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Reproductive Status of the American Lobster in Southwest Nova Scotia and the Bay of Fundy (Lobster Fishing Areas 34-38)

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The historical reproductive status of the American lobster, *Homarus americanus*, for Lobster Fishing Areas (LFAs) 34-38 was examined in the form of size-at-onset-maturity, egg production indices and other aspects of lobster reproduction (size structure, sex ratio, proportion of ovigerous females, mating success). A significant downward shift in size-at-onset-maturity was observed when comparing an unpublished dataset between 1978-79 and 2011 from North Head Grand Manan (LFA 38). A re-estimate of size-at-50%-maturity (SoM50) for 1978-79 indicates it was 99 mm carapace length (CL) rather than the published estimate of 108.1 mm CL. The estimate for 2011 indicated a decline of approximately 7 mm to 92.5 mm. This shift was consistent with the observation that sizes of smallest ovigerous females have gradually declined over past 30-year in the Bay of Fundy and Southwest Nova Scotia. The sea sampling time-series have shown a dramatic increase of lobster over time and, combined with the shift in SoM50, the reproductive potential has increased dramatically in the Bay of Fundy. There is no clear trend in LFA 34. Reproductive potential of large females has slightly declined over time but was largely compensated by the increased potential of the smaller size group. Despite the overall increase in the egg production potential in the Bay of Fundy, observed egg production calculated from ovigerous females catch rates and fecundity-at-size only increased slightly or was steady when comparing the initial five-year of the time series to the past five years for the Bay of Fundy areas. The discrepancy between the two indices may be related to lower mating rates among mature females in recent years in comparison to 1978-79. Observed mating success had a positive size-dependent relationship among mature females and, thus, the contribution of small sizes females (i.e. below SoM50) to observed egg production was substantially lower than their reproductive potential. In LFA 34, the observed egg production indices were variable but showed no upward trend. This work suggests that increasing the minimum legal size would not have a significant effect on increasing egg production unless the increase is substantial. Instead, it may be more effective to protect larger females that appear more successful at mating. In addition, protecting large males may contribute to increased egg production as there are indications based on mating success and proportion of ovigerous females that sperm limitation may be occurring in within LFAs 34-38.

État reproducteur du homard d'Amérique dans le Sud-Ouest de la Nouvelle-Écosse et de la Baie de Fundy (Zones Pêche du Homard 34-38)

RÉSUMÉ

L'état reproducteur historique du homard de l'Atlantique, *Homarus americanus*, des zones de pêche du homard (ZPH) 34 à 38 a été examiné relativement aux aspects suivants : taille à l'aube de la maturité, indices de production d'œufs et autres aspects de la reproduction du homard (structure des tailles, sexe ratio, proportion de femelles œuvées, succès des accouplements). Un changement à la baisse important dans la taille à l'aube de la maturité a été observé en comparant un ensemble de données inédit de 1978-1979 à 2011 de North Head à Grand Manan (ZPH 38). Une réestimation de la taille à 50 % de la maturité pour l'année 1978-1979 indique que la longueur de carapace était de 99 mm, plutôt que l'estimation publiée de 108,1 mm. L'estimation pour 2011 indiquait un déclin de 7 mm environ, pour atteindre 92,5 mm. Ce changement cadre avec l'observation selon laquelle les tailles des plus petites femelles œuvées ont diminué graduellement au cours des 30 dernières années dans la baie de Fundy et le sud-ouest de la Nouvelle-Écosse. La série chronologique d'échantillonnage en mer montre une augmentation importante de homards au fil du temps et en tenant compte du changement dans la taille à 50 % de la maturité, le potentiel de reproduction a augmenté considérablement dans la baie de Fundy, mais sans aucune tendance claire dans la ZPH 34. Le potentiel de reproduction des femelles de grande taille a baissé légèrement au fil du temps, mais cette baisse a été largement compensée par l'augmentation du potentiel du groupe de femelles de plus petite taille. Malgré l'augmentation globale du potentiel de production d'œufs dans la baie de Fundy, la production d'œufs observée et calculée uniquement à partir des taux de prise de femelles œuvées et de la fécondité à la taille a augmenté légèrement ou est restée stable si l'on compare la série chronologique initiale de cinq ans avec les cinq dernières années des zones de la baie de Fundy. L'écart entre les deux indices peut être associé à des taux d'accouplement plus faibles parmi les femelles matures au cours des dernières années comparativement à l'année 1978-1979. Il y avait une relation positive entre le succès des accouplements observé et la taille des femelles matures et, par conséquent, la contribution de femelles de petite taille (taille inférieure à la taille à 50 % de la maturité) relativement à la production d'œufs observée était beaucoup plus faible que leur potentiel de reproduction. Dans la ZPH 34, les indices de production d'œufs variaient, mais il n'y avait aucune tendance à la hausse. Le présent article laisse entendre qu'augmenter la taille légale minimale n'aurait pas d'impact important sur l'augmentation de la production d'œufs, à moins que l'augmentation soit substantielle. Il serait peut-être plus efficace de protéger les femelles de plus grande taille semblant avoir plus de succès pour s'accoupler. De plus, le fait de protéger les mâles de grande taille peut faire augmenter la production d'œufs, car il y a des indications basées sur le succès d'accouplement et la proportion de femelles œuvées selon lesquelles il y a peut-être limitation du sperme dans les ZPH 34 à 38.

