys Cove 45.0857°N, 66.6461°W	0.59±0.13	42	0	0	0	0	0
West Isles 45.0322°N, 66.9321°W	0.22±0.11	45	0	0	0	0	0
All low areas	0.31±0.15	137	8	0	0	0	8
Total		281	15	0	0	8	23

In addition to catching lobster larvae, the traps caught a suite of other invertebrates such as green crab (*Carcinus maeanas*, Linnaeus 1758) zoea (all five stages) and megalope larvae and Atlantic rock crab (*Cancer irroratus*, Say 1817) zoea (all five stages) and megalope, euphausiids (mostly *Meganyctiphanes norvegica*, Sars 1857, in very high numbers), mysis shrimp, amphipods and isopods (*Idiotea* spp.). The traps also caught several fish species, including 55 juvenile lumpfish (*Cycloptera lumpus*), two tomcods (*Microgadus tomcod*) and a snailfish (*Liparis* spp.). Zoea larvae of both green crab and rock crab were found from early August to early September, with the peak in abundance around the third week

of August (Figure 2.3.7). The last larval stage, the megalope, started to appear a bit later, in middle of August, and it peaked in late August/early September (Figure 2.3.7). Green crab larvae were mainly found in one area, Passamaquoddy Bay, while rock crab larvae were found in all areas with no distinctive spatial pattern. Northern krill was mostly limited to one of the low lobster settlement areas, West Isles, where over 1600 individuals were caught. Krill abundance peaked in early August, when over 900 individuals were caught, and no individuals were caught after 11th of September (Figure 2.3.7).

Table 2.2.4. Comparison of the number of stage I, stage IV and total (stages I to IV) lobster larvae caught by light traps in this study (first row) and larval tow studies reviewed by Fogarty (1983) that included information on number of tows and tow duration (rows 2-7). Sampling effort was estimated as the cumulative number of hours the sampling devices (light traps or plankton nets) were in the water (e.g., 47 light traps x 1848 hours/light trap = 86,856 hours). Working hours represents the time at sea necessary to acquire the samples from the light traps or to conduct the larval tows (does not include time to travel to and from study sites).

Study	Region	Sampling effort (h)	Working hours (h)	Larvae caught (n)			Larvae/effort			Larvae/working hours		
				I	IV	Total	I	IV	Total	I	IV	Total
Light traps												
Current study	Bay of Fundy	86856	44	15	8	23	0.00017	0.000092	0.00026	0.34	0.18	0.52
Larval tows												
Lund and Stewart 1970	Long Island Sound	72.5	72.5	474	245	1366	6.5	3.4	18.8	6.5	3.4	18.8
Lund and Stewart 1970	Offshore New England	48	48	57	11	119	1.18	0.23	2.47	1.18	0.23	2.47
Scaratt 1973	Northumberland Strait	224	224	10616	60	11955	47.4	0.26	53.4	47.4	0.26	53.4
Harding et al. 1982	Nova Scotia	26.73	26.73	644	16	924	24.1	0.60	34.6	24.1	0.60	34.6
Sherman and Lewis 1967	Gulf of Maine	109	109	295	65	368	2.7	0.6	3.4	2.7	0.6	3.4
Scaratt 1968	Nova Scotia	50	50	1883	6	1984	37.7	0.1	39.7	37.7	0.1	39.7
Scaratt 1969	Nova Scotia	50	50	673	55	746	13.5	1.1	14.9	13.5	1.1	14.9

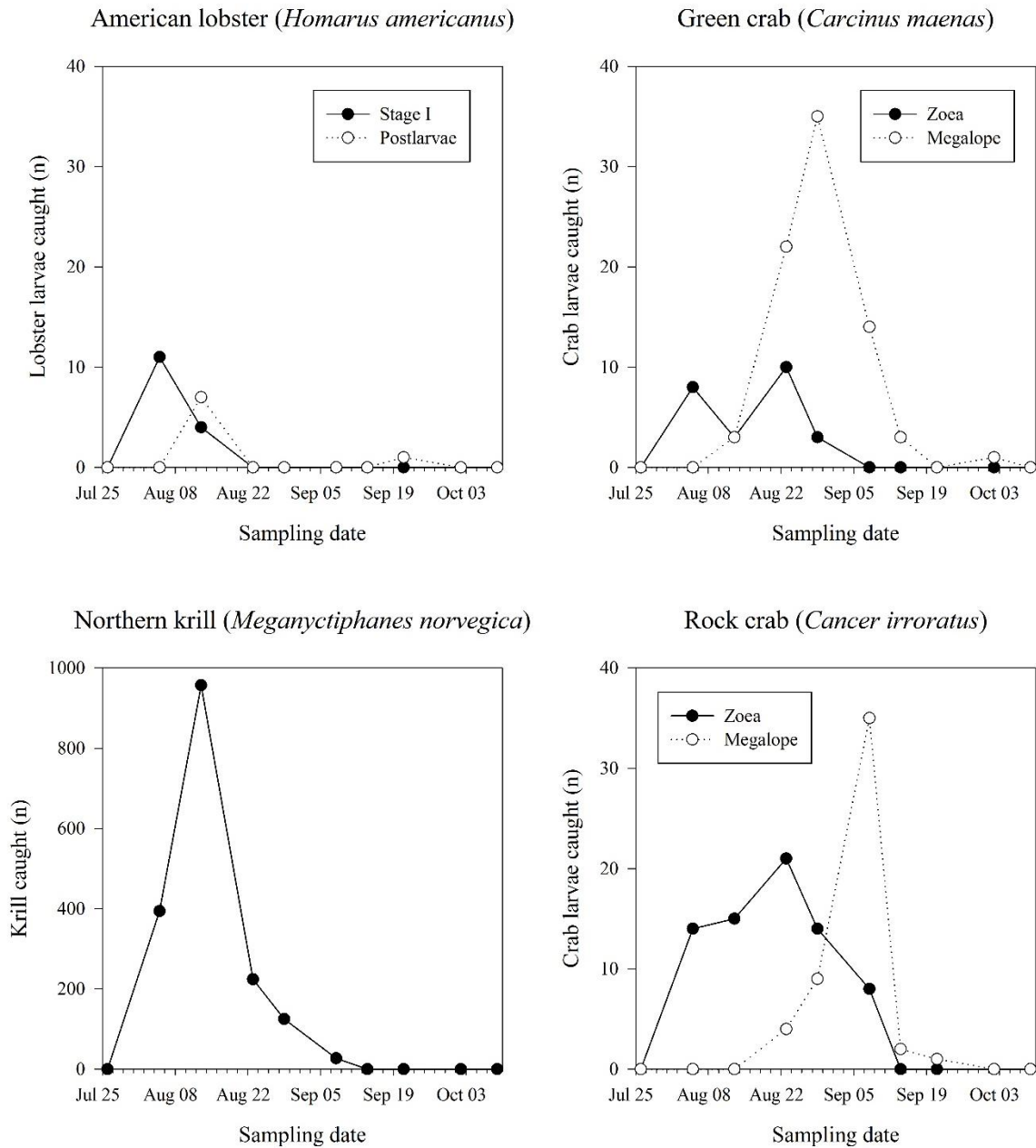


Figure 2.3.7. Catches (n) of four crustacean species commonly found in the light traps over the duration of the study: American lobster, green crab, rock crab and northern krill. For the three decapod species, catches of both early larval stages (black circle) and the final larval stage (white circle) are shown. Note the different scale on the y-axis on the northern krill graph.

Discussion

Our findings show for the first time that light traps can be used to capture American lobster larvae and postlarvae in nature. We were positively surprised to catch stage IV postlarvae as Øresland (2007) only caught larval stages I and II of the closely related *Homarus gammarus* in his light traps, even though his sampling covered the period when stage III and IV larvae were expected to be present in the plankton. Our study, therefore, represents the first reported catches of *Homarus spp.* postlarvae in a light trap.

The light traps did not catch stage II or III lobster larvae. As all lobster larval stages are positively phototactic, apart from the final part of stage IV when postlarvae begin to search for suitable habitat on the bottom (Factor 1995), we are unable to explain the absence of stage II and III larvae in the traps. However, these larval stages have also historically been found in relatively low numbers in larval tow studies. For example, in a review of 13 published accounts of American lobster larval sampling programs conducted from southern New England to Newfoundland between 1936 and 1978, stage II and stage III larvae represented on average only 9% and 8.1% of the larvae caught, respectively (Fogarty 1983).

The total number of lobster larvae captured by the light traps was relatively low (23 larvae in 281 light-trap hauls), and lower than numbers typically caught by larval tows (Fogarty 1983), especially when capture rates are compared on the basis of time the sampling devices spend in the water. However, this particular comparison might not be the most relevant, in terms of utility of these different sampling tools to assess spatial and temporal

patterns in the abundance of lobster larvae, as it ignores a fundamental difference between them, which is that one (the light trap) samples passively and continuously over relatively long periods of time whereas the other (the larval tow) samples over relatively short periods of time and only when being actively pushed through the water by a boat with crew. When catch rates were compared in terms of human work hours, the light trap used in this study seemed to perform fairly similarly to larval tows. Given that operating the light traps is easier than conducting larval tows, particularly if many areas are to be sampled simultaneously and over long periods of time, this new tool could complement larval tows to study lobster larvae. In particular the light trap could prove to be a cost effective method to study spatio-temporal dynamics of lobster larvae and important processes such as pelagic-benthic coupling (e.g. Doherty 1987).

There are other reasons why the relatively low number of lobster larvae caught in our study understates the light trap's potential as a tool to sample lobster larvae. First, given our main interest was in stage IV postlarvae, our deployments were timed to the presence of this particular larval stage in the water and as such would have missed stage I larvae from earlier hatches of the season; hatching was estimated to start in early July in the area the year of our study (M.L. Haarr, University of New Brunswick, unpublished data), whereas we started deploying light traps on the 26th of July. Second, given one of our objectives was to link spatial variability in postlarval abundance to settlement, half of our sites were selected specifically because they were expected, based on previous work, to have very low numbers of postlarvae. Third, visibility in the Bay of Fundy is notoriously poor

(sometimes less than 0.30 m based on Secchi observations) due to plankton concentrations, sediment transport, and turbidity of the bay (Dadswell et al. 1983), and it is likely that the traps would work better in most other areas where lobster larvae are found. Finally, we expect improvements can be made to the light trap design that will increase both catchability as well as retention (see below).

The laboratory experiments demonstrated that lobster postlarvae have a relatively high propensity to enter the light traps. We did not continuously monitor the tanks, and are thus unable to say how quickly they entered and left the traps, but after the 24-hour time period an average of 55% of the postlarvae were found in the traps, and this value did not differ between light intensity treatments. Given the proportion of larvae that were found to escape the traps over a 24-hour period (see below), we estimate that at least 68% of the postlarvae entered the traps at some point over the 24-hour experimental period. Catchability has been previously identified as one of the limitations of light traps (Meekan et al. 2000). For example, trials in a mesocosm (1.8 m diameter, 2.5 m deep) study on the coral reefs of Australia showed that capture rates averaged 38% for invertebrates (i.e., polychaetes, euphausiids, mysids, amphipods, stomatopods, isopods and decapod shrimps) and were somewhat lower for various fish species (Meekan et al. 2000). Catchability of lobster postlarvae by our traps is thus relatively high, and could perhaps be further improved by reducing losses (see below) and using a more intense light source. We found no effect of light intensity on the capture and escape rates of postlarvae during our laboratory experiment, in which postlarvae were bound to detect the light source given the relatively

small size of the tanks, but in open water the area from which the postlarvae could be attracted would undoubtedly increase with intensity of the light source. In our field study we placed the flashlight at the lowest intensity of 4 lumens, to increase its longevity, but the flashlight came with a variety of settings, the highest being 110 lumens. Experiments should be conducted to compare the efficacy of the traps in nature using different light intensities, to help optimize study design considering the trade off between area of attraction and longevity of the light source.

It is possible that changes to the trap design could reduce escapes. We suggest, in particular, that a longer and narrower funnel could possibly reduce escapes, as the opening on our traps was fairly wide (24 mm diameter) in comparison to the size of the lobster postlarvae (ca. 2-3 mm across). Also, an additional chamber in the trap, made by adding a second funnel inside the pipe, could perhaps also increase larval retention after capture. Given the relatively high rate of escapes it is likely worthwhile to experiment with different trap designs to attempt to reduce these losses.

Our results suggest that light traps could eventually complement larval tows in American lobster larval research, especially if the tool's sampling efficacy can be improved. In particular, the abundance of stage IV postlarvae caught by the traps could be a good index of spatial and temporal variability in settlement (assuming adequate settlement substrate). Lobster larvae drift for 11 days (at 22°C) to 54 days (at 10°C) and can disperse > 200 km before they are competent (i.e., physiologically ready) to settle (Ennis 1995; Cobb and Castro 2006; Chassé and Miller 2010; Incze et al. 2010), suggesting the abundance of stage

I individuals in an area is not going to be a good indicator of settlement in that area. Not surprisingly, then, the abundance of stage I larvae in our light traps was clearly not related to lobster settlement in our different study areas. In contrast, lobster larvae settle only ca. 2-6 days after moulting into the stage IV postlarva (Cobb et al., 1989), and hence the presence of stage IV larvae in the plankton could be a good index of settlement potential in an area, which is corroborated by our results where more postlarvae (in light traps) were found in areas where densities of young-of-year settlers (in cobble-filled collectors) was greatest.

In conclusion, we built a simple and relatively inexpensive light trap that can be used to sample pelagic larvae of the American lobster. More work needs to be done to increase the sampling efficacy of the tool, which may enable its use to study pelagic-benthic coupling in the species. It is also noteworthy that the traps captured some fishes and numerous other species of invertebrates, including all larval stages of certain species of crabs and a great abundance of euphausiids.

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Figure Legends

Figure 2.1.5 Diagram of the light trap used in this study. The main body of the trap (hatched area) was made of white PVC pipe, while its opening was made from the top of a clear 2L plastic soda bottle. The other end of the trap was sealed with a rubber cap held down with a hose clamp. The flashlight was secured close to the middle of the pipe using the hard plastic ring from the bottom of the soda bottle.

Figure 2.2.6 Percentage of postlarvae captured (A) and retained (B) after 24 hours in the high (110 lumens) and low (4 lumens) light intensity treatments of two laboratory experiments testing the efficiency of the light trap.

Figure 2.3.7 Catches (n) of four crustacean species commonly found in the light traps; American lobster, Green crab, Rock crab and Northern krill over the duration of the study. For the three decapod species, catches of both early larval stages and the final larval stage is shown. Note the different scale on the y-axis on the northern krill graph.

Table Legends

Table 2.1.3 Catches of the four larval stages of American lobster *Homarus americanus* in the light traps and densities of recently settled (young of year) lobster in cobble-filled settlement collectors. Light traps and settlement collectors were both deployed in 2011 in three areas where settlement has been high in the last 4 years (0.8-2.5 settlers/m²) and three areas where it has been low (0-0.6 settlers/m²) (Sigurdsson and Rochette, unpublished data).

Table 2.2.4 Comparison of the number of stage I, stage IV and total (stages I to IV) lobster larvae caught by light traps in this study (first row) and larval tow studies reviewed by Fogarty (1983) that included information on number of tows and tow duration (rows 2-7). Sampling effort was estimated as the cumulative number of hours the sampling devices (light traps or plankton nets) were in the water (e.g., 47 light traps x 1848 hours/light trap = 86,856 hours). Working hours represents the time at sea necessary to acquire the samples from the light traps or to conduct the larval tows (does not include time to travel to and from study sites).

Chapter 3: Processes affecting American lobster benthic recruitment in the southwest Bay of Fundy

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Abstract

Indices of benthic recruitment are used for forecasting in some of the most commercially important fisheries in the world, including those supported by lobster. There is, however, generally limited understanding of the factors responsible for spatial and temporal variation in benthic recruitment. The objective of this study was to conduct a broad analysis of factors that could explain recently reported patchiness in benthic recruitment of American lobster (*Homarus americanus*) at the scale of 0.4 - 4 km² in the southwest Bay of Fundy. We addressed this objective using two modeling approaches, based on 10 abiotic factors and one biotic factor considered over different time periods, for a total of 48 potential model variables. After exclusion of correlated and collinear variables, 11 variables were used for model building. The best model resulting from this exercise comprised four variables, the North Atlantic Oscillation Index (NAO) over the larval period, fetch of the study area, juvenile abundance, and sea surface temperature over the larval period. The best purely physical model comprised the same variables with the exception that juvenile abundance was replaced by wind driven fetch in October. Of these variables, the NAO index seemed important in explaining inter-annual variation in recruitment patterns, while juvenile abundance showed promise in explaining the spatial variation. Sea surface temperature and fetch seemed to be spuriously related to recruitment. Density predictions by the best biophysical model and the best purely-physical model correlate relatively well with observed densities, suggesting that these models hold some promise to be useful for forecasting. These models could also be useful for selection of sites to conduct annual recruitment surveys.

Introduction

The development of tools to predict trends in the abundance of commercially exploited species is one of the main goals of fisheries science, and various recruitment indices are the cornerstone of modern stock assessment. Lobsters now support some of the most valuable fisheries worldwide. In 2018, 304,478 tonnes of lobsters of 39 different species were caught (FAO 2020), with landed value of those lobsters exceeding 9 billion dollars (FAO 2020). These species begin their free-living existence as larvae that swim and develop in the water column for weeks up to ca. two years before they settle on the sea floor and adopt a benthic mode of existence (Butler et al. 2006). For such species, indices of larval benthic recruitment (settlement and early survival) are almost certainly going to be markedly more useful for forecasting to the fishery than indices based on earlier life stages, such as larvae caught in the plankton or eggs produced by females (Miller 1997), due to the many biotic and abiotic processes that affect the transition from the water column to the benthos (Ennis 1995). Such benthic recruitment indices are currently used for forecasting in several of the most commercially important lobster fisheries, such as that for the western rock lobster (*Panulirus cygnus*) in Australia (Caputi et al. 1995) and the southern rock lobster (*Jasus edwardsii*) in New Zealand (Booth and McKenzie 2009). Similar indices are also in development for the Caribbean spiny lobster (*Panulirus argus*) fishery in the Caribbean (Acosta et al. 1997; Eggleston et al. 1998) and the American lobster fishery in North America (ALSI 2020, Oppenheim et al. 2019).

The American lobster (*Homarus americanus*) fishery is the largest and most valuable fishery in northeastern United States and Canada, with landed value in Canada alone surpassing 1.4 million CA\$. Landings in much of Atlantic Canada and the Gulf of Maine have surged to record high numbers over the past 20-30 years, while landings in the southern range of the species have markedly declined since the late 1990s/early 2000s and are showing no signs of recovery (Wahle et al. 2009, ASFMC, 2020). Benthic recruitment seems to be a strong driver of fisheries recruitment in American lobster. For example, a recent study in the Gulf of Maine has found a significant correlation between annual estimates of benthic recruitment and time-lagged (based on temperature-driven growth) landings in 10/12 fisheries management areas (Oppenheim et al. 2019). Importantly, mediation of this relationship by climate-driven change in temperature may be contributing to large-scale shifts in the species' distribution. In particular, a collapse of landings in the southern part (New York, Rhode Island, Massachusetts) of the lobster's range (Wahle et al. 2009) seems to be at least partly related to a downturn in benthic recruitment, caused by excessively high temperatures in shallow coastal areas, and mortality of adults from shell disease, which reduces reproductive output, whereas at the northern end of the species' range (Quebec's north shore and in Labrador) requests are being made for new fishing licenses, most likely due to increasing benthic recruitment due to warming temperatures (Sainte-Marie, DFO Québec, pers. comm.). It also seems that the epicenter of lobster harvest may be shifting northwards, with record landings and very high benthic recruitment being observed in the southern Gulf of St. Lawrence (around Prince Edward Island) in recent years (DFO 2020; ALSI 2020), while the historical hotspot of lobster landings in

the Gulf of Maine has recently seen a decrease in numbers of benthic recruits that is causing concerns over future landings there (Oppenheim 2019; ALSI 2020). Despite the profound importance of benthic recruitment to the fishing industry, factors that affect this process are poorly understood.

