LONG-TERM EFFECTS OF MARINE RESERVE PROTECTION ON THE POPULATION STRUCTURE, DENSITY, AND REPRODUCTIVE POTENTIAL OF THE AMERICAN LOBSTER (*Homarus americanus*) IN BONAVISTA BAY, NEWFOUNDLAND

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by

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Abstract

Marine reserves provide a means of implementing the precautionary principle in support of sustainability objectives. Many reserves have been established for several commercially significant species of spiny lobster, but are less frequently employed for Homarid lobsters. In 1997, two small reserves for American lobster, *Homarus americanus*, were established in Bonavista Bay, Newfoundland – one at Round Island, and one at Duck Islands. They were designated as Marine Protected Areas (MPAs) in 2005. Relatively short-term studies, employing 3 to 5 years of data, revealed significant differences in lobster density and/or mean size between populations within the reserves and similar reference locations, but did not examine differences in reproductive output. Using over ten years of data, I investigated differences in density, population structure (i.e. size; sex ratios), and reproductive potential between protected and unprotected populations of American lobster at both study sites. At the Round Island site, lobster density inside the reserve was greater than that of the adjacent reference area. Observed sex ratios in reserve and reference locations differed at both sites, with a greater bias towards females in reference locations. At Round Island and Duck Islands study sites, both male and female lobsters were significantly larger in protected populations, and mean sizes continued to increase over time. The increased female size in protected populations led to consistently greater reproductive potential inside these reserves, though the difference between protected and unprotected populations was small, averaging 10 % for Round Island and 14 % for Duck Islands. The results of this study

provide further evidence that the Eastport MPAs promote sustainability of the resource through increased density, mean size and reproductive potential of lobsters.

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Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1: Introduction

1.1 The precautionary principle and marine reserves in fisheries management

Many exploited populations in coastal habitats have declined precipitously as a consequence of overfishing (Dayton *et al.* 1995). In most cases, the declines were associated with traditional fisheries management methods, involving control of effort or catch (Stefansson and Rosenberg 2005). The large degree of uncertainty associated with fisheries stock assessments and the study of marine ecosystems, combined with the uncontrollability of catches and incidental mortality, necessitates a more precautionary approach to fisheries management, to safeguard against these uncertainties and mitigate the possibility of a stock collapse (Ludwig *et al.* 1993; Lauck *et al.* 1998). The precautionary principle stresses the importance of caution and careful consideration in fisheries management where scientific information is uncertain, unreliable, or inadequate. It asserts the importance of accounting for environmental fluctuations and excessive, unreported fishing mortality in the design and implementation of fisheries management strategies (Lauck *et al.* 1998). Application of the precautionary principle, or precautionary approach, has typically been achieved through the use of harvest control rules, which adjust catch quotas or effort levels in response to reference points based on estimates of biomass and/or rates of fishing mortality (Hilborn *et al.* 2001). Such control rules are best applied to fisheries characterized by data-rich stock assessments, but many stock assessments lack sufficient information or certainty to derive necessary control rules and associated reference points (Cadrin and Pastoors 2008). Establishment of marine no-take reserves is another method of implementing the precautionary principle in fisheries management (Lauck *et al.* 1998). More effective management and, thus, greater sustainability of fisheries can be achieved through the use of marine reserves as a complement to traditional fisheries management practices, which sometimes fail to prevent overexploitation, or even collapse, of harvestable stocks (Davis 1989; Bohnsack 1993; Agardy 1994; Guénette *et al.* 1998; Lauck *et al.* 1998; Roberts *et al.* 2005; Stefansson and Rosenberg 2005).

Reserves have the potential to benefit target species and ecosystems in a number of ways. Targeted species can benefit from the establishment of such refugia as abundance, mean individual size (and age), and reproductive output can be increased (Dugan and Davis 1993). Recruitment both inside and outside the refugia can be enhanced, as can fishery yields in adjacent harvested grounds (Dugan and Davis 1993). Additionally, the genetic diversity and population structure (sex ratio and size structure) of stocks can be maintained as a consequence of protecting a portion of the stock within a reserve (Bohnsack 1992; Dugan and Davis 1993; Bohnsack 1998).

Although marine reserves have the potential to conserve exploited populations through a variety of general effects on ecosystems and targeted species, specific and direct benefits to the fishery can be achieved in two principal ways. First, reserves may act as sources of recruitment to regional fishery stocks, exporting larvae to areas that are open to commercial harvesting (Roberts and Polunin 1991; Rowley 1994). This is often viewed as the primary benefit of reserves in the context of fisheries management, as they may provide "insurance" against poor recruitment seasons (Roberts and Polunin 1991;

DeMartini 1993; Dugan and Davis 1993). Recruitment benefits from the protected spawning stock within reserves can also aid in the rehabilitation of the stock following a collapse due to unfavorable environmental conditions or recruitment overfishing (Roberts and Polunin 1991; Carr and Reed 1992; Rowley 1994; Russ and Alcala 1996). Secondly, marine reserves may enhance local catches via the "spillover" effect, as harvestable biomass contained within the reserve disperses and enters adjacent harvesting grounds (Rowley 1994; Russ and Alcala 1996). This "spillover" may increase yield and counteract the effects of growth overfishing, replenishing exploited stocks through the movement of older life stages across reserve boundaries (Polacheck 1990; Roberts and Polunin 1991; Rowley 1994; Russ and Alcala 1996).

Design and implementation of such harvest refuges requires careful consideration and dedicated research and evaluation. Reserves that are poorly designed and/or do not contribute to the enhancement of a fishery will serve as inefficient use of resources, and unnecessarily restrict the range of the fishery (Carr and Reed 1992). Therefore, it is important that the effectiveness of such reserves be evaluated and monitored, to ensure that resources and effort are optimally expended, and the fishery is not compromised.

Marine reserves have been implemented for a variety of species in response to the realization that traditional fisheries management approaches are characterized by a considerable, and often irreducible, degree of uncertainty (Guénette *et al.* 1998; Lauck *et al.* 1998). Multiple studies involving marine reserves of varying sizes and locations have demonstrated that the abundance/density, mean size, and fecundity of heavily fished resident species tend to be greater within reserve boundaries, as compared to nearby reference areas (Roberts and Polunin 1991; Dugan and Davis 1993; Rowley 1994; Halpern and Warner 2002). Many of these studies have focused on the impacts of protection for a number of populations of commercially significant species of spiny lobster. Increases in abundance and/or mean size of populations in reserves have been demonstrated for *Jasus edwardsii* (Cole *et al.* 1990; Kelly *et al.* 2000; Davidson *et al.* 2002; Barrett *et al.* 2009), *Panulirus argus* (Acosta and Robertson 2003; Cox and Hunt 2005), and *Palinurus elephas* (Goni *et al.* 2001). Additionally, increased reproductive potential has been reported for protected populations of *Jasus edwardsii* in New Zealand (Kelly *et al.* 2000; Davidson *et al.* 2002), *Panulirus argus* in Florida (Bertelson and Matthews 2001), *Panulirus cygnus* in Western Australia (Babcock *et al.* 2007), and *Palinurus elephas* in the western Mediterranean, off the coast of Spain (Goni *et al.* 2003). In contrast, fewer reserves exist for populations of clawed lobsters such as the American lobster, *Homarus americanus*, despite its commercial significance. In Canada, the commercial fishery for the American lobster is valued at approximately one billion dollars annually.

1.2 American lobster (*Homarus americanus*) biology

The American lobster (*Homarus americanus*) is distributed along the continental shelf and upper slope of the northwestern Atlantic, ranging from the Straits of Belle Isle to Cape Hatteras (Lawton and Lavalli 1995). It is a decapod crustacean characterized by a complex life cycle, which is dominated by a benthic period that may continue for more than 30 years (Lawton and Lavalli 1995). Growth is achieved through molting, and frequency of molting depends on the age of the animal. Adolescent and juvenile lobsters may molt 15 to 20 times before reaching reproductive maturity (Wilder 1953). Older animals, however, molt less frequently and the interval between molts increases with the size of the lobster (Cobb 1995).

Mating in this species occurs in the months of July to September, immediately after the summer molt, and the female extrudes eggs roughly one year subsequent to mating (Waddy *et al.* 1995). The eggs are carried in clutches on the underside of the female's abdomen, and the ovigerous (egg-bearing) animal protects and maintains the eggs for a period of 9-12 months (Ennis 1995). Thus, female lobsters are characterized by an alternate year molt/lay sequence (*i.e.* biennial molt-reproductive cycle), though mature female lobsters at the lower end of the size range sometimes molt and spawn within the same summer (Ennis 1984). As is the case with many species of fish and marine invertebrates, fecundity of females increases logarithmically with size (and age), and eggs from larger lobsters tend to contain more energy per unit weight than those of smaller females (Aiken and Waddy 1980*a*, 1980*b*; Waddy and Aiken 1986; Attard and Hudon 1987; Estrella and Cadrin 1995). This suggests that larvae hatched from eggs of larger animals are better equipped to deal with, and survive, adverse conditions. Larger ovigerous females also undertake migrations to expose their developing eggs to less extreme and variable temperatures, which may affect timing of hatching, larval release and, therefore, postlarval settlement (Cowan *et al.* 2007). This may have implications for survival of offspring.

Hatching occurs during a four month period extending from late May through most of September, and newly hatched prelarvae undergo an initial molt to Stage I before being released by the ovigerous female (Ennis 1995). Once released, larvae swim upward and undergo a series of three molts during a 6-8 week pelagic phase, during which most mortality is thought to occur (Scarratt 1964; Ennis 1995). With the third molt, a metamorphosis occurs and the newly developed postlarvae (Stage IV) make the transition from pelagic to benthic existence.

Newly-settled lobster postlarvae progress through three juvenile stages and an adolescent phase before reaching adulthood (Lawton and Lavalli 1995). The adult lobster is thought to have few natural predators; commercial harvesting accounts for the greater proportion of adult mortality (Fogarty 1995). The American lobster is believed to be one of the most heavily exploited marine species in the world (Cobb 1995).

1.3 Management of the American lobster (*Homarus americanus*) fishery

The Canadian lobster fishery is closely regulated, and is based largely on input controls, rather than quotas. These include regulatory measures such as minimum and maximum size limits, limited entry, restrictions on trap numbers, and the prohibition against landing of ovigerous females. In November of 1995, the Fisheries Resource Conservation Council (FRCC) published a report to the Minister of Fisheries and Oceans Canada entitled, "A Conservation Framework for Atlantic lobster". In this report, the FRCC expressed concerns about the future viability of Atlantic Canada's lobster stocks, suggesting that high exploitation rates, combined with the considerable harvesting of immature animals, could result in decreased egg production and recruitment failure in periods characterized by adverse environmental conditions (FRCC 1995). Exploitation rates were estimated to be as high as 85%, and estimates of egg production stood at about 1-2% of what would be expected in an unfished population (FRCC 1995). The FRCC concluded that the lobster fishery was operating under a very high-risk management regime and recommended that steps be taken to both enhance egg production and decrease exploitation rates.

The FRCC suggested numerous conservation measures aimed at increasing egg production, reducing exploitation rates and effective fishing effort, improving stock structure, and minimizing waste. One such suggestion was the establishment of no-take reserves - protected areas where lobsters would be allowed to live and breed naturally in the absence of commercial harvesting. The FRCC also recommended other measures, such as an increase in the minimum legal carapace size required for retention, and proposed the implementation of V-notching programs. V-notching involves the cutting of a shallow notch in the endopodite of the right uropod of ovigerous lobsters. It is illegal to land V-notched lobsters and, since the mark is typically retained through two or more molts (DeAngelis *et al.* 2010), the practice allows females to attain larger sizes, and greater fecundity (Daniel *et al.* 1989). The FRCC strongly recommended that a precautionary approach be adopted as a required element of lobster conservation plans, to increase the level of egg production while reducing exploitation rates and effective fishing effort (FRCC 1995).

1.4 Eastport Peninsula lobster conservation initiatives

The Eastport Peninsula is located on the northeast coast of Newfoundland, in the centre of Bonavista Bay (48.65°N, 53.70°W). The waters surrounding the peninsula have traditionally served as lobster fishing grounds for harvesters from seven small communities in the area (Burnside, Eastport, Happy Adventure, Salvage, Sandringham, Sandy Cove and St. Chad's). The Eastport Peninsula Lobster Protection Committee was formed in 1995, in response to concerns raised by the FRCC report. The committee, comprised of local lobster harvesters, was established to implement some of the conservation practices outlined in the FRCC report, in an attempt to increase egg production and reduce exploitation rates. In 1996, approximately 1500 ovigerous females were V-notched and released in the area (Rowe 2000). In 1997, the Eastport Peninsula Lobster Management Area was formed, and two small marine reserves were established in Bonavista Bay, around the Duck Islands and in the waters surrounding Round Island (see Figure 1 in Chapter 2). The committee formed a partnership with Fisheries and Oceans Canada, Memorial University of Newfoundland, and Parks Canada, in order to integrate scientific and traditional ecological knowledge and evaluate the effectiveness of these areas.

After the reserves had been established, tagging studies commenced in the fall of 1997, using uniquely numbered polyethylene streamer tags to mark individual animals. With data obtained during the first three years following establishment of the reserves, various aspects of the lobster populations, and movement of animals between the commercially harvested and reserve areas, were quantified. The data revealed significant differences in mean size and lobster density between reserve and commercially exploited populations (Rowe 2002). Janes (2009) compared data from the first year of reserve establishment to later years, 2004-2007, and reported that males and females at the Duck Islands site, and males at the Round Island site, were significantly larger inside the reserves. Overall, these relatively short-term studies suggest that the implementation of the precautionary principle, through the establishment of marine reserves in Eastport, could potentially offer considerable benefits to the local fishery, and facilitate increased survival of lobsters in the area. However, further research, employing a longer time series of data, is necessary in order to determine if these short-term results carry through to longer term impacts on density and population structure. Given that a major benefit of reserve establishment is the production and export of larvae, fecundity and reproductive potential of females within the reserve should also be investigated.

Hypotheses

The hypotheses of this study are as follows:

1) Lobster density will be greater inside each of the reserves, as compared to reference areas. In addition, density inside the reserves will increase over time.

2) Sex ratios inside and outside the reserves will differ significantly. Since ovigerous and V-notched females are protected from commercial harvesting, there should be a biased sex ratio, towards females, in the reference area.

3) The mean size of lobsters will be significantly greater inside the reserves, as opposed to that of reference areas, and will increase over time.

4) Reproductive potential will be greater inside the reserves due to increased mean size of females, and will increase over time.

Chapter 2 will address hypotheses 1, 2, and 3. Chapter 3 will address hypothesis 4. Chapter 4 will summarize key conclusions and directions for future research.

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Chapter 2: Population structure and density of American lobster (*Homarus americanus*) in protected and unprotected populations in Bonavista Bay, Newfoundland.

2.1 Introduction

A number of exploited populations in coastal habitats have declined precipitously as a consequence of overfishing (Dayton *et al.* 1995). The large degree of uncertainty associated with fisheries stock assessments and the study of marine ecosystems, combined with the uncontrollability of catches and incidental mortality, necessitates a more precautionary approach to fisheries management, to safeguard against these uncertainties and mitigate the possibility of a stock collapse (Ludwig *et al.* 1993; Lauck *et al.* 1998). The establishment of marine no-take reserves is one method of implementing the precautionary principle in fisheries management (Lauck *et al.* 1998). Over the past 30 years, marine reserves and fishery refugia have gained popularity as an alternative, or complement, to conventional fisheries management practices, which sometimes fail to prevent overexploitation, or even collapse, of harvestable stocks (Davis 1989; Bohnsack 1993; Agardy 1994; Guénette *et al.* 1998; Lauck *et al.* 1998; Roberts *et al.* 2005; Stefansson and Rosenberg 2005). Interest in the use of reserves as a fishery management tool is focused on two potential direct benefits to the fishery: 1) the production and export of larvae from the protected area, and; 2) the direct emigration of harvestable biomass from reserves, commonly referred to as "spillover" (Rowley 1994).

Both larval export and "spillover" can be difficult to demonstrate. Attempts to quantify the efficacy of marine reserves (and, in turn, the effects of fishing) have often focused on comparisons between protected and commercially exploited populations, and changes in these populations over time, using measures of abundance and/or density, mean sizes, size structure, and sex ratios. A number of these studies have focused on commercially significant species of spiny lobster, including *Jasus edwardsii*, *Panulirus argus*, *Panulirus cygnus* and *Palinurus elephas*. Reserves for these highly exploited species of spiny lobster have been established since the mid 1970s. Studies of these reserves have demonstrated increased abundance and/or density of spiny lobsters within protected areas compared to exploited areas (Cole *et al.* 1990; Kelly *et al.* 2000; Goñi *et al.* 2001; Davidson *et al.* 2002; Babcock *et al.* 2007; Barrett *et al.* 2009), increases in mean size and shifts in population structure to favour larger, more fecund, individuals (Cole *et al.* 1990; Kelly *et al.* 2000; Bertelsen and Matthews 2001; Davidson *et al.* 2002), and changes in population sex ratios (Goñi *et al.* 2001; Davidson *et al.* 2002).

By comparison, fewer reserves have been established for the protection of clawed lobsters, such as the American lobster, *Homarus americanus.* In 1997, two small marine reserves for the American lobster were established in Bonavista Bay, Newfoundland. Tag-recapture studies from 1997-1999 revealed significant differences in lobster population parameters (mean size and density) between protected and unprotected populations, but no differences in sex ratios (Rowe 2002). Janes (2009) compared data from the first year of reserve establishment to later years, 2004-2007, and reported significant differences in size between protected and unprotected populations. This study addresses changes in population structure and lobster density over the long-term, by including data from 2000-2002, as well as recent data from 2008 mark-recapture sampling.

Hypotheses

The hypotheses of this study are as follows:

1) The mean size of lobsters will be significantly greater inside the reserves, as opposed to that of reference areas, and will increase over time.
2) Sex ratios inside and outside the reserves will differ significantly. Since ovigerous and V-notched females are protected from commercial harvesting, there should be a biased sex ratio, towards females, in the reference area.
3) Lobster density will be greater inside each of the reserves, as compared to reference areas. In addition, density inside the reserves will increase over time.

2.2 Materials and methods

2.2.1 Study areas

The Eastport Peninsula Lobster Management Area, located in the waters surrounding the Eastport Peninsula in Bonavista Bay, Newfoundland (48.65° N. 53.70° W), contains two marine reserves, one at Round Island, and one at Duck Islands. Through harvester initiative, the reserves were established in 1997 for the protection of the American lobster, and were designated as Marine Protected Areas (MPAs) by Fisheries and Oceans Canada in 2005.

2.2.2 Sampling design

Data were assembled for 1997-2008. During September 18 – September 28 of 2000, mark-recapture research tagging of lobsters took place at both the Round Island and Duck Islands study sites. Sampling was conducted inside the reserves and in the adjacent reference areas, which were open to commercial harvesting. These areas are identified in Figure 1. Participating harvesters were asked to spread traps out within each reserve and reference location, and set them at commercially fished depths. A total of 25 wood-lath parlour traps were set in each of the reserves, and 25 traps were set in each nearby reference area. Traps were hauled daily, except in circumstances of inclement weather, and baited using fresh or salted herring (*Clupea harengus*), mackerel (*Scomber scombrus*), winter flounder (*Pseudopleuronectes americanus*) or cod (*Gadus* spp.).