1. INTRODUCTION

Despite a long standing high exploitation rates, lobster landings in the Bay of Fundy and Southwest Nova Scotia are at an all-time high. The high resilience of lobster stocks to fishing pressure has been attributed to the existence of spatial refugia and larva source-sink dynamics (Anthony and Caddy 1980, Fogarty and Idoine 1988), favourable environmental conditions (Fogarty 1995), the release of predation pressure, and good conservation measures (protection of ovigerous females and v-notching). However, there are concerns that fishing pressures are shifting to those refugia, potentially depleting the broodstock (e.g. Cowan 2012, DFO unpublished document). If the current environmental conditions that are favourable to lobsters deteriorate, a reduction of the reproductive capacity may have direct consequences on the recruitment processes, therefore impacting the productivity of the stock and the fishery.

Despite the current high abundance of lobsters in LFAs 34-38 (Tremblay et al. 2013), there are long standing concerns about recruitment overfishing among fishery managers for the LFAs 34-38 stock for two main reasons: the stock is under a moderate to high level of exploitation and the gap between minimum legal size (MLS), set at 82.5 mm carapace length (CL) and size-at-onset-maturity (SoM) is one of the widest in the Maritimes (FRCC 2007). Estimates of the size at which 50% of females in the Bay of Fundy reach maturity (SoM50) range from 101 (Comeau 2003) to 108 mm CL (Campbell and Robinson 1983). For LFA 34, FRCC (2007) reported SoM50 to be 94 mm CL. Despite the concept that MLS should be based on biological data to allow animal to reproduce at least once prior legal size (Jamieson 1993), MLS in the Bay of Fundy and LFA 34 is based on history and marketing factors, not biology. This is because SoM50 estimates are substantially higher than the typical market needs.

The possibility of recruitment overfishing for exploited lobster stocks has promoted the implementation of conservation measure towards protecting the breeding females (e.g. size refuge, prohibition of landings ovigerous and v-notched females). However, there is a possibility that male reproductive capacity may be insufficient at fulfilling the female reproductive potential due to sperm limitation (Levitan and Petersen 1995, Wedell et al. 2002). Sperm limitation may arise when the operational sex ratio is biased towards females and/or male availability is too low, so females fail at mating, or mate with a male having a depleted reserve of sperm from multiple mating. In many other crustacean species, sperm limitation has been identified as a limiting factor to egg production: spiny lobster, snow crab, and blue crabs (Hines et al. 2003, MacDiarmid and Butler 1999, Sainte-Marie et al. 2002, Wedell et al. 2002). For the American lobster, there are some evidences suggesting sperm limitation may occur in some populations because of those conservation measures. For instance, Gosselin et al. (2003) found that large females accumulated more ejaculate when mated with large males. They also found the occurrence of multiple paternity in female clutches which might indicate sperm is a limiting factor to egg production (Gosselin et al. 2005).

To ensure the long-term sustainability of the fishery, the concern about recruitment overfishing needs to be addressed. Fishing pressure is considered high in most LFAs but a potential downward shift in size-at-maturity, as suggested by fishermen observation, may increase egg production (Landers et al. 2001). This document provides an historical assessment of the lobster reproductive capacity for LFAs 34-38 with a focus on the Bay of Fundy. It provides a re-evaluation of size-at-maturity and mating success in Grand Manan for two time periods, 1978-79 and 2011. In addition, time-series of potential egg production based on sizes from at-sea samples and the new estimates of size-at-maturity are provided and compared with observed egg production (from ovigerous females in at-sea samples). This information is relevant in the context of the lobster precautionary approach as it may help determine what management measures would be the most effective at maintaining and/or improving reproductive potential so productivity and/or stock resilience is optimized.