The life cycle of the American lobster involves both pelagic (in the water column) and benthic (on the bottom) life phases. Mating usually occurs after a female moults during summer months, following mating rituals performed by the male, who then protects the female until her shell has hardened. In the typical 2-year reproduction cycle, females store the sperm until the following summer, when eggs are fertilized externally as they are extruded onto the female's abdomen, where they develop over the following 9-11 months (Atema and Voight 1995). After the embryo hatches from its egg, it moults into a stage I larva, which leaves the female and swims into the water column (Talbot and Helluy 1995). This larva then undergoes an additional three moults in the water column, at which point it metamorphoses into the postlarva (stage IV larva). The entire larval phase can last between approximately 2 to 18 weeks, depending on water temperature (Ennis 1995). When the postlarva is "competent" (i.e., physiologically ready) to settle on the benthos, it starts to periodically dive to the bottom in search of suitable shelter in which to settle. After settlement, the juvenile lobsters are thought to remain cryptic in nursery habitats for the first few to several years of their lives and to increasingly venture further from their shelters as they grow (Lawton and Lavalli 1995), although a recent tracking study suggests this ontogenic shift may not be as gradual as might have been assumed (Morse and Rochette,

2016). In different parts of the species' range, American lobsters reach sexual maturity at approximately 4-10 years of age and they recruit to the fishery at 5-9 years of age (based on sizes from Aiken and Waddy 1995).

Research on settlement and benthic recruitment of lobster postlarvae has followed two broad approaches: lab experiments to investigate factors that affect settlement decisions, and field sampling to assess spatial and temporal patterns of settlement. In the laboratory, Botero and Atema (1982) showed that settling postlarvae prefer cobble bottom over mud and sand, while Boudreau et al. (1991, 1993) showed the importance of predator avoidance, temperature, and thermocline on settlement decisions. In the field, Wahle and Steneck (1991) were pioneers in sampling recently settled American lobster, and their work in New England, United States, showed that benthic recruitment was patchy and mostly limited to complex rocky habitat (cobbles and eel grass reefs) (Wahle and Steneck 1991; Wahle 1993). Palma et al. (1999) extended this work by studying benthic recruitment of American lobster (and rock crab) at different spatial scales, and they suggested that spatial patterns were mostly driven by oceanographic processes at large spatial scales (≈ 100 km) and substrate characteristics at smaller spatial scales (≈ 0.0001 km). In a more recent study, Sigurdsson et al. (2016) assessed spatial patterns in benthic recruitment of American lobster on "good settlement bottom" in the Canadian Gulf of Maine and found marked patchiness of young-of-year at intermediate scales ($0.4-4.0$ km², distance 10-80 km), significant but much lower patchiness at the largest scale investigated (140 km), and very little spatial patterns in recruitment at the smaller scales investigated (0.001-5 km).

Our understanding of factors and processes that are responsible for spatial and temporal variation in benthic recruitment of American lobster in nature is very incomplete. While much has been learned concerning factors affecting settlement decisions of postlarvae in the laboratory, much less is known concerning the factors that drive spatio-temporal patterns of lobster benthic recruitment in nature. Investigations into this question have thus far individually focused mostly on a small number of factors, such as sea surface temperature (Jaini et al. 2018), sea surface temperature and geopotential height (Pershing et al. 2012), wind driven surface currents (Wahle and Incze 1997), bottom temperature (Annis et al. 2013), and the presence of juvenile conspecifics (Burdetts-Coutts et al. 2014). One exception is the recent study by Carloni et al. (2018), which simultaneously assessed the relation between YoY recruitment in 10 areas in the Gulf of Maine (or vicinity) between 1989-2015 and the abundance of the copepod *Calanus finmarchicus*, other potential zooplankton prey, gelatinous predators and some environmental indicators such as sea surface temperature, wind transport and the North Atlantic Oscillation index.

In this study we used a holistic ecological modelling approach in an attempt to explain spatio-temporal patterns in lobster benthic recruitment recently observed in southwest Bay of Fundy, Canada (Sigurdsson et al. 2016). First, we identified 11 abiotic and biotic factors that have been proposed to potentially affect lobster benthic recruitment, and we estimated 48 different variables reflecting variation in these factors over different time periods in each of four years. We then shortened this list by excluding strongly correlated parameters, and we used the remaining 11 parameters to build multiple models to explain variability in

lobster benthic recruitment in 6 geographic areas in southwest Bay of Fundy between 2010 and 2013 (Sigurdsson et al. 2016). Finally, we contrasted these different models using AIC model selection methods (Anderson 2008).

Methods

Benthic recruitment sampling

The data on “benthic recruitment” (i.e. density of young-of-year within a few months post-settlement) of American lobster used in this study were mainly derived from the first chapter of this thesis, which comprises data on the abundance of young-of-year (YOY) lobster in “bio collectors” (see below) deployed at a hierarchy of spatial scales near the mouth of the Bay of Fundy, Canada, in 2010, 2011 and 2012 (see also Sigurdsson et al. 2016). That study analyzed patterns of abundance of YOY lobsters on both the New Brunswick and Nova Scotia sides of the Bay of Fundy, although in this study we only used YOY data from the former because some of the abiotic factors of interest were not available for all Nova Scotia samples (e.g., bottom temperature). In addition to these data between 2010 and 2012, we added new YOY abundance data for 2013.

We attempted to explain variability in YOY density among six “study areas” in southwest Bay of Fundy (Fig. 1), varying between 0.4-4.0 km², as this is the spatial scale at which most variability in YOY abundance was observed between 2010 and 2012 (Chapter 1, Sigurdsson et al. 2016). These six study areas had been selected mainly on the basis of availability of suitable cobble habitat for lobster settlement (see Chapter 1 or Sigurdsson et al. 2016 for details of site selection process). Two sites (0.003-0.23 km²) were sampled within each of these areas every year, with the exception of one area where three sites were sampled in all four years, for a total of 13 sites/year (Table 3.1.5). The same sites were sampled in 2010-2012, but the 2013 data was also intended for a different project and

comprised 2 sites (out of 13) that were not the same as in 2010-2012, although these 2 “new sites” were in proximity (within 1-7 km) to the “old sites”. The use of two new sites in 2013 did not complicate analyses, because these were all based on average values of the 2 or 3 sites in each study area (see below). In order to ensure this small discrepancy in location of study sites did not affect our inferences we compared the results of separate analyses run with the 2010-2012 and 2010-2013 data.

Table 3.1.5. Name and coordinates (N, W) of the sites sampled in each of the six study areas, along with the year(s) each site was sampled.

Area Site	Coordinates	Years sampled
Passamaquoddy Bay		
Birch Cove	45.1435, 67.0323	2010-2013
Dicks Island	45.1399, 66.9989	2010-2012
Hardwood II	45.1216, 66.9922	2013
West Isles		
Simpson Island	45.0001, 66.9083	2010-2013
Hardwood Island	45.0151, 66.9216	2010-2012
Mascarene	45.0843, 66.9192	2013
Deadmans Harbour		
I	45.0497, 66.7821	2010-2013
II	45.0471, 66.7851	2010-2013
Beaver Harbour		
East	45.0679, 66.7194	2010-2013
West	45.0613, 66.7340	2010-2013
Center	45.0694, 66.7227	2010-2013
Seeleys Cove		
Control area 1	45.0876, 66.6446	2010-2013
Control area 2	45.0890, 66.6374	2010-2013
Maces Bay		
Pocologan Island	45.1091, 66.5656	2010-2013
No name rock	45.1097, 66.5612	2010-2013

Benthic recruitment was quantified based on the abundance of YOY lobsters found in passive “bio-collectors” deployed on shallow cobble bottom (5-15 meters depth relative to 0 chart datum, depending on availability of suitable substrate) between the first week of July and the last week of October. Each year we deployed 15-25 bio-collectors at each site, depending mainly on the area of cobble bottom available for the work. The bio-collectors followed the design by Wahle et al. (2009). They are made of wire mesh and they resemble a flattened lobster trap with the following dimensions: 91.4 cm long, 61 cm wide, and 15.2 cm high (5 cm diagonal mesh opening). They are filled with \approx 5-22 cm round quarry rock, to mimic optimal substrate for lobster postlarvae and juveniles (Botero and Atema 1982; Wahle et al. 2009). These collectors have been shown to sample, on quality cobble substrate, comparable numbers of YOY and juvenile lobsters as suction sampling by SCUBA divers, with the exception that they catch slightly lower numbers of the smallest juvenile lobsters (<25 mm CL), which are referred to as “shelter restricted” lobsters and not believed to leave shelter often (Wahle et al. 2009; Wahle et al. 2013). We considered that all lobsters that were \leq 13.0 mm Carapace Length (CL) were YOY, based on visual inspection of size frequency distributions of lobsters sampled in 300 collectors deployed in 2009 (see Chapter 1). This 13 mm cut off agrees well with results of a Bayesian model developed by the Department of Fisheries and Oceans (Toby Surette, Gulf Fisheries Centre, personal communication), which estimates, based upon the size of all lobsters found in our bio-collectors between 2009-2012, a cut off of 12.2-12.9 mm for YOY in our region over this time period. The modelling exercise was based on annual numbers of YOY lobsters (\leq 13 mm CL) in each study area, which were estimated as the mean of the

densities obtained in the bio-collectors at the different (two or three) sites sampled in a given area and year.

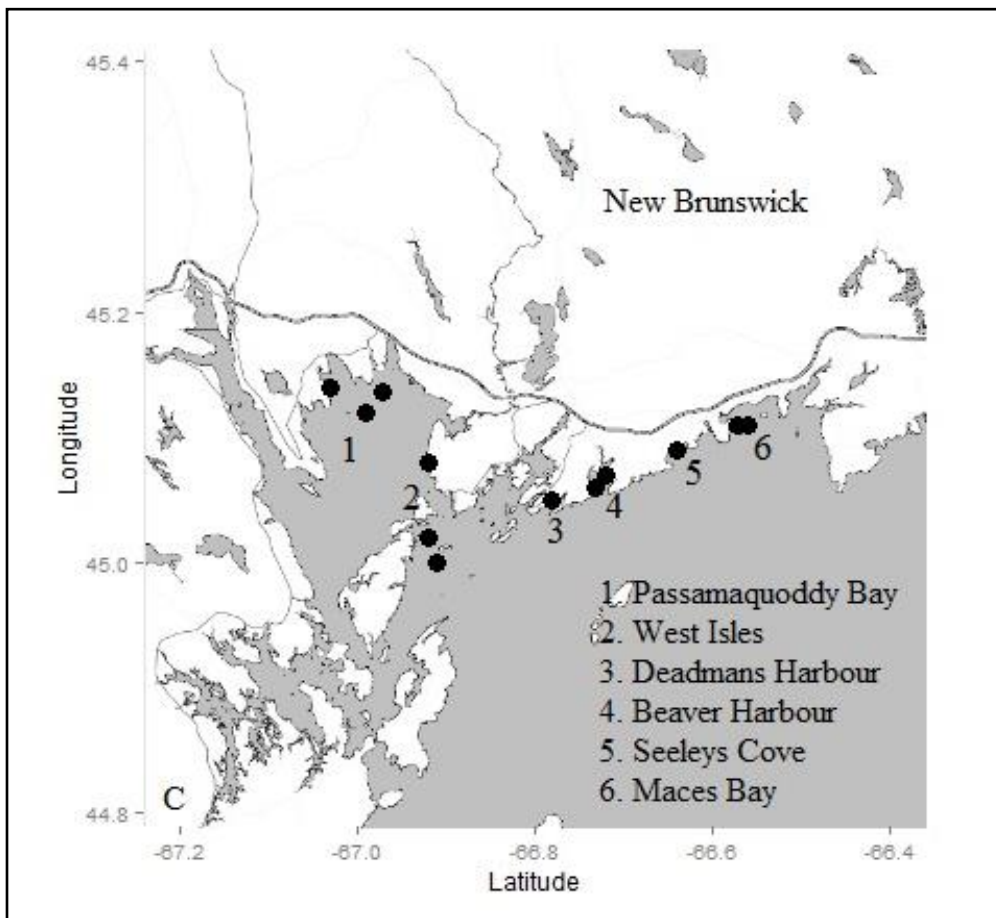
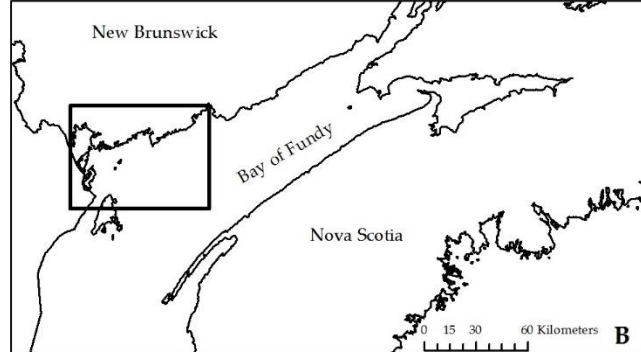
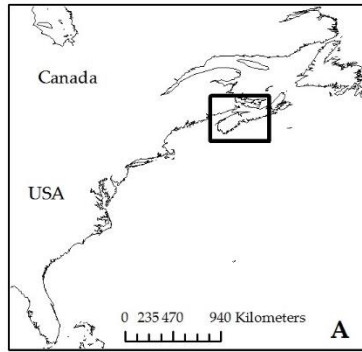


Figure 3.1.8. Maps showing where benthic recruitment of American lobster (i.e., abundance of YOY [≤ 13 mm CL]) was quantified annually, from 2010 to 2013. Maps A and B situate the study region within North America and the Bay of Fundy, respectively, whereas map C shows the location of the 6 study areas and 15 study sites (black circles) in southwest Bay of Fundy. In each study area, two or three sites and between 30-60 collectors (15-25 per site) were sampled annually (Table 3.1.5).

Physical parameters

We considered a total of 11 factors to explain spatial (among study areas) and temporal (among years) variability in benthic recruitment (density of YOY) of American lobster, 10 physical and one biological (Table 3.2.6). We used these 11 factors to calculate a total of 48 variables based on estimates of these factors over relevant time periods (Table 3.2.6), including i- monthly (some or all of June, July, August, September, October), ii- over the bio-collector deployment period (early July to late October), and iii- over the estimated larval period (June to late October when bio-collectors were retrieved) (Table 3.2.6).

Bottom temperature was recorded by 2-6 HOBO temperature loggers in each area (average = 4, at least one in each site), which logged temperature every 10 minutes throughout the period that collectors were in the water. We first estimated the mean daily temperature of each logger, then averaged these daily values over different time intervals (monthly, bio-collector deployment period, larval period; see Table 3.2.6) for each logger, then averaged these period-based values among loggers of a same site, and finally averaged these values among sites of a same area. Maximum and minimum daily temperature over the deployment period were similarly estimated for each logger, and then averaged among loggers of a same site and then among sites of a same area. To test whether the hypothesized 12°C thermal threshold for settlement (Annis et al. 2013) contributed to spatio-temporal

patterns in settlement during our study, we counted for each logger the number of days when average daily temperature exceeded 12°C during the period the bio-collectors were in the water, which covered the lobster settlement period, and then averaged these values among loggers of a same site and finally among sites of a same study area.

Estimates of sea surface temperature (SST) were obtained at 30 min intervals over the study period from Fisheries and Oceans Canada's St. Lawrence Global Observatory (www.slgo.ca) and used to estimate, as described above, monthly and larval period SST values for each area.

The depth of each collector was estimated using boat sonar, correcting for the state of the tides at deployment, and then depth values were averaged among collectors in each site, and then across sites of a same area.

Fetch, which can be defined as the distance travelled by wind or waves over open water, was calculated based on a method described by Håkanson (1981), which involved measuring the distance from the center of each site to the nearest mass of land in each of 8 cardinal directions (N, NE, E, SE, S, SW, W, NW), with distances evaluated for each of 9 vectors per cardinal direction (1 perfectly aligned with the cardinal direction, and 4 at 6° angle on each side of it). Each distance measurement was weighed by the sine of the angle, to give more weight to vectors more closely aligned with each cardinal direction. These 72 values were then averaged to obtain a single fetch value for each site within an area. These site-level fetch values were also averaged to obtain a mean value for each study area, while

the largest site fetch value was considered maximum fetch for each area. We also estimated a wind-adjusted value of fetch for each site by multiplying the fetch values estimated in each 6° orientation by maximum hourly wind speeds observed in each of these orientations, then averaging values obtained for each orientation of a particular cardinal direction, and finally averaging values for the different cardinal directions. Average hourly and daily wind speeds in each of these orientations were also tested in place of maximum hourly winds for the wind driven fetch calculations, but these did not reveal different trends. Wind data were acquired from Environment Canada weather stations (Government of Canada 2014), using the nearest weather station for each area (St. Stephen weather station: sites in Passamaquoddy Bay and West Isles; Grand Manan weather station: sites in Deadmans Harbour and Beaver Harbour; Point Lepreau weather station: sites in Seeleys Cove and Maces Bay).

Values of the North Atlantic Oscillation Index (NAO), which is measured as the difference in atmospheric pressure between weather stations in Stykkishólmur, Iceland, and Lisbon, Portugal, and thought to drive strength and direction of westerly storms and winds in the North Atlantic, were included to potentially explain inter-annual variability in YOY abundance. The NAO values were acquired from the US National Weather Service for each month (June-October) and year; monthly values were used separately in the models, and also to calculate a mean NAO value for the entire larval period (US National Weather Service 2015). Note that the NAO index does not vary spatially and was only used to attempt to explain inter-annual variability in lobster benthic recruitment.

700 mb geopotential height data, which is another large-scale weather index that is measured as the atmospheric height (km) at which the atmospheric pressure is 700 mb, was gathered for each month (June-October) and then averaged for the entire larval period. The geopotential height monthly values were obtained from NOAA’s Earth System Research Laboratory (NOAA 2013) for centroids of each study area, not individual sites, because sites within areas were too close together to distinguish based on this factor.

Table 3.2.6. List of biotic and abiotic factors included as independent variables in the model building process, along with their definition and the time periods over which they were estimated, as well as sources of the different data. In different years (2010-2013) post-larval bio-collectors were deployed and retrieved between 1-8 July and 20-30 October, respectively. Independent variables included in the model were calculated i- monthly (July, August, September, and October for “benthic parameters”, and the same plus June for “pelagic parameters”), ii- over the bio-collector “deployment period” (early July to late October), and iii- over the estimated “larval period” (June till retrieval of bio-collectors). P indicates the number of variables considered for each factor based on the number of relevant time periods for each of these factors.

Factors	Definition	Time period	Source
Average daily bottom temperature (°C) (p=5)	Average daily value at each site, over different time periods, then averaged among sites of a same study area	-Monthly (July-October) -Deployment period	This study
Minimum daily bottom temperature (°C) (p=5)	Average minimum daily temperature at each site, over different time periods, then averaged among sites of a same study area	-Monthly (July-October) -Deployment period	This study
Maximum daily bottom temperature (°C) (p=5)	Average maximum daily temperature at each site, over different time periods, then averaged among sites of a same study area	-Monthly (July-October) -Deployment period	This study
Number of days with bottom temperature above 12°C (p=5)	Number of days with bottom temperature above 12°C at each site, over different time periods, then averaged among sites of a same study area	-Monthly (July-October) -Deployment period	This study
Average sea surface temperature (°C) (p=6)	Average daily values of SST at each site, over different time periods, then averaged among sites of a same study	-Monthly (June-October) -Larval period	Fisheries and Oceans Canada

Average depth of collectors (m) (p=1)	Average depth of collectors at each site, then averaged among sites of a same study area	-Deployment period	This study
Average fetch (km) (p=1)	Average distance (km) to nearest land measured from 9 angles around each of the 8 cardinal directions each study site, then average among study sites of a same area	-Deployment period	This study
Average wind driven fetch (km ² /h) (p=6)	Daily fetch measured from 9 angles around each of the 8 cardinal directions multiplied by wind velocity in each 6° orientation, averaged over different time periods, then averaged among sites of a same study area	-Monthly (June-October) - Larval period	This study and Environment Canada
North Atlantic Oscillation Index (kPa) (p=7)	Difference in sea level atmospheric pressure (kPa) between Portugal and Iceland. This large-scale atmospheric index does not vary spatially, and we used it only to explain inter-annual variability in benthic recruitment	-Annually -Monthly (June-October) -Larval period	US National Weather Service
Average 700 mb geopotential height (km) (p=6)	Average atmospheric height (km) at which the atmospheric pressure is 700 mb in centroids of each study area over different time periods. We used this large-scale atmospheric index to explain spatial and inter-annual variability in benthic recruitment	-Monthly (June-October) -Larval period	NOAA
Average density of juvenile lobster (lobsters/m ²) (p=1)	Average density of lobsters >13 mm CL among collectors of a same site, then averaged across sites of a same study area	-Deployment period	This study

Note: Calendar year was also included as a random term in the model building exercise

Biological parameters

The density of juvenile lobsters in each site was estimated by counting the number of lobsters larger than 13 mm CL in each bio-collector, estimating their density by dividing the number of lobsters by the bio-collectors area cover and then averaging these values across the collectors of a site, and then averaging across sites of a same area. These lobsters were likely too large to be young-of-the-year that settled in the bio-collectors as postlarvae, and instead had likely crawled into the collectors from the benthos as juveniles.