For each new lobster captured during the research tagging periods, the following information was recorded: date of capture, location of capture, sex, and carapace length (CL). Carapace length was defined as the length of the cephalothorax, from the base of the right eye-socket to the end of the carapace, and was measured in millimeters (mm) using vernier calipers. Females were also examined in order to determine reproductive condition (*i.e.* ovigerous or not). New captures were marked with uniquely numbered polyethylene streamer tags. Each tag was inserted, with the aid of an attached embroidery needle, into the thoraco-abdominal membrane and abdominal muscle on one side, and threaded over the dorsal artery and through the abdominal muscle on the opposite side, as described by Moriyasu *et al.* (1995). In the case of larger animals, *circa* 100 mm or larger, the tag was inserted through one muscle band only. With the tag properly inserted, the needle was detached and discarded. Once tagged, lobsters were released immediately.

Often, lobsters tagged in previous years were recaptured, in which case the original tag number was recorded, along with the aforementioned information. This protocol was repeated during Fall of 2001 (23 September – 5 October) and Fall of 2002 (2 October – 10 October). Similar protocols were used in Fall (September/October) of 1997-1999, and 2004-2008. Sampling was not conducted at either site in 2003, and no data were available.

2.2.3 1997-1999 data

Because data from the 1997-1999 study were not available, it was necessary to make use of values from figures and tables published in Rowe (2002). Estimates of population size, and associated confidence limits, were obtained from taking measurements of figures published in Rowe (2002). Estimates of annual mean sizes of males and females in both protected and unprotected populations, at each study site, were obtained in a similar fashion. However, published confidence limits were not consistent with results of ANCOVA and other regression analyses in the publication, which revealed significant differences in mean sizes between protected and unprotected populations (*e.g.* males at Duck Islands), and increases over time (*e.g.* females in Round Island reserve), in some cases. Confidence limits for means estimated from 2000-2002 and 2004-2008 data were on the order of several mm, as opposed to ten or twenty mm.

Therefore, values for confidence limits from 1997-1999 data were not used to back calculate standard errors or variances.

2.2.4 Population structure

Recaptures occurred frequently during each sampling period, but each lobster was counted only once per year for the analyses. Due to differences in growth rates between the sexes (Waddy *et al.* 1988; Ennis *et al.* 1989; Comeau and Savoie 2001), data from males and females were analyzed separately. When mean carapace lengths for males and females were plotted against year, no consistent observable trends were evident. ANOVA was used to compare mean sizes between reserve and reference locations for males and females at both study sites. The tolerance for Type I error was set at 5%. Residuals were checked for independence, normality and homogeneity. Because data from the 1997-1999 study were unavailable, the 2000-2002 and 2004-2008 data were pooled to obtain a MS error. The MS error was then used to estimate F ratios based on main effects from means weighted by associated sample sizes, using data from 1997-1999, 2000-2002, and 2004-2008. Appendix A shows computational flow. When interpreting multifactor ANOVA results, interaction terms were examined first, before main effects.

The proportion of each sex inside reserve and reference areas, for both study sites, was calculated for each year of the study. The proportions were statistically analyzed using binary logistic regression with a logit link function to determine if the differences in sex ratios between protected and unprotected populations, at each study site, were significant.

2.2.5 Population size and density

Estimates of lobster population size within the reserves and in adjacent reference areas were carried out using the Schumacher and Eschmeyer (1943) method, a multiple markings and recaptures method. To obtain accurate estimates of population size using this method, five assumptions must hold: (i) The population must be closed, (ii) all animals must have an equal chance of being caught in the first sample, (iii) the marking of individuals does not affect their catchability, (iv) animals do not lose marks between sampling periods, and (v) all marks are reported upon discovery in the second sample (Krebs 1999). Rowe (2000) reviewed the extent to which these assumptions were met in the 1997-1999 study, and concluded that adjustments could be made to limit the effects of the potential violations. Rowe (2000) also concluded that the assumptions that could not be tested directly did not introduce serious bias. Because the same sampling methods were employed in subsequent years, the conclusions were adopted (with one exception). The method was used to estimate population size for data from 2000-2002 and 2004-2008.

The assumption of a closed population was not met during the 2000-2002 and 2004-2008 studies. A total of 5 animals crossed the reserve boundary at the Round Island study site, and a total of 8 moved across the boundary at the Duck Islands site. These animals were removed from all analyses.

For each sampling period, a regression plot of the proportion of marked animals on the number previously marked was used to test for violations of the assumptions. A linear plot indicated that assumptions of the method were fulfilled, while a curvilinear plot indicated that the assumptions were violated, in that catchability was not constant, or the population was not closed (Krebs 1999). Data from protected and unprotected sampling areas for both Round Island and Duck Islands were plotted in this fashion for 5 of the 8 years of available data (Appendix B). Of the 20 plots, curvilinearity was evident in 5. An additional 2 plots showed slight curvilinearity. The method was used to obtain population size estimates.

To estimate density, the population size estimates obtained by the Schumacher and Eschmeyer method (1943) were divided by the estimated size of each reserve and reference location in the two study sites. Rowe (2002) employed both a Global Positioning System and a Geographic Information System, combined with the local ecological knowledge of Eastport Peninsula lobster harvesters, to estimate the size of each reserve and reference location in the two study sites. More detailed maps published in Janes (2009) suggested that the sizes of the study areas were underestimated by Rowe (2002), and that the sizes of the reference areas had changed over time at both Duck Islands and Round Island study sites. It was necessary to reexamine the size of protected and reference areas at both study sites, and assess any temporal changes. To achieve this, a grid of 100m x100m (1 ha) squares was overlaid on the maps published in Janes (2009). Using the shoreline as the inner boundary of the study area, and the edge of the 10m depth contour as the outer boundary, the number of squares contained within the boundaries of the protected and reference areas for both Duck and Round Islands was summed. Using maps from 1997-1999 (Rowe 2002) and 2000-2002 (Figure 1) studies, the procedure was repeated to estimate the size of each reference area used for these earlier investigations. This procedure was repeated three times to obtain an average. Since the boundaries for the reserves remained fixed from 1997-2008, it was not necessary to evaluate the size of the protected areas for each of the three study periods.

2.3 Results

2.3.1 Population structure

For females at the Round Island study site, the interaction term was not significant (ANOVA; Protection x Year: $F_{10, 1600} = 1.49$, $p = 0.136$). Female lobsters inside the reserve (91 mm CL) were significantly larger (ANOVA; Protection: $F_{1, 1600} = 30.61$, $p < 0.001$) than those in the reference area (88 mm CL). In addition, there were significant differences across years (ANOVA; Year: $F_{10, 1600} = 23.55$, $p < 0.001$). Mean size of female lobsters at the Round Island reserve increased over time (Figure 2).

For females at the Duck Islands site, the interaction term was not significant (ANOVA; Protection x Year: $F_{10, 1274} = 1.16$, $p = 0.311$). Female lobsters inside the reserve (94 ml CL) were significantly larger (ANOVA; Protection: $F_{1, 1274} = 35.13$, $p < 0.001$) than those of the adjacent reference area (90 mm CL). There were also significant differences across years (ANOVA; Year: $F_{10, 1274} = 16.51$, $p < 0.001$). Mean size of female lobsters at the Duck Islands reserve increased over time (Figure 3).

For males at Round Island, the interaction term was significant (ANOVA; Protection x Year: $F_{10, 1508} = 3.02$, $p < 0.001$). This was due to an increase in the magnitude of difference between mean sizes of reserve and reference populations over time (Figure 4). From 1997 to 2008, the percent difference in mean size (reserve relative to reference) increased from 1.9% to 15.4%. Male lobsters in the reserve (97 mm CL) were significantly larger (ANOVA; Protection: $F_{1, 1508} = 95.72$, $p < 0.001$) than those of the adjacent reference area (91 mm CL). In addition, there were significant differences across years (ANOVA; Year: $F_{10, 1508} = 14.88$, $p < 0.001$). Mean size of male lobsters at the Round Island reserve increased over time (Figure 4).

For males at Duck Islands, the interaction term was significant (ANOVA; Protection x Year: $F_{10, 1927} = 2.16$, $p = 0.018$). This was due to an increase in the magnitude of difference between mean sizes of reserve and reference populations (Figure 5). From 1997 to 2008, the percent difference in mean size (reserve relative to reference) increased from 3.7% to 15.7%. Male lobsters in the reserve (99 mm CL) were significantly larger (ANOVA; Protection: $F_{1, 1927} = 226.04$, $p < 0.001$) than those of the adjacent reference area (89 mm CL). In addition, there were significant differences across years (ANOVA; Year: $F_{10, 1927} = 13.69$, $p < 0.001$. Mean size of male lobsters at the Duck Islands reserve increased over time (Figure 5).

Observed sex ratios for lobsters captured during 1997-1999, 2000-2002 and 2004-2008 are presented in Table 1. There were significant differences in sex ratios between reserve and reference areas at both study sites, with a bias toward females in the reference locations (Table 2).

2.3.2 Population size and density

At the Round Island site, population size in the reference area was greater than that of the reserve in 1997, but decreased in 1998 (Figure 6). The reserve population was larger than the reference population in 2004. An average population size for the entire time series, from 1997 to 2008, was 473 lobsters in the reserve, and 506 lobsters in the reference area. At the Duck Islands site, population sizes for the reserve and reference areas varied without trend (Figure 7). Protected populations were larger than those of the reference area in 1999, 2004, 2006, and 2007. An average population size for the entire time series, from 1997 to 2008, was 844 lobsters in the reserve, and 486 lobsters in the reference area. Estimates of population size do not account for changes in the size of the study areas over time. Estimates of size of the reserve and reference areas for both Round Island and Duck Islands are presented in Table 3. At Round Island, the size of the reference area decreased between study periods. At Duck Islands, the size of the reference area increased between each of the three study periods.

At the Round Island site, lobster density was consistently greater inside the reserve from 1998 to 2008 (Figure 8). An average density for the entire time series was 17 lobsters/ha in the reserve, and 5 lobsters/ha in the reference area. At the Duck Islands site, no differences in lobster density were observed between reserve and reference areas (Figure 9). From 1997-2008, the reserve averaged 10 lobsters/ha and the reference area averaged 9 lobsters/ha, for each year of the study. At both study sites, lobster densities did not increase over time. At the Duck Islands site, from 1997-2002, estimated densities were typically higher in the reference area but, from 2004-2008, reserve densities were consistently higher than those of the reference area.

2.4 Discussion

The population structure and density of American lobsters (*Homarus americanus*) from two marine reserves and adjacent reference locations, from 1997 to 2008, were compared. As predicted, mean sizes of males and females were greater inside the reserves, as compared to adjacent reference areas. Mean size of males and females in both Round Island and Duck Islands reserves increased over time, but the most pronounced response to protection occurred for males at both study sites. Observed sex ratios in reserve and reference locations differed at both sites, with a greater bias towards females in the reference areas. Lobster densities at the Duck Islands site were similar for reserve and reference locations, while densities at the Round Island site were greater inside the reserve, as compared to the adjacent reference area. Contrary to predictions, estimated densities of lobsters at each reserve did not increase over time.

The presence of larger lobsters in the reserves at both Round Island and Duck Islands is consistent with previous studies of lobsters in the Eastport reserves. Rowe (2002) reported that, during the first three years of reserve establishment, males and females inside each reserve were larger than those of the adjacent reference areas. Using data from 1997 and 2004-2007, Janes (2009) reported that males and females at the Duck Islands site, and males at the Round Island site, were significantly larger inside the reserves.

Between 1997 and 2008, increases in mean size were observed for both sexes in protected populations at both study sites. Using ANCOVA, Rowe (2002) reported that increases in mean size of lobsters during the first three years of reserve establishment depended upon sex, presence of protection, and the study site. The mean size of males increased over a three year period, from 1997 to 1999, in both the reserve and reference areas of the Round Islands site, and the reserve at Duck Islands (Rowe 2002). For females, mean size increased in the reserve population at Round Island, but remained unchanged for populations in the Round Island reference area and at the Duck Islands site (Rowe 2002). The change in size over time in the present study, in contrast to Rowe (2002), may have been a consequence of different analytical approaches (ANOVA vs. ANCOVA), or a difference in the duration of the studies. ANCOVA was not used in the present study, as the data did not warrant an assumption of a straight line increase.

From 1997-2008, the greatest response to protection, with respect to size, was associated with males at both reserves. This may be due to a number of factors. Males typically grow faster than females (Waddy *et al.* 1988), especially after the onset of sexual maturity, as the female allocates more energy to reproductive demands and assumes a biennial molt-reproductive cycle (Templeman 1933; Aiken and Waddy 1980*a*, 1980*b*). In Newfoundland, females may be subject to a lower rate of exploitation in the commercial fishery (DFO 2009), possibly due to the prohibition against landing ovigerous (egg-bearing) lobster. Ovigerous females must be immediately released upon capture and thus are afforded an additional opportunity to molt before becoming vulnerable to harvest in a subsequent fishing season. Additionally, the implementation of a comprehensive V-notching program in Eastport in 1996 resulted in increases in the mean size of females in commercially harvested areas (Whiffen 2010). The practice of V-notching involves cutting a shallow mark in the endopodite of the right uropod of the female's tail, which is then typically retained for two or more molts (DeAngelis *et al.* 2010). This enhances egg production by rendering the female ineligible for harvest, even when not brooding eggs externally, allowing her to attain larger sizes and greater fecundity (Daniel *et al.* 1989). Given that approximately 1500 ovigerous females in the Eastport area were V-notched in 1996 (Rowe 2000), and that V-notched lobster were caught at both study sites during fall sampling, in multiple years; the less pronounced difference in female size between protected and unprotected populations may have been the result of females in the reference areas attaining larger sizes over time as a consequence of this conservation measure.

Given that male lobsters are generally more catchable than females (Miller 1989, 1990, 1995; Tremblay and Smith 2001; Tremblay *et al.* 2006), and that females are afforded additional protection in the commercial fishery when bearing eggs or V-notched, and that mortality appears to be higher for males in Newfoundland lobster populations (DFO 2009), it was expected that the observed sex ratio in reference areas, which are subject to commercial harvesting, would be skewed in favour of females. The results of the present study support this hypothesis. Observed sex ratios in reserve and reference locations differed at both sites, with a bias towards females in reference locations. These results are inconsistent with those of Rowe (2002), who reported no difference in sex ratios between reserve and reference populations after the first three years of reserve establishment. The difference between the results of the present study and those of Rowe (2002) may be due to different analytical approaches, or differences in the duration of the studies.

In the absence of commercial harvesting, it was expected that densities of lobsters would be greater inside the reserve. Studies of numerous marine reserves, established for a variety of species, have repeatedly demonstrated greater average population densities when compared to those of reference sites, regardless of reserve size (Halpern 2003). At the Round Island site, reserve densities were much higher than those of the adjacent reference area. However, at the Duck Islands site, densities of lobsters in protected and unprotected populations were comparable. These longer term results are consistent with those from an earlier short term study of these two reserves. Rowe (2002) reported that differences in density were pronounced at the Round Island study site during the first three years of reserve establishment, with an average of 165 lobsters/ha in the reserve, as opposed to 42 lobsters/ha in the reference area. At the Duck Islands study site, lobster densities in reserve and reference locations were similar. The Duck Islands reserve contained an average of 68 lobsters/ha, while the reference area contained an average of 85 lobsters/ha (Rowe 2002). These density estimates were much greater than those obtained in the present study, due to substantial differences in estimates of the size of reserve and reference areas at each study site, but the observed trends were similar.

Population response to protection, in terms of density, appeared to be contingent upon the study site. While there were differences in density between reserve and reference areas at Round Island, there were no detectable differences at the Duck Islands site, despite the substantial sampling effort over 11 years. Differences in topography and substrate between the two study sites may result in differences in suitable habitat, or shelter availability (Rowe 2000). Lobsters compete for shelters, in which they spend much of their time (O'Neill and Cobb 1979; Karnofsky *et al.* 1989). Shelter availability may limit local carrying capacity (Cobb 1971; Atema and Cobb 1980; Steneck 2006), and the availability of suitable shelters is of particular importance during molting and mating periods (Karnofsky *et al.* 1989; Lawton and Lavalli 1995). Additionally, there is some indication that exploitation rates were lower around the Duck Islands reserve (Rowe 2001). If the amount of suitable lobster habitat is similar in reserve and reference locations at the Duck Islands site and/or exploitation rates in this area are lower, then reserve density may not differ greatly from that of the adjacent commercially fished area.

Contrary to predictions, lobster densities did not increase over time at either reserve location. Rowe (2002) found that, during the first three years of reserve establishment, population density remained stable in the Round Island reserve, but increased between 1997 and 1998 in the Duck Islands reserve. Halpern and Warner (2002) reviewed 112 independent measurements of 80 reserves, and found that species density was significantly higher inside the reserves relative to the reference areas, but there was no indication of changes in density over time. The data suggest that response to protection can occur rapidly, within 1-3 years of reserve establishment (Halpern and Warner 2002). This may be particularly true for species which are heavily targeted and subject to high rates of exploitation, as fishing would be the primary factor limiting population size and structure (Polacheck 1990; Carr and Reed 1993; Rowley 1994; Halpern and Warner 2002). Given that no baseline data were collected prior to reserve establishment, it is possible that population response to protection occurred within the first year of protection at Round Island, and that carrying capacity of this relatively small area was reached quickly. Although there were no overall increases in density at the Duck Islands reserve, there was an increase between 1997 and 1998, and a decrease after 2002. It may have taken slightly longer for the larger Duck Islands reserve to reach carrying capacity. The decrease in density that occurred after 2002 may have been the result of movement of lobsters from the reserve. Although both Rowe (2001) and Janes (2009) reported low rates of movement from both reserves, it is possible that undetected spillover into the adjacent reference area has been taking place, particularly in recent years. Janes (2009) assessed movement based on annual fall sampling at each of the study sites. Spring sampling was conducted in only one year (2004). Given the bathymetry at both study sites, exchange between reserve and reference locations seems likely, but especially for the Duck Islands site, as the extent of contact of the reserve perimeter with that of the reference area is greater. Since the commercial fishery is prosecuted during the spring and summer, before the fall mark-recapture sampling, animals crossing reserve boundaries into commercially harvested areas may have been captured in the commercial fishery and gone unreported to the researchers.

Inferences about size structure, sex ratio and density from studies that rely on trap sampling should be judicious in nature, as certain components of the population can be underrepresented due to differences in catchability. Catchability of *Homarus americanus* is influenced by a number of factors, including sex and size of the animal, as well as agonistic encounters in and around traps (Richards *et al.* 1983; Karnofsky and Price 1989; Miller 1990; Jury *et al.* 2001). It has been repeatedly demonstrated that females are less vulnerable to traps than males (Miller 1989, 1995; Tremblay and Smith 2001; Tremblay *et al.* 2006). Generally, smaller lobsters are underrepresented in trap catches (Smith 1944; Ennis 1978; Miller 1989, 1995; Tremblay and Smith 2001; Tremblay *et al.* 2006). Miller (1990) suggested that, for decapod crustaceans, a logistic curve best describes the relationship between catchability in traps and size, with the possibility that animals at very large sizes are characterized by decreased catchability due to potential mechanical difficulties associated with entering the trap. Using parlour traps, Pezzack and Duggan (1995) reported a decline in *Homarus americanus* catchability at sizes above 120 mm in carapace length. Using direct observation of behavioural responses to traps, Karnofsky and Price (1989) determined that wood lath traps were very inefficient at capturing lobster. Approximately 40% of the legal-sized lobsters in their study were never caught, and 30% of the lobsters that approached a trap, without entering, left in response to agonistic interactions with conspecifics outside the trap. There is evidence to suggest that trap saturation occurs as a consequence of lobster behaviour in and around traps, and the presence of lobsters in traps can reduce the catch of other lobsters (Richards *et al.* 1983; Karnofsky and Price 1989; Jury *et al.* 2001). Larger lobsters in traps have been shown to prevent entry by smaller conspecifics (Jury *et al.* 2001). Agonistic encounters, which affect the rate of entry into traps, and the saturation effect can influence the catch and, thus, estimates of density and size, as well as observed sex ratios. However, if these biases in catchability are consistent across reserve and reference locations, then differences between protected and unprotected populations can be interpreted free of the bias.