2. METHODS

2.1. SIZES OF THE SMALLEST OVIGEROUS FEMALES

Lobster from commercial fishing trips were sampled in each of five regions from the early 1980s to 2011 for the Bay of Fundy and from the early 1990s in LFA 34. Only the late spring data was used (i.e. the last month of the fishing season) because of the possibility that females can lose their clutch (e.g. Campbell and Brattey 1986) and to be consistent with the egg production indices (see section 2.4.1). These data reside in the CRIS (Crustacean Research Information System) database (from DFO). Carapace length measured to the nearest mm, sex, and presence of eggs were recorded for every lobster. These data on ovigerous females were used for size distribution, sex ratio, and catch rates. It was determined the size of the smallest ovigerous females annually by calculating the 5th percentile.

2.2. SIZE-AT-ONSET-MATURITY

The SoM in North Head, Grand Manan was re-estimated, based on data from 1978-79 (Waddy, unpublished data) containing information on ovary stages. Females with ovary development greater than stage 4b (Waddy and Aiken 2005) were deemed to be mature according to criteria from Waddy and Aiken (2005). For the 2011 data, maturity was based on cement gland development and females with stage 2 and above glands were considered mature (Waddy and Aiken 2005). The maturity ogive was estimated by applying a Generalized Linear Model with a *logit* link using the statistical package R (Reeves et al. 2011). The estimated 1978-79 ogive was then compared to Campbell and Robinson's ogive (1983) and to a 2011 maturity ogive from North Head (Silva et al. unpublished document[1]) to determine if a shift in size-at-maturity has indeed occurred.

2.3. MATING SUCCESS

Mating status was determined by inserting a pair of forceps into the seminal receptacle of females to determine whether or not they were inseminated (Waddy and Aiken 1990). In the size-at-maturity and sea sampling trip conducted in 2011 in the Bay of Fundy, mating status of all females were recorded. Mating status was also recorded from the maturity work conducted in North Head in 1978-79 using the same method. Information on mating success in LFA 34 was not collected.

2.4. REPRODUCTIVE INDICES

A variety of indices on reproduction was used to determine broodstock health status based on data available from the at-sea sample program. These indices were developed for four reference areas in the Bay of Fundy (North Head, Seal Cove, Dipper Harbour, and Alma) and two grid areas in LFA 34 (Table 1). A time-series of egg production is provided but since the annual sampling coverage was generally modest over the years, their current broodstock health status was evaluated by comparing the average of an historical time period to a few recent years. Based on coverage, years of the historical and recent time periods are variable among

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[1] Unpublished working paper by A.M. Silva, J. Gaudette, M.J. Tremblay, and D.S. Pezzack, "Recent female lobster size at maturity estimates for Southwest Nova Scotia (LFA 34), and Bay of Fundy, New Brunswick (LFA 35, LFA 36, LFA 38): 2010 – 2011" (2013).

the reference areas. Table 1 provides the years to which the time periods correspond for the different regions.

Table 1. Reference regions for the development of reproductive indices including the type of fishery those regions are relying on and corresponding years for the historical and current time periods for each reference area. Numbers of years for each time period are between parentheses. Lobster Bay area 4A and 2A refer to grid groups in LFA 34 (Tremblay et al. 2013).

Reference Areas	LFA	Fishery relying on	Time Periods	
			Historical	Recent
Alma	35	Mature lobster[1]	1979-1985 (5)	2009-2011 (3)
Dipper Harbour	36	Recruitment[1]	1980-1987 (7)	2007-2011 (5)
North Head	38	Mature lobster[1]	1977-1983 (7)	2005-2011 (7)
Seal Cove	38	Recruitment[1]	1980-1986 (7)	2005-2011 (7)
Lobster Bay / 4A	34	Recruitment[2]	1991-1995 (5)	2004-2009 (4)
Lobster Bay / 2A	34	Recruitment[2]	1990-1994 (5)	2006-2012 (5)

[1] As described by Robichaud and Campbell (1991) and Lawton et al. (2001).