Statistics

Removal of correlated variables

As a first step to simplify the model selection process, we built a correlation matrix of the 48 variables (11 factors measured over different time periods) estimated in each area and year (see Table 3.2.6) and removed highly correlated parameters ($r \geq 0.70$); if two variables were highly correlated, we discarded the variable that showed greater correlation with the other suite of variables. As a second step, we tested the variables retained for collinearity and excluded those with a variance inflation factor (VIF) ≥ 2 (Kutner et al. 2004); the VIF provides an estimate of how much smaller the standard error of the dependent variable would be if a predictor variable was uncorrelated with the other predictor variables in the model. These two steps reduced the total number of variables from 48 to 11.

Model building

We used two approaches, stepwise multiple regression and automated stepAIC, to identify “candidate models” considering all 11 variables that were retained through the correlation and collinearity screening processes (Table 3.3.7). In addition to these 11 variables, calendar year and study area were included as random variables to account for unexplained spatio-temporal variability in benthic recruitment. We also used these two approaches to identify candidate models based exclusively on abiotic parameters, given the relative ease with which these can be measured (compared to juvenile density) and the practical implications this could have. The response variable was in all cases the number of YOY lobsters divided by the total area of the bio-collectors (YOY density) in a particular year

and study area. Generalized linear mixed (GLM) models with Gaussian distribution and identity-link are presented in the Results, but GLMs with Poisson distribution and log link were also tested in the stepwise multiple regression approach for comparison.

The traditional stepwise multiple regression approach (Crawley 2012) was run backwards, and p-values ($\alpha = 0.05$) were used to remove parameters iteratively until a candidate model was achieved in which all parameters had a p-value < 0.05 . Similarly, the automated stepAIC approach was used to select the candidate model based on AIC scores (removing or adding variables in backward and forward directions, respectively, resulted in the same “best model”). This exercise resulted in four candidate models to be studied further, two derived by stepwise regression and two by AIC, with one of each being based exclusively on physical parameters. Further “manual” additions or removals of variables failed to identify a better model than these four candidate models. A fifth and final candidate model was considered for comparison, which included all 11 variables retained through the correlation/collinearity screening process (Table 3.3.7).

Table 3.3.7. List of the 11 variables retained through the correlation and collinearity parameter-screening processes, which were used in the model building exercise.

Annual NAO index (kPa)
Larval period NAO index (kPa)
Depth of collectors (m)
Deployment period daily average bottom temperature (°C)
Deployment period maximum bottom temperature (°C)
Number of days when bottom temperature was $> 12^{\circ}\text{C}$ over the study period (n)

Juvenile lobster density (n/m ²)
Larval period 700 mb geopotential height (km)
Fetch (km)
Wind-driven fetch (km ² /h)
Larval period sea surface temperature (°C)

Model comparisons

Once the five candidate models were identified, we used three separate and complementary approaches to identify our “best model”. First, we calculated an AIC value corrected for small sample size (i.e., AICc) for each candidate model by adding to its AIC value a correction factor $(\frac{2k(k+1)}{n-k-1})^2$ based on sample size (n) and the number of model parameters (k), and we compared AICc scores of our five candidate models; using uncorrected AIC values in cases where sample size is not many times larger than the number of parameters squared increases the chance of overfitting (i.e., selecting a model that has variables that are not truly useful) (Burnham and Anderson 2002). Lower AICc values indicate better fit. We also estimated AICc weights for each model, which represent the relative likelihood of a model when compared to the other candidate models, given the data at hand (Burnham and Anderson 2002). The second approach we used to compare our five candidate models, and to get a better understanding of their explanatory power, was to estimate the error rate of each model using a cross-validation approach, which estimated the accuracy of the model by leaving out a specified portion of the dataset, building the model from the remaining portion, and then predicting the portion that was left out. A root mean squared cross-validation prediction error for each of the five candidate models was calculated, both

using leave-one-out validation (1 sample left out, model built, 1 [excluded] sample predicted, error estimated, repeating 24 times leaving out a different sample each time), and 6-fold validation (4 randomly-obtained samples left out, model built, 4 [excluded] samples predicted, error estimated repeating 6 times leaving out 4 different samples each time). Cross validation involving leaving out 1 single datum (24-fold validation here) is traditionally done in cross validation testing, but also using a smaller number of folds (6 here) provides information concerning the robustness of the model; a much higher error rate with the 6-fold than with the 24-fold cross validation would suggest that our best model is not robust and excessively driven by 1 or a few data points. The third and final approach we used to compare our five candidate models was to correlate the YOY densities predicted by each of the five candidate models with the observed densities.

Once the single best model was identified by the three model-comparison approaches outlined above, we used model coefficients of determination to assess the relative importance of each variables in explaining variability in YOY abundance. We contrasted the coefficient of determination of the full model with that of reduced models, after removing each variable one at the time. The variable which removal resulted in the largest change in the coefficient of determination was determined to have the most importance.

All analyses were done in R (R developmental core team 2013) using the MASS (stepAIC function, Venables and Ripley 2013), ppcor (Kim 2015), car (Fox et al. 2020), AICcmodavg (Mazerolle 2015), and boot (Canty and Ripley 2015) packages.

Further investigation into the effect of the NAO

Results of this model selection exercise indicated a significant relation between inter-annual variability in lobster benthic recruitment and the NAO index. To investigate this relationship further, we used a 30-year time series (1991-2020) of young-of-year lobsters obtained by the Department of Fisheries and Oceans, based on SCUBA-assisted suction sampling in one of our six study areas, i.e., Beaver Harbour. These data were compared using simple linear correlations ($\alpha = 0.05$) to the NAO index over several time periods: monthly from June to October (larval period), two (consecutive)-month averages over the same period, three-month averages over the same period, average of the entire larval period (June-October), and finally the average for the winter (December-March) before the larval period. One year (2005) was excluded from these analyses, as the YOY density that year was 4x higher than the mean and 7x higher than the median, and was found to be a significant statistical outlier (Grubbs test, `grubbs.test` function from the R package `outliers` [Komzta, 2011]).

Results

Benthic recruitment patterns

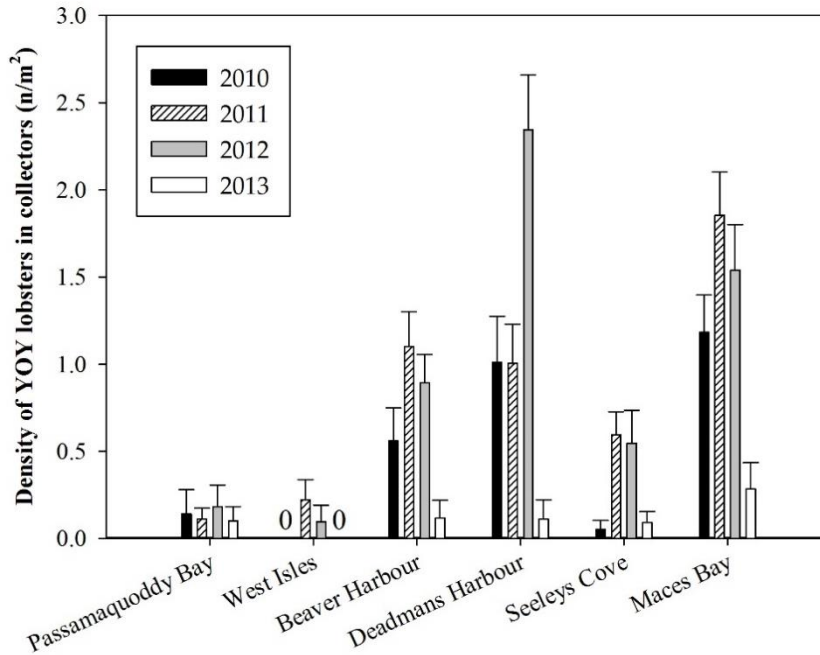


Figure 3.2.9. Density +SE (number/m²) of young-of-year lobsters (< 13.0 mm CL) in the 6 areas sampled over the four years of the study (2010-2013).

The average density of young-of-year (YOY) lobsters varied markedly over the 6 areas and 4 years of the study, from a low of 0 ind./m² in the West Isles in 2010 and 2013 to a high of 2.33 ind./m² in Deadmans Harbour in 2012 (Figure 3.2.9). Average density among study areas varied by nearly an order of magnitude across years, with a low of 0.14 ind./m² in 2013 and a high of 0.99 ind./m² in 2012. Three of the six study areas consistently had higher densities of YOY during the study (Beaver Harbour, Deadmans Harbour and Maces Bay), and two consistently had much lower YOY densities (Passamaquoddy Bay and West

Isles), although these spatial differences were much less pronounced in 2013, when benthic recruitment was lower in all areas. The decrease in benthic recruitment in 2013 was quite pronounced, especially in Deadmans Harbour, where the mean density of YOY dropped an order of magnitude from 2.4 lobsters/m² in 2012 to 0.25 lobsters/m² in 2013.

Model selection

Considerable overlap in variables was observed between the four candidate models that were derived from the different model-selection approaches. Using the traditional stepwise multiple regression approach, the best model to explain variability in the abundance of YOY lobsters among areas and years comprised four parameters: average density of juvenile lobsters, Atlantic Oscillation Index during the larval period, fetch, and average sea surface temperature during the larval period. The best model based on the automatic stepAIC approach had five parameters, including the four parameters just mentioned for the stepwise regression model in addition to the average depth of the areas. Neither calendar year nor study area were retained in either model selection approach, although the study area was the last variable removed in the traditional multiple regression approach.

The best purely physical model derived from the traditional stepwise multiple regression and the full stepAIC model included the same physical parameters as the “full model” derived using each approach, and therefore only differed from these with respect to the omission of the juvenile lobster parameter.

The exact same parameters made up each of the four candidate models whether the 2013 data were included or not, with one single exception (geopotential height was added in the stepAIC method when 2013 was excluded), indicating that these results are robust to the slight change in exact location of two of the 13 study sites in 2013 relative to 2010-2012. The same two candidate models were also obtained through the traditional stepwise multiple regression approach whether a GLM with Gaussian distribution and identity-link or with a Poisson distribution and log-link was used.

When the four candidate models were compared, along with the model that included all 11 variables retained following the correlation/collinearity variable-exclusion process, the latter was by far the worst, with markedly higher AICc score, virtually no AICc weight and the greatest cross-validation error (Table 3.4.8). This model would be expected to have very low predictive power, and its high coefficient of determination was the result of overfitting. The remaining four candidate models performed more similarly to one another, although the two models that included juvenile density clearly outperformed the models based on physical parameters alone, possessing lower AICc scores and lower cross-validation errors than the latter. The two top models also performed differently from one another, with the one obtained from the traditional stepwise approach clearly outperforming the one derived using the stepAIC method (same factors plus depth). More specifically, the model obtained with the traditional stepwise method and critical alpha levels had the lowest AICc score of all models and 83% of the AICc weight, compared to only 15% for the stepAIC model. The model obtained by stepwise regression also had

somewhat lower cross-validation error than that obtained by the stepAIC approach, for both the 24-fold (0.132 versus 0.151 YOY/m²) and the 6-fold (0.133 vs 0.144 YOY/m²) cross-validation estimates. The fact that the errors associated with the 24-fold and 6-fold cross-validation estimates were very similar suggests that the models are robust and not driven by one or a few data points. The cross-validation error for the stepwise model was 23% of the mean value for the density averaged across all years/areas (0.58 n/m²), while the cross-validation error for the stepAIC model was 26% of the mean. Taken together these results indicate that the biotic-abiotic model derived by stepwise regression is the best of the five candidate models we compared (one based on all 11 uncorrelated factors and four based on the 4-5 most useful factors), and we will hereafter refer to this model as the “best model”.

Table 3.4.8. Table comparing five candidate models to explain variation in abundance of YOY lobsters among six study areas in southwest Bay of Fundy in 2010, 2011, 2012 and 2013. The first four models were the best models derived from the model selection exercise (see Methods), and the fifth included all 11 non correlated/co-linear variables quantified during this study (Table 3.3.7); models 1 and 2 were based on (non correlated/non co-linear) biological and physical variables, and were identified using (1) traditional stepwise multiple regression and (2) stepAIC automated model selection, whereas models 3 and 4 were based on physical parameters only, and were identified using (3) traditional stepwise multiple regression and (4) stepAIC automated model selection. The models displayed here were all generalized linear mixed (GLM) models with Gaussian distribution and identity-link. n = sample size, K = number of variables in the model + 2 (see details in Anderson, 2008), AIC = uncorrected AIC scores, AICc = AIC scores corrected for small sample size, Pseudo R² (relative goodness of fit for the model compared to other models), CV error = Cross validation error for 24 folds and 6 folds of the dataset (see Methods).

#	Model	n	K	AIC	AICc	ΔAICc	AICc weight	Pseudo R ²	CV error	
									k = 24	k = 6
1	Juveniles+NAO larval+Fetch+SST	24	6	20.89	25.83	0.00	0.83	0.63	0.132	0.133
2	Juveniles+NAO larval+Fetch+SST+Depth	24	7	22.23	29.23	3.39	0.15	0.62	0.151	0.144
3	NAO larval+Fetch+SST+Depth	24	6	29.29	34.23	8.40	0.01	0.49	0.194	0.211
4	NAO larval+Fetch+SST	24	5	43.18	46.52	20.68	0.00	0.17	0.364	0.347
5	All 11 variables	24	13	17.93	46.29	20.46	0.00	0.79	0.198	0.220

Correlations between predicted and observed YOY densities.

YOY densities predicted by the best biophysical model in our six study areas and four years are strongly correlated to those predicted by the best physical model ($R^2 = 0.849$), and the slope of this relationship was not significantly different from 1 ($t_{19} = 0.24$, $p = 0.80$) and its intercept was not significantly different from 0 ($t_{19} = 0.18$, $p = 0.86$), indicating similarity of predictions made by these two models.

Observed YOY densities correlate relatively well with values predicted by the best biophysical and the best physical models, with the former ($R^2 = 0.79$) performing slightly better than the latter ($R^2 = 0.70$) (Figure 3.3.10). Both models have slopes that differ significantly from 1 (biophysical: $t_{19} = 23.35$, $p < 0.001$; physical: $t_{19} = 19.85$, $p = p < 0.001$) and intercepts that differ significantly from 0 (biophysical: $t_{19} = 3.7$, $p = 0.002$; physical: $t_{19} = 3.9$, $p = 0.001$), indicating some bias in predicted YOY densities. Overall, both models tend to over-estimate lower YOY density values ($< 0.5 \text{ n/m}^2$) and underestimate higher values ($0.5\text{-}1.5 \text{ n/m}^2$).

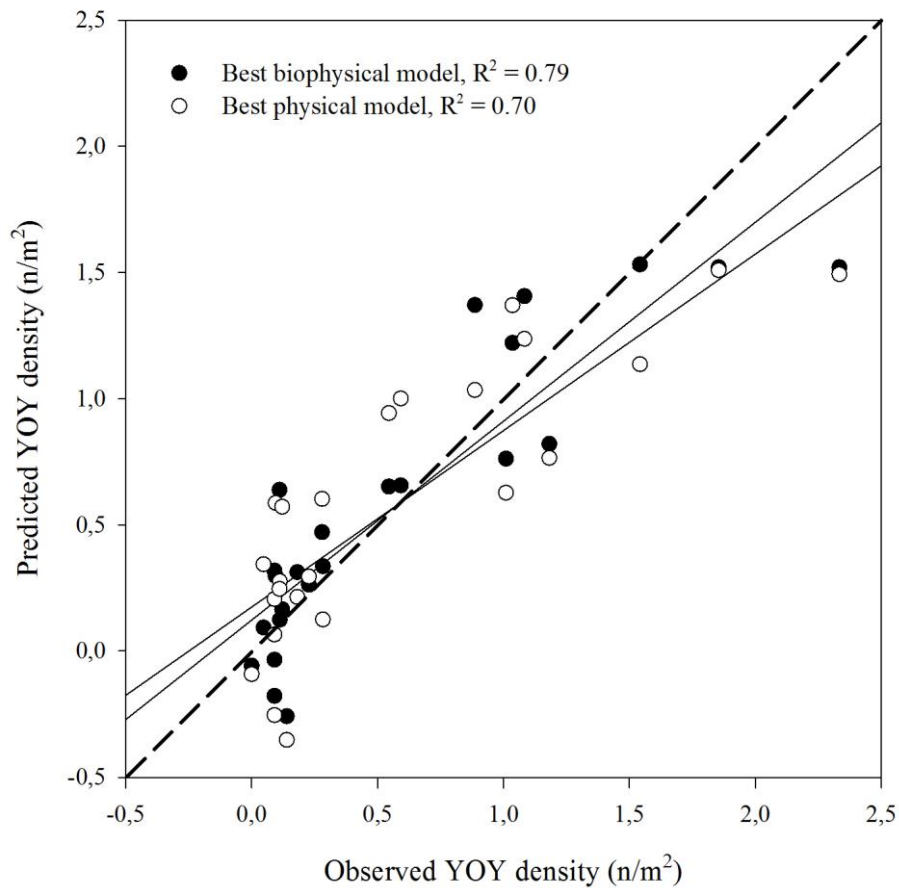


Figure 3.3.10. Correlations between observed YOY density and YOY density predicted by the best (see Methods) biophysical (black circles) and physical (open circles) models. The dotted line has a slope of 1 and intercept of 0 and is plotted to indicate perfect correspondence between observed and predicted values.

Relative importance of different parameters in the best model

Coefficient of determination yielded consistent results concerning the relative importance of the four variables of our best model in explaining variation in YOY density. The most important variable was the Atlantic Oscillation Index over the larval period ($R = -0.79$, $p < 0.0001$; 0.38 change in model R^2), with average YOY density during the three negative NAO years being markedly higher (0.73 n/m^2) than during the single positive NAO year (0.13 n/m^2). The second most important parameter was

sea surface temperature over the larval period ($R = -0.66$, $p = 0.001$; 0.18 change in model R^2), with YOY density decreasing with increasing temperature. Juvenile density was the third most important ($R = 0.64$, $p = 0.002$; 0.14 change in model R^2), indicating a relatively strong tendency for the abundance of juveniles and YOY to positively covary. Finally, fetch of the study was the least important factor ($R = -0.53$, $p = 0.01$, 0.08 change in model R^2), with YOY density tending to be greater in areas where fetch was lower.

Further investigation into the effect of the NAO

When the longer Department of Fisheries and Oceans' time series (1991-2020) of lobster benthic recruitment in Beaver Harbour (one of our six study areas) was compared to annual values of the North Atlantic Oscillation (NAO) index, it became evident that a negative correlation existed between these two variables. This negative correlation was consistent with the one observed in our more temporally restricted (4 years, 2010-2013), but more spatially extensive (six areas instead of one) analyses, where higher NAO index values also resulted in lower YOY densities. After YOY density in 2005 was excluded as an outlier (gruber test, see Methods), two significant ($p < 0.01$) correlations were observed between YOY values and the NAO index over different time periods, one based on the mean monthly NAO over the larval period (June-October) (Fig. 3.3.11) and the other based on the mean monthly NAO in June-August, with the former yielding a slightly stronger correlation than the latter ($R = -0.53$ vs -0.49). When the 2005 outlier year was kept in the model, these correlations were marginally insignificant ($R = -0.33$, $p = 0.07$).