It is also possible that depth of trap placement may have biased the sex ratio estimates by targeting males. For inshore lobster populations, adult females appear to undertake movements to deeper water earlier in the fall, before adult males (Campbell and Stasko 1986; Robichaud and Campbell 1991; Roddick and Miller 1992). Templeman (1939) reported that in the fall, immediately following the molt, males predominated in trap catches at depths of 8-10 m, and females predominated at 15-22 m. Since the depth at which traps were set was not standardized within or across years, but appeared to be 10 m or less (Janes 2009), then it is possible that traps were not set at sufficient depths during the study periods to effectively target female lobsters. However, if these trap biases are consistent across reserve and reference locations, then differences between protected and unprotected populations can be interpreted free of the bias.

Issues with trap sampling, catchability of lobsters, and trap saturation, may warrant the use of alternate census techniques, as biases may have influenced the catch, as well as observed sizes and sex ratios. If trap sampling is to be used in future studies, an attempt should be made to set traps at a broader range of depths, if possible, to determine if female lobsters are being adequately sampled.

Habitat heterogeneity, and changes in the size of the reference areas at both study sites, may have influenced the results. Suitable habitat may not be uniformly distributed in either of the reference areas, and changes in the boundaries of the reference areas may have influenced the outcome of the study, by affecting the sizes, and numbers, of animals caught due to habitat heterogeneity. The boundaries of the reference areas should remain constant in further studies of the reserves. It would also be beneficial to quantify differences in habitat quality and shelter availability between reserve and reference locations at both sites, as these may have biased the results.

Additional conservation measures that were implemented around the same time as the establishment of the reserves may have influenced the structure and abundance of animals in the reference areas. In 1996, approximately 1500 ovigerous female lobster were V-notched on commercial fishing grounds in the Eastport area (Rowe 2000). Since it is illegal to retain a V-notched lobster, and the notch persists through the molt, these females were afforded an additional degree of protection from fishing mortality for many years. This resulted in an accumulation of larger females in the reference area that likely would not have been present had an intensive V-notching program not been carried out (Whiffen 2010). In addition, partway through the 1998 fishing season, a 1.5 mm increase in the minimum legal size was imposed for all Newfoundland Lobster Fishing Areas (LFAs), thus reducing mortality on animals in the commercially exploited areas outside the reserves and increasing average size of lobsters in the reference populations. Hence, additional conservation measures that were implemented in the Eastport area may have confounded the study.

Any substantial exchange of lobsters between reserve and reference areas could have influenced the estimates of size and observed sex ratios, as well as the density estimates. Although movement of lobsters in Bonavista Bay appears to be relatively restricted (Ennis 1984*a*, 1984*b*), and previous studies of the reserves have demonstrated low rates of exchange (Rowe 2001; Janes 2009), undetected movement across reserve boundaries may be taking place. Any unreported tag return information associated with commercial fishing activities in the spring may result in an underestimation of spillover. Since spillover is an expected result of marine reserve establishment, and may provide the most localized benefits for stakeholders, the issue deserves further investigation if reserve effects are to be accurately quantified.

As is the case with many studies involving marine reserves, the lack of baseline data limits the strength of the conclusions one can make about the effectiveness of protection for commercially exploited species. Given that no baseline data were collected prior to reserve establishment, it is also possible that any population differences between reserve and reference areas were pre-existing. It is also possible that establishment of reserves erased pre-existing differences between the study areas.

Increased size as a consequence of protection is one of the expected benefits of marine reserves, and this response has been demonstrated for a variety of marine fish and invertebrates (Halpern and Warner 2002). In the absence of commercial exploitation, animals will live longer and attain larger sizes. This is of particular significance for a heavily exploited species such as *Homarus americanus*, for which the fishery in Newfoundland depends heavily on incoming recruitment (DFO 2009). Commercial fishery data from Newfoundland suggests a truncated size structure, with a relative lack of large animals in the population (DFO 2009). Numerous studies have examined the implications of truncated age/size structures for exploited species, and determined that the lack of large mature animals renders a population more vulnerable to environmental variability, resulting in an increased risk of recruitment failure due to associated fluctuations in recruitment levels and population size (Birkeland and Dayton 2005; Hseieh *et al.* 2006; Anderson *et al.* 2008).

Many efforts aimed at improving size structure and promoting growth to larger sizes have focused on the importance of females, specifically. Egg production increases logarithmically with increasing female size (Aiken and Waddy 1980*a*, 1980*b*; Waddy and Aiken 1986; Estrella and Cadrin 1995), and larger females produce eggs that contain more energy per unit of weight, which may confer survival advantages to their offspring (Attard and Hudon 1987). Additionally, while females less than 120 mm in CL are characterized by a biennial molt-reproductive cycle, larger females often spawn twice between intervening molts (consecutive spawning), thus enabling them to make a greater relative contribution to population egg production through more frequent spawning (Waddy and Aiken 1986). Explicit protection for males is generally not emphasized in conventional management regimes for American lobster, which can result in skewed sex ratios in commercially harvested areas (Campbell 1992; Gendron and Savard 2000). When the sex ratio is biased toward females, dominance hierarchies form between males (Lawton and Lavalli 1995), and females will stagger their molts to mate with larger, dominant males (Cowan and Atema 1990). A scarcity of suitable males could limit reproductive potential through a reduction in mating success or sperm availability (Gosselin *et al.* 2003, 2005). Larger males typically transfer more ejaculate than smaller ones, and appear to allocate more ejaculate to larger females (Gosselin *et al.* 2003). Large females, in particular, may be susceptible to sperm limitation if the number of large males is insufficient to mate with all females, or these males deplete their sperm through successive matings with multiple females (Gosselin *et al.* 2003). Also, larger males tend to cohabit with pre- and postmolt females for longer periods, which may provide additional protection for the females, and minimize risks of molt-related mortality (Gosselin *et al.* 2003). Conventional management measures emphasize the importance of protecting reproductive capacity of females, including the prohibition against landing ovigerous females, and the use of the V-notch. Marine reserves appear to provide additional protection for both male and female lobster, and may potentially safeguard, or enhance, reproductive potential. The attainment of large sizes for males and more balanced sex ratios may be among the most important effects of such reserves.

The length of the time-series of available data fortifies the conclusions of this study, as the available data spanned more than a decade. The findings concur with those of numerous other studies of reserve impacts, involving a variety of species, in that population response to protection arose rapidly and/or persisted over time. Overall, the results of this study indicate that these reserves promote sustainability of the resource through increased density and mean size of lobsters, as well as more balanced sex ratios. This should positively influence recruitment through increased reproductive success, larger clutch sizes and, consequently, greater overall egg production.

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Table 2.1: Observed sex ratios for lobsters captured at Round Island and Duck Islands study sites during 1997-1999, 2000-2002 and 2004-2008.

	Reserve		Reference	
	n	**% female**	**n**	**% female**
Round Island				
1997	231	0.44	241	0.53
1998	234	0.51	158	0.51
1999	255	0.50	182	0.47
2000	234	0.50	190	0.61
2001	193	0.50	124	0.69
2002	186	0.46	122	0.52
2003	-	-	-	-
2004	271	0.54	101	0.45
2005	265	0.55	120	0.53
2006	270	0.50	179	0.46
2007	251	0.44	190	0.40
2008	229	0.41	163	0.62
Duck Islands				
1997	141	0.45	78	0.55
1998	218	0.44	154	0.49
1999	335	0.41	193	0.50
2000	280	0.36	238	0.44
2001	175	0.40	134	0.47
2002	160	0.40	124	0.48
2003	-	-	-	-
2004	219	0.35	138	0.36
2005	185	0.37	82	0.41
2006	328	0.44	190	0.45
2007	366	0.36	226	0.45
2008	230	0.34	160	0.36

Table 2.2: Dependence of sex ratio on protection where sex ratio is analyzed as odds (female), Odds = %female/(1-%female). Odds ratio is change in odds due to each source of variation. The value of p is based upon normal approximation using a Z score.

	N Total	N female	% female	Odds	Odds Ratio	Z	p
Round Island							
Reserve	2619	1279	0.49	0.95	0.87	-2.19	0.029
Reference	1770	924	0.52	1.09			
Duck Islands							
Reserve	2637	1032	0.39	0.64	0.79	-3.77	<0.001
Reference	1717	771	0.45	0.81			

Table 2.3: Estimates of size, in hectares (ha), of reserve and reference areas for Round Island and Duck Islands study sites from 1997-1999; 2000-2002; and 2004-2008.

	Round Island		**Duck Islands**	
	Reserve	**Reference**	**Reserve**	**Reference**
1997-1999	28	114	87	45
2000-2002	28	102	87	51
2004-2008	28	89	87	62

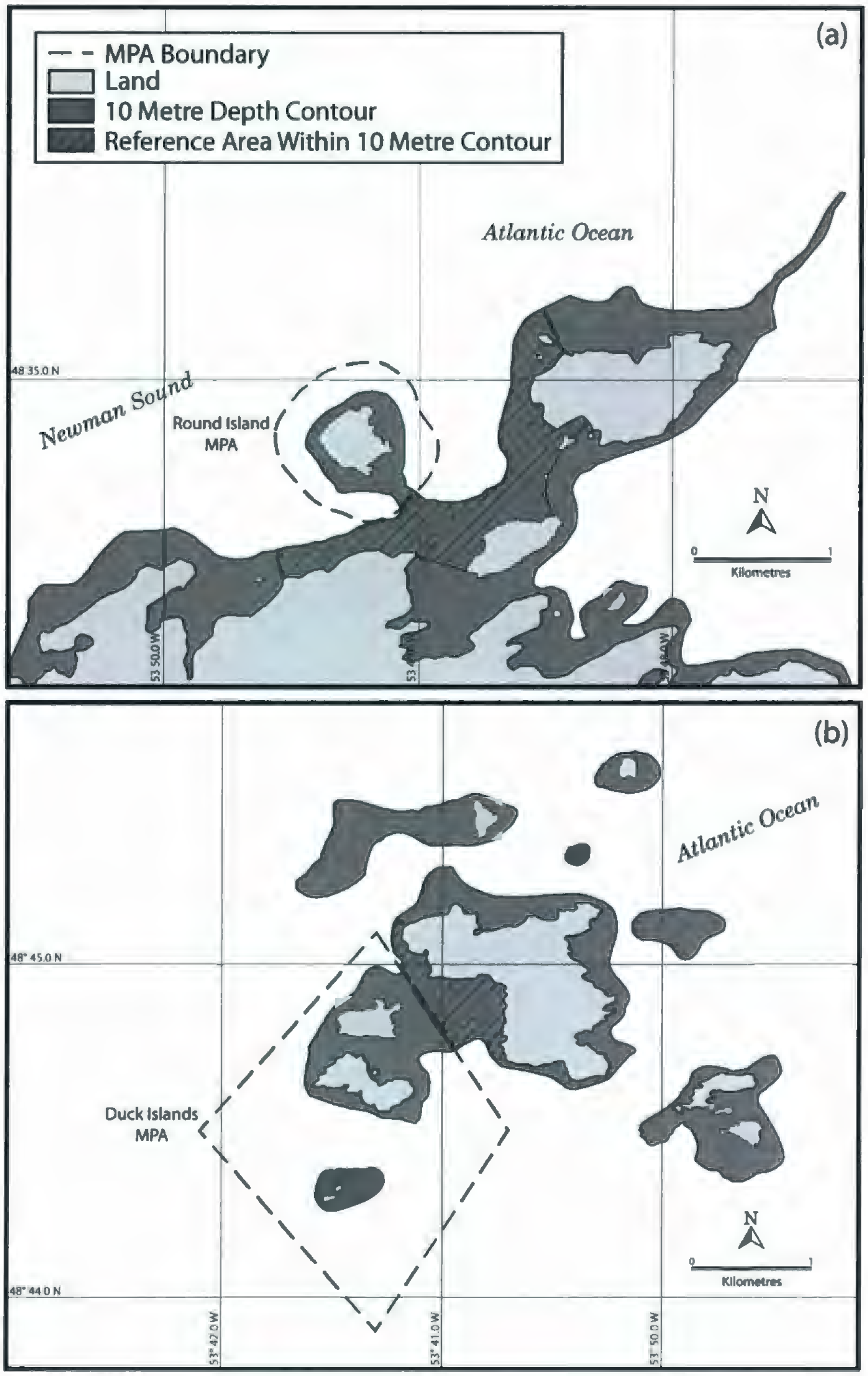


Figure 2.1: Study areas within reserve and reference locations at Round Island (a) and Duck Islands (b) study sites in Bonavista Bay, Newfoundland.

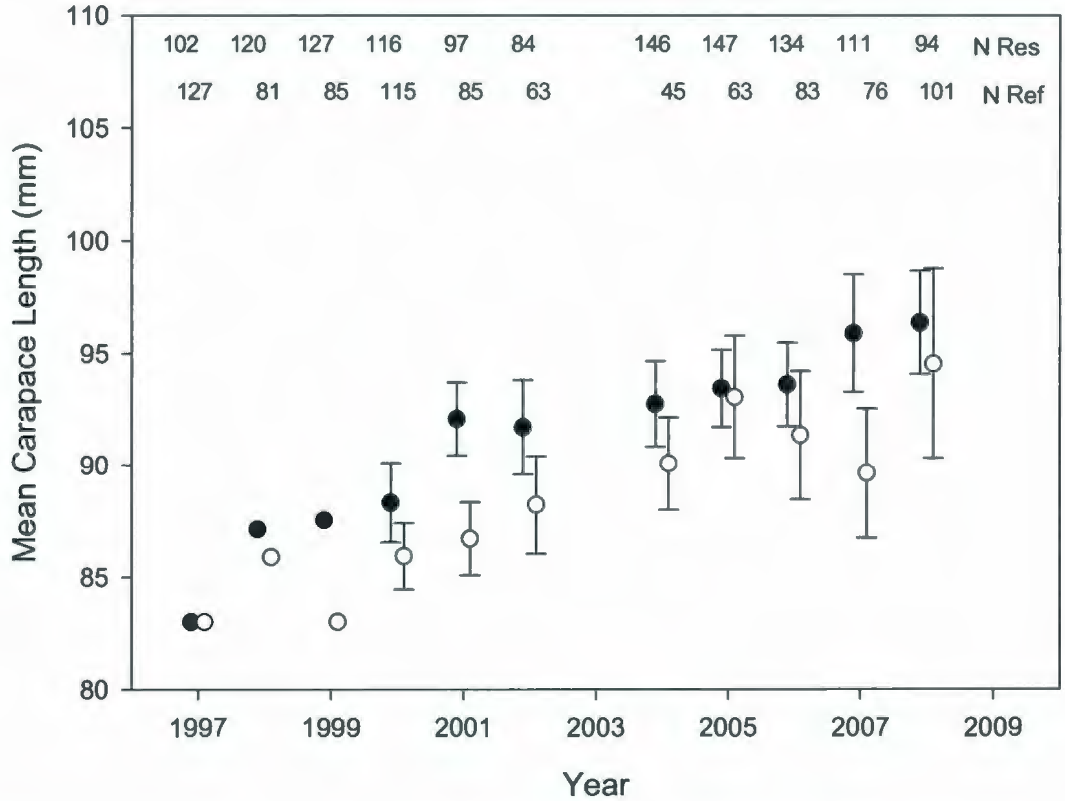


Figure 2.2: Size (mean ± 95% confidence limits) of female lobsters in reserve (●) and reference (○) locations at Round Island, Bonavista Bay, Newfoundland, 1997-2008. Sample sizes provided above estimates.

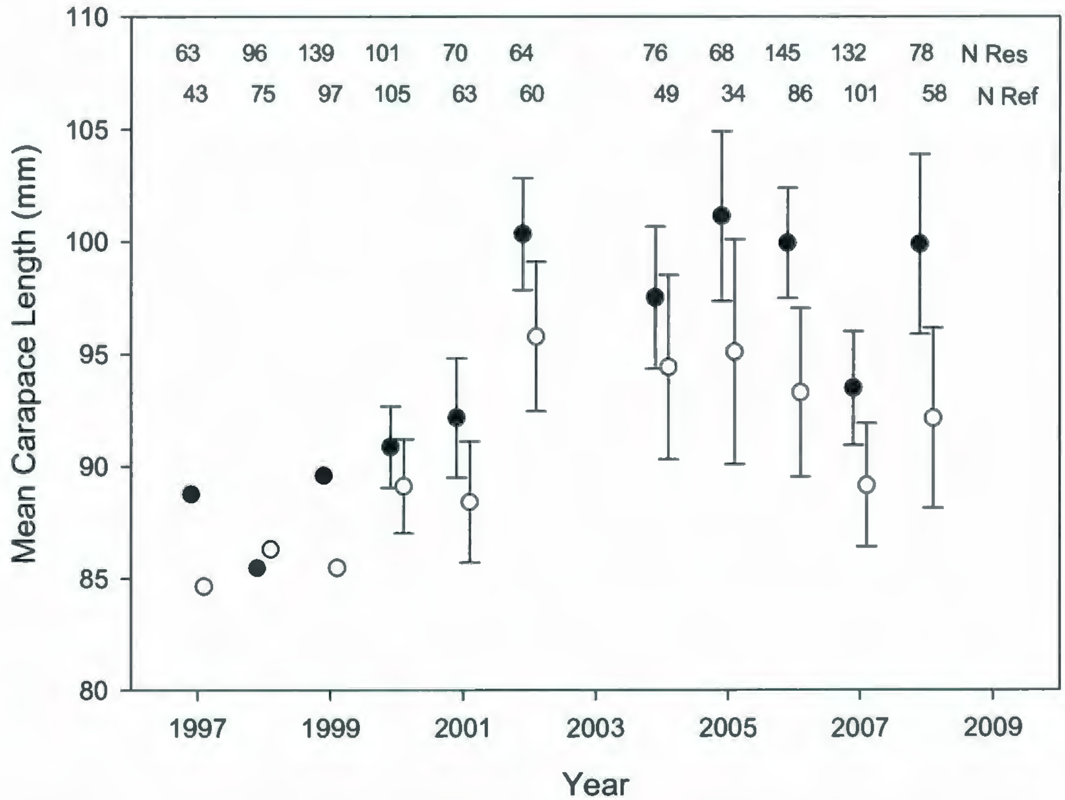


Figure 2.3: Size (mean ± 95% confidence limits) of female lobsters in reserve (●) and reference (○) locations at Duck Islands, Bonavista Bay, Newfoundland, 1997-2008. Sample sizes provided above estimates.