[2] Tremblay et al. (2013).

2.4.1. Egg Production and Size-class Contribution to the Productivity

Data used to determine egg production came from the at-sea sample program. Only sampling trips conducted in June (just prior to the fishing closure and the onset of spawning and egg hatching) were used to calculate the egg production indices in the Bay of Fundy. This was to ensure consistency across years on the abundance estimates and population size structure. For LFA 34, at-sea sampling data from May was used since the fishery closes May 31.

Two distinct egg production estimates were compared: potential and observed. The Potential Egg Production (PotEP) index was based on non-ovigerous females. It is an index predicting the egg production for the next year.

Potential Egg Production for a given year was calculated from:

$$PotEP = \sum_i Cn_i \cdot Pm_i \cdot F_i$$

where Pm_i is the proportion of female lobster mature in size-class *i* for a given year and location based on maturity ogive; F_i is the fecundity of size-class *i* based on fecundity-at-size from Campbell and Robinson (1983); and C_i is the catch rates of non-ovigerous female lobster for size-class *i* observed for a given year. PotEP is calculated in 1-mm size-class bins but summed in 5-mm bins afterward for clarity. Because the sizes of the smallest ovigerous females has gradually declined in recent decades, (see result section, Figure 1), it is assumed the shift at size-maturity occurred progressively. Therefore, annual maturity ogives were interpolated between the 1978-79 ogive from North Head (because it is the only historical ogive information available for LFAs 34-38) and 2011 ogive estimates from their respective regions (Silva et al. unpublished document[2]). For Dipper Harbour and Alma regions, the 2011 maturity ogives are

[2] Unpublished working paper by A.M. Silva, J. Gaudette, M.J. Tremblay, and D.S. Pezzack, “Recent female lobster size at maturity estimates for Southwest Nova Scotia (LFA 34), and Bay of Fundy, New Brunswick (LFA 35, LFA 36, LFA 38): 2010 – 2011” (2013).

more uncertain because of low sample sizes and the possible occurrence of false immature females (i.e. mature females with cement gland development stages <2; see section 4.1 for information) may have shifted upward the maturity estimates. Instead, the maturity ogive information from Grand Manan (i.e. combining information from Seal Cove and North Head) was used as a maturity ogive proxy for these two regions. Since temperature is the major factor of size-at-maturity (Little and Watson 2005, Waddy and Aiken 1995) and the Bay of Fundy has relatively homogenous temperature because of its massive tidal mixing, it is assumed that maturity ogive estimates across Bay of Fundy regions should be similar.

As to the Observed Egg Production (ObsEP) index, it is based on ovigerous female catch rates, size structure, and fecundity. Thus, it is an index of the current egg production for a given year.

Observed Egg Production was calculated from:

$$ObsEP = \sum_i Co_i \cdot F_i$$

where Co_i is the catch rates of ovigerous females of size-class *i* and F_i is the fecundity of size-class *i*. Both egg production indices are expressed in term of eggs per trap hauled. Size-classes are the same as PotEP.

2.4.2. Broodstock Catch Rates, Sex Ratio, and Ovigerous Proportion

Male and female catch rates was calculated by combining the total count of animals sampled divided by the number of traps hauled in a given year. Rates was calculated per 5-mm size-class and averaged for their respective time periods.

Proportion of males was calculated by 5-mm size-class for all the years relevant to the time period comparison. Sum of males in one size-class was divided by total amount of lobsters within the size-class for each year of the studied time periods. Annual proportions were then averaged for their respective time periods.

Proportion of ovigerous females (i.e. count of ovigerous female divided by count of non- and ovigerous females) was calculated the same way as the male proportion. An average was calculated for each reference time period.

3. RESULTS

3.1. SIZES OF THE SMALLEST OVIGEROUS FEMALES

The smallest ovigerous females in the at-sea samples (5^{th} percentile) showed a decreasing trend over the time period in some LFAs, suggesting a decrease in the size-at-onset of maturity (Figure 1). The trend is strongest in the south and west (i.e. LFAs 34-41). In the eastern-most LFA (27) there was no indication of a decline. The trends are mostly linear in LFA 34-41, which suggests the shift was gradual.

3.2. SIZE-AT-ONSET-MATURITY

The maturity ogive estimate from the 1978-79 dataset is substantially different from that in Campbell and Robinson (1983). Size-at-50%-maturity from 1978-79, estimated at 99.8 mm CL was almost 10 mm lower than Campbell and Robinson's estimate (Figure 2A).