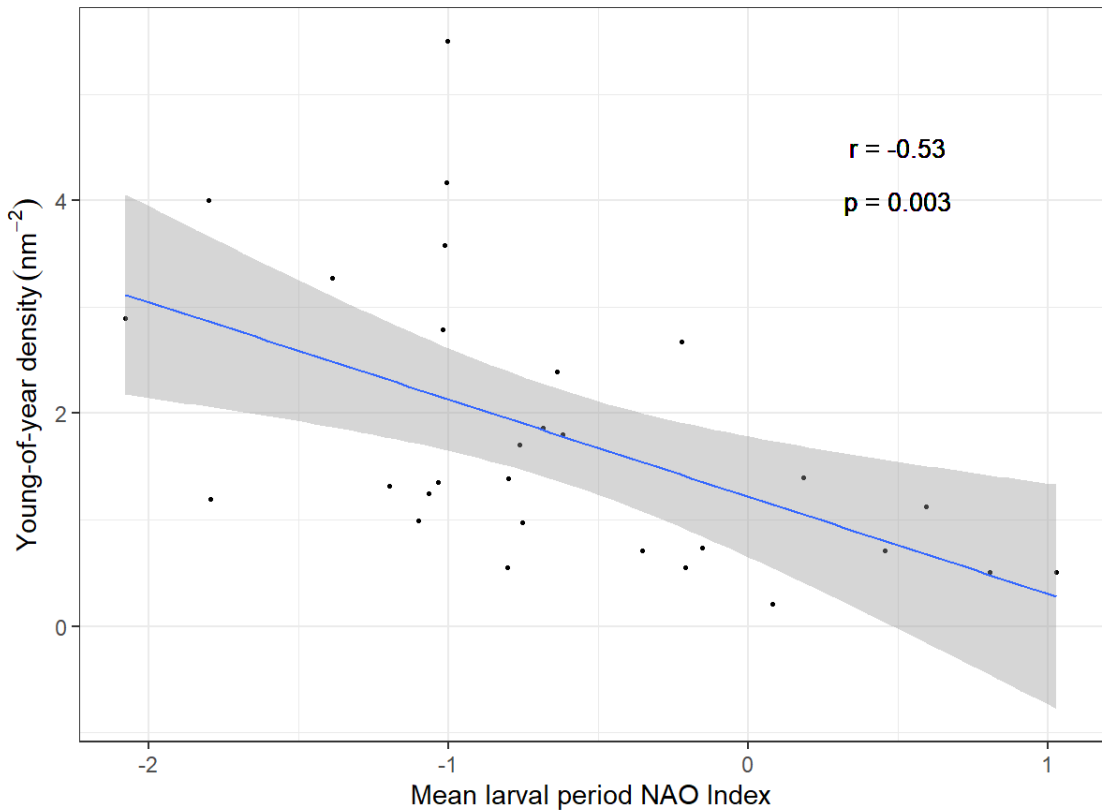


Figure 3.3.11. Correlation between the mean monthly NAO index over the lobster larval period (June-October) between 1991 and 2020, and YOY density in Beaver Harbour, which is one of the six study areas included in this study. Each point is one year. The shaded area indicates a 95% confidence interval around the trendline. Suction sampling YOY density data was graciously provided by Peter Lawton of the Department of Fisheries and Oceans Canada. One extreme outlier in the YOY densities (the value for 2005) was removed before the analysis was conducted.

Discussion

The “best model” at predicting YOY density resulting from the model selection exercise, which was derived with the traditional stepwise multiple regression approach, rose above the other models tested in terms of AICc weight and cross validation error. It comprised four variables: density of juveniles, Atlantic Oscillation Index over the larval period, fetch, and sea surface temperature over the larval period. The best model comprised the same four variables if the 2013 data were excluded, indicating that the small difference in exact location of study sites in that year did not affect the outcome of the model selection exercise. The best model had nearly all the AICc (83%) weight and the lowest cross-validation error (0.132 versus 0.151 for the second-best model). The cross-validation error of this biophysical model was approximately 23% of the overall average of young-of-year (YOY) density over the six areas and four years of the study (0.58 ind/m²), which suggests it could become useful to predict absolute densities of YOY lobsters, and not only relative densities, if the model can be further improved (see below). This conclusion is further supported by the relatively strong positive correlation ($r = 0.79$) obtained between the observed and predicted YOY densities (Figure 3.3.10), although this correlation does still imply considerable error in point predictions and the model also shows some bias, as the intercept was significantly different from 0 and the slope different from 1. This error and this bias are at least partly related to unexplained annual differences in YOY density, as even though the random year term was not retained (i.e., $p > 0.05$) in the model selection exercise, it did slightly increase the coefficient of determination and rendered the intercept and slope terms non-significant (result not shown).

The second best of the candidate models, which was obtained using the automated stepAIC function and differed from the best model by including depth, had much lower AICc weight (15%) and higher cross-validation error (0.151 versus 0.132) than the best model. That the cross-validation error only differed slightly between the two top models is perhaps not surprising, given these shared four variables, but the fact that the inclusion of depth to this second model did not improve its AICc score, and that the R^2 of these two models was similar, suggests that the second-best model is over-fitted.

Not surprisingly, given that the best overall model included juvenile density as a variable, the two best models that were based exclusively on physical parameters performed worse than the two models that included the density of juvenile lobsters, having almost no AICc weight and considerably higher cross validation error (0.194-0.364 versus 0.132-0.151). The best purely-physical model comprised the Atlantic Oscillation Index during the larval period, fetch, average depth, and sea surface temperature during the larval period. Although this purely-physical model was weaker than the biophysical model, it still generated a relatively strong relationship between predicted and observed YOY values ($R^2 = 0.70$) and could prove useful to identify areas of high and low YOY densities, given its ease of application. In the rest of our discussion, we will focus on the factors that were retained in our best models, including consideration of processes they might underlie, and we will consider the forecasting potential of both the best biophysical and the best purely-physical models identified.

Factors related to benthic recruitment of American lobsters

The North Atlantic Oscillation index (NAO) over the larval period was the most important variable in our best model, accounting for the largest change in coefficient of

determination. It was also the variable with the strongest correlation with YOY abundance ($R = -0.79$). This was somewhat surprising, given that this parameter can only explain temporal (i.e., among years) and not spatial (i.e., among areas) variability in YOY abundance. The relationship between the NAO index and YOY abundance was negative, as the single positive NAO index value (0.72) was observed in 2013, when we observed the lowest average benthic recruitment (0.13 n/m^2), and negative NAO index values were observed in 2010, 2011 and 2012 (-2.80 to -0.30), when we observed much greater average benthic recruitment (0.73 n/m^2) across areas. This relationship was confirmed when we compared NAO index values to benthic recruitment estimates made by the Department of Fisheries and Oceans using SCUBA-assisted suction sampling in Beaver Harbour, NB, between 1991 and 2020. A similar trend can be seen in this longer dataset, where higher NAO values over the larval period resulted in lower YOY abundance.

The NAO index is associated with, and often used as a proxy for, large-scale weather patterns in the Northwest Atlantic, because it influences the strength and frequency of westerly winds and storms in the region (Mann and Drinkwater, 1995). A negative correlation between NAO index values and recruitment of Atlantic Cod on the northern Grand Banks and Labrador shelf has been reported, possibly due to colder winter sea temperatures in negative NAO years (Mann and Drinkwater, 1995). Our results similarly suggest that negative NAO values over the larval period have a positive effect on benthic recruitment of American lobsters in the Bay of Fundy, while a positive NAO seems to generally result in lower benthic recruitment. Although winds and storm events certainly influence the distribution of larvae and postlarvae in the water, and

hence their potential recruitment to the sea floor, the actual mechanisms underlying this relationship are unclear. Interestingly, in a recent study Carloni et al. (2018) did not find a significant correlation between the NAO index and postlarval densities at multiple locations in the Gulf of Maine over a similar (although not the same) time-period (1988-2015) as that considered in this study (1991-2020). There are several possible explanations for why their results differ from ours. First, they used a slightly shorter “larval period” to estimate the NAO index (July-September) than we did (June-October), and we excluded one year (2005) as a statistical outlier in YOY density, whereas they did not. However, we do not believe this is the main reason for the difference in outcome of these two studies, as they observed a (non-significant) positive correlation ($r = 0.16$, $p = 0.43$), and we still observed a negative correlation when we re-ran our analyses by calculating the NAO index over the same three months and same years they used, whether we kept ($r = -0.17$, $p = 0.38$) or removed ($r = -0.35$, $p = 0.06$) the 2005 statistical outlier. Secondly, they correlated the NAO index to the abundance of postlarvae, and not YOY, and whereas they did find a significant correlation between the postlarval and YOY abundance, this difference in endpoint may certainly have contributed to differences in study outcomes. Thirdly, it is possible that the NAO index has a greater impact on lobster postlarvae and YOY in the northern part of the Gulf of Maine, where our study was conducted, than in its southern part, where theirs was mostly conducted.

Sea surface temperature over the larval period (June-October) was the second most important variable of our best model, accounting for ~23% of the explained variance in YOY abundance. Somewhat surprisingly, however, YOY density tended to decrease

with increasing sea surface temperature in our dataset, as reflected by the negative partial correlation coefficient ($R = -0.66$). This result is unexpected, because growth and survival of larvae and postlarvae increase over the range of temperatures (10.5-15 °C) observed during our study (reviewed by Ennis, 1995; Mackenzie, 1988; Jaini et al. 2018). We are inclined to believe that this relationship is a spurious one, driven by differences in lobster settlement among our study areas that are confounded with, but driven by other factor(s) than, differences in temperature. The relationship between sea surface temperature and lobster settlement seems to arise mainly because our two study areas where lobster settlement was lowest had the greatest average sea surface temperatures during larval development (West Isles: 13-14°C; Passamaquoddy Bay: 14-15°C), while our other four study areas had lower temperatures (10-12.5°C) and more variable but generally higher density of YOY lobsters. Our two warmer study areas are, however, also each quite distinct from the four colder areas. First, Passamaquoddy Bay is a very large ($\approx 180 \text{ km}^2$) embayment that is partially isolated from the outer Bay of Fundy by the narrows and strong currents of the West Isles and Passages (Fig. 3.1.8), and which may be exposed to markedly different sources of larvae than our four “outer” study areas. Similarly, our West Isles study area is within a complex archipelago that experiences exceptionally strong tidal currents ($\approx 11 \text{ km/h}$), which may affect larval supply and benthic recruitment. In contrast, our other four study areas are all relatively small ($\approx 1.5\text{-}3.6 \text{ km}^2$) embayments with a similar orientation relative to the outer Bay of Fundy (Fig. 3.1.8). If we exclude our two warmer areas from the analysis, the correlation between YOY abundance and sea surface temperature becomes positive ($R = 0.11$), although not significantly so ($p = 0.791$).

Although we believe that the negative relationship between sea surface temperature and lobster settlement is a spurious one, we obviously cannot exclude the possibility that it does reflect a causal relation. One possibility is that lobsters from the cool waters of the Bay of Fundy are adapted to colder waters than lobsters from the studies mentioned earlier that showed a positive relation between temperature and larval/postlarval development, and which were from Maine and other warmer parts of New England. Interestingly, evidence of local adaptation to temperature has recently been provided for lobster larvae, where larvae hatched from “cold-origin” females in the Gaspé region in Québec developed faster in colder water, but more slowly in warmer waters, than larvae in previous studies that had been hatched from warmer-origin females (Quinn and Rochette 2015). But even these results are not consistent with the temperature-settlement relation documented in our study, because although the temperature-development relations for “cold-origin” and “warm-origin” larvae were found to intersect in the study by Quinn and Rochette (2015), they both showed greater development in warmer waters.

The density of juvenile lobsters in an area-year was positively correlated ($R = 0.63$) with the density of YOY in the same area-year and accounted for approximately 19% of the explained variance in YOY abundance over the course of the study. At least two markedly different processes could be responsible for this positive association. First, oceanographic circulation or other large-scale physical processes could cause inter-annual consistency in postlarval supply at our area scale (0.4-4.0 km², distance 10-80 km), in which case the strong correlation between YOY and older juvenile densities would not reflect a causal relationship. The second possibility is that the postlarvae

actively seek out and select habitats where juvenile lobsters are already present, and the relationship between juvenile and YOY density is causal. In the laboratory, settling lobster postlarvae have been observed to swim towards odors of conspecifics, providing support for the possibility of the causal relationship (Boudreau et al. 1993). In nature, Wahle et al. (2013) found a statistically significant correlation between YOY and juvenile densities in 39 sampling areas that were monitored using diver based suction sampling or passive bio-collectors between 2007 and 2009 across New England and the Canadian Maritimes, and Burdett-Coutts et al. (2014) found a statistically significant spatial association between YOY recruitment and juvenile densities at a regional scale (10-100s of km) in an 8-year time series from New England. In both cases the association between lobster settlement and juvenile abundance was hypothesized to be caused by spatial consistency in large-scale circulation-driven patterns of larval supply, and hence not to reflect a causal link. However, in addition to the association found at the “region scale”, Burdett-Coutts et al. (2014) also found significant association between the two life phases between quadrats only a few meters apart, which is unlikely to be the result of consistency in larval supply (at such small scale) and rather likely reflects attraction of settling postlarvae towards juvenile conspecifics. Such attraction towards older conspecifics by settling larvae is well known in a suite of marine invertebrates (Rodriguez et al. 1993), and there is some limited evidence from laboratory studies that lobster postlarvae are attracted to adult odour plumes given a choice in a Y-maze (Boudreau et al. 1993). It is therefore possible that both processes, inter-annual consistency in postlarval supply and attraction towards conspecifics, are responsible for spatial patterns in settlement of lobster postlarvae at different spatial scales. However, given the spatial scale at which our study was conducted (~10 km

between study areas), it is more likely that the positive association between YOY and juvenile abundance was due to some level of consistency in spatial patterns of supply of competent postlarvae rather than to YOY gregarious behaviour. Whatever the mechanism(s), however, this spatial consistency in YOY and juvenile densities suggests that some areas are disproportionately important to benthic recruitment of American lobster, and that there may be value in identifying and monitoring some such areas for forecasting purposes, potentially in combination with some sampling locations selected more randomly and changing from year to year, to take advantage of benefits both sampling designs afford.

Fetch had the lowest importance of the variables retained by our best model, accounting for 11% of the explained variance. It is difficult to recognize the pattern suggested by the significantly negative correlation ($R = -0.53$) between fetch and YOY abundance. Our study areas fall roughly into three categories in terms of fetch values, with Passamaquoddy Bay and West Isles having very low fetch distances (< 10 km), Beaver Harbour and Deadmans Harbour having moderate fetch distances (~ 90 km) and Maces Bay and Seeleys Cove having high (> 150 km) fetch distances. The two high fetch areas had low to medium (Seeleys Cove) and high (Maces Bay) YOY abundance, the moderate fetch areas had high YOY abundance (Beaver Harbour and Deadmans Harbour), while the two low fetch areas (Passamaquoddy Bay and West Isles) had low YOY abundance. Lower fetch areas therefore had lower settlement and moderate to high fetch areas had variable but mostly medium to high settlement. This could reflect lower wind-driven supply of postlarvae to areas with low fetch, or potentially another spurious relationship driven by the two low fetch areas.

Of the 48 variables that were considered but excluded by the model selection process, we were most surprised that those related to bottom temperatures (deployment period bottom temperature, deployment period maximum bottom temperature, number of days above 12°C) did not figure in our final best model, because laboratory experiments have shown that settlement, survival and growth of lobster postlarvae are affected by temperature (Mackenzie 1988). For example, after exposing postlarvae to five constant temperatures between 10 and 22°C, highest growth rates and survival were observed at 15 and 18°C, while slower growth and reduced survival were observed at 10°C and 22°C (Mackenzie 1988). It was therefore surprising that the areas where we observed the lowest YOY recruitment were the two areas closest to the optimal temperatures suggested in this laboratory study. For example, one of our lowest benthic recruitment areas, Passamaquoddy Bay (0.13 n/m²), was in fact 14.5°C on average (range: 10 – 21°C) over the collector deployment period, which was the temperature at which highest growth and survival was observed in the lab study, while our coldest area, Seeleys Cove (mean: 11.2°C; range: 8 – 15°C), experienced moderate benthic recruitment (0.5 n/m²). These results suggest that outside of the laboratory, other factors may play a larger role than bottom temperature in influencing where postlarvae recruit, such as post-larval supply (chapter 2, Carloni et al. 2018), presence of conspecifics or predators (Boudreau et al. 1993), or other yet-unidentified factors.

The number of summer days above 12°C (degree days) also did not explain variability in YOY abundance among our study areas and years ($R^2 = 0.08$, $p = 0.16$), and was not retained as an explanatory variable by any of our best models. This was somewhat surprising, as Annis (2005) and Annis et al. (2013) provided evidence that 12°C

represents a “thermal threshold” for successful benthic recruitment of lobster. In his 2005 study, Annis suggested a 12°C settlement threshold based on in-situ observations of lobster postlarvae in the Gulf of Maine, where he rarely observed postlarvae dive below the 12°C isotherm while actively following released wild caught larvae. In a more recent paper, Annis et al. (2013) observed higher YOY densities at warmer “inshore” sites compared to colder “offshore” sites (10-16 0.5 m² quadrats per site), which differed in the number of days (46.1 vs 5.1) spent above 12°C over a two-month period. Importantly, larval tows demonstrated that “inshore” and “offshore” sites had similar densities of postlarval lobsters in the water column, which led the authors to propose that the postlarvae avoided, or suffered higher post-settlement mortality at, the sites where the average temperature was below 12°C. Despite this evidence, the number of days above 12°C during the larval period, or the total degree days over this period, did not provide significant explanation for the spatial patterns and/or inter-annual differences observed in our study. This obviously does not mean that lobster settlement behavior is not affected by temperature, or even potentially disproportionately so by fluctuations in the vicinity of 12°C, but only that this “threshold” played little to no role in the establishment of spatial and interannual settlement patterns in our study. It is for example possible that such effects were not observed because the number of days above 12°C did not vary much among years (mean across areas 49-75) or areas (mean across years 55-76) in our study.

Could these models be used for forecasting?

One of the longer-term motivations behind our work is the development of a model that could be used to predict spatial and/or inter-annual variability in lobster benthic

recruitment, or at least areas of high YOY densities, for example to help identify benthic recruitment monitoring sites. Although the density of juvenile lobster was found to be a good predictor of YOY density, this is nearly as difficult to quantify as YOY density, such that it does not represent a particularly useful variable to simplify the task of predicting benthic recruitment. We therefore decided to also identify the best model based exclusively on easily measured physical variables. That model, which comprised 4 variables (depth, annual NAO, fetch, sea surface temperature over the larval period), was clearly outperformed by, and had considerably higher cross-validation error than (0.132 vs 0.194 YOY/m²), the model including juvenile density. However, this purely physical model still explained 49% of the variability in YOY abundance among years and study areas. Most of the explanatory power of that model comes from the annual NAO index. As stated above, it seems that positive NAO years result in poor benthic recruitment of lobster in our study areas on the east coast of Canada, and as such can help explain and predict variability in year class strength of lobster. If the NAO index is removed from this purely physical model, the explanatory power of the model drops markedly, to 11%. Most of this (low) explanatory power is related to sea surface temperature, but as stated above, we believe this to be due to a spurious correlation and unlikely to explain variation in lobster benthic recruitment elsewhere than in the areas used in this study. It may be possible to complement the NAO index in some areas with on-going monitoring of juvenile lobster abundance based on ventless traps or trawl surveys, to predict not only annual but also spatial variability in recruitment. The spatial patterns in YOY and juvenile lobster densities observed in this study suggest strong consistency in recruitment among areas, which may be related to other not quantified

in this study, such as current speed and direction and size and orientation of embayments in relation to those currents.

Conclusion

This holistic correlative study identified two variables that explained a fair proportion of variability in benthic recruitment of American lobster we documented among four years and six areas in southwest Bay of Fundy. First, the North Atlantic Oscillation (NAO) index accounted for 47% of the variability in settlement among our four study years, and this association was confirmed with a 30-year time series of lobster settlement in one of our study areas ($R = -0.53$). This study provides the first evidence that benthic recruitment of American lobster is related to the NAO index. Second, the abundance of juvenile lobsters accounted for 19% of the variability in benthic recruitment among our six study areas, which most likely reflects a certain level of inter-annual consistency in larval supply. Even though these variables show relatively strong (particularly the NAO index) correlations to benthic recruitment, much of the variability remains unexplained or lies in possible spurious correlations (fetch and sea surface temperatures), which speaks to our limited understanding of the factors affecting benthic recruitment of lobsters in nature. Somewhat surprisingly, spatial patterns of YOY density were not related to various bottom temperature variables (degree days, bottom temperature threshold, bottom temperature over larval period) that have been hypothesized or shown to be important to lobster benthic recruitment in field and laboratory studies. Temporal variability in benthic recruitment remained largely unexplained in this study, leaving the field open to further testing of factors such as annual egg production of females (Gendron et al. 2019, but see Carloni et al. 2018) and abundance of planktonic prey (Carloni et al. 2018). Likewise, drivers of spatial variability in benthic recruitment remain largely unknown, and factors such as current speeds and direction, along with size and orientation of nursery-area embayments in

relation to these currents, may be worth investigating. Most importantly, as more data on lobster benthic recruitment becomes available, it will be necessary to test the predictive ability of these models on new datasets, to determine how useful these models can be for forecasting, and more generally how much we really understand about the processes affecting settlement (Houlahan et al. 2017).