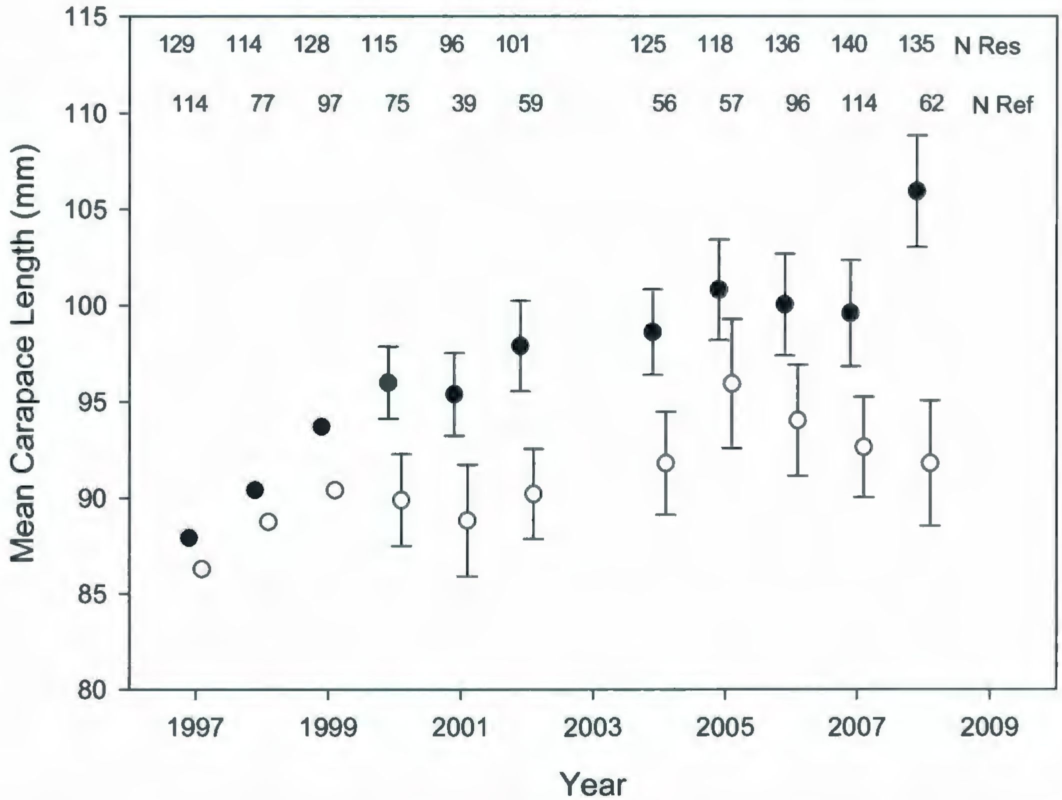


Figure 2.4: Size (mean ± 95% confidence limits) of male lobsters in reserve (●) and reference (○) locations at Round Island, Bonavista Bay, Newfoundland, 1997-2008. Sample sizes provided above estimates.

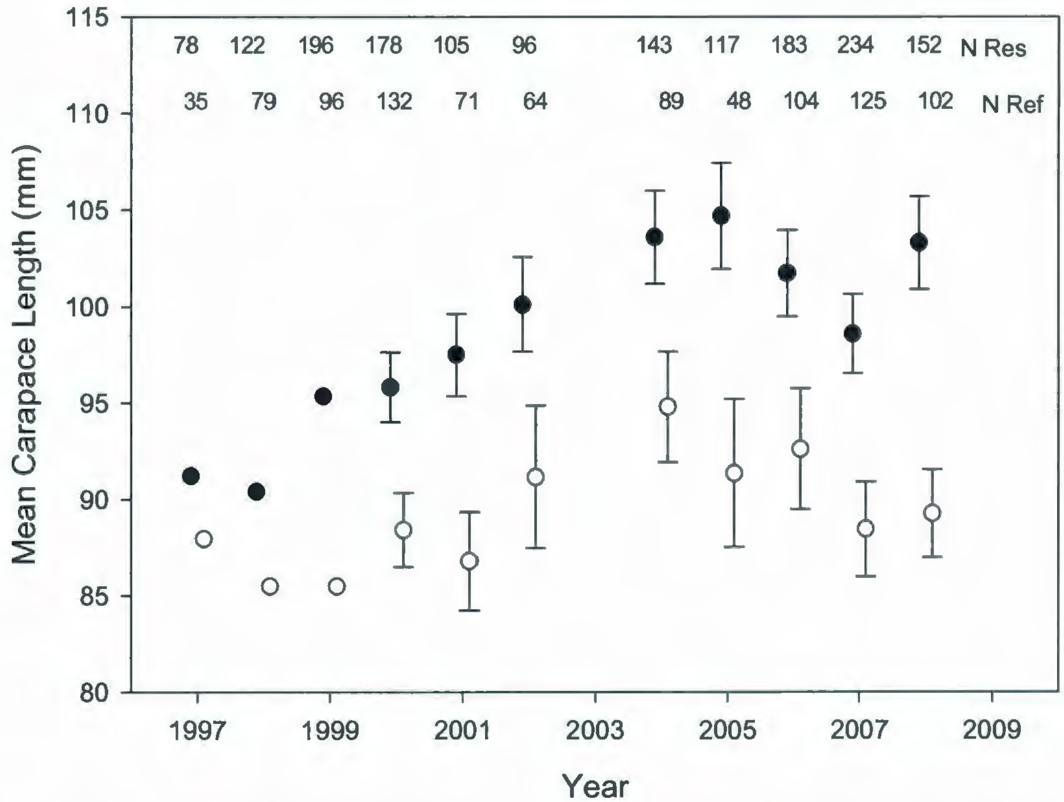


Figure 2.5: Size (mean ± 95% confidence limits) of male lobsters in reserve (●) and reference (○) locations at Duck Islands, Bonavista Bay, Newfoundland, 1997-2008. Sample sizes provided above estimates.

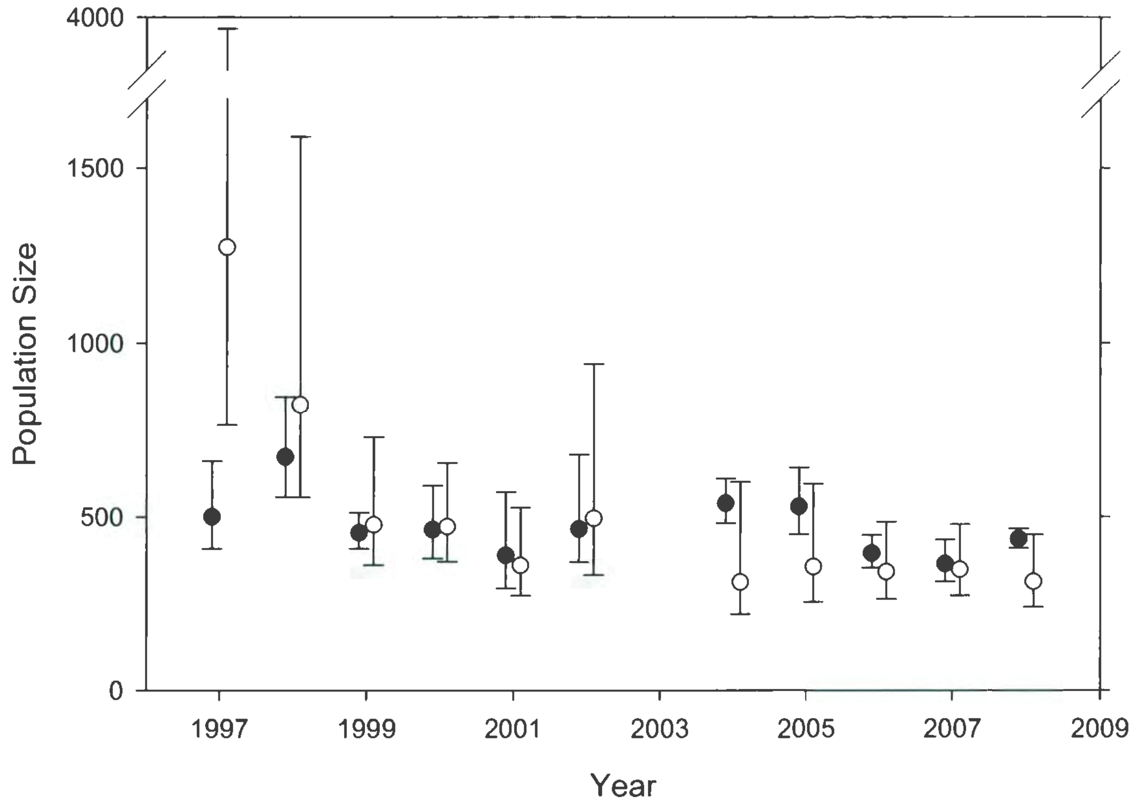


Figure 2.6: Population estimates (± 95% confidence limits) for lobsters in reserve (●) and reference (○) locations at Round Island, Bonavista Bay, Newfoundland, 1997-2008.

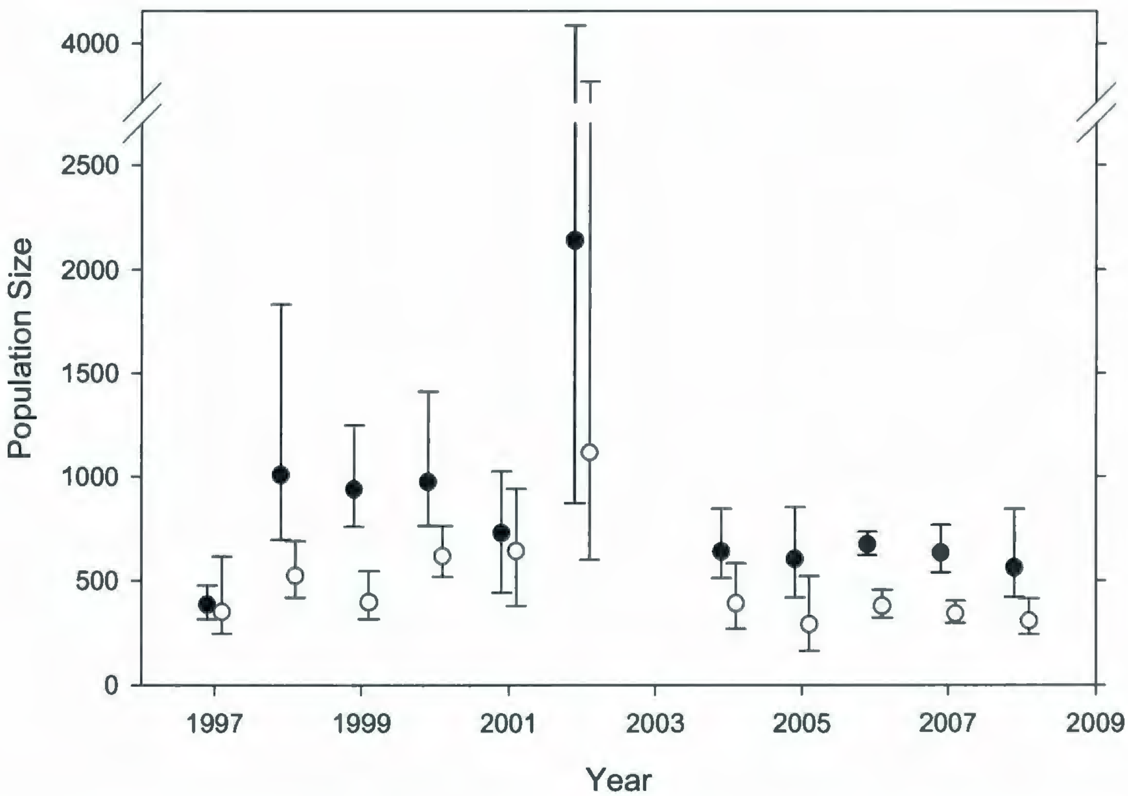


Figure 2.7: Population estimates (± 95% confidence limits) for lobsters in reserve (●) and reference (○) locations at Duck Islands, Bonavista Bay, Newfoundland, 1997-2008.

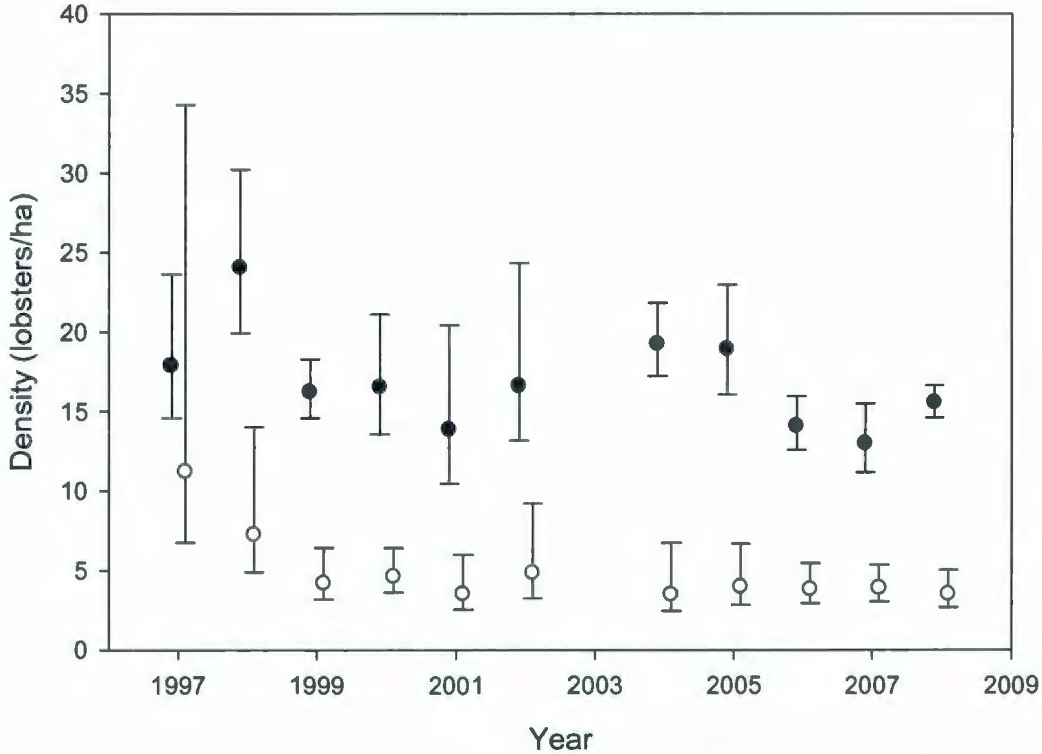


Figure 2.8: Estimates of lobster density (± 95% confidence limits) in reserve (●) and reference (○) locations at Round Island, Bonavista Bay, Newfoundland, 1997-2008. Density calculated using estimates of population size, and size of study areas within reserve and reference locations.

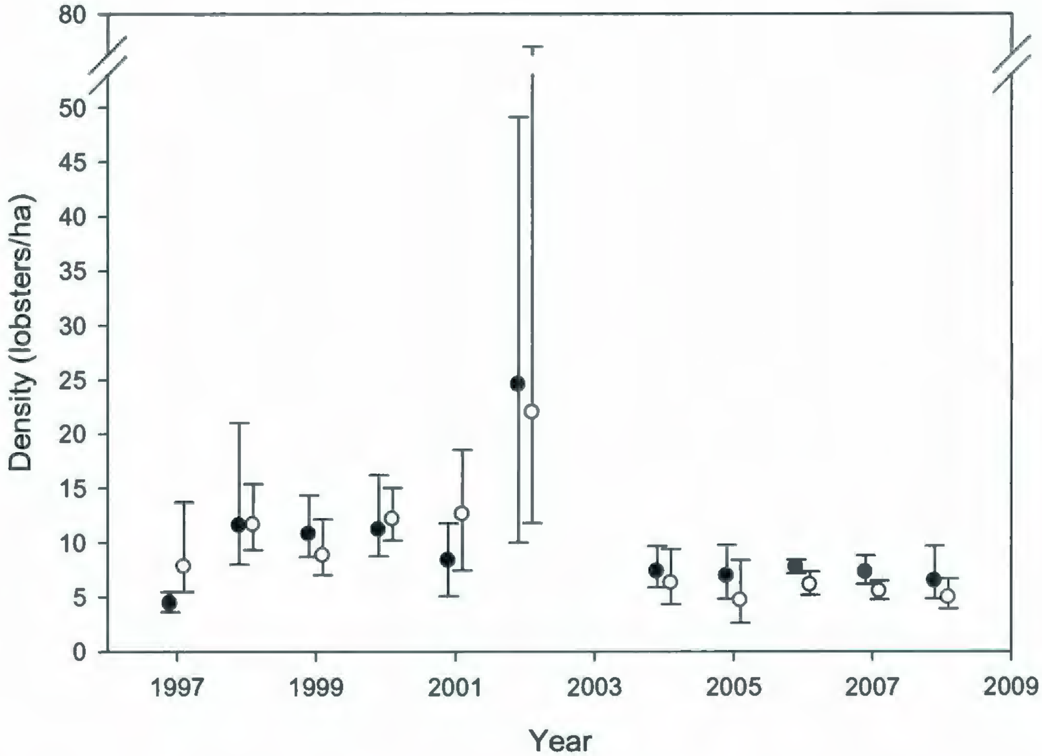


Figure 2.9: Estimates of lobster density (± 95% confidence limits) in reserve (•) and reference (○) locations at Duck Islands, Bonavista Bay, Newfoundland, 1997-2008. Density calculated using estimates of population size, and size of study areas within reserve and reference locations.

Appendix A: Analyses of Variance (ANOVAs) on carapace length for males and females at Round Island and Duck Islands study sites.

Table A1. Analysis of variance (ANOVA) on carapace length for females at Round Island study site, for years with complete datasets (2000-2002 and 2004-2008).

Source of Variation	df	Seq. SS	Adj. SS	Adj. MS	F	p
Protection (yes, no)	1	3649.7	3332.6	3332.6	26.32	<.001
Year	7	9546.2	9656.7	1379.5	10.90	<.001
Year x Protection	7	1250.7	1250.7	178.7	1.41	0.196
Error	1600	202563.3	243383.3	126.6		
Total	1615	217009.9				

Table A2. Analysis of variance (ANOVA) on carapace length for females at Round Island study site, for all years (1997-1999; 2000-2002; and 2004-2008). Adjusted MS Error from Table A1.

Source of Variation	df	Seq. SS	Adj. SS	Adj. MS	F	p
Protection (yes, no)	1	5528	3874.6	3874.6	30.605	<.001
Year	10	30009.8	29816.1	2981.6	23.551	<.001
Year x Protection	10	1888.3	1888.3	188.8	1.491	0.136
Error	1600	*	*	126.6		
Total						

Table A3. Analysis of variance (ANOVA) on carapace length for males at Round Island study site, for years with complete datasets (2000-2002 and 2004-2008).

Source of Variation	**df**	**Seq. SS**	**Adj. SS**	**Adj. MS**	**F**	**p**
Protection (yes, no)	1	19298.4	17982.2	17982.2	100.02	<.001
Year	7	9062.3	6500.9	928.7	5.17	<.001
Year x Protection	7	2395.4	2395.4	342.2	1.90	0.065
Error	1508	271115.5	271115.5	179.8		
Total	1523	301871.6				

Table A4. Analysis of variance (ANOVA) on carapace length for males at Round Island study site, for all years (1997-1999; 2000-2002; and 2004-2008). Adjusted MS Error from Table A3.

Source of Variation	**df**	**Seq. SS**	**Adj. SS**	**Adj. MS**	**F**	**p**
Protection (yes, no)	1	20089.9	17211	17211	95.72	<.001
Year	10	32767.7	26750.7	2675.1	14.88	<.001
Year x Protection	10	5429.8	5429.8	543	3.02	<.001
Error	1508	*	*	179.8		
Total						

Table A5. Analysis of variance (ANOVA) on carapace length for females at Duck Islands study site, for years with complete datasets (2000-2002 and 2004-2008).