The maturity ogive for 2011 was even lower than the ogive for 1978-79. The estimate of SoM50 for 2011 was 92.5 mm CL in North Head (Figure 2A). The slope of the 1978-79 maturity curve was steeper than the other two (Figure 2A).

3.3. MATING RATES

Coherent with the apparent downward shift in size-at-onset-maturity, mating occurrence at smaller sizes was higher in 2011 than in 1978-79 (Figure 2B). However, the slopes of the mating ogives between 1978-79 and 2011 were different, the historical ogive being steeper. The historical mating ogive predicts that at 100 mm CL, almost 100% of the non-ovigerous females are mated; the ogive for 2011 predicts that just about 80% were mated at that size.

The difference in mating rates between the two times periods is more obvious when comparing the maturity ogives with the mating ogives (Figure 3). In 1978-79, the ogives were mostly parallel with the maturity ogive shifted about 10 mm to the right to the mating ogive (Figure 3A). The size at which 50% are mated and 50% are mature in 1978-79 are substantially different (90.9 versus 99.5 mm CL respectively). In 2011, the ogives were closer to each other (size at 50% mated was 89.4 mm CL versus SoM50 of 92.5 mm CL; Figure 3B) and the mating ogive slope was more steep than the maturity ogive. Above 98 mm CL, the proportion of mature females was unexpectedly higher than the proportion of mated females. The differences between the two times periods suggests mating opportunities for females are lower now than in 1978-79. The mating rates among mature non-ovigerous females from North Head in 1978-79 was 100%; in 2011 the mating rates in Bay of Fundy areas varied from 88% at North Head, 86% at Seal Cove and just 63% in Southwest New Brunswick.

Mating success rates in relation to size for both immature and mature females show the existence of linear relationships for both immature and mature females within the size ranges of 70-110 mm in 2011 (Figure 4). This positive relationship was observed at multiple sites among the mature females (Figure 5). However, at similar sizes, mating rates inside the 70-110 mm size range were consistently greater for the mature individuals than the immature ones (Figure 4).

3.4. FEMALE CATCH RATES

As an index of abundance, females catch rates (Figure 6) were used. For most of the regions, catch rates of small females (< 100 mm CL) are substantially higher in recent time periods compared to historical time periods. In LFA 34 2A, this increase was less important and above 85 mm CL, recent catch rates were actually lower than earlier time periods. For medium size (100-120 mm CL), catch rates were substantially higher in North Head only. In Dipper Harbour and Seal Cove, catch rates for females in the size range of 100-110 mm CL were marginally higher, but catch rates were nonetheless low. Recent catch rates were lower than historically in Alma and in the grid groups 4A, 2A. For the large females (>120 mm CL), catch rates were lower in North Head. In Alma and Dipper Harbour, catch rates of large females were low in both periods but marginally higher in the historical time periods. Overall, there is a downward shift in the size structure of the catch suggesting that compared to the earlier periods, abundance of smaller females has increased and abundance of larger females has decreased.

3.5. EGG PRODUCTION TIME-SERIES

Egg production potential was variable from year to year. This was probably caused by within-season sampling variability and the low number of sampling trips per year, together with annual differences in catchability. Nevertheless, it is apparent that the reproductive potential in the Bay of Fundy has increased substantially over the time period, especially in the recent years (Figure 8). In LFA 34, the sea sampling time-series were shorter and the production potential has been also variable so no trend was apparent.

In contrast to the egg production potential, the observed egg production, based on the catch rates and size of ovigerous females, shows different trends with smaller amplitude (Figure 7). In

Alma and in LFA 34 2A, there were downward trends. In Dipper Harbour, North Head, and LFA 34 4A, trends were relatively stable. It is only in Seal Cove where an increase of egg production was apparent.