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**Chapter 4: How do benthic movements, including their ontogeny,
affect the spatial distribution of sub-adult American lobster *Homarus
americanus*?**

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Abstract

We quantified the abundance of four life-history phases of sub-adult American lobsters *Homarus americanus* at a hierarchy of spatial scales to determine the contribution of ontogenetic changes in behaviour to demographic patterns observed in nature. The first three life-history phases showed similar spatial patterns, but these differed markedly from those displayed by the fourth phase. This “ontogeny of spatial patterns” was corroborated by a density correlation matrix, which revealed significant spatial correlations in the density of the first three phases, but not between any of these and the fourth phase. These results are largely consistent with ontogenetic behavioral changes proposed in the literature, based mostly on laboratory observations, albeit suggesting a less gradual change in behavior than some schemes. They suggest that the distribution of the first three benthic phases (juveniles) is largely driven by larval supply and early survival, while the distribution of the fourth phase (adolescents) is further influenced by benthic movements. Our study highlights the importance of nursery grounds to juvenile lobsters, and the contribution of adolescent movements to connectivity among populations.

Résumé

Nous avons quantifié l'abondance de quatre stades subadultes du homard Américain *Homarus americanus* à différentes échelles spatiales afin de déterminer la contribution de leurs mouvements aux patrons de distribution observés en nature. Les trois premiers stades ont démontré des patrons similaires, mais différents de ceux démontrés par le quatrième stade. Cette "ontogénie des patrons spatiaux" fut corroborée par une matrice de corrélation, qui a démontré des corrélations significatives entre la densité des trois premiers stades, mais pas entre ces derniers et le quatrième stade. Ces résultats sont généralement congruents avec l'ontogénie comportementale proposée dans la littérature, basée principalement sur des expériences de laboratoire, quoique suggérant une ontogénie moins graduelle. Ils suggèrent que la distribution des trois premiers stades (juvéniles) est principalement déterminée par l'apport larvaire et la survie post-déposition benthique, alors que la distribution du quatrième stade (adolescents) est aussi influencée par les déplacements benthiques. Notre étude met en évidence l'importance des pouponnières pour les homards juvéniles, et de la contribution des mouvements benthiques des homards adolescents au niveau de la connectivité entre les populations.

Key words

Sub-adult American lobster, *Homarus americanus*, movements, spatial patterns, patchiness, spatial scale, from individual behavior to population patterns

Introduction

Animal behavior can be important to ecological processes and is increasingly being studied to further our understanding of population structure and dynamics (Grimm and Railsback, 2005). In this growing field, the behaviour of individuals is quantified and/or modelled, and its contribution to characteristics of the population is estimated. Such individual-focused approaches and resulting models have shed considerable light on a variety of demographic patterns and processes in nature (Sutherland 1996). For example, in the marine environment, biophysical models that combine physical oceanic processes and various behavioural attributes such as swimming speed and diurnal movement have been used to predict large-scale patterns of larval dispersal and connectivity for many species, including commercially important fish and invertebrate species (Cowen et al., 2006; Kough et al., 2013; Quinn et al., 2017). While behaviour is increasingly incorporated in models to predict spatial patterns, using observed spatial patterns to elucidate behaviour of animals has less frequently been done. In one of the few studies that have done this, Bergström et al. (2002) used spatial patterns and abundance correlations between taxa and age groups of Baltic sea zoobenthos (mostly amphipods and bivalves) to infer biotic interactions.

The life cycle of the American lobster *Homarus americanus* is similar to that of many other benthic invertebrates with a pelagic larval phase. Larvae hatch from eggs carried under the abdomen of the female before being released into the water column (Talbot and Helluy, 1995), where they undergo three moults (Ennis, 1995) over a period of 1-12 weeks (depending mainly on water temperature) before metamorphosing into the postlarva, which morphologically resembles the adult and makes the transition to the

seafloor (i.e., benthos). In laboratory trials, settling postlarvae have shown strong preference for cobble over other more uniform substrates such as sand or mud (Botero and Atema, 1982). In nature, recent settlers have mainly been found in shallow cobble habitat (Wahle and Steneck, 1991; Wahle and Incze, 1997; Palma et al., 1999), and efforts to find them elsewhere have resulted in very few animals being found (MacKay, 1926; Wahle, 1993).

The terminology used to describe the various life-history phases of the American lobster has been revised frequently, as knowledge of their physiological, morphological, behavioural and/or ecological traits has improved. The first life-history scheme was proposed by Herrick in 1895, who used the term “larva” for the three larval stages and the morphologically different postlarval stage, “adolescent” for the benthic phase up to ~40-50 mm carapace length (CL), and “adults” for individuals ~50 mm CL and larger. In 1987, Hudon proposed a new scheme based on behavioral responses to the threat of capture, using the term “larva” for the first three larval stages and the pelagic phase of the postlarval stage, the term “postlarva” for recently-settled individuals (~4-25 mm CL) that are cryptic and flee for cover when startled, the term “juvenile” for lobsters from ~25-73 mm CL, and “adult” for lobsters larger than ~73 mm CL. One year later, in 1988, Barshaw and Bryant-Rich proposed a different scheme solely for the early stages of lobster (< 50 mm CL). They recognized the differences between “larvae” and “postlarvae” in the water column, and then distinguished between the cryptic “early” and “late” juveniles, based on undifferentiated (early juveniles) and differentiated (late juveniles) claws. In 1991, Wahle and Steneck revisited the life-history phases based on their extensive *in situ* observations in the Gulf of Maine. They

kept the terms larvae and postlarvae for the first four larval stages, and then used the term “early benthic phase” for lobsters ~10-40 mm CL, which are generally found in shelter-providing habitats (cobble, eelgrass, etc.). They then used the term “adolescent phase” for lobsters larger than ~40 mm CL but smaller than ~80 mm CL, when they become reproductive adults (~80 mm CL). In 1994, Cobb and Wahle modified this life-history scheme slightly, by starting the adolescent phase earlier (~20 mm CL), to coincide with their proposed onset of movement away from nursery areas, and by starting the reproductive phase earlier (~45 mm CL), to better align with physiological maturity of lobsters.

In 1995, Lawton and Lavalli summarized these earlier schemes and proposed the life-history scheme that is probably most widely used today (see Selgrath et al. 2007; Tang et al., 2015; Comeau and Benhalima 2019 as examples). They kept the terms larvae and postlarvae for the first four stages, and then divided the early life-history of sub-adult lobsters following settlement into four phases based on energetic requirements, susceptibility to predation and perhaps most importantly, activity levels (Lawton and Lavalli, 1995). In the ~8-12 months following settlement, lobsters are thought to remain strongly associated with shelter in the cobble nursery areas where they settled, during a life-history phase Lawton and Lavalli (1995) called “shelter-restricted juvenile” (~4-14 mm CL). During this phase, the lobsters are thought to rarely exit their cobble shelter and feed on microscopic animals in suspension in the water or on carrion leftover from older lobsters on the nursery ground (Lawton and Lavalli, 1995; Sainte-Marie and Chabot, 2002). As the lobsters grow, they enter according to this scheme a phase called “emergent juvenile” (~15-25 mm CL), which is thought to start emerging from shelters

to search for food and ambush prey. This stage is, however, still considered relatively vulnerable to predation and thought to be mostly confined to shelter because of this. As the juveniles grow further, they are considered “vagile juvenile” (~25-40 mm CL), which are thought to move out of shelters more extensively for food, because they have greater energetic requirements and fewer predators, due to their larger size. After the three juvenile phases, the “adolescent” phase is characterized by physiological maturity (i.e., maturation of gonads and reproductive organs) but not functional maturity (i.e., mating behaviour and subsequent mating), at sizes varying between ~40-60 mm CL based in part on regional differences in gonadal maturation. The adolescent phase is thought to be very active and not shelter restricted, and to participate in seasonal movements with adult lobsters in areas where those occur (Lawton and Lavalli 1995; Morse et al. 2018). It is important to note, however, that this categorical life-history scheme proposed by Lawton and Lavalli (1995) is almost entirely based on laboratory work and short-term SCUBA observations, given the difficulty of observing and monitoring these cryptic animals in nature over longer time intervals.

The goal of this study was to quantify spatial patterns of different life phases of American lobster at different spatial scales to investigate the contribution of ontogenetic changes in behaviour to demographic patterns in nature. We divided the lobsters into phases based on the Lawton and Lavalli (1995) life-history scheme, as it is the most recent and widely used, and also because it is derived from lab and field observations made close to our study areas. Note however that the results are largely interpretable in relation to the other proposed schemes, given the considerable overlap between them. Based on the Lawton and Lavalli life-history scheme, we expect a rather gradual change

in spatial patterns with ontogeny/phase, with patterns becoming increasingly dissimilar as juveniles grow through the three juvenile phases, and then more markedly different once they reach the more mobile adolescent phase. Similarly, we expect a decrease in the strength of the spatial correlation between the abundance of different sub-adult stages with increasing “distance” between these stages, and a particularly marked decrease between the three juvenile phases and the adolescent phase. This study is the first to attempt to link, empirically, a relatively large body of literature concerning the early life history of lobster (e.g., Herrick, 1895; Hudon, 1987; Barshaw and Bryant-Rich, 1988; Wahle and Steneck, 1991; Cobb and Wahle, 1994; Lawton and Lavalli, 1995) and their distribution patterns in nature.

Methods

We quantified the abundance of Lawton and Lavalli's (1995) four life-history phases of sub-adult lobsters (shelter restricted, emergent, vagile, and adolescent) over three consecutive years at a hierarchy of spatial scales (Figure 4.1.11 and description below) using passive bio-collectors designed to mimic optimal habitat for lobster postlarvae and sub-adults (Wahle et al., 2009; Wahle et al., 2013). The bio-collectors resemble a flattened lobster trap, made of wire mesh, with the following dimensions: 91.4 cm long, 61 cm wide and 15.2 cm high. Each bio-collector was filled with cobble (round river-bed rocks 10-25 cm in diameter) to mimic optimal substrate for lobster postlarvae and sub-adults. Although these bio-collectors are passive sampling devices, they have been shown to provide density estimates of lobster postlarvae and sub-adults (up to approximately 50 mm carapace length) that are comparable to densities estimated using active suction sampling by SCUBA divers, with the exception that juveniles between 13 and 17 mm CL are slightly underrepresented in the bio-collectors, likely due to their cryptic nature and limited tendency to venture outside of their shelters (Wahle et al., 2009; Wahle et al., 2013). During this study, bio-collectors were deployed on high quality cobble habitat in less than 12 meters of water (relative to 0 chart datum). The general study areas were first determined based on traditional ecological knowledge from fishermen and scientists that have worked in the region for decades, and the actual study sites with proper substrate were then confirmed using a combination of SCUBA diving, bottom grabs, and ROV videos. The bio-collectors were deployed in late June-early July and recovered in late October-early November in 2010 (n = 413 collectors total), 2011 (n = 553) and 2012 (n = 452). Upon recovery the bio-collectors were carefully inspected, and all lobsters found were measured for carapace length (CL),

from the eye socket to the back of the thorax, and then categorized as shelter restricted (≤ 15 mm), emergent (15.1-25 mm), vagile (25.1-40 mm) and adolescent (40.1-50 mm) (Lawton and Lavalli, 1995). Lobsters larger than 50 mm CL were considered adults, and not included in this study, because most adults are too large to enter the bio-collectors.

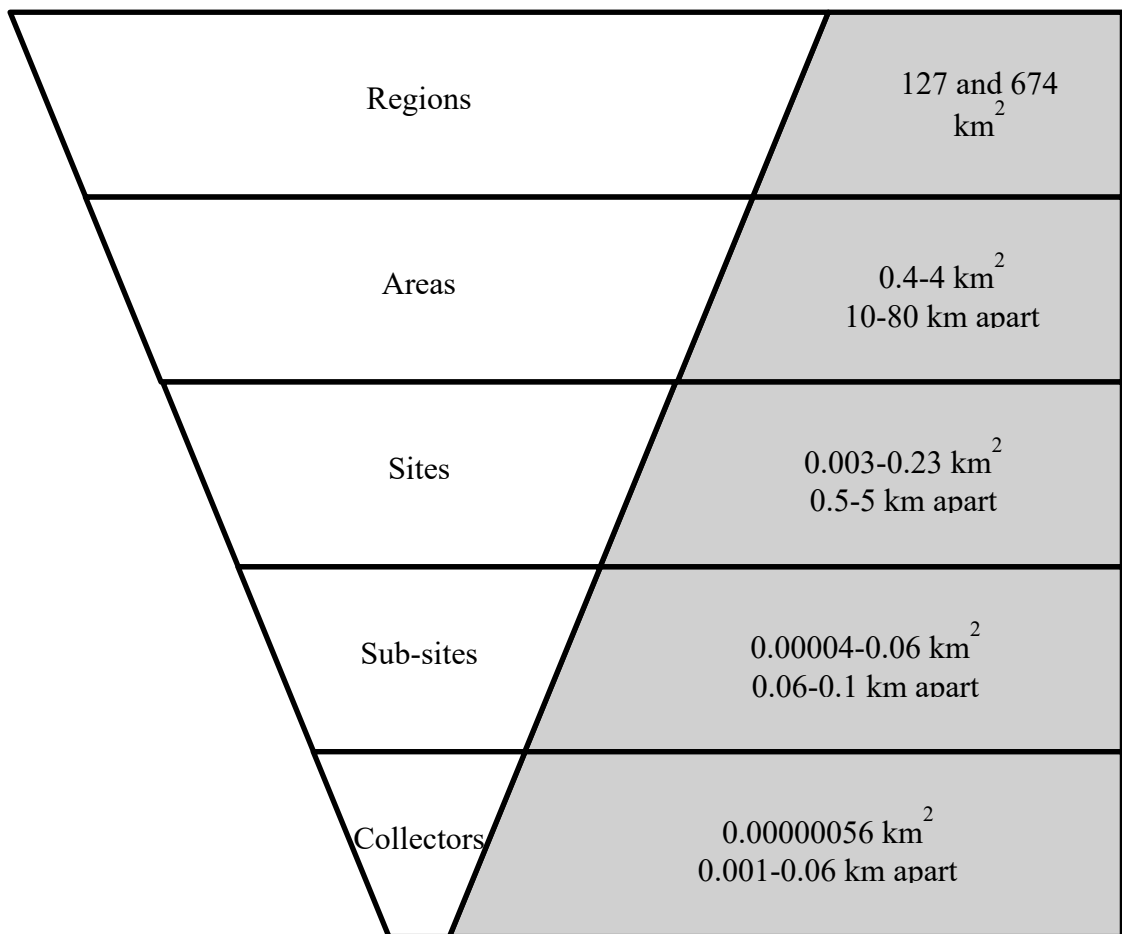


Figure 4.1.11. Hierarchy of spatial scales sampled in this study, showing area of seabed covered by replicates at each scale and distance between replicates (based on Sigurdsson et al. 2016).

Spatial scale hierarchy

The sampling scheme is described in Sigurdsson et al. (2016), which focused on spatial patterns of lobsters under 13 mm CL, corresponding roughly with the shelter-restricted (≤ 15 mm) lobster category used in this study.

Regions

Our sampling design consisted of two large regions in Atlantic Canada, south New Brunswick (SNB) and southwest Nova Scotia (SWNS). The minimum convex polygon made from the different sampling areas of the SNB region covers ca. 127 km² of seabed, while that for the SWNS region covers ca. 674 km². The straight-line distance between the centres of the two regions is 143 km (Figures 4.1.11 and 4.2.12).

Areas

We selected 11 sampling Areas within these Regions, six within SNB and five within SWNS. The seabed area of the minimum convex polygons made up from the different sites of a given area ranged from 0.4-4 km², and the Areas within the Regions were 10-80 km apart middle to middle.

Sites

We used 2-3 sampling sites within each Area. The seabed area of the sites' minimum convex polygon made from the different bio-collectors within each site ranged from 0.003-0.23 km², and the sites within each area were 0.5-5 km apart.

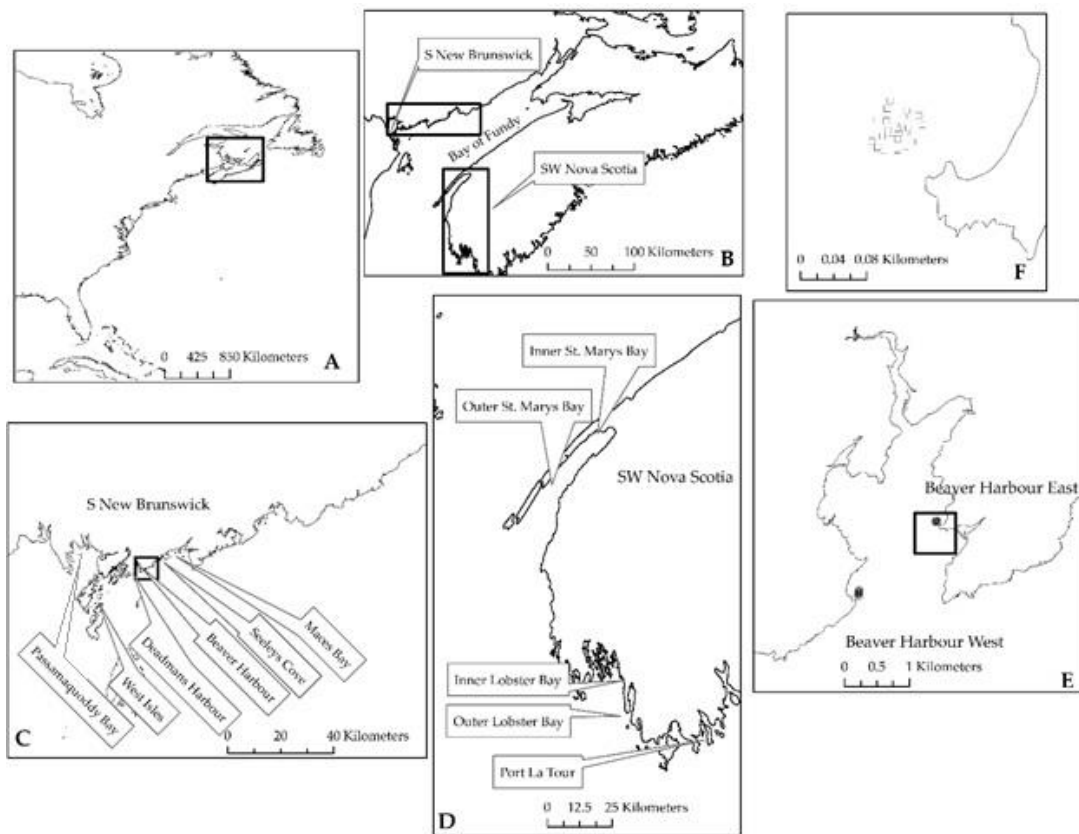
Sub-site

To bridge the gap in spatial scale between the Bio-collector and the Site scale, we divided all our sites post-hoc into sub-sites. In dividing each site into two sub-sites effort was made to keep the number and coverage of bio-collectors in each sub-site as similar as possible. Coverage of each sub-site was 0.00004-0.06 km² of seabed, and distance between sub-sites of a same site was 0.06-0.1 km.

Bio-collectors

We deployed 15-25 bio-collectors within each site, each covering 0.00000056 km² (0.56 m²). The different bio-collectors within each site were 0.001-0.06 km apart.

Figure 4.2.12. Maps showing the hierarchy of spatial scales sampled in this study. Map A highlights the lower Bay of Fundy on the east coast of North America. Map B shows the two study “Regions”, south New Brunswick (SNB) and south-west Nova Scotia (SWNS). Map C and D show study “Areas” within the SNB and SWNS study regions, respectively. Map E shows two study “Sites” (cluster of 25 bio-collectors) within the Beaver Harbour study area, and map F shows “Bio-collectors” that make up the eastern site within the Beaver Harbour study area (from Sigurdsson et al., 2016).



Statistical analyses

Nested analysis of variance and variance component analysis (VCA) were used to elucidate the effect of spatial scale (region, area, site, subsite) on the density of all sub-adult lobsters (4-50 mm CL), and then separately for each of the four life phases. The denominator of the F statistic for each scale was the MS of the scale that is nested within it (e.g., F for Region = $MS_{\text{Region}}/MS_{\text{Area}} [\text{Region}]$), with the model error representing variability among bio-collectors of a same subsite. We initially ran these

analyses with a year term, which resulted in some significant year by spatial scale interaction terms that provided no useful insights into the question at hand, given they spoke to variation in the magnitude of differences among scales between years, rather than change in direction of those differences. We then analyzed each year separately, and we found similar results. Therefore, for simplicity, we present here a model with the year term included, but with interactions omitted.