Source of Variation	df	Seq. SS	Adj. SS	Adj. MS	F	p
Protection (yes, no)	1	8287.2	6368.6	6368.6	33.34	<.001
Year	7	13661.2	12811.5	1830.2	9.58	<.001
Year x Protection	7	1119.2	1119.2	159.9	0.84	0.557
Error	1274	243383.3	243383.3	191		
Total	1289	266450.9				

Table A6. Analysis of variance (ANOVA) on carapace length for females at Duck Islands study site, for all years (1997-1999; 2000-2002; and 2004-2008). Adjusted MS Error from Table A5.

Source of Variation	df	Seq. SS	Adj. SS	Adj. MS	F	p
Protection (yes, no)	1	8163.3	6709.3	6709.3	35.13	<.001
Year	10	34722.1	31533.2	3153.3	16.51	<.001
Year x Protection	10	2224	2224	222.4	1.16	0.311
Error	1274	*	*	191		
Total						

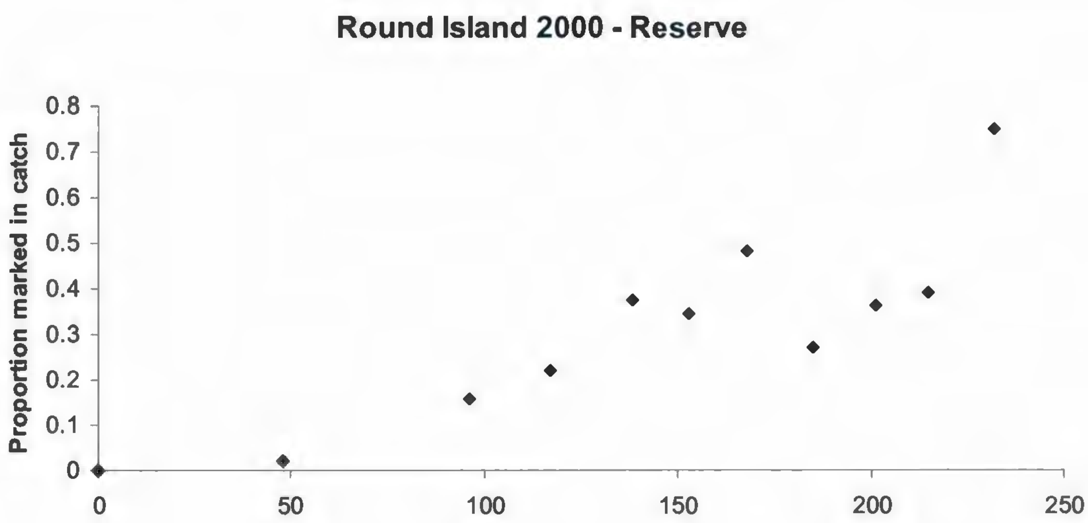
Table A7. Analysis of variance (ANOVA) on carapace length for males at Duck Islands study site, for years with complete datasets (2000-2002 and 2004-2008).

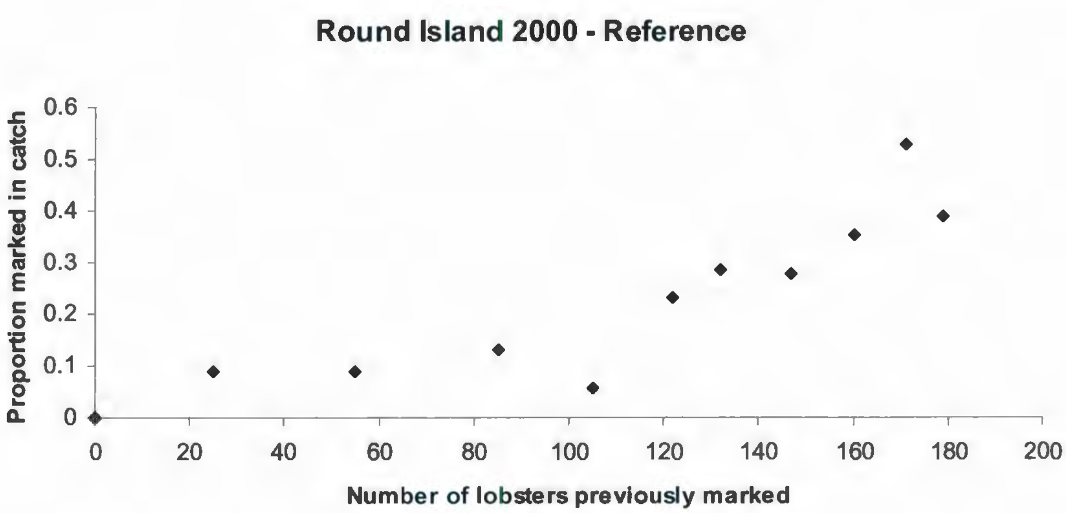
Source of Variation	**df**	**Seq. SS**	**Adj. SS**	**Adj. MS**	**F**	**p**
Protection (yes, no)	1	48201.4	44049.5	44049.5	228.66	<.001
Year	7	12831.5	11290.1	1612.9	8.37	<.001
Year x Protection	7	2075.1	2075.1	296.4	1.54	0.15
Error	1927	371213.8	371213.8	192.6		
Total	1942	434321.9				

Table A8. Analysis of variance (ANOVA) on carapace length for males at Duck Islands study site, for all years (1997-1999; 2000-2002; and 2004-2008). Adjusted MS Error from Table A7.

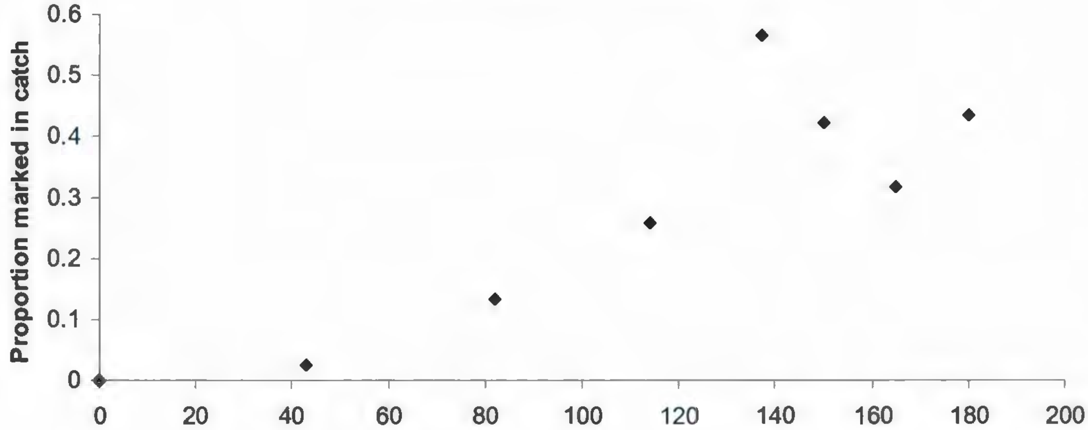
Source of Variation	**df**	**Seq. SS**	**Adj. SS**	**Adj. MS**	**F**	**p**
Protection (yes, no)	1	53402.8	43535.7	43535.7	226.04	<.001
Year	10	32550.2	26370.7	2637.1	13.69	<.001
Year x Protection	10	4157.7	4157.7	415.8	2.16	0.018
Error	1927	*	*	192.6		
Total		89110.7				

Appendix B: Graphical evaluation of assumptions of the Schumacher-Eschmeyer (1943) method. Assumptions violated if plot is curvilinear.

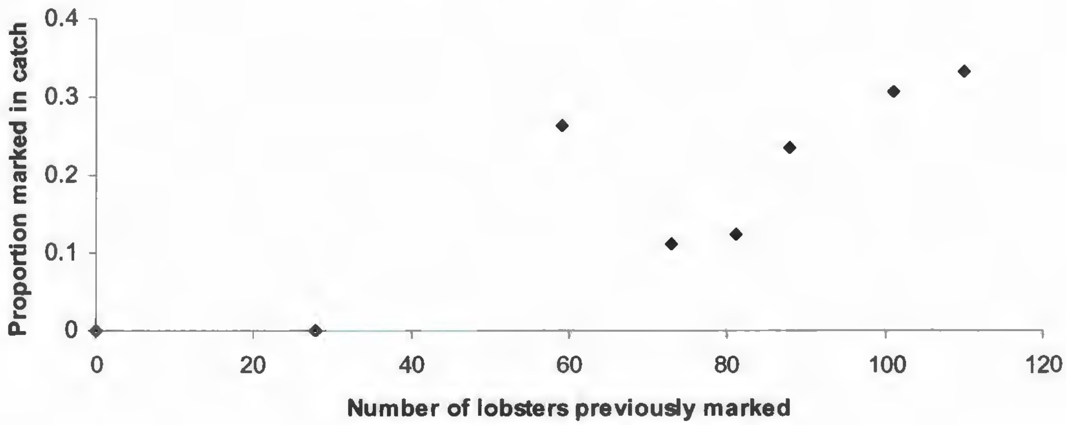


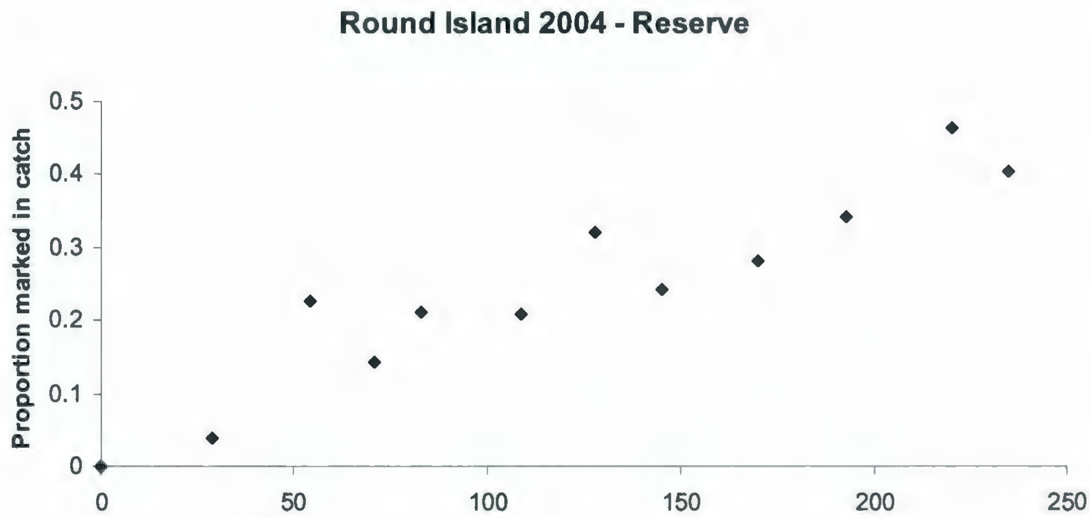


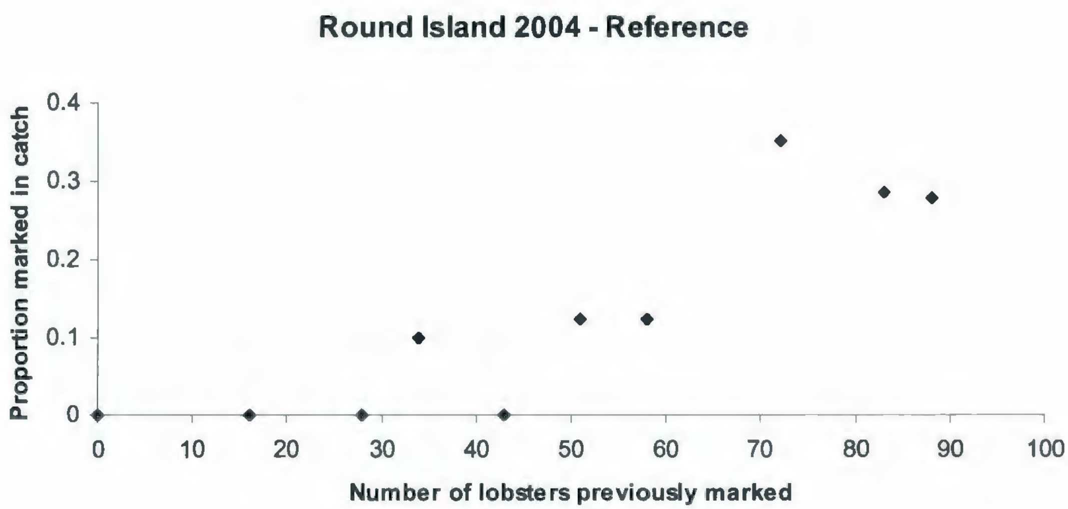
Round Island 2001 - Reserve



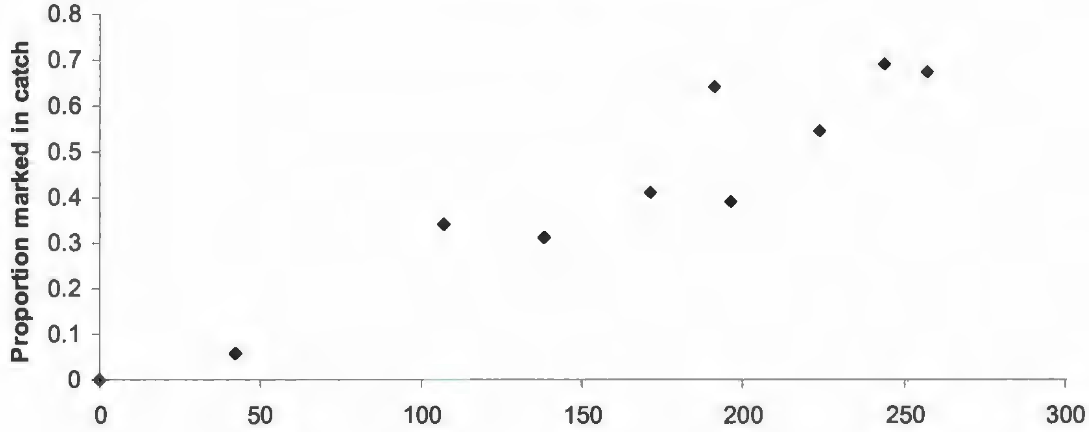
Round Island 2001 - Reference




Round Island 2004 - Reserve
Proportion marked in catch
0.5
0.4
0.3
0.2
0.1
0
0
50
100
150
200
250


Round Island 2004 - Reference
Proportion marked in catch
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
70
80
90
100
Number of lobsters previously marked

Round Island 2006 - Reserve



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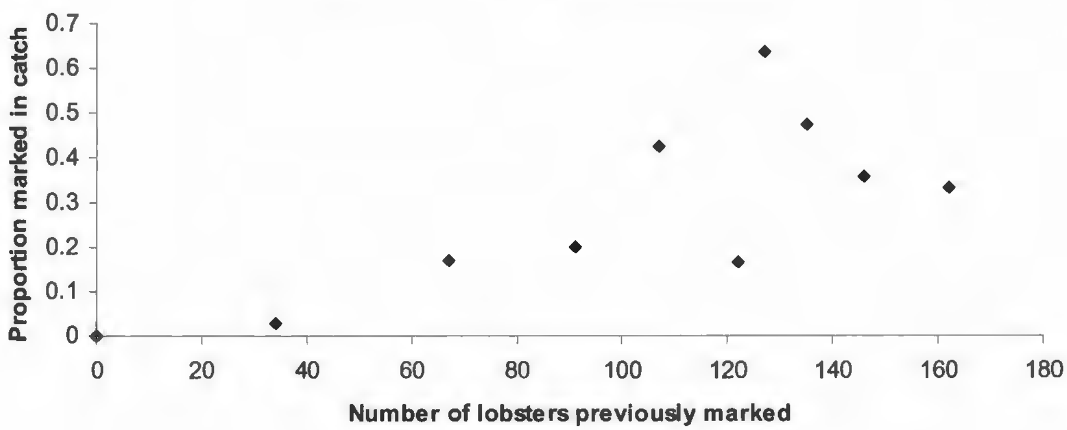
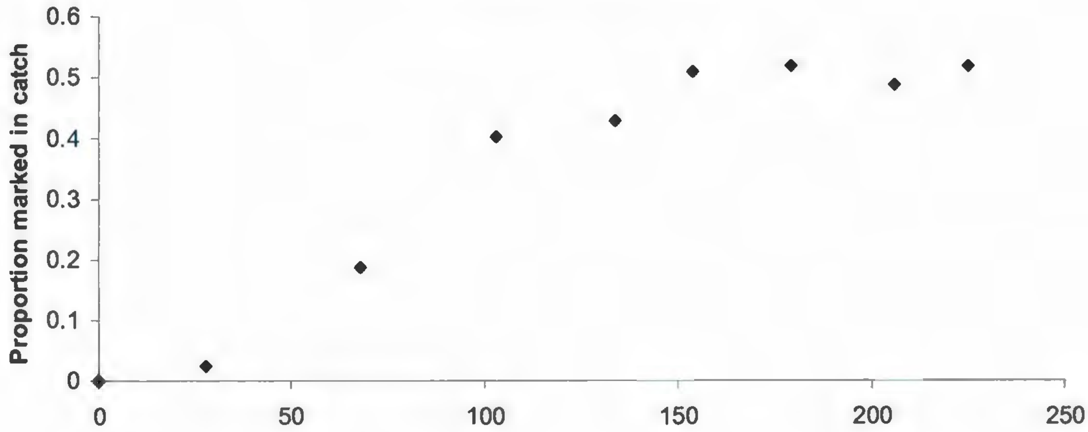
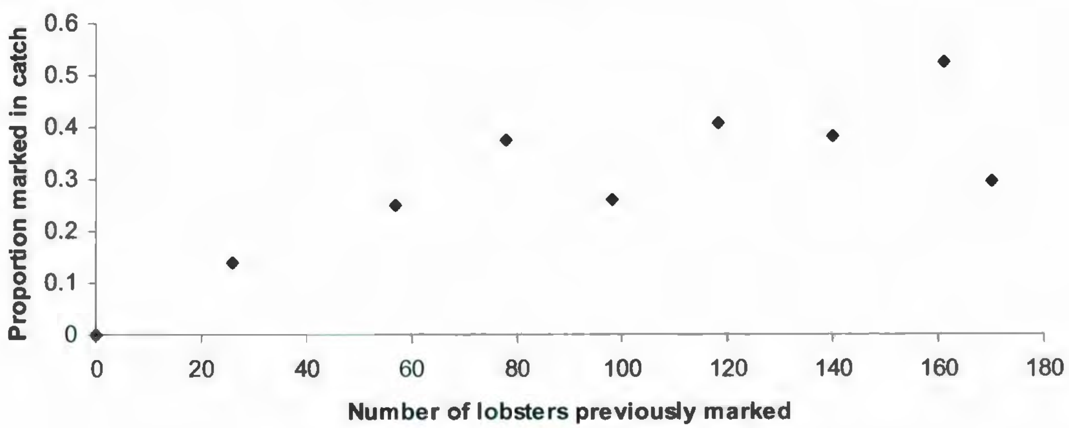
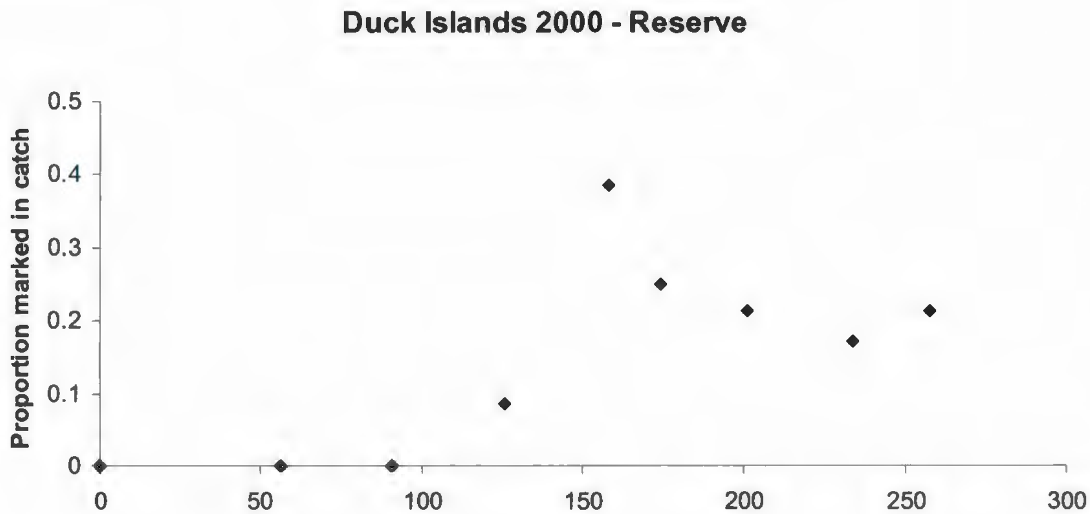