3.6. CONTRIBUTION OF DIFFERENT SIZES TO EGG PRODUCTION

Changes in the contribution of different sizes to potential egg production are most obvious when comparing the recent past (4-7 years) to an historical time period (i.e. the first 5-7 years of the egg production time-series). Total potential egg production was higher for the recent time period in the Bay of Fundy (Figure 8). The potential was 2 to 4.7 times higher for Alma and Dipper Harbour respectively. Most of the increase in the potential egg production came from the contribution of smaller females and compensated for lower production in the larger size categories (Figures 8, 9). In Dipper Harbour, the potential egg production also increased for the medium size category up to 115 mm CL but declined for the larger females (Figures 8, 9). In Grand Manan, the egg production potential increased by a factor of 1.6 in North Head and almost 8 in Seal Cove (Figures 8, 10). Most of the increase came from the 90-130 mm CL size-class in North Head (Figure 10). In Seal Cove, the increase came from smaller size-categories up to 110 mm CL (Figure 10).

In contrast to the Bay of Fundy, there was no increase in the total potential egg production for both grid groups of LFA 34 (Figure 8). In 4A, reproductive potential of the small females increased by a factor of 2.9 but the potential of the medium size category decreased by 68% so that overall, the total potential were similar between the historical period versus recent years (Figures 8, 11). In grid group 2A, there was decreased potential for the medium size category, which resulted in an overall decrease in the total egg production potential (Figures 8, 11).

The trends in observed egg production were substantially different from the trends in potential egg production. In Alma and North Head, observed egg production decreased by 58% and 42% respectively (Figures 12, 13). This reduction was caused by a decreased contribution from the medium and larger size categories in Alma (Figures 9-bottom left panel, 13), which is consistent with the drop of the egg production potential for those size categories (Figures 8, 9-upper left panel). However, the contribution of the smaller size category to observed egg production was far below its potential (Figure 14) so that overall, the total observed egg production was lower in recent years. In North Head, the reduction in the observed egg production came from (*i*) a lower contribution of the large females (Figures 10-bottom left panel, 13) and (*ii*) a smaller contribution than expected of the medium size category (Figure 14). For Dipper Harbour and Seal Cove, observed egg production increased but to a smaller extent than potential egg production (1.6-fold increase for Dipper Harbour versus 4.7 for the potential; 6-fold increase for Seal Cove versus 8-fold for the potential; Figure 12). Dipper Harbour had a decrease in the observed egg production from the larger females (>120 mm CL; Figures 9, 13) but, more importantly, the anticipated contribution of the smaller females did not materialise into observed eggs (Figure 14). In Seal Cove, the anticipated egg production from the smaller females was also considerably lower than their potential (Figures 8, 10, 13).

For LFA 34, the observed egg production index was more consistent with the potential egg production index (Figures 8, 13). Total observed egg production was similar between the two time periods in grid group 4A but smaller sizes contributed more eggs in the later period (Figure 11). In grid group 2A, the observed egg production decreased by 53% (Figure 13) due to a decline in the contribution from the medium size category (Figures 11, 13).

The contribution to egg production of smaller females (i.e. below SoM50) was below their potential in all studied regions with the exception of North Head where most females were larger than SoM50 (Figure 14). The under-contribution to egg production by smaller females is obvious in Alma, Dipper Harbour and Seal Cove and it seems to occur in grid group 4A and 2A as well, although to a lesser extent.

In North Head, the egg production potential versus size agrees well with the observed egg production for the historical time period (Figure 14-top panel). However, for the recent time period, gap between the potential and observed egg production indices is visible between 95-120 size-classes (Figure 14-lower panel).

3.7. PROPORTION OF OVIGEROUS FEMALES

The proportion of ovigerous females in the two time periods was inconsistently different in most of the studied regions (Figure 15). The proportion was generally higher in recent years in Seal Cove and LFA 34 2A for most of the size-classes. However, the proportion was only marginally higher in Seal Cove for the females smaller than 95 mm CL despite the shift in size-at-maturity. In LFA 34 4A, the ratio was higher for the size range of 95-115 mm CL and dropped thereafter. In Dipper Harbour and North Head, ratio of ovigerous females was considerably lower for larger size females in the recent years. In Alma, ratio was roughly similar, with a marginal increase for females smaller than 105 mm CL.

3.8. MALE AVAILABILITY

Male catch rates in recent years were higher than historically for the smallest size categories across all the regions (Figure 16). For the medium size category, recent catch rates were higher in Alma, Dipper Harbour, and North Head than the historical time period. Recent catch rates of the medium sized males were slightly lower in LFA 34 2A and 4A and similar in Seal Cove. For larger sizes (>140 mm CL) of males, catch rates were lower in North Head in recent years. In other regions, catch rates were low overall and recent rates were in general slightly lower if at all.