Annual spatial patterns were further investigated using a randomization approach that enabled us to assess patchiness at each spatial scale, while accounting for the effect that low abundance could have on results of the VCA (i.e., a small number of individuals distributed among a relatively large number of replicates will unavoidably result in high variance among replicates). The randomization approach is described in Sigurdsson et al. (2016), but in essence is based on the variance in abundance among replicates of a particular “spatial unit” (e.g., the different areas of a particular region) as a metric for patchiness, and randomization (10,000 times) of the data (i.e., individual lobsters of a particular life phase) among bio-collectors of that spatial unit (i.e., areas of a same region) to assess the likelihood of the observed or greater variance (p-value) under the null hypothesis that lobster abundance patterns were random within that particular spatial unit, and given the total number of lobsters observed and the number of bio-collectors among which these were distributed (see thoughts on conventional indices of patchiness, and why we chose to use this randomization method in Sigurdsson et al. 2016).

Finally, correlations were used to investigate, at each spatial scale separately, the relation between the abundance of each life-history phase in a year and the abundance

of the other life-history phases in the same and other years; we investigated correlations among all years, because the lobsters in the different phases and years were of unknown and overlapping ages (e.g., Gendron and Sainte-Marie, 2006). Comparisons were made at the area, site, and sub-site scales, but not at the region scale because we only sampled two regions. The correlations at a particular scale were done on density deviations relative to means of the spatial scale above it (e.g., density of a particular area minus density of the region within which this area occurs), rather than observed density values, given that patchiness at a particular spatial scale is confounded by patchiness at the scale “above it” (i.e., patchiness among all areas will be high if patchiness between regions is high, even if areas within a same region have a similar density of lobsters).

All statistical models and tests were run in R (R Development Core Team, 2018), and an alpha level of 0.05 was used in all inferential tests. The function `aov` within the base stats package in R was used to run the nested analysis of variance while the `anovaVCA` function in the VCA package (Schuetzenmeister and Dufey, 2020) was used for the variance component analysis.

Ethics approval

This study was approved by the University of New Brunswick (Saint John) Animal Care Committee (protocol # 2010-EA-13).

Results

Nested Analysis of Variance and Variance Component Analysis

Results of the Nested ANOVAs assessing the significance of variation in density of lobsters at different spatial scales can be found in Table 4.1.9. When all sizes of sub-adult lobsters were considered together, density varied highly significantly among areas of a same Region ($p < 0.0001$), marginally non-significantly between Regions ($p = 0.07$) and among Sites of a same Area ($p = 0.08$), and clearly not among Subsites within a Site ($p = 0.99$) (Figure 4.3.13). Similar spatial patterns were observed when the three younger life phases of lobsters were considered separately, while the oldest life phase showed less spatial structure. More specifically, the density of shelter-restricted ($p < 0.0001$), emergent ($p < 0.0001$) and vagile ($p = 0.003$) lobsters all varied highly significantly at the Area scale, whereas that of adolescents did not ($p = 0.12$). The density of shelter-restricted lobsters also varied marginally significantly at the Region scale ($p = 0.04$), and that of vagile lobsters at the Site scale ($p = 0.02$), while all other combinations of life stages and spatial scales were non-significant (all $p > 0.09$). Year had a significant effect on the density of all phases (all $p \leq 0.017$).

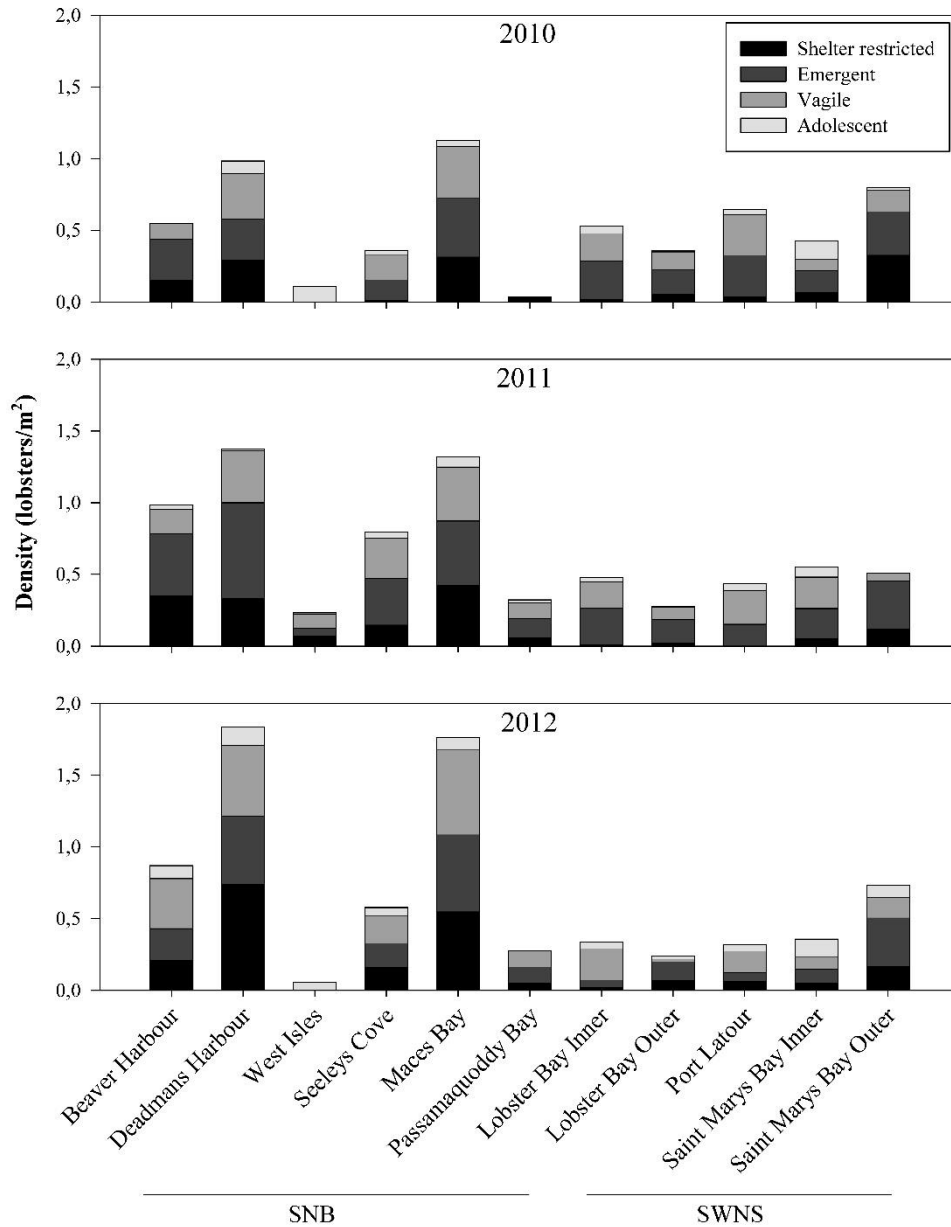


Figure 4.3.13. Density (lobsters/m²) of the four different sub-adult lobster life-history phases (shelter restricted, emergent, vagile, and adolescent) in 11 Areas of two Regions (south west Nova Scotia [SWNS] and south New Brunswick [SNB]) over the three years (2010-2012) of the study. Each bar comprises density of each of the four juvenile phases.

Table 4.1.9. Results of the five nested analyses of variance of the density of sub-adult lobsters overall, and of each of the four life history phases separately, across the hierarchy of spatial scales used in the study from 2010-2012.

Phase/ Spatial scale	Year			Region			Area			Site			Sub-site			Residuals
	df	F	p	df	F	p	df	F	P	df	F	p	df	F	P	df
All sub-adults	2	6.75	0.002	1	2.49	0.07	9	23.53	<0.001	16	2.20	0.08	26	0.45	0.99	73
Shelter restricted	2	5.25	0.007	1	3.82	0.04	9	11.83	<0.001	16	1.95	0.14	26	0.57	0.55	73
Emergent	2	4.30	0.017	1	1.21	0.19	9	15.21	<0.001	16	1.59	0.32	26	0.54	0.46	73
Vagile	2	7.19	0.001	1	2.23	0.09	9	5.02	0.003	16	2.86	0.02	26	0.63	0.74	73
Adolescents	2	7.48	0.001	1	0.21	0.75	9	2.21	0.12	16	2.06	0.11	26	0.65	0.83	73

The Variance Component Analysis (VCA) results (Table 4.2.10) were mostly consistent with those just outlined for the nested ANOVAs. The year term explained a relatively small amount of variation in the density of all life history phases, from 3% for shelter-restricted and emergent lobsters up to 10% for adolescents (3% for all sub-adults pooled). The error term (Bio-collector scale) explained a considerable amount of variation for all life history phases, from 35% for shelter-restricted up to 71% for adolescents (Table 4.2.10). This variation, however, likely does not reflect any biological or physical process, but rather is probably largely if not entirely due to the relatively small number of lobsters found among collectors of a particular sub-site (see results of randomization tests below). The error term aside, most of the variation in density of sub-adult lobsters (all life history phases combined) was at the Area scale (54%), followed by the Regional scale (13%), while there was little variation at the Site (3%) and Sub-site scales (0%). Broken up by life history phase, the Area scale was most important for the shelter restricted (38%), emergent (53%), and vagile lobsters (30%), and of lower importance for adolescents (9%). The Region scale explained 20% of the

variance for shelter-restricted individuals, but considerably less (0-7%) of the variance for the three older life phases. The Site scale accounted for some (10-12%) of the variation among the two older life phases, and less (3-4%) among the two younger phases. The Sub-site scale explained no variance (0%) in abundance of any of the life phases (Table 4.2.10).

Table 4.2.10. Partitioning of the total variation in density of the four sub-adult lobster phases, as well as all these life phases pooled (i.e., sub-adults), across the hierarchy of spatial scales used in the study from 2010 to 2012.

Phase Scale	Shelter restricted	Emergent	Vagile	Adolescent	All sub- adults
Year	3%	3%	6%	10%	3%
Region	20%	0%	7%	0%	13%
Area	38%	53%	30%	9%	54%
Site	4%	3%	12%	10%	3%
Sub-site	0%	0%	0%	0%	0%
Error (collector)	35%	41%	48%	71%	27%

Randomization

The percentage of randomization “tests” at each spatial scale (e.g., Areas in each of 2 Regions sampled in each of 3 years = 6 “tests” at the Area scale) that showed significant

patchiness varied between the different spatial scales and life history phases (Table 4.2.11). In contrast to the results of the VCA, our randomization approach revealed close to no significant patchiness at the smallest spatial scale of the Bio-collector, suggesting that the considerable variability observed in the VCA at this scale was due to low sample size, and did not arise as a result of any biological or physical process (see Discussion). But as was observed in both the VCA and Nested ANOVAs, the first three life-history phases showed very similar patterns, with strong evidence of patchiness at the Area and Region scales, much less evidence of patchiness at the Site scale (Table 4.2.11), and close to no evidence of patchiness at the Sub-site and Bio-collector scales (Table 4.2.11), while the adolescents showed virtually no evidence of patchiness at any spatial scale (Figure 4.3.13, Table 4.2.11).

Table 4.2.11. Percentage of “tests” at each spatial scale that showed significant ($\alpha = 0.05$) patchiness in abundance of each of the four sub-adult lobster life-history phases (shelter restricted, emergent, vagile, and adolescent) in addition to all sub-adult lobsters together, based on our index of patchiness and randomization of the lobster data (see Methods). The number of tests conducted at each scale (shown in parenthesis under each scale name) is the number of larger units within which this scale is nested (i.e., Areas are nested in two Regions) multiplied by the number of years (3) in which patchiness was tested (2 Regions x 3 years = 6 tests at Area scale).

Phase Scale	Number of tests	Shelter restricted	Emergent	Vagile	Adolescent	All sub- adults
Region (n = 2)	3	66.7	66.7	66.7	0.0	33.3
Area (n = 11)	6	83.3	66.7	66.7	0.0	66.7

Site (n = 20-23)	33	16.7	4.2	20.8	4.2	7.8
Sub-site (n = 38-46)	60-69	3.4	1.7	1.7	0.0	3.2
Collector (n = 413-559)	114-138	3.3	8.2	0.0	1.6	2.9

Density correlations

Evidence of spatial coherence in the density of different life phases of sub-adult lobsters over the three years of this study (i.e., densities of two life phases co-varying among Sub-sites, Sites, or Areas in the same or different years) varied markedly according to the spatial scale considered, being stronger at the area scale than at the Sub-site and Site scales, and to some extent among life phases, being stronger for the three earlier life phases than for adolescents. More specifically, at the Sub-site scale most correlations (54/66) between life phases were not statistically significant, and correlation coefficients were equally frequently positive as they were negative (Figure 4.4.14, left panel), whether considering all comparisons (33 negative versus 33 positive) or only the relatively small number of comparisons that were statistically significant (6 versus 6). Nevertheless, the 12 significant correlations were significantly ($\chi^2(1) = 4.95$, $p = 0.03$) more than expected by chance (3.3 out of 66 correlations) under the null hypothesis of no spatial co-variance between life stages, at the set alpha level of 0.05. The limited spatial coherence at the Sub-site scale was true for all life phases, as the number of significant correlations was the same for shelter-restricted (6/30), emergent

(6/30) and adolescent (6/30) lobsters, and only slightly lower for vagile (3/30) lobsters. Similarly, at the Site scale most correlations between life phases (57/66) were not statistically significant, and the correlation coefficients were equally frequently positive as they were negative (Figure 4.4.14, middle panel), whether considering all comparisons (31 negative versus 35 positive) or only the relatively small number of comparisons that were statistically significant (4 negative versus 5 positive). The 9 significant correlations are not significantly more ($\chi^2(1) = 2.64, p = 0.1$) than expected by chance (3.3 out of 66). Again, the absence of spatial coherence at the site scale applied to all life stages, as the number of significant correlations was similar for shelter-restricted (2/30), emergent (3/30), vagile (4/30) and adolescent (6/30) lobsters. In marked contrast, at the Area scale more than half (37/66) of the correlations between life phases were statistically significant, and the vast majority of correlation coefficients were positive (Figure 4.4.14, right panel), both when considering all comparisons (60 positive versus 6 negative) or only those that were statistically significant (all 37 positive). The 37 significant correlations are significantly more ($\chi^2(1) = 28.18, p < 0.0001$) than expected by chance. Importantly, this spatial coherence at the Area scale varied among lobster life phases, as shelter-restricted (21/30), emergent (21/30) and vagile (19/30) had a much higher number of significant correlations with other sub-adult life phases at this scale than did adolescents (4/30), and all negative correlations involved adolescents. Across all life stages more correlations were observed than expected by chance ($p < 0.05$), with the exception of correlations involving adolescents,

which were not statistically different from what would be expected by chance ($\chi^2(1) = 1.13, p = 0.29$).

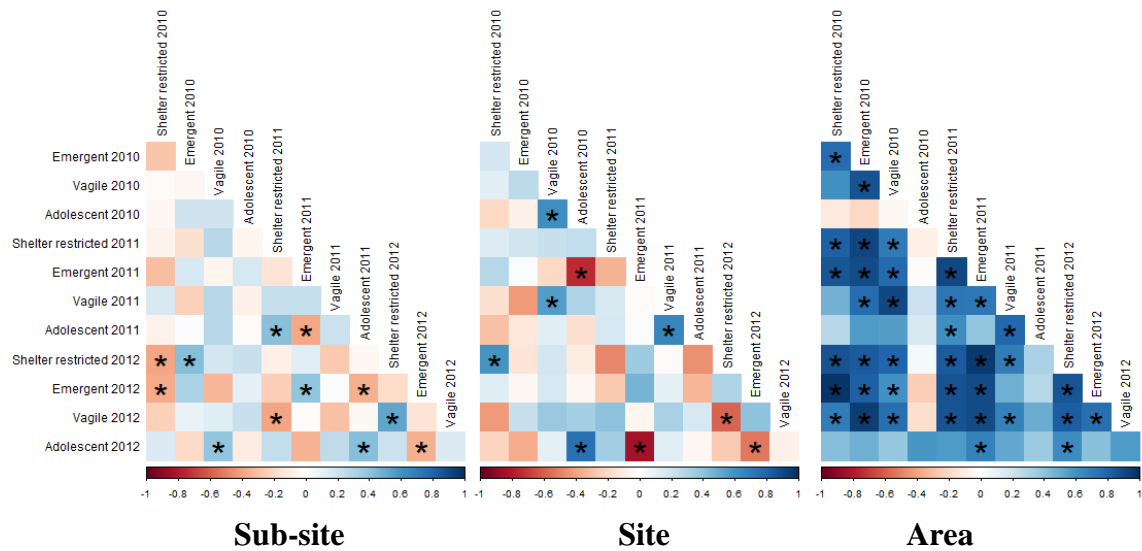


Figure 4.4.14. Matrices showing, at three different spatial scales (Sub-site, Site and Area), the correlation between the “scale-adjusted density” of the four sub-adult lobster life-history phases over the three years of the study. Densities for a particular “sample” (e.g., each sub-site in a particular year for the leftmost panel) and life phase were adjusted by expressing them as the difference from the mean value of the scale within which the unit is first nested (e.g., site in the leftmost panel), to ensure that correlations reflected patterns at the scale of interest (e.g., variation among sub-sites of a same site) rather than the outcome of patterns at a higher spatial scale (e.g., variation among sub-sites from different sites). The color associated with each pairwise correlation reflects the value of the Pearson correlation coefficient (r); red and blue indicate negative and positive correlations, respectively, and darker colors reflect stronger correlations (higher r), with asterisks indicating correlations that were statistically significant at alpha level of 0.05.

Discussion

Our study provides data on patchiness in the abundance of different size sub-adult American lobsters (4-50 mm CL) at a hierarchy of spatial scales on suitable nursery grounds in the lower Bay of Fundy, and it allows evaluation of the contribution of ontogenetic changes in lobster behaviour to these demographic patterns. All three analytical approaches we used indicated that the abundance of sub-adult lobster over our study domain varied most at the scale of 0.4-4.0 km², which we referred to as the “Area” scale, followed by the scale of 127-674 km², which we referred to as the “Region” scale. The data randomization approach indicated that 67% of the comparisons of sub-adult abundance between different areas of a same region were significant, followed by 33% for the region scale, and only 8% and 3% at the smaller “Site” (0.003-0.23 km²) and “Sub-site” (0.00004-0.15 km²) scales, respectively. Similarly, the Variance Component Analysis (VCA) indicated that 54% of the variance in sub-adult abundance was explained by the Area scale, compared to 13% by the Region scale, and only 3% and 0% by the Site and Sub-site scales, respectively. Finally, 58% of the correlations of abundance of different lobster life phases were statistically significant at the Area scale, all showing positive associations between different life phases, compared to only 14% and 18% for the Site and Sub-site scales, respectively, with approximately half of these being positive and half negative; this analysis could not be conducted at the Region scale given we studied two regions only.

As will be discussed in more detail below, our three analytical approaches revealed considerable consistency in the spatial pattern of the first three benthic life phases of lobster (i.e., shelter restricted, emergent and vagile), and a more pronounced difference in the distribution of the fourth and oldest sub-adult benthic life phase (i.e., adolescents). We will argue that these spatial and ontogenetic patterns are best interpreted as being the result of large-scale oceanographic processes affecting larval supply and settlement to different areas of our two study regions, followed by relative stability of post-settlement patterns over the first ca. 3-5 years of the lobsters' benthic life due to limited movement and mortality of juvenile lobsters over this period (or at least similar impact of these processes in different areas), and finally a disruption of these patterns due to increased movement of older adolescent-phase lobsters.

Benthic recruitment: spatial scale and mechanisms

The youngest benthic life phase studied, i.e., shelter-restricted lobsters (4-14.9 mm CL), showed greatest patchiness at the Area scale, followed by the Region scale, with little to no evidence of process-driven (see below) patchiness at finer spatial scales. The data randomization approach indicated that 83% (5/6) of the comparisons of the abundance of shelter-restricted lobsters in different areas of a same region, and 67% (2/3) of the comparisons between regions, were statistically significant, and the VCA indicated that these scales accounted for 38% and 20% of the variability in the abundance of this life phase, respectively. Whereas 17% of randomization tests at the Site scale were statistically significant, this scale only accounted for 4% of the variance in the VCA, and there was no

patchiness at the Sub-site scale. Importantly, a considerable amount of variability in the VCA (36%) was at the Bio-collector scale, but the randomization tests indicated that this was the unavoidable numerical outcome of a relatively small number of lobsters being distributed among a relatively large number of bio-collectors (only 3.3% of randomizations at the Bio-collector level were significant at $\alpha = 0.05$), and therefore likely not the result of any particular physical or biological process. Excluding the patchiness estimated at the Bio-collector scale, the Area and Region scales accounted for 61% and 31%, respectively, of the variability in the abundance of shelter-restricted lobsters across spatial scales.