Round Island 2007 - Reserve



Round Island 2007 - Reference





Duck Islands 2000 - Reserve
Proportion marked in catch
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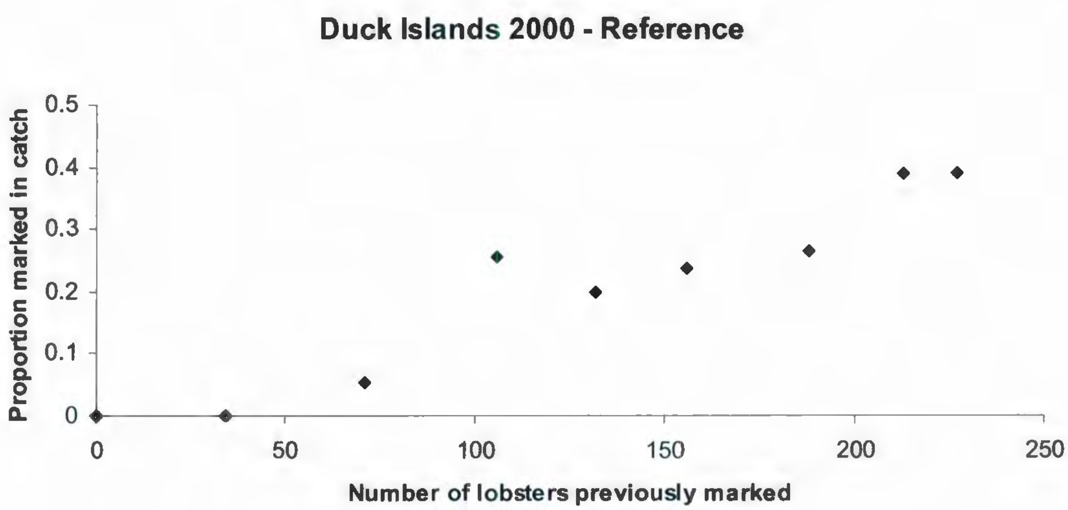
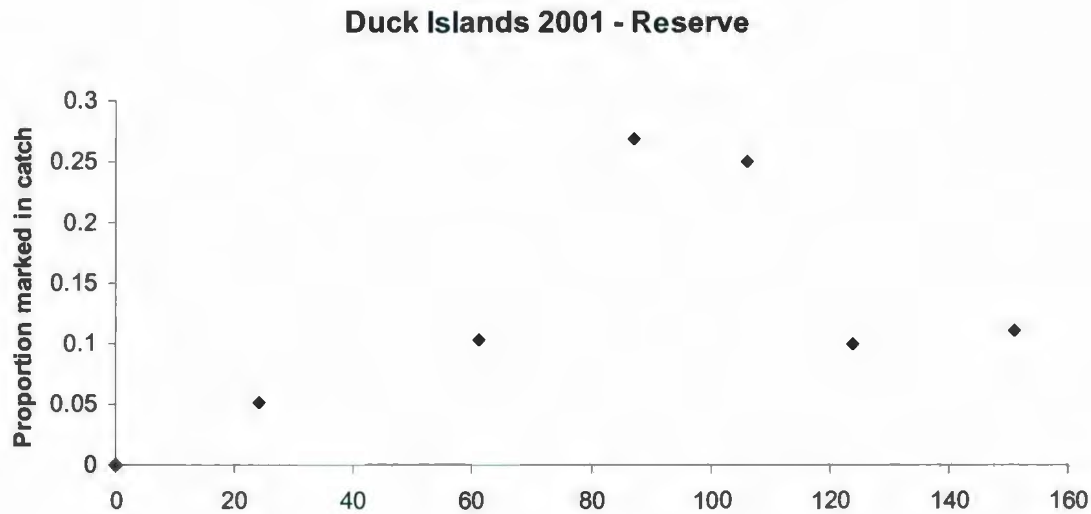
0.4
0.3
0.2
0.1
0
0
50
100
150
200
250
300



Duck Islands 2000 - Reference
Proportion marked in catch
0.5
0.4
0.3
0.2
0.1
0
0
50
100
150
200
250
Number of lobsters previously marked



Duck Islands 2001 - Reserve
Proportion marked in catch
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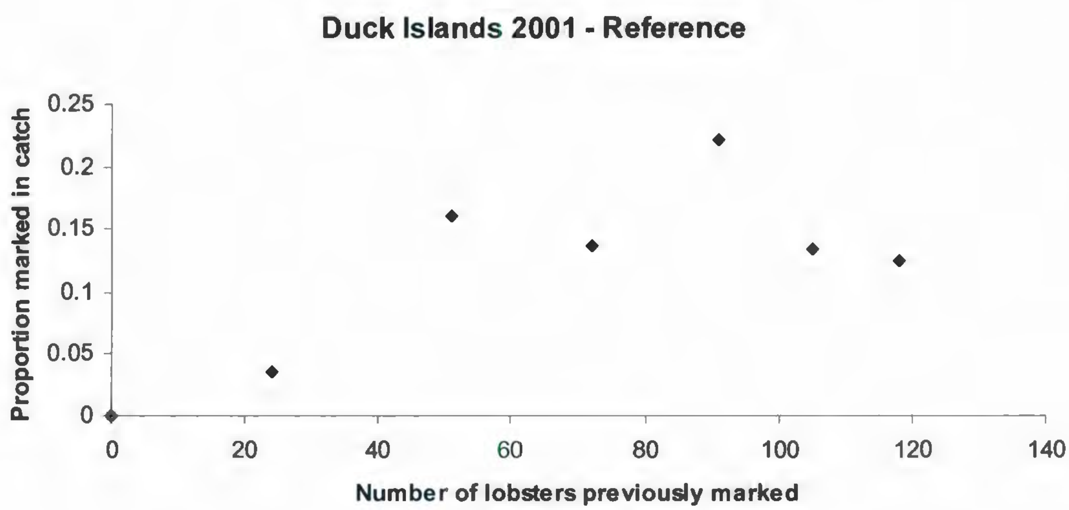
0.25
0.2
0.15
0.1
0.05
0
0
20
40
60
80
100
120
140
160



Duck Islands 2001 - Reference
Proportion marked in catch
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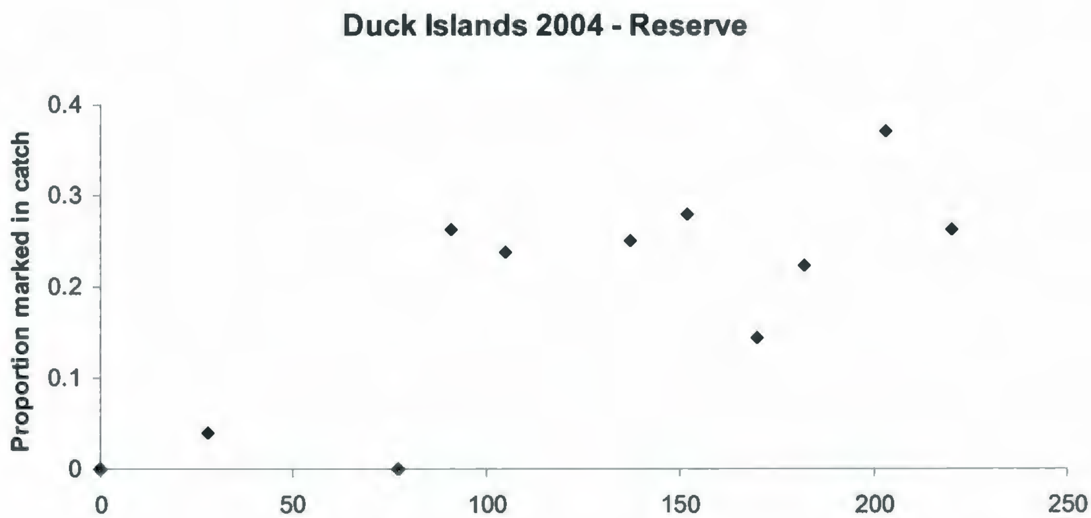
0.1
0.05
0
0
20
40
60
80
100
120
140
Number of lobsters previously marked


Duck Islands 2004 - Reserve
Proportion marked in catch
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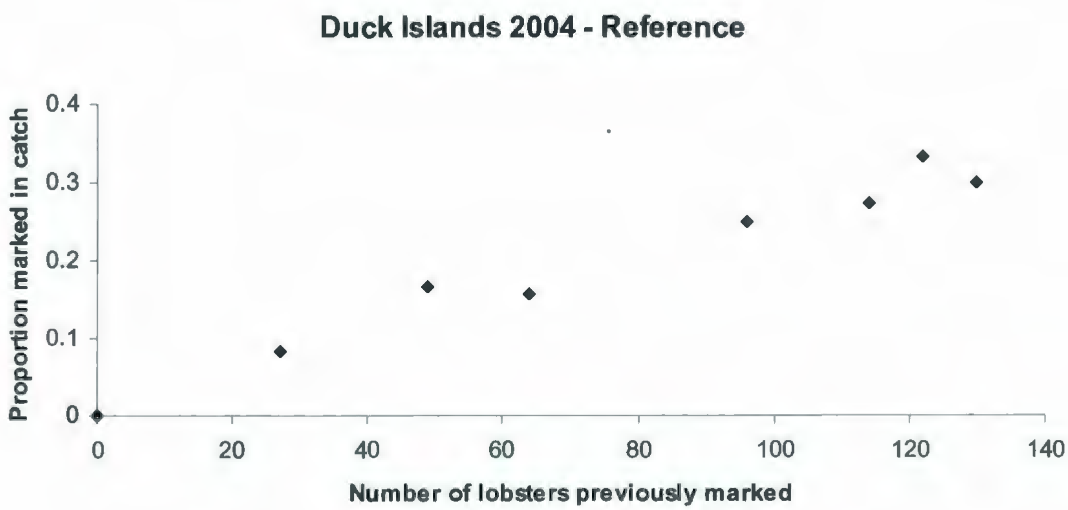
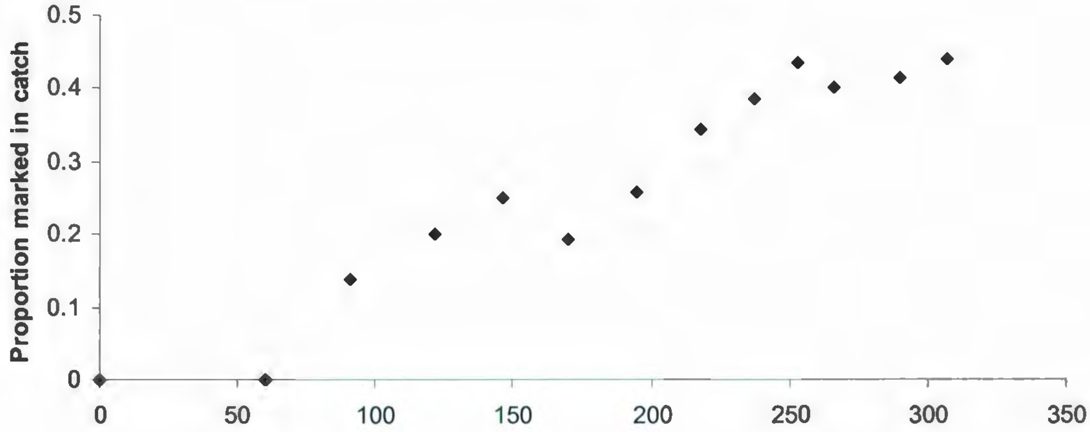
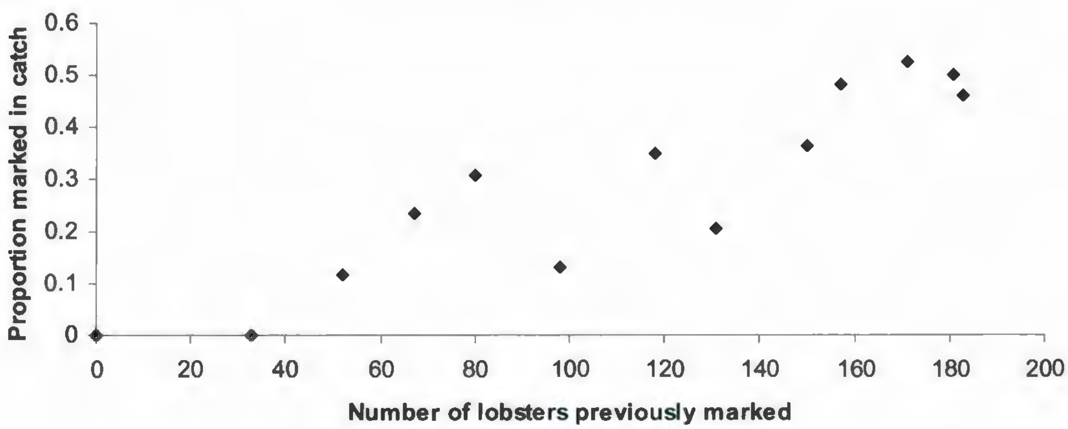
0.2
0.3
0.4
0
50
100
150
200
250

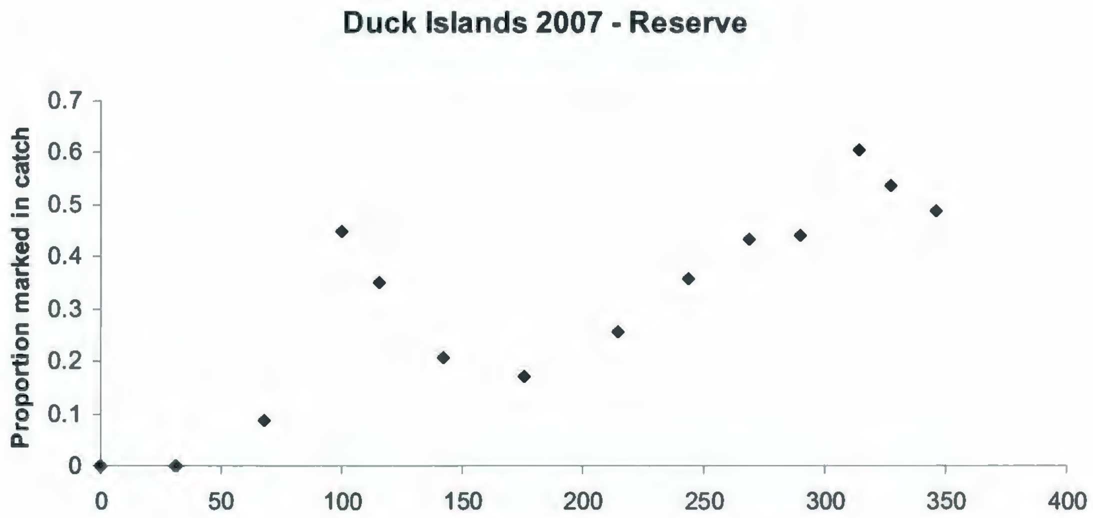

Duck Islands 2004 - Reference
Proportion marked in catch
0
0.1
0.2
0.3
0.4
0
20
40
60
80
100
120
140
Number of lobsters previously marked

Duck Islands 2006 - Reserve

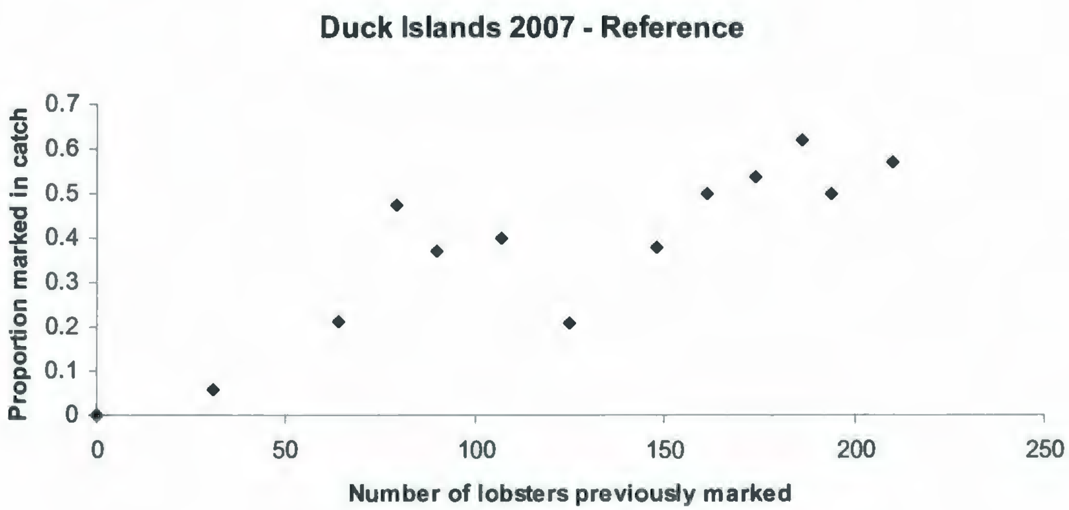


Duck Islands 2006 - Reference





Duck Islands 2007 - Reserve
Proportion marked in catch
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
50
100
150
200
250
300
350
400



Duck Islands 2007 - Reference
Proportion marked in catch
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
50
100
150
200
250
Number of lobsters previously marked

Chapter 3: Reproductive potential of American lobster (*Homarus americanus*) in protected and unprotected populations in Bonavista Bay, Newfoundland.

3.1 Introduction

A more precautionary approach to fisheries management is increasingly being advocated as a safeguard against uncertainty in fisheries stock assessments (Ludwig *et al.* 1993; Lauck *et al.* 1998). Overfishing has resulted in precipitous declines in many exploited populations in coastal habitats, and conventional fishery regulations may not provide adequate protection to ensure sustainability (Bohnsack 1993; Dayton *et al.* 1995; Lauck *et al.* 1998). Marine reserves can serve as powerful tools for promoting recovery and sustainability of world's fisheries (Agardy 1994; Allison *et al.* 1998; Guénette *et al.* 1998; Roberts *et al.* 2005).

Marine reserves have the potential to provide direct benefits to the fishery in at least two major ways (Rowley 1994). Firstly, "spillover" may occur as harvestable biomass disperses from reserves into commercially exploited areas. Secondly, reserves may act as sources of recruitment, exporting larvae to areas that are open to commercial harvesting. In the context of fisheries management, larval export is viewed as the primary benefit of marine reserves as it may provide "insurance" against poor recruitment periods (Roberts and Polunin 1991; DeMartini 1993; Dugan and Davis 1993). Larval export can be extremely difficult to demonstrate, however, and the time from hatching to recruitment to the fishery can take a decade or more. For these reasons, many attempts to assess the efficacy of marine reserves have focused on changes in the structure of the population contained in the reserves, with the knowledge that greater numbers of larger animals (which are generally more fecund) have the potential to greatly enhance population egg production. Multiple studies involving marine reserves of varying sizes and locations have demonstrated that the abundance, density, and mean size of commercially exploited species tend to be greater within reserve boundaries, as compared to nearby reference areas (Roberts and Polunin 1991; Dugan and Davis 1993; Rowley 1994; Halpern and Warner 2002). Many of these studies have focused on commercially significant species of spiny lobster, including *Jasus edwardsii*, *Panulirus argus*, *Panulirus cygnus* and *Palinurus elephas*. Reserves for highly exploited species of spiny lobster have been established since the mid 1970s. Studies of these reserves have demonstrated increased size, abundance and/or density of spiny lobsters within protected areas as compared to exploited areas (Cole *et al.* 1990; Kelly *et al.* 2000; Goñi *et al.* 2001; Davidson *et al.* 2002; Babcock *et al.* 2007; Barrett *et al.* 2009), as well as changes in population sex ratios (Goñi *et al.* 2001; Davidson *et al.* 2002).

Fewer studies have directly examined changes in lobster fecundity and/or reproductive potential as a consequence of protection. In addition to increases in mean density and mean size, Kelly *et al.* (2000) reported an increase in egg production for spiny lobster, *Jasus edwardsii*, in four different reserves in New Zealand, but no time-series data were available for three of the reserves, and temporal patterns were inferred from reserve ages (ranging from 3-21 years). At the Tonga Island reserve in New Zealand, a two-year study revealed a ninefold increase in size-specific fecundity for *Jasus edwardsii* (Davidson *et al.* 2002). In a three-year study of fecundity dynamics of female spiny lobster, Bertelsen and Matthews (2001) reported larger clutch sizes in a protected population of *Panulirus argus,* as compared to an exploited population. Bertelsen *et al.* (2004) reexamined data from various monitoring projects carried out in Florida reserves for *Panulirus argus*. These data were collected for discrete periods between 1973 and 2002 and, in most cases, revealed greater fecundity in reserve locations, as compared to reference locations (Bertelsen *et al.* 2004). Goñi *et al.* (2003) found that size-specific fecundity in a protected population of *Palinurus elephas* from the Western Mediterranean was greater than that of exploited populations in the region over a three-year period. In a two-year study, Babcock *et al.* (2007) reported that egg production for an unfished population of *Panulirus cygnus* in Western Australia was significantly higher than in adjacent fished areas.

Although reserves have been established for clawed lobster species, *Homarus americanus* and *Homarus gammarus*, they have not been evaluated for their potential to contribute to population egg production. Previous studies on marine reserves for American lobster (*Homarus americanus*) have examined changes in population structure, abundance/density, mean size and sex ratios (Rowe 2002; Janes 2009), but have not examined the effect of protection on reproductive output. Hence, long-term effects of reserve protection on egg production are largely unknown for this commercially significant species. This study quantifies the effect of 11 years of protection on the reproductive potential of a population of American lobster.

Hypothesis

The hypothesis of this study is as follows:

1) Reproductive potential will be greater inside the reserves due to increased size of female lobsters, and will increase over time.

3.2 Materials and methods

3.2.1 Study areas

The Eastport Peninsula Lobster Management Area, located in the waters surrounding the Eastport Peninsula in Bonavista Bay, Newfoundland (48.65° N. 53.70° W), contains two marine reserves, one at Round Island, and one at Duck Islands. The reserves were established in 1997 for the protection of the American lobster, and were designated as Marine Protected Areas (MPAs) by Fisheries and Oceans Canada in 2005.

3.2.2 Sampling design

Data were assembled for 1997-2008. During September 18 – September 28 of 2000, mark-recapture research tagging of lobsters took place at both the Round Island and Duck Islands study sites. Sampling was conducted both inside the reserves and in the adjacent reference areas, which were open to commercial harvesting. These areas are identified in Figure 1. Participating harvesters were asked to spread traps out within each reserve and reference location, and set them at commercially fished depths. A total of 25 wood-lath parlour traps were set in each of the reserves, and 25 traps were set in each nearby reference area. Traps were hauled daily, except in circumstances of inclement weather, and baited using fresh or salted herring (*Clupea harengus*), mackerel (*Scomber scombrus*), winter flounder (*Pseudopleuronectes americanus*) or cod (*Gadus* spp.).

For each new lobster captured during the research tagging periods, the following information was recorded: date of capture, location of capture, sex, and carapace length (CL). Carapace length was defined as the length of the cephalothorax, from the base of the right eye-socket to the end of the carapace, and was measured in millimeters (mm) using vernier calipers. Females were also examined in order to determine reproductive condition (*i.e.* ovigerous or not). New captures were marked with an individually numbered polyethylene streamer tag. The tag was inserted, with the aid of an attached embroidery needle, into the thoraco-abdominal membrane and abdominal muscle on one side, and threaded over the dorsal artery and through the abdominal muscle on the opposite side, as described by Moriyasu *et al.* (1995). In the case of larger animals, *circa* 100 mm or larger, the tag was inserted through one muscle band only. With the tag properly inserted, the needle was detached and discarded. Once tagged, lobsters were released immediately.

Often, lobsters tagged in previous years were recaptured, in which case the original tag number was recorded, along with the aforementioned information. This protocol was repeated during Fall of 2001 (23 September – 5 October) and Fall of 2002 (2 October – 10 October). Similar protocols were used in Fall (September/October) of 1997-1999, and 2004-2008. Sampling was not conducted at either site in 2003, and no data were available.

3.2.3 Length-fecundity relationships

Reproductive potential was evaluated using a power law as follows, Eggs = $\alpha(CL)^{\beta}$. Because no length-fecundity relationship has been developed for Bonavista Bay lobster, reproductive potential was evaluated using relationships derived for other areas of Newfoundland. Due to relative proximity to Bonavista Bay, size and egg count data from Leading Tickles, in Notre Dame Bay (Ings, unpublished data), were used to derive two length-fecundity relationships, one using all available data (LT1), and one with two outliers removed (LT2). Carapace length and fecundity estimates were ln transformed and subjected to regression analysis. The linearized version of the power curve was fitted to the set. The relationship was then applied to datasets collected from the research fishing at both study sites. Due to the potential for geographic variability in fecundity, reproductive potential was also evaluated using published length-fecundity relationships for Paradise in Placentia Bay, NL and the Northwest Coast of Newfoundland (Ennis 1981).

3.2.4 Reproductive potential

Recaptures occurred frequently during each sampling period, but each lobster was counted only once per year for the analyses. Data collected from 2000-2002 was combined with data from 1997-1999 and from 2004-2008 to examine changes in reproductive potential over time. For the majority of these years, full datasets were available. In these circumstances, estimates of reproductive potential were calculated by applying the Leading Tickles length-fecundity relationship to each female in the dataset.

An average number of eggs per individual was then determined by summing these values and dividing by the total number of females in the dataset (Method 1).

In the absence of complete datasets for 1997-1999, reproductive potential was evaluated by obtaining mean carapace lengths for females from figures published in Rowe (2002), which were then used to estimate the annual reproductive potential for an average female in reserve and reference locations at the two study sites for these three years (Method 2). This method of evaluating reproductive potential was also applied to data from 2000-2002, to assess the extent to which estimates of reproductive potential differed between each of the two methods. This would then determine whether the estimates from 1997-1999 could be included in the overall analyses.

3.3 Results

For the 2000-2002 data from the Round Island study site, estimates of annual reproductive potential from Method 1 and Method 2 were sufficiently similar to warrant inclusion of 1997-1999 data in the overall analyses (Table 1). Results from the Duck Islands site were similar to those from Round Island site. In all cases, the percent difference between the two estimates of reproductive potential for 2000-2002 data lay within the 95% confidence limits associated with annual mean reproductive potential for those years (Method 1).

Table 2 presents estimates of parameters for two length-fecundity relationships derived from Leading Tickles data, as well as those from Paradise, in Placentia Bay, and the Northwest Coast, originally published in Ennis (1981). Explained variance ranged from 36% to 88%, depending on source of data. Estimates of β varied, depending on location of data collection (*e.g.* Paradise vs. Northwest Coast). They also depended on whether outliers were included in the regression analysis (*i.e.* LT1 vs. LT2).

These differences in parameter estimates did not result in large differences in estimates of reproductive potential (Table 3). For LT1, percent differences in reproductive potential between reserve and reference locations ranged from 0% to 24% for the Round Island study site, and from -3% to 30% for the Duck Islands study site. Percent differences obtained from the other three relationships, ranged from 0% to 23% for Round Island, and from -3% to 30% for Duck Islands.

At both Round Island and Duck Islands study sites, reproductive potential was generally greater in the reserves, and increased over time in both reserves (Figure 2; Figure 3). At the Round Island site, differences in reproductive potential averaged 10% from 1997-2008, with values ranging from 0% to 24% (Table 3). At the Duck Islands site, differences in reproductive potential averaged 14% from 1997-2008, with values ranging from -3% to 30% (Table 3).

3.4 Discussion

Estimated annual reproductive potential was generally greater in the reserves at both study sites, and increased over time for protected populations at both study sites. This supports the hypothesis that the benefits of marine reserves, with respect to larval production and export, will increase annually as larger animals accumulate inside the reserve boundaries. It appears that these reserves have a cumulative effect over time, as greater numbers of eggs are generally produced inside the reserve each year.

Often, the development of size-fecundity relationships for American lobster has involved the use of logarithmic transformation to linearize size and fecundity data, thus facilitating the estimation of parameters for a power function in the form, Eggs = $\alpha(CL)^{\beta}$ (*e.g.* Ennis 1981). However, the use of logarithmic transformations to linearize the data results in biased estimates of parameters α and β (Smith 1984, 1993; Packard 2009). Sprugel (1983) proposed the use of a correction factor to address this bias, which was applied to more recent fecundity studies of American lobster (Estrella and Cadrin 1995). In this study, this bias was consistent in that the same parameter estimates were used for both reserve and reference areas. Table 3.3 shows that percent differences in reproductive potential between reserve and reference populations were very similar despite differences in the parameters used.

Issues with the use, and placement, of traps may have biased the results of the study. Lobster catchability can be affected by the size, sex, and reproductive condition of the animal (Miller 1990). Smaller lobsters are often underrepresented in trap catches (Smith 1944; Ennis 1978; Miller 1989, 1995; Tremblay and Smith 2001; Tremblay *et al.* 2006), but catchability may decrease at very large sizes, as well. Using parlour traps, Pezzack and Duggan (1995) reported a decline in *Homarus americanus* catchability at sizes above 120 mm in carapace length. Miller (1990) suggested that, for decapod crustaceans, a logistic curve best describes the relationship between catchability in traps and size, with the possibility that animals at very large sizes are less catchable as they may be physically incapable of entering the trap. Females are generally less vulnerable to traps than males (Miller 1989, 1995; Tremblay and Smith 2001; Tremblay *et al.* 2006), and ovigerous females may be less catchable than males and non-ovigerous females (Templeman and Tibbo 1945; Miller 1990). Given that females larger than 120 mm in carapace length tend to spawn more frequently than smaller females (Waddy and Aiken 1986), it is possible that these large females were underrepresented, as they allocate more time and energy to reproduction through consecutive spawning, and may be less catchable while brooding eggs externally. In addition, behavioural interactions can strongly influence observed catch. Agonistic encounters between lobsters outside of traps can affect the rate of entry into traps, and the presence of lobsters in traps can reduce the catch of other lobsters (Richards *et al.* 1983; Karnofsky and Price 1989; Jury *et al.* 2001). Due to seasonal movements and sex segregation by depth, placement of traps may have also influenced the results of the study. Ennis (1984) found that lobster in Bonavista Bay undergo seasonal movements to deeper water in the fall, presumably in response to increased turbulence associated with inclement weather and the breakdown of the thermocline. There is evidence that, for inshore lobster populations, adult females move to deeper water earlier in the fall than their male counterparts (Campbell and Stasko 1986; Robichaud and Campbell 1991; Roddick and Miller 1992). Templeman (1939) reported that in the fall, immediately following the molt, males predominated in trap catches at 8-10 m, and females predominated at 15-22 m. Since the depth at which traps were set was not standardized within or across years, but appeared to be 10 m or less (Janes 2009), then it is possible that some traps were set too shallowly during the study period to effectively target female lobsters. However, if the biases associated with use and placement of traps are consistent across reserve and reference locations, then differences between protected and unprotected populations can be interpreted free of the biases.

Changes in the size of the reference areas at both study sites may have affected the results. A small expansion of the reference area at the Duck Islands study site occurred between 1997-1999 and 2000-2002. The size of reference area at the Duck Islands study site increased further for 2004-2008, while the size of the Round Island reference area decreased between 1997-1999 and 2000-2002, and again between 2000-2002 and 2004-2008. Suitable habitat may not be uniformly distributed in either of the reference areas. Lobsters spend the majority of their time individually occupying shelters, and shelter size is often related to the size of the animal (Cobb 1971; Karnofsky *et al.* 1989). Male and female lobsters cohabit during molting and mating periods, and the protection afforded by shelters is of particular importance during this time (Karnofsky *et al.* 1989; Lawton and Lavalli 1995). Therefore, changes in the boundaries of the reference areas may have influenced the outcome of the study, by affecting the sizes, and numbers, of animals caught due to habitat heterogeneity and spatial differences in shelter availability.

Additional conservation measures that were implemented around the same time as the establishment of the reserves may have enhanced the reproductive potential of the unprotected population. This would have served to reduce any observed effect of protection on reproductive potential, as the magnitude of difference between reserve and reference populations with respect to size and, thus, reproductive potential, would have been reduced. In 1996, approximately 1500 ovigerous female lobster were V-notched on commercial fishing grounds in the Eastport area (Rowe 2000). It is illegal to retain V-notched lobsters, and the notch is typically retained through two or more molts (DeAngelis *et al.* 2010). Therefore, these females were rendered ineligible for commercial harvest for a number of years, and attained larger sizes as a consequence (Whiffen 2010). This would have resulted in greater reproductive potential of lobsters in the reference locations. In addition, during the 1998 fishing season, an increase in the minimum legal size, from 81 mm CL to 82.5 mm CL, was imposed for the Newfoundland lobster fishery. This would have increased survival and mean size of females in the commercially exploited areas outside the reserves. Hence, the additional conservation measures that were implemented in the Eastport area may have confounded the study, by increasing the average size, and thus reproductive potential, of females in reference locations.

In addition to observed increases in reproductive potential, it is possible that some unquantified benefits of protection may be occurring in the reserves. Given the long brooding interval for American lobster, egg loss is common and anywhere from 30-50% of a clutch will typically be lost between extrusion and hatching (Perkins 1971; Campbell and Brattey 1986). Capture in traps, handling, and subsequent release of berried females may contribute to significant clutch attrition (Herrick 1909). It has been estimated that natural attrition of up to 36% can be attributed to normal activity, capture and release from traps, and similar factors (Perkins 1971). Since lobster in commercially exploited regions can be subject to capture in traps for up to 10 weeks during the Newfoundland lobster fishing season, this may represent a significant source of egg loss. Female lobsters in reserves would not be subject to the same intensive fishing pressure, and thus may be less prone to clutch attrition over the brooding period. Consequently, they may produce a greater number of larvae from a given clutch. In addition, females in reserves may be benefiting from the presence of larger males in the protected populations. Due to differences in catchability, and commercial fishery regulations prohibiting the landing of ovigerous or V-notched females, males may be subject to greater rates of fishing mortality and a more truncated size-structure (Miller 1990; Campbell 1992; Gendron and Savard 2000). Since larger males tend to transfer more ejaculate than smaller ones, and appear to tailor ejaculate proportionately to female size, it is possible that sperm limitation may occur in populations if there are insufficient numbers of large, dominant males to mate with females, or if the available males deplete their sperm reserves through repeated matings (Gosselin *et al.* 2003). Larger females may be particularly susceptible to such sperm limitation (Gosselin *et al.* 2003). Large males also spend a greater period of time cohabitating with females during the molting and mating period, which may reduce the risk of molt-related mortality for those animals that mate with larger males (Gosselin *et al.* 2003). Thus, although reproductive potential is generally greater inside the reserves due to increased female size, it is also possible that other factors are contributing to increased reproductive output in protected populations.

Several studies have demonstrated increased egg production as a consequence of reserve protection for commercially significant spiny lobster species (Kelly *et al.* 2000; Bertelsen and Matthews 2001; Davidson *et al.* 2002; Goñi *et al.* 2003; Bertelsen *et al.* 2004; Babcock *et al.* 2007). In a study of the effects of protection on *Jasus edwardsii*, Davidson *et al.* (2002) estimated that almost nine times more eggs were produced in the reserve, as compared to reference areas. Bertelsen and Matthews (2001) reported an average clutch size of 0.8 million eggs in a protected population of *Panulirus argus,* while females in a fished population averaged 0.3 million eggs per clutch. While the present study revealed that reproductive potential of American lobster was generally greater in reserve locations, differences between reserve and reference populations were small, by comparison. This is likely related to differences in species fecundity. The fecundity of both *Jasus edwardsii* and *Palinurus elephas* ranges from tens of thousands to hundreds of thousands of eggs (MacDiarmid 1989; Goñi *et al.* 2003). The fecundity of *Panulirus argus* is measured in the hundreds of thousands of eggs (Fonseca-Larios and Briones-Fourzán 1998) while size-fecundity relationships for *Panulirus cygnus* estimate 800 000 eggs at 95 mm CL, the size at 50% maturity (Hall and Chubb 2001; Babcock *et al.* 2007). The fecundity of the American lobster is low relative to these other species, and ranges from a few thousand eggs in a young (smaller) female, to several tens of thousands in older (larger) individuals (Aiken and Waddy 1980*a*, 1980*b*). Therefore, any absolute difference in egg production between protected and unprotected populations would be expected to be smaller in *Homarus americanus*. Given the low fecundity of *Homarus americanus,* relative to other crustacean species, it is possible that even a small increase in egg production that results from protection may be biologically significant, and may have an appreciable impact on recruitment.

This study has several implications for future research on the effects of marine reserves. Like a number of other studies on reserve effects, this study was conducted without the collection of baseline data regarding the abundance and population structure of lobster in the areas designated for protection. Given that population characteristics may have differed between the reserve and reference populations prior to the establishment of the closure, future studies should ensure that baseline data is collected prior to the establishment of the reserve.

A lack of consistency in the research design may have introduced a bias, since the greater reproductive potential observed for reserve populations may have been related to minor changes in research protocol and not the effects of protection. The lack of standardization in the size of the study areas may have influenced the results of the study. Efforts should be made to set traps at consistent and appropriate depths, where possible. In addition, the boundaries of the reference areas for both research sites should be standardized, and the amount of available habitat in each should be quantified.

The implementation of additional conservation measures immediately before, and during, the course of the study also may have biased the results. The introduction of a broad-scale V-notching program and changes to commercial fishery regulations would have impacted reproductive potential in commercially exploited populations, and thus influenced the observed differences between protected and unprotected populations.

Where possible, the implementation of additional conservation measures should be delayed until the effects of the reserve can be quantified.