The spatial patterns observed for shelter-restricted lobsters were very similar to those reported in Sigurdsson et al. (2016), which focused on young of year (YOY) individuals. For example, the randomization approach returned the same percentage of significant comparisons at the Area scale (83%), and very similar percentages at the Site scale (15% vs 17%), for shelter-restricted and YOY lobsters. This is not surprising, given the considerable overlap in size range of these two groups of young lobsters (YOY: 4-13 mm CL, shelter restricted: 4-15 mm CL). In fact, and notwithstanding the uncertainty surrounding the actual “cut off” of YOY in a given sampling year, the vast majority of the shelter-restricted lobsters in this study were likely YOY lobsters (98% \leq 13 mm), i.e., individuals that settled to the sea floor in the few months before the bio-collectors were retrieved, and probably very few were 1+ year of age.

The spatial patterns of shelter-restricted lobsters were largely consistent across years, despite inter-annual variability in their density (CV = 30%) and a significant year effect in the Nested ANOVAs. In particular, in the three years of the study, between 58-71% of all shelter-restricted lobsters were sampled in three sampling areas, despite these comprising only 27% (3/11) of the areas surveyed; we refer to these three areas as “settlement hotspots”. In contrast, 55% (6/11) of the areas consistently combined for less than 5% of the annual abundance of shelter restricted lobsters; we refer to these six areas as “settlement coldspots”.

The patchiness of shelter-restricted lobsters we observed at the area (and to a lesser extent the region) scale in the outer Bay of Fundy is likely heavily influenced by current-mediated larval supply, as suggested by a recent study that showed a positive spatial correlation between the abundance of stage IV postlarvae caught in light traps and the abundance of YOY recruits sampled in bio-collectors across six study areas in southwest Bay of Fundy (Sigurdsson et al. 2016). This conclusion is similarly supported by a study done on the Scotian Shelf (Miller 1997), which found high spatial correlation between postlarvae in plankton tows and fishery recruits in commercial catch several years later, as well as in the Gulf of Maine, where a correlation was observed between the number of lobster postlarvae found in plankton tows and the abundance of early benthic life phases found on different sides of an island in the same years (Wahle and Incze, 1997) and at the same sampling location in different years (Carloni et al., 2018).

Although the spatial patterns of shelter-restricted lobsters are likely mainly the result of physical processes, the behavior of postlarvae could also have played a role. While active directed swimming of the postlarvae towards a particular area is unlikely to be a major driver behind the patterns observed (but see Rooney and Cobb, 1991), given the distances in question and the swimming capabilities of the postlarvae, it is likely that decisions by postlarvae could affect their recruitment to our different study areas. Rejection of an area by postlarvae due to poorer substrate or other cues could increase the likelihood that they drift to other areas, including some with better substrates. Given the duration of the pelagic postlarval stage (17-27 days based on equation in Quinn et al. 2017), and the tendency of postlarvae to “reject” featureless substrates in the lab (Botero and Atema, 1982), passive drift and substrate selection by postlarvae over several weeks could have affected patterns at both the Area and Site scales. That such behaviors affected patterns in our study may at first seem unlikely, given that the bio-collectors provided a high-quality and comparable settlement substrate in all areas, and they were all deployed (in all areas) on sites with structurally complex cobble bottoms. Although different sites undoubtedly varied to some extent in the quality/coverage of settlement substrate, there is good empirical evidence that differences in background structural complexity at this spatial scale would have had little or no effect on the likelihood of lobster postlarvae settling in the bio-collectors deployed at each site (Ellis et al., 2015). Nevertheless, it is possible that habitat characteristics (e.g., prevalence of mud versus cobble) between these quality settlement “patches” (i.e., sites) in our different study areas could have had such an effect, at least to a small degree, in which case patchiness among areas could in principle be partly due to behavioural settlement

decisions made by settling postlarvae. It similarly seems possible, and perhaps even more likely, that postlarval behaviour could have contributed to the (relatively modest) evidence of patchiness we observed for shelter-restricted lobsters at the site scale, considering the relatively small distances (0.5-5 km), and unavoidable variability in habitat quality, among our sites. Spatial differences due to the quality of the substrate of a site or area would be more likely to be observed on natural substrate than in our study design due to the uniformity of the substrate provided by the bio-collectors.

Benthic recruitment patterns: maintenance during ontogeny and implications

Spatial patterns in the abundance of the second and third lobster benthic life phases, i.e., emergent (~15-25 mm CL) and vagile (~25-40 mm CL) juveniles, were similar to those of the first, shelter-restricted, life phase. In particular, all three phases showed greatest patchiness at the Area scale. Their abundance varied highly significantly among Areas (Nested ANOVAs), and for all three of these life phases the Area scale i- explained the greatest percentage of process-driven (i.e., excluding bio-collector scale) variance in lobster abundance (VCA), ii- most frequently showed patchiness in the randomization tests (i.e., after accounting for the relatively small lobster to bio-collectors ratio), and iii- showed the greatest “spatial coherence” (i.e., correlation tests) in the abundance of the same or different life phases among sampling units (i.e., Areas with “high” or “low” abundance of different life phases). Importantly, these patterns differed markedly from those observed for adolescent lobsters, as will be discussed below. The first three juvenile phases also

showed significant patchiness at the Region scale in the randomization tests and the Nested ANOVA, although this was markedly less pronounced than that observed at the Area scale.

Not only was the scale of patchiness of emergent and vagile juveniles similar to that of shelter-restricted individuals, the actual identity of the areas where these three phases were most abundant was the same. The five areas that we identified as benthic recruitment hotspots (87% of shelter-restricted individuals in 45% [5/11] of the Areas sampled) also had a disproportionate number of emergent (71%) and vagile (65%) lobsters, in comparison to the six benthic recruitment coldspots. Also, the significant area-scale correlations in the abundance of the first three life-phases are not exclusively based on the same cohorts of individuals at different points in time (e.g., shelter-restricted in 2010 correlated with emergent in 2011 and vagile in 2012), but rather are based on all combinations of life-stages and years, suggesting that not only do patterns that are established at benthic recruitment persist through the juveniles life history in the years that follow, but also that some areas seem to consistently have higher benthic recruitment levels than others.

The consistency in spatial patterns of the first three life-history phases of American lobster suggests that ontogenetic changes in lobster activity among these phases are not consequential to dominant distribution patterns in nature, at least at the spatial scales investigated in this study. Whereas laboratory and SCUBA observations have found young lobsters to more frequently leave shelter as they increase in size over the size range (4-40 mm) covered by these three phases (reviewed by Lawton and Lavalli, 1995), likely due to decreased vulnerability to predation and increased energetic requirements, this was not

evident in the distribution patterns we observed in nature; patterns that were established at settlement remained largely unchanged in shelter-restricted, emergent, and vagile juveniles.

Two recent acoustic telemetry studies, which were conducted over somewhat larger temporal and spatial scales than the laboratory and field observations mentioned above, similarly found no evidence of change in activity level among the first three life phases of juvenile lobsters. These studies involved young juvenile and adolescent lobsters that were tracked for 21 and 72 days on nursery grounds in the Bay of Fundy (Morse and Rochette, 2016; 10 lobsters 20-47 mm in CL) and the Gulf of St. Lawrence (Morse et al., 2018; 6 lobsters 28-41 mm CL). Whereas these studies were done in two very different regions of the species' range, and notwithstanding the relatively small sample size involved, both showed that the amount of time the juvenile lobsters (i.e., excluding adolescents) spent outside of shelter (\approx 2-40 % of each day), their daily home range (\approx 10-200 m²), study-length home ranges (\approx 50-700m²), daily displacements (\approx 5-50 m) and study-length displacements (\approx 50-400 m), did not vary with their body size, as may have been expected based on earlier laboratory and field observations (reviewed by Lawton and Lavalli, 1995).

Given the above, when considering the impact of behavior on lobster distribution patterns in nature, we propose grouping the first three juvenile life phases (4-40 mm in C) into a single group called “early benthic phase” (EBP) lobsters (sensu Wahle and Steneck (1992). Once they have settled on a quality nursery ground, it seems that lobsters generally do not move to a “new patch” of quality habitat (i.e., Site) within the same or a different

embayment (i.e., Area) while they remain in this EBP phase. This is consistent with the two telemetry studies mentioned earlier, for reasons already discussed, but also because the tracked juveniles (20-41 mm CL) behaved as central place foragers, displaying movements from and to shelters that prevented dispersal from their nursery habitat. This should obviously not be taken to mean that movements of EBP lobsters are entirely inconsequential to their distribution patterns in nature, only that they have a relatively minor impact on patterns established at settlement at the Site scale or larger (see below concerning patchiness at smaller spatial scale). For example, we did find some evidence of marginally greater patchiness at the Site scale for vagile than for shelter-restricted juveniles (Nested ANOVA: shelter-restricted $p = 0.4$ vs vagile $p = 0.02$; VCA: shelter-restricted 4% variance vs vagile 12%; randomization tests: shelter-restricted 16.7% significant vs vagile 20.3%), suggesting that ontogenic increases in movement among EBP lobsters may have had some impact on patchiness at the Site scale, but these differences were much weaker than those observed between EBP lobsters and adolescents (at the Area scale). Some of these Site-scale movements by EBP lobsters may arise when a nursery patch exceeds its' carrying capacity, and sub-dominant (generally smaller) individuals are forced to leave the patch and search for a new one where competition for shelter is lower (Wahle and Incze, 1997).

We may have expected to observe lobster patchiness at the smaller scale of the Sub-site, and potentially variation in the extent of this patchiness across the three juvenile life phases (EBPs), given that movements over the distances involved (Sub-sites of a same Site are

contiguous and 40,000-60,000 m² large) can certainly be achieved by these animals over relatively short periods of time (see numbers above for studies by Morse and Rochette, 2016; Morse et al., 2018). We believe that the lack of lobster patchiness at the Sub-site scale likely reflects relatively low levels of substrate heterogeneity at this scale, in part because the main criterion used for the selection of our study Sites was that they needed to have a good coverage of cobble. Similarly, the lack of patchiness at the bio-collector scale does not imply that lobsters cannot move between bio-collectors, but rather likely arose because all our bio-collectors provided similar high-quality cobble substrate. Our study therefore almost certainly under-estimates patchiness of young lobsters at these smaller scales, and hence the potential contribution of behavioral ontogeny to these patterns, which may be expected based on earlier and smaller-scale laboratory and field observations (reviewed by Lawton and Lavalli, 1995)

Benthic recruitment patterns: disruption during ontogeny and implications

Our analyses revealed a marked disruption of spatial abundance patterns between the first three benthic life phases (4-40 mm), i.e., EBP lobsters, and the fourth phase, i.e., adolescent lobsters (40-50 mm CL in this study). In particular, whereas the first three life phases showed significant spatial structure at the Area scale (see above), 0% (0/6) of the randomization tests involving adolescents were statistically significant at this scale (compared to 67-83% for the first three life phases), which only accounted for 10% of the variance in the abundance of adolescent lobsters (versus 30-50% for the first three life phases). This disruption was also evident in the correlation analyses, where only 12%

(4/33) of the area-scale correlations involving adolescents were statistically significant, in comparison to 70% for shelter-restricted, 70% for emergent, and 63% for vagile individuals. These differences were not simply due to the fact that these correlations are not strictly based on the same cohorts of individuals (discussed further below), given that 75% (9/12) of the correlations involving 2012 shelter-restricted individuals (i.e., the youngest lobsters sampled in the last year of this study) were significant, even though none of these correlations involved same-cohort individuals (they are all based on later life stages sampled in earlier years), compared to only 0% (0/11), 18% (2/11) and 18% (2/11) of the comparisons involving 2010, 2011 and 2012 adolescents, respectively.

Adolescent individuals not only showed much less patchiness at the Area scale than all other life stages, but they also showed markedly less spatial structure overall. In particular, there were very few significant randomization tests overall for this phase, and not more than would be expected under the null hypothesis of no patchiness using an alpha of 0.05 (1.6%, 4.6%, 0% and 0% of tests at the Bio-collector, Site, Area and Region scales, respectively), suggesting these can be considered to be type I errors. Similarly, in the variance component analysis, only 22% of the variance in abundance of adolescents was not associated with the error term (10% for Area and 12% for the Site scales), compared to 52-64% for the other three life phases. These results indicate that adolescents were relatively uniformly distributed across spatial scales and units covered in this study, in contrast to younger life phases that were mostly aggregated at the Area scale, and to a lesser extent at the Region (and even lesser extent Site) scales. It is worth mentioning that fishing

would not be affecting the spatial patterns of this phase, since they are still considerably below the legal size (82.5 mm CL in the Bay of Fundy), and lobsters of this size that would be caught are released.

This abrupt change in spatial abundance patterns between adolescent lobsters (more uniform) and younger juveniles life phases (patchier) is consistent with the proposed shift in life history (e.g., susceptibility to predation, energetic requirements, activity level) between these phases (Wahle and Steneck, 1991; Lawton and Lavalli, 1995). We propose, in particular, that this change is caused by marked differences in movement patterns between adolescent lobsters and EBP lobsters, and more specifically a tendency for these younger lobsters to remain within settlement nursery grounds until they become adolescents, at which time they start moving more broadly, including undertaking seasonal migrations with adult individuals. This same mechanism was proposed by Wahle and Incze (1997) to explain patterns in abundance of different life phases of young lobsters within a $\approx 1.5 \text{ km}^2$ area in the southwestern Gulf of Maine, where lobsters were observed to settle almost exclusively on one side of an island (Damariscove island, east of Portland, Maine) over four consecutive years, and differences in abundance of different-size young lobsters on the two sides of the island persisted until individuals reached approximately 30 mm in CL. They proposed that densities of lobsters $> 30 \text{ mm CL}$ were similar on the two sides of the island because these individuals moved more broadly, disrupting abundance patterns established at settlement. While the size ($>30 \text{ mm}$) at which this change occurred is somewhat smaller than the minimum size considered for adolescents in this study (40 mm),

the patterns observed are very similar, and it is possible that the difference is in part related to differences in temperature between the two study regions, and associated differences in lobster growth rates and size at onset of sexual maturation. A similar ontogenetic change in movement was observed in the recent acoustic telemetry study in the Baie des Chaleurs that was mentioned earlier (Morse et al., 2018), which simultaneously tracked the activity and movements of 14 lobsters measuring 28-81 mm CL for 74 days from late summer through fall. For example, and notwithstanding that not all lobsters were successfully tracked for the entire study duration, the six juvenile lobsters (28-41 mm) were only recorded travelling between \approx 55-320 m from their tagging location, in comparison to \approx 340-2020 m for the 4 adolescent lobsters (41-67 mm) and \approx 200-2060 m for the 4 adult lobsters (74-80 mm). Importantly, these numbers undersell, and probably considerably so, the importance of the difference in movements of juveniles versus adolescents and adults, because 3 of 4 adolescents and 2 of 4 adults left the tracking area before the end of the study, whereas none of the 6 juveniles are thought to have done so. Importantly, these 5 adolescent and adult lobsters, along with one additional adult individual (i.e., 6/8 adolescent/adults lobsters) migrated towards the deeper portion of the study area over the course of the study, presumably undertaking autumn migrations from shallow to deeper waters that older lobsters in the region are known to undertake as temperature decrease and storm events increase at this time of the year in the Gulf of St. Lawrence (e.g., Munro and Therriault, 1983; Comeau and Savoie, 2002; Bowlby et al., 2007). Whereas similar migrations would presumably also benefit smaller juvenile lobsters from the perspective

of the temperature they experience, these individuals are thought to not undertake such migrations because of their greater susceptibility to predators (Spanier et al., 1998).

Conclusion

This study investigated the relationship between ontogenetic changes in behaviour and abundance patterns of early life stages of American lobster at different spatial scales in the lower Bay of Fundy. Our findings indicate that spatial abundance patterns established at settlement in this region are largely unchanged over the first three life-history phases of young lobsters, which probably cover the first 3-5 years of their life in this part of the species' range (Tang et al., 2015). This is consistent with a relatively large body of literature on the early life history of lobsters (e.g., Wahle and Steneck, 1991; Lawton and Lavalli, 1995), as well as more recent acoustic telemetry tracking studies (Morse and Rochette, 2016, Morse et al., 2018). Importantly, whereas structurally complex cobble bottom is believed to represent a demographic bottleneck to lobster benthic recruitment (Wahle and Steneck, 1992), our results suggest that some such nursery grounds are consistently more important to this process than others. This finding helps explain recent evidence that settlement trends on relatively small patches (4-12 sites of ~6-10 m²) of quality cobble bottom can in some cases forecast fisheries landings over whole lobster management units covering 1000s of km² (Oppenheim et al., 2019). Our findings also show that spatial patterns of abundance of young lobster change rather abruptly at the adolescent

phase, likely because of the more extensive movements these lobsters undertake, including seasonal migrations. This finding is also largely consistent with literature on the early life history of lobsters (review by Lawton and Lavalli, 1996), field observations (Ennis, 1984) and two more-recent acoustic telemetry tracking studies (Morse and Rochette, 2016; Morse et al., 2018). It highlights the importance of this phase to connectivity and fisheries recruitment over large areas, following successful benthic recruitment on select and relatively small quality nursery grounds. Taken together, our findings argue for the importance of identifying, protecting and monitoring hotspots of lobster benthic recruitment, as a means of safeguarding and forecasting fisheries recruitment.

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Competing interests

The authors declare there are no competing interests.

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Appendix 1. Variance Component Analysis by life history phase and spatial scale for all three years separate

Phase Scale	Shelter restricted	Emergent	Vagile	Adolescent	Shelter restricted	Emergent	Vagile	Adolescent	Shelter restricted	Emergent	Vagile	Adolescent
Year	2010				2011				2012			
Region	0%	0%	0%	0%	13.98%	1.36%	0.64%	0%	9.97%	0.53%	5.76%	0%
Area	18.12%	4.74%	5.82%	1.68%	18.7%	20.21%	8.12%	2.14%	10.71%	12.73%	12.11%	0%
Site	0.47%	3.49%	4.88%	8.73%	1.35%	0.7%	6.41%	2.44%	13.92%	8.36%	5%	5.89%
Sub-site	1.92%	3.76%	3.08%	0	0.16%	0%	0.02%	0%	0%	0%	1.3%	0.79%
Error (collector)	79.49%	88.01%	86.22%	89.59	65.8%	77.73	84.81%	95.42%	65.39%	78.39%	75.83%	93.32%

Appendix 2. Summary table of the three main results obtained by the nested analysis of variance (Anova), variance component analysis (VCA), and the randomization approach (Patchiness).

Phase / Scale	Region			Area			Site			Sub-site			Collector		
	Anova	VCA	Patchiness	Anova	VCA	Patchiness	Anova	VCA	Patchiness	Anova	VCA	Patchiness	Anova	VCA	Patchiness
Shelter restricted		0%	2/3	2010	18%	5/6		0%	18%		2%	0		80%	0
		14%		2011	18%			1%			0%			65%	
		10%		2012	11%		2012	14%			0%			65%	
Emergent		0%	2/3		5%	4/6		3%	18%		4%	0		88%	5
		2%		2011	20%			1%			0%			78%	
		1%		2012	12%		2012	8%			0%			78%	
Vagile		0%	2/3		5%	4/6		5%	20%		3%	0		86%	0
		1%			8%			6%			0%			84%	
		6%			12%			5%			1%			76%	
Adolescent		0%	0/3		2%	0/6		8%	5%		0%	0		90%	0
		0%			2%			2%			0%			95%	
		0%			2%			6%			1%			93%	

General discussion

Elucidating spatio-temporal patterns in the abundance of organisms in nature, and the processes that drive those patterns, are the cornerstone of ecology as a scientific discipline. Ecology differs from other scientific disciplines in its high dependence on scale, where different patterns and processes occur at certain scales, but not others. This is very different from physics for example, where many of the same laws, principles and hypotheses apply to atoms and galaxies. This dependence on scale tends to complicate understanding and generalizations in ecology, as patterns at different scales can be driven by different processes. As an example, at the scale of oceans, feeding patterns of bottlenose dolphins are defined by physical characteristics of the ocean floor, such as seabed slope and shelf fronts, while at the smaller scale of bays and coves individual prey selection is the main driver (Pirotta et al. 2013). Another example is the quest to explain species richness patterns in avian ecology, which has spawned more than 100 different hypotheses, depending in part on the scale being considered, where some processes are good predictors at certain scales and not at others (Rahbek and Graves 2001). This thesis focuses on spatial patterns in the abundance of early benthic phases of lobster (*Homarus americanus*) in nature, and how we can use these patterns to gain valuable insight into the ecology of Canada's and eastern North America's most socio-economically important marine species (Rochette et al. 2017).