The length of the time-series of available data strengthens the conclusions of this study. Previous studies of reserve effects on reproductive potential in spiny lobster populations have generally been short-term in nature, or have lacked continuous time-series data. The available data for this study spanned more than a decade. This study has established that differences in reproductive potential of *Homarus americanus* between reserve and reference areas were quick to arise, and that these differences persisted over time. This provides evidence for the potential of reserves to promote the sustainability of commercially exploited lobster populations through sustained increased reproductive output.

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Table 3.1: Comparison of two methods for estimating annual reproductive potential (RP) for female lobsters at the Round Island study site, from 1997-2002. Mean sizes for 1997-1999 from Rowe (2002). Percent difference calculated as (Method 2-Method 1)/Method 2.

Year	RP: Method 1	Confidence Limit	N	Mean Carapace Length (mm)	RP: Method 2	% difference
Reserve						
1997	-	-	102	83	11364	-
1998	-	-	120	87	13246	-
1999	-	-	127	88	13445	-
2000	14391	± 911	116	88	13831	-4.1
2001	16210	± 917	97	92	15785	-2.7
2002	16188	± 1185	84	92	15580	-3.9
Reference						
1997	-	-	127	83	11364	-
1998	-	-	81	86	12660	-
1999	-	-	85	83	11364	-
2000	13067	± 783	115	86	12679	-3.1
2001	13387	± 835	85	87	13047	-2.6
2002	14244	± 1209	63	88	13781	-3.4

Table 3.2: Estimated parameters for power law equations relating fecundity to female carapace size, $Eggs = \alpha(CL)^{\beta}$.

Source	N	Size Range (mm)	Parameters β	α	r^2
Leading Tickles 1 (Ings, unpublished data)	30	74-113	3.17	Exp(-4.67)	.55
Leading Tickles 2 (Ings, unpublished data)	28	74-113	2.52	Exp(-1.7)	.63
Paradise, NL (Ennis 1981)	72	75-139	3.10	Exp(-4.37)	.88
Northwest Coast, NL (Ennis 1981)	63	70-107	2.32	Exp(-0.92)	.36

Table 3.3: Differences in annual reproductive potential between reserve and reference areas at Round Island and Duck Islands study sites, for four different length-fecundity relationships. See text for explanation of sources of estimates.

Year	Reproductive Potential (based on LT1)		% difference (Reserve - Reference)/Reference)			
	Reserve	**Reference**	**LT1**	**LT2**	**Paradise**	**NW Coast**
Round						
1997	11364	11364	0.0%	0.0%	0.0%	0.0%
1998	13246	12660	4.6%	3.7%	4.5%	3.4%
1999	13445	11364	18.3%	14.3%	17.9%	13.1%
2000	14391	13067	10.1%	7.8%	9.9%	7.1%
2001	16210	13387	21.1%	16.4%	20.6%	15.0%
2002	16188	14244	13.7%	10.6%	13.3%	9.7%
2003	-	-	-	-	-	-
2004	17066	15407	11.0%	8.0%	10.0%	7.0%
2005	17283	17090	1.1%	0.9%	1.1%	0.9%
2006	17421	16546	5.3%	4.9%	5.3%	4.7%
2007	19262	15545	23.9%	18.7%	23.3%	17.1%
2008	19497	19003	3.0%	3.0%	3.0%	3.0%
Duck						
1997	14054	12093	16.0%	13.0%	16.0%	12.0%
1998	12469	12853	-3.0%	-2.4%	-2.9%	-2.2%
1999	14471	12469	16.1%	12.6%	15.7%	11.5%
2000	15664	14995	4.5%	4.0%	4.4%	3.8%
2001	16610	14587	13.9%	11.0%	13.5%	10.0%
2002	21420	19000	12.7%	10.7%	12.5%	10.0%
2003	-	-	-	-	-	-
2004	20247	18434	10.0%	7.9%	9.6%	7.3%
2005	22990	18854	21.9%	17.1%	21.4%	15.6%
2006	22015	18514	18.9%	16.1%	18.6%	15.1%
2007	17998	15524	15.9%	12.7%	15.6%	11.6%
2008	22651	17365	30.0%	23.0%	30.0%	21.0%

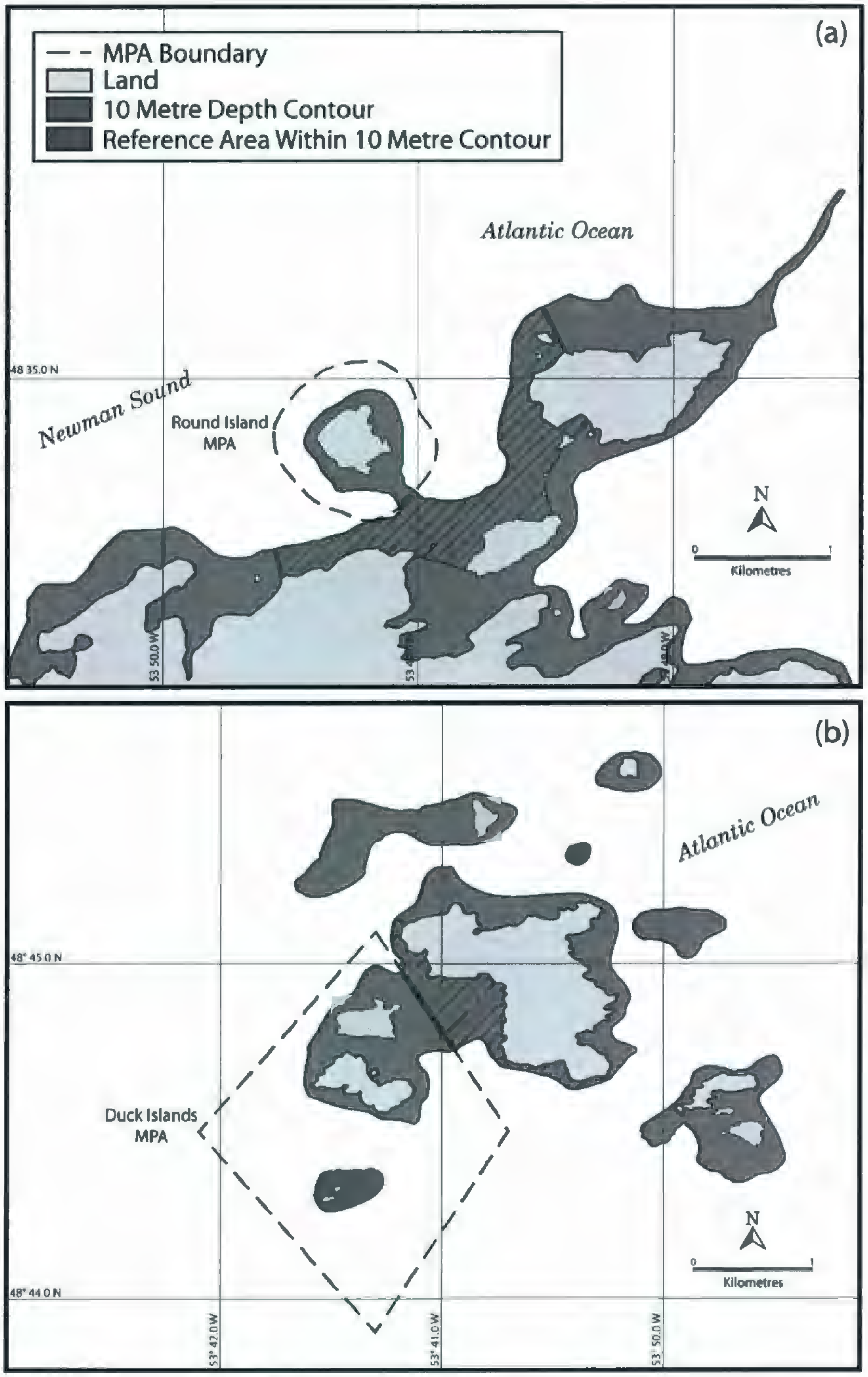

Figure 3.1: Study areas within reserve and reference locations at Round Island (a) and Duck Islands (b) study sites in Bonavista Bay, Newfoundland.

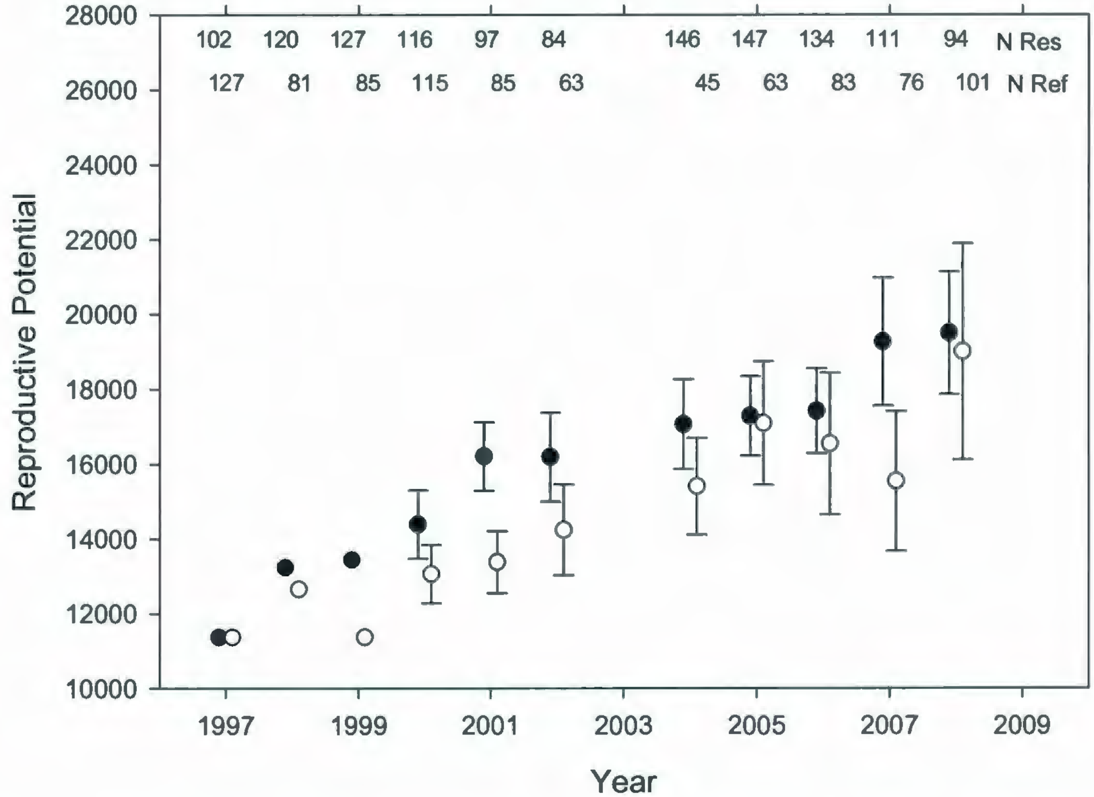

Figure 3.2: Reproductive potential (mean ± 95% confidence limits) of female lobsters in reserve (●) and reference (○) locations at Round Island, Bonavista Bay, Newfoundland, 1997-2008.

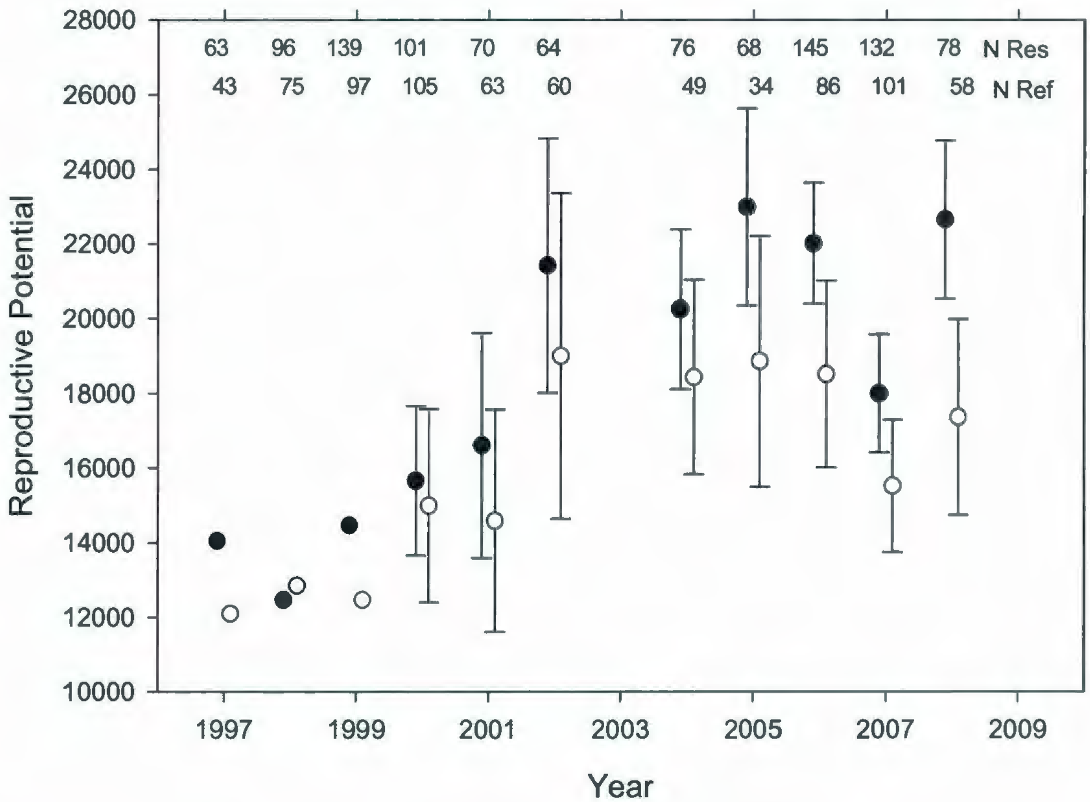

Figure 3.3: Reproductive potential (mean ± 95% confidence limits) of female lobsters in reserve (●) and reference (○) locations at Duck Islands, Bonavista Bay, Newfoundland, 1997-2008.

Chapter 4: Summary, Conclusions and Future Work

The results of this study provide further evidence that the Eastport Marine Protected Areas (MPAs) have the potential to promote sustainability of the resource through increased density, mean size and reproductive potential of lobsters. At the Round Island site, lobster density inside the reserve was greater than that of the adjacent reference area. Observed sex ratios in reserve and reference locations differed at both sites, with a bias towards females in reference locations. At Round Island and Duck Islands study sites, both male and female lobsters were significantly larger in protected populations, and mean sizes continued to increase over time. The increased female size in protected populations led to consistently greater reproductive potential inside these reserves, though the difference between protected and unprotected populations was small.

Previous studies of the Eastport MPAs have demonstrated differences in density and mean size of lobsters between reserve and reference locations (Rowe 2002; Janes 2009), but were relatively short-term in nature. Moreover, they did not directly examine changes in reproductive potential, which is a key indicator of a reserve's ability to enhance recruitment. Measures of reproductive potential are important because recruitment as a consequence of protection is difficult to quantify. The protracted pelagic larval period for American lobster increases the potential for considerable dispersal. Newly-settled postlarvae, and juveniles, are cryptic in nature, and hence difficult to census. Additionally, it can take 8 years or more for a lobster to recruit to the fishery (DFO 2009). Survival and recruitment are unpredictable because they are heavily influenced by environmental conditions (Caddy 1979; Ennis 1986).

These results have considerable implications for the management of American lobster (*Homarus americanus*) populations. Many of the concerns that were raised by the Fisheries Resource Conservation Council (FRCC) in 1995 (FRCC 1995), regarding the sustainability of lobster stocks in Atlantic Canada, are still relevant today. In 2007, the FRCC reiterated their concerns regarding impact of high exploitation rates on population egg production and the size structure of the lobster resource in Atlantic Canada, and suggested that a "network of reasonably sized and spaced reserves" be developed to enhance the sustainability of the resource (FRCC 2007). In 2008, DFO published a document outlining a conservation rationale and biological basis for the protection of large lobsters, both male and female, citing concerns about the potential impacts of a truncated size structure on reproductive success and population egg production, where truncation could lead to recruitment failure in periods associated with adverse environmental conditions (DFO 2008). The document also recommended the establishment of MPAs as a potential means of allowing male and female lobster to attain larger sizes (DFO 2008).

The conclusions of this study would have been strengthened had baseline data been available prior to reserve establishment. Pre-existing differences between reserve and reference populations may have influenced the results, but the time series of available data lends support to the hypothesis that observed differences were influenced by the presence of protection. The implementation of other conservation measures just prior to, and shortly after, reserve establishment presented a confounding factor that likely influenced the results. These measures would have served to increase the abundance, and mean size, of lobsters in commercially exploited areas, and thus reduce the ability to detect differences between reserve and reference locations. Because baseline data were not collected and because other conservation measures were implemented, it would be difficult to attribute increases in catch to any one conservation measure.

This study supports the hypothesis that American lobster populations can benefit from the establishment of marine reserves. However, further work is required to strengthen the conclusions. Changes in the size of both reference areas over time introduced a degree of bias that was controlled by some degree by standardizing density estimates by area. However, changes in the boundaries of the reference areas may have influenced the outcome of the study, by affecting the sizes, and numbers, of animals caught due to habitat heterogeneity. The boundaries of these reference areas at both study sites should be standardized for further research. Additionally, since there is some evidence for sex segregation by depth in the fall (Templeman 1939; Campbell and Stasko 1986; Robichaud and Campbell 1991; Roddick and Miller 1992), it is possible that traps were set too shallowly to effectively sample female lobsters. In future, traps should be set at appropriate depths to target both male and female components of the population, so that sex ratios, and size of female lobsters, can be examined more appropriately. Once the boundaries of the study sites have been standardized by lateral extent and depth, further research will be required to identify the amount of available lobster habitat in both reserve and reference locations.

Lobster catchability is influenced by many factors, including size, sex, and agonistic encounters both in, and around, traps (Richards *et al.* 1983; Karnofsky and Price 1989; Miller 1990, 1995; Jury *et al.* 2001). Additionally, some lobsters never enter traps (Karnofsky and Price 1989). The use of alternate census techniques may be warranted to cross-check estimates of abundance and density.

The contiguous nature of the boundaries of reserve and reference locations at both study sites indicates the potential for spillover. Thus far, studies to quantify the degree of exchange between reserves and commercially harvested locations have reported low rates of movement (Rowe 2001; Janes 2009), but have been limited by either a relatively short time-series of data, or limited and inconsistent rates of tag reporting during the commercial fishery (Janes, pers. comm.). Since spillover is an expected result of protection, and may provide localized benefits to stakeholders, further efforts should be made to obtain tag return information from the commercial fishery, to quantify movement of lobster across reserve boundaries. This will provide both a direct quantification of spillover, and a measure of lobster retention in the reserve, which can indirectly provide a means to further assess the reserves' potential to enhance recruitment.

The 1995 FRCC report contained explicit considerations of the precautionary approach as it pertains to Atlantic lobster populations. In 2001, the United Nations *Agreement on Straddling and Highly Migratory Fish Stocks* (UNFA) came into effect, thus committing Canada to employ a precautionary approach in managing both domestic and straddling stocks. In 2009, the Sustainable Fisheries Framework for Fisheries and Oceans Canada renewed this commitment though a specific policy for the development of a fishery decision-based framework incorporating the precautionary approach. The conservation and sustainable use of resources are of paramount importance in the management of current fisheries, as well as in the development of future ones. The establishment of marine reserves represents a promising approach to the implementation of the precautionary approach for American lobster.

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