Sampling of recently settled American lobster postlarvae started in the late 1980s through the pioneering work of Wahle and Steneck (1991), and before this thesis only three studies

had quantified patchiness in benthic recruitment of American lobster, and they had done so at three very different spatial scales. Firstly, Wahle and Incze (1997) found pronounced differences in the abundance of recently settled lobsters on two sides of a small island in the Gulf of Maine, which they suggested were due to differences in larval supply, most likely because of wind-driven surface currents, since they found no difference in habitat characteristics or post-settlement mortality between the two sides of the island (Wahle and Incze 1997). Secondly, Palma et al. (1999) looked at patchiness in benthic recruitment of American lobster (as well as rock crab and Jonah crab) at spatial scales ranging from a few centimeters to hundreds of kilometers on three different substrates in the Gulf of Maine, finding patchiness at small scale (mainly between different substrate types), but also at “regional scale” (hundreds of km) and at an intermediate scale around 10-100 km apart. Finally, a more recent study involving greater spatial coverage, ranging from southwest Nova Scotia in the north to Rhode Island in the south, contrasted benthic recruitment between several regions in the Gulf of Maine, and found stark contrast between these regions (roughly 200 km apart) (Wahle et al. 2013). These three studies did not investigate the similarity of these patterns across different juvenile life phases, the consistency of the spatial patterns over multiple years, or the contribution of different processes at those different spatial scales. The work presented here is the most comprehensive investigation of spatial patterns of young American lobsters as it covers different life stages, multiple years, and multiple spatial scales over a relatively wide geographic area.

In the first chapter of my thesis, I quantified spatial patterns of young-of-year (YOY) American lobster on structurally-complex cobble bottom at a hierarchy of spatial scales in the Canadian Gulf of Maine. This study was the first to assess spatial patterns in benthic recruitment of American lobster at multiple spatial scales over multiple years. I quantified spatial patterns of benthic recruitment using three quantitative approaches (a nested analysis of variance, a variance component analysis and a randomization approach), which all indicated greatest patchiness of benthic recruits at the “area” scale (0.4-4 km²), followed by the “region” scale (127 and 674 km²), and virtually no significant variation in abundance at the two smaller spatial scales considered (site: 0.003-0.23 km²; sub-site: 0.00004-0.06 km²). Importantly, despite inter-annual variability in benthic recruitment, spatial patterns and scales of patchiness were largely consistent across years, and several “hotspots” and “coldspots” of American lobster benthic recruitment in the Canadian Gulf of Maine were identified.

My findings concerning the spatial scale of patchiness in lobster benthic recruitment are generally consistent with the three published studies that provide comparable data (Wahle and Incze 1997, Palma et al. 1999, Wahle et al. 2013). In particular, the striking difference in benthic recruitment Wahle and Incze (1997) observed on two sides of an island in the Gulf of Maine was at a spatial scale (ca. 1 km²) most similar to the area scale of my study (0.4-4 km²), which is the scale at which I found greatest patchiness of benthic recruits. Similarly, Palma et al. (1999) reported low variation in lobster settlement at a scale that roughly corresponds with my site scale (ca. 1-10 km, versus 0.5-5 km in this study),

moderate variation at a scale similar to my region scale (ca. 120 km, versus 140 km in this study), and markedly more variation at a scale similar to my area scale (ca. 10-100 km, versus 10-80 km in this study). The most recent study (Wahle et al. 2013), which was conducted at a scale similar to my region scale (ca. 200 km, versus 140 km in this study), found variation in benthic recruitment between Rhode Island, mid coast Maine, southwest New Brunswick and southwest Nova Scotia, similar to the variation observed between the two regions in my study. It is noteworthy that these congruent results were observed even though scale was represented in two different ways in these studies, first as the area of the “patches” surveyed (Wahle and Incze 1997; this study) and second as the distance between these patches (Palma et al. 1999; Wahle et al. 2013; this study).

The results of the first chapter show not only how the abundance of lobster benthic recruits varies at different spatial scales, but that at the scale where patchiness is greatest (i.e., area, or 0.4-4 km²), there is some consistency in the identity of “patches” with “high” (i.e., hotspots) and “low” (i.e., coldspots) recruitment success. Three areas had between 58-71% of all YOY lobsters sampled over the three years of the study, while comprising only 27% of the areas surveyed. Similarly, six areas consistently had fewer than 5% of the annual abundance of YOY, while comprising 73% of the areas surveyed. This consistency was observed even though mean benthic recruitment varied among years. These findings are somewhat surprising, given that all areas were sampled with the same cobble filled bio-collectors deployed on cobble bottom thought to be ideal for lobster benthic recruitment, which suggests that all areas with suitable settlement substrate are not equally important to

benthic recruitment of American lobsters. However, and as already mentioned, this is consistent with Wahle and Incze (1997), who observed (although in a single sampling year) striking difference in recruitment on quality cobble patches on two sides of an island.

In the second chapter of this thesis, I built light traps to investigate whether larval (stages I-III) and postlarval (stage IV) supply were responsible for variability in benthic recruitment between areas designated as benthic recruitment “hot-spots” and “cold-spots” in the first chapter of the thesis. Studies on the spatial or temporal link between the abundance of American lobster larval stages, postlarvae, and benthic stages are few. Miller (1997) conducted a very large number of larval tows (351-445 annually) in seven large coastal areas over a total of 190 km of the eastern shore of Nova Scotia over 2-4 years with the goal of linking postlarval abundance and fisheries landings. His study was very labour intensive, given the nature and frequency of the sampling, but it showed a strong correlation (r ranged between 0.81-0.94 depending on years and depth) between postlarval abundance in the plankton and the abundance of recruits to the fishery. Wahle and Incze (1997) also used surface tows to confirm their hypothesis that postlarval supply was responsible for the stark differences in benthic recruitment reported earlier, on two sides of an island in the Gulf of Maine. In a recent study, Carloni et al. (2018) used extensive multiyear datasets from plankton tows and SCUBA suction sampling in conjunction with landings data to investigate linkages from 1988 to 2013-2015 between lobster spawning stock biomass (SSB), the abundance of lobster larvae, postlarvae, and YOY, and the abundance of planktonic prey. They found a positive correlation between SSB and the

abundance of stage I larvae in plankton tows, but while both increased over the study period, the abundance of postlarvae in the water and YOY on the sea floor decreased. They also found that both postlarval and YOY abundance were significantly correlated with the abundance of the copepod *Calanus finmarchicus*, suggesting that the decrease in lobster benthic recruitment that occurred despite increasing egg and larval production was the result of impoverished feeding conditions for lobster postlarvae in the plankton.

Results of the light trap study in my second chapter suggest that postlarval supply markedly affects patterns of American lobster benthic recruitment, as all (100%) the postlarvae caught in the plankton were caught in the two of three benthic recruitment hotspots, where 34% of the pelagic light trap sampling effort was concentrated, and none (0%) were caught in the three benthic recruitment coldspots, where 49% of the pelagic light trap sampling effort was concentrated. No postlarvae were found in one of the high benthic recruitment areas where 17% of the sampling effort was concentrated. These findings were consistent with those of Miller (1997), Wahle and Incze (1997), Carloni et al. (2018) and older studies in the Northumberland strait (Scarratt 1973, Robinson 1979, Harding et al. 1982) that indicated that postlarval supply can be linked with later stages (benthic recruitment, fisheries recruitment, landings). These studies were also similar to mine in suggesting that the supply of stage I larvae does not influence the number of recruits on the bottom; the majority (57%) of the stage I larvae in my study were found in areas where no or low benthic recruitment was observed, where 18% of the sampling effort was concentrated, while the

rest of the stage I larvae (43%) were found in one of the high benthic recruitment areas, where only 18% of the sampling effort was concentrated.

While the results of these earlier studies are largely consistent with mine, their methodology differed markedly. More specifically, these studies used surface tows by boat to catch lobster larvae and postlarvae, while I used light traps. While plankton tows can be very successful at catching larvae and postlarvae, they generally are labour intensive and fairly costly, in time and money, given the relatively long larval period and the patchy distribution of larvae/postlarvae. Light traps of this design were first used in Sweden to sample larvae of the Norwegian lobster *Nephrops norvegicus* (Oresland, 2007) and my study was the first to use a modified/simplified design of these traps to successfully capture American lobster larvae and postlarvae. These traps provide a possible alternative for labour-intensive and costly larval tows for sampling of American lobster larvae/postlarvae, especially if the suggested design changes can be implemented to increase retention and catchability of the traps. These traps could then be used for example by community groups or fishermen's organizations to monitor larval/postlarval abundance locally at relatively low cost.

In the third chapter of this thesis, I considered a broad range of biological and physical factors to identify processes that may be responsible for spatial patterns in American lobster benthic recruitment observed at the area scale in chapter 1. Various physical and biological processes are responsible for spatial patterns observed in nature. As an example, large-scale patterns in the abundance of phytoplankton can be broadly explained by the presence

of nutrient-rich cold water, while the formation of coral reefs in the tropics is limited by physical factors such as water temperature, light availability, and currents, as well as biological factors such as recruitment and competition with other biota (Harriot and Banks 2002). Our understanding of physical and biological factors that are responsible for spatial and temporal variation in benthic recruitment of American lobster in nature is very incomplete. While much has been learned concerning factors affecting settlement decisions of postlarvae in the laboratory (e.g. Botero and Atema 1982, Boudreau et al. 1991, Boudreau et al. 1993), much less is known concerning the factors that drive spatio-temporal patterns of lobster benthic recruitment in nature. Investigations into this question have thus far individually focused on a small number of factors, such as sea surface temperature (Jaini et al. 2018), sea surface temperature and geopotential height (Pershing et al. 2012), wind-driven surface currents affecting postlarval supply (Wahle and Incze 1997), bottom temperature (Annis 2005, Annis et al. 2013), and the presence of juvenile conspecifics (Burdett-Coutts et al. 2014).

In my study, I first reviewed the literature on factors influencing settlement of marine invertebrates and identified a suite of candidate biological and physical factors that could potentially explain the abundance patterns of lobster benthic recruitment described in Chapter 1. Various candidate models were then compared using AICc until two models stood out, the best biophysical and the best purely physical models. The best biophysical model resulting from this exercise comprised four variables, the North Atlantic Oscillation Index (NAO) over the larval period, fetch of the study area, juvenile abundance, and sea

surface temperature over the larval period. Some of these variables have been suggested as drivers of patterns of benthic recruitment of American lobster in other studies, while others have not been suggested before for American lobster (see below). According to variance explained, the NAO index seemed most important in explaining the recruitment patterns, followed by sea surface temperature and juvenile abundance, while fetch was least useful. However, it seems that the relationship between the benthic recruitment patterns and both sea surface temperature and fetch might reflect a spurious correlation.

While the NAO index has not been associated with benthic recruitment of American lobster before, it has been associated with variation in recruitment of various species of fish and invertebrates (see review by Solow 2002), such as Atlantic cod (Brander and Mohn, 2004; Brander 2005), North Atlantic swordfish (Mejuto 2002), anchovy (Santojanni et al. 2006), and short finned squid (Dawe et al. 2000). In these studies, the index acts as a proxy for general weather patterns (e.g., wind direction and strength) in the regions in question, and the mechanistic link between the index and recruitment is therefore generally unknown and likely varies. This is also the case in my study, but it might be related to dominant wind directions that push larvae toward or away from the shoreline.

I observed a negative correlation between benthic recruitment and sea surface temperature over the larval period (June-October). This result is somewhat surprising, given that growth and survival of larval stages and recently-settled postlarvae have been shown to increase with temperature over the range observed in our study (reviewed by Ennis 1995). Our results are therefore not consistent with the positive relationship between YOY densities

and temperature observed in other studies (Jaini et al. 2018, Pershing et al. 2012). Although we believe that the negative relationship between sea surface temperature and lobster settlement is a spurious one, we obviously cannot exclude the possibility that it does reflect a causal relation. One possibility is that lobsters from the cool waters of the Bay of Fundy are adapted to colder waters than lobsters from the studies mentioned here, which were from Maine and other warmer parts of New England.

The density of older juvenile lobsters in an area was positively correlated with benthic recruitment of American lobster in my modelling exercise. Two markedly different processes could be responsible for this positive association. Oceanographic circulation or other large-scale physical processes could cause some inter-annual consistency in differences in postlarval supply among my different study areas, in which case the correlation between the density of recent settlers and older juveniles would not reflect a causal relation. The second possibility is that the postlarvae actively seek out and select habitats where juvenile lobsters are already present, as a sign of “quality habitat”, in which case the relation between juvenile density and benthic recruitment density would be causal. Laboratory studies have shown that settling lobster postlarvae swim towards odors of conspecifics (Boudreau et al. 1993), and in nature a positive association has been found among quadrats (a few meters apart) of a same site between the abundance of young-of-year individuals and of older juveniles, providing support for the possibility of the causal relation. It is possible that both processes, inter-annual consistency in postlarval supply and

attraction to conspecifics, are responsible for spatial patterns in lobster benthic recruitment, but at different spatial scales.

Fetch showed a weak positive relationship with YOY abundance, and it had the lowest importance of the variables retained in my modelling exercise. While fetch has not been directly associated with benthic recruitment of American lobster before, studies mentioned earlier (Wahle and Incze 1997; Pershing et al. 2012) have found a relationship between wind, surface currents and settlement patterns in this species. It is possible that high fetch creates wind driven surface currents that push pelagic postlarvae into certain areas. Lower fetch areas (areas more closed off) could that way receive lower larval supply due to topography. This is particularly likely for one of the low recruitment areas in my study, Passamaquoddy bay, which is closed off from the rest of the Bay of Fundy by a corridor of islands and skerries which could block drifting larvae. In stark contrast, one of the highest recruitment areas, Maces Bay, is a wide and rather exposed bay in the Bay of Fundy, which could potentially receive drifting larvae from multiple directions and sources. It should be noted though that the relationship observed was rather weak/unclear, and warrants further investigation.

In the fourth and final chapter of this thesis I used spatial patterns of different life phases of juvenile American lobster to gain insight into the contribution of ontogenetic changes in the species' behaviour to its demography. The behaviour (*sensu lato*) of individual animals can be important to ecological processes and is increasingly studied to further our understanding of population structure and dynamics (Grimm and Railsback 2005). In this

growing field, the behaviour of individual animals is quantified, and its contribution to characteristics of the population is established. Such individual-focused approaches and resulting models have shed considerable light on a variety of demographic patterns and processes in nature (Sutherland 1996). For example, they have predicted patterns of recruitment (into the spawning stock) in fishes in lakes and rivers based on the size, foraging, and growth of young, individually tracked individuals (DeAngelis and Grimm 2014). In the marine environment, biophysical models that combine physical oceanic processes and various behavioural attributes such as swimming speed and diurnal movements have been used to predict large-scale patterns of larval dispersal and connectivity for several species, including commercially important fishes and invertebrates (Cowen et al. 2006, Kough et al. 2013). In these studies, observed behaviour is used to predict or model population dynamics, but in the last chapter of this thesis I have turned this idea on its head, and used observed spatial patterns of different life stages to investigate the contribution of ontogenetic changes in behaviour to demographic patterns of sub-adult American lobster in nature. I found that spatial patterns established at settlement (Chapter 1) are largely unchanged over the first three life-history phases of young lobsters, which probably cover the first 3-5 years of their life. These patterns then change when the lobsters reach adolescence, presumably because these individuals start to move over larger areas and hence disrupt spatial patterns established at settlement. This interpretation is largely consistent with a body of literature on the behaviour and early life history of the American lobster (e.g. Wahle and Steneck 1991; Lawton and Lavalli 1995). However, whereas these studies and reviews have generally predicted a rather gradual increase in movement and

activity of young lobsters until adolescence, my results indicate that changes in behavior before the adolescent phase have limited impact on spatial patterns in nature. My results are in fact more consistent with those of two recent acoustic telemetry tracking studies, which have shown that although earlier life phases are fairly active, they behave as central place foragers and stay within their nursery areas, and don't start moving more broadly until they reach adolescence and adulthood (Morse and Rochette 2016, Morse et al. 2018). This highlights the importance of the adolescent phase to connectivity and fisheries recruitment over larger areas, following successful benthic recruitment and subsequent development over the first 3-5 years in relatively rare and small nursery grounds. Taken together, the results of this chapter show the importance individual behaviour has on population patterns of American lobster in nature.

Conclusion

The four chapters of my thesis enhance our understanding of benthic recruitment in American lobster in the lower Bay of Fundy, and they highlight the importance of quality nursery grounds to fisheries recruitment of this species. These areas seem to be relatively rare, and their monitoring and preservation could help manage lobster stocks.

The first chapter shows how the abundance of lobster benthic recruits varies at different spatial scales, and that at the scale where patchiness is greatest there is some inter-annual consistency in “high” (i.e., hotspots) and “low” (i.e., coldspots) recruitment success among “patches” of seafloor. The fourth chapter shows that these “hotspots” are critical for the first 3-5 years in the lobster’s life, as the juveniles remain within those nurseries until the onset of adolescence. The importance of juvenile presence in explaining the recruitment patterns in my third chapter, and the correlation between the abundance of juveniles and recent settlers in the study by Burdett-Coutts et al. (2014), further emphasize the importance of certain patches of seafloor to benthic recruitment. These areas are likely to be important for fisheries recruitment locally, which should be kept in mind while managing coastal areas for human activities such as aquaculture or construction of breakwaters or harbours. The use of benthic recruitment to predict fisheries recruitment is used in management of the spiny lobsters in Australia (Linnane et al. 2013), and there are studies that have shown that similar predictions can be used to forecast fisheries recruitment for American lobster as well (Wahle 2003, Oppenheim et al. 2019).

While protecting and monitoring these nursery areas is essential, it is also important to stay vigilant and monitor the areas where benthic recruitment is lower, as results of the second chapter show the importance of larval supply for benthic recruitment, and rapid climate change is affecting the distribution of both the species and its fishery, as well as environmental conditions essential for larval development (Steneck and Wahle, 2013; Goode et al. 2019). For example, increasing temperatures in the southern parts of the species' range has caused an increase in the prevalence of shell disease, and the main fishing areas for lobster have consequently shifted northwards, from southern New England (Rhode Island and Massachusetts) to northern parts of Maine and the Atlantic provinces in Canada (Wahle et al. 2015). Lobsters have also been observed to settle in deeper waters due to increases in availability of thermally suitable habitat associated with warmer summers (Goode et al. 2019). These observed changes are likely to continue, and monitoring recruitment is therefore of high and increasing importance.

Results of the second and third chapters, along with information from the literature, demonstrate that despite considerable effort, our understanding of the factors and processes that affect benthic recruitment success is limited. Supply of postlarvae seems, however, to be a key driver. The four variables identified in the third chapter (NAO index, sea surface temperature, juvenile abundance, fetch) are all likely to influence postlarval abundance in the plankton. The NAO index, in particular, shows promise in explaining annual variation in YOY abundance. In addition to these variables, a recent study has shown the importance of postlarval food sources, in the form of copepod abundance, in explaining YOY

abundance in suction sampling (Carloni et al. 2018). This further shows the importance of postlarval abundance and survival to the YOY abundance patterns, and some index of copepod abundance (collected for example in oceanographic surveys) in addition to other parameters influencing postlarval survival could potentially be incorporated into a model similar to that which I developed in chapter three to predict spatial and/or temporal variability in benthic recruitment. Validating such a model by testing its predictive ability on a new dataset is an important and logical next step for this work, as ecological models are often built to predict, but too rarely validated and tested elsewhere/later. Continuing monitoring of the areas sampled in this thesis is therefore important, for all the reasons discussed above, but also to allow future validation of hypotheses concerning ecology and biology of early life phases of the American lobster in the region.

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Publications:

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2019 – Mcleod, K., Königson, S., Kingston, A., Pinto, C., Sigurdsson, G.M. The impact of spatial scale on the scale of impact: Harbour porpoise *Phocoena phocoena* bycatch in the Celtic Seas. World Marine Mammal Conference, Barcelona, Spain, December 2019.

2019 - Sigurðsson, G.M., Haney, G. Testing of two commercially available porpoise bycatch reduction devices in a sub-Arctic bottom set gillnet fishery. World Marine Mammal Conference, Barcelona, Spain, December 2019.

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2015 - Sigurðsson, G.M., Tremblay, M.J., Rochette, R. Botntaka humars í Fundyflóa: Ferlar og mynstur. Líffræðiráðstefnan 2015. Reykjavík, Iceland. November 2015.

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Poster presentations

Hanley, P., Morse, B.M., Sigurðsson, G.M., Rochette, R. Thermal histories and migration of ovigerous lobsters, *Homarus americanus*, from Grand Manan, N.B. revealed using

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