Male availability in relation to females (i.e. proportion of males) was higher for the recent time period in Alma, Dipper Harbour and the grid group 2A of LFA 34 (Figure 17). These results are surprising in Alma and Dipper Harbour as the recent mating success seems lower than historically, and the proportion of ovigerous females was not necessarily higher at in those regions (Figure 15). In North Head, male sex ratio was significantly lower for sizes below 100 mm CL largely because of the increase abundance of females. For the larger lobsters (>120 mm CL), male proportion were higher because of the lower abundance of females (Figure 6). In Seal Cove and grid group 4A, there was no clear trend although in Seal Cove, male ratio appears higher now than historically between the size rage of 120 and135 mm CL. In grid group 4A, recent ratios were higher between 105 and 115 mm CL.

4. DISCUSSION

4.1. DIVERGENCE BETWEEN THE EGG PRODUCTION INDICES

Landings are currently at their highest levels of all time and simultaneously, size-at-maturity has declined. This higher abundance combined with lower size-at-maturity should have increased egg production as indicated by the potential egg production index. Instead, the observed egg production, based on ovigerous female catch rates and fecundity-at-size, either did not increase to the extent predicted by the potential or did not increase at all. Below, four hypotheses are provided to explain the divergence between the potential and observed egg production indices.

The first hypothesis is that male mating choice influences the size-class contribution to egg production. In this study, it is observed that immature females mate regularly (Figure 4) and this has been observed by others in the past (e.g. Aiken and Waddy 1980a, Krouse 1973, Pugh et al. 2013). However, the implications of this on the lobster mating system has never been discussed in the literature (e.g. Factor 1995). Since vulnerability to predators is higher following the molt (Cobb 1995), a potential benefit for immature females to attempt mating may be to receive protection from a guarding male during the molting process (see Atema and Voigt 1995). Thus, mating behavior for females may occur at sizes below physiological maturity and the maturity and mating ogives illustrated this clearly (Figure 3). From the male perspective, however, mating with an immature female provide no fitness gain as there are costs associated with mating, such as establishing a mating shelter and guarding its mate (Atema and Voigt 1995) as well as producing sperm (Dewsbury 1982). However, Pugh et al. (2013) suggested recently that male may practice mating and potentially attract other females to their shelter. Nevertheless, the positive size-dependent relationship in mating success that was observed among both mature and immature females (Figure 4) suggests that:

1. the capacity of male lobsters to assess female maturity status at a given size is limited (but not totally lacking as mature females are generally mated at an higher rates compared to immature counterpart of similar sizes), and
2. males select mating partner based on sizes to reduce the risk of mating with immature individuals.

This hypothesis is in contrast to the dominant role attributed to females in the mate selection process (reviewed by Atema and Voigt 1995) and challenges the role of a sexual pheromone in mating activity (Bushmann and Atema 1997). It also contradicts the long time belief that males are capable of distinguishing female ovary stages and maturity status (Waddy and Aiken 1990, Pugh et al. 2013). An important implication of this male mating choice on egg production is that the contribution of small mature females might be disproportionately lower than their potential (Figure 14). In LFA 34, the gap between the potential and observed egg production indices was not as important as in the Bay of Fundy. This could be caused by the skewed size structure toward small mature lobsters in LFA 34, which may relax the male mating choice criteria (i.e. a size-structure dependent effect on male mating choice (Kokko and Rankin 2006)).

A second non-exclusive hypothesis to explain the divergence between the potential and observed egg production indices is a shortage of males causing mating failure. In North Head in particular, there were signs indicating that a shortage of males was limiting recent egg production. The first indication was the gaps between the potential and observed egg production curves in the size range of 100-120 mm CL for the recent time period (Figure 14). The second sign was the proportion of ovigerous females, considerably lower for the past years in comparison to the early 1980s (Figure 15; also note the similar pattern in Dipper Harbour). Third, the shape and position of the mating ogive in relation to the mating ogive for North Head in 2011 suggests that male availability for mating is lower than in 1978-79 (Figure 3). Fourth, mating success among the mature female of larger size was also lower in 2011 (around 88% in 2011) than in 1978-79 when the mating rates for large females was at 100%. The possibility of a shortage of males limiting egg production was also mentioned in a different study looking at multiple paternity rates (Gosselin et al. 2005). The cause of the sperm limitation is unclear and may be due to a shortage of large males in some of mating grounds.

The shortage of male availability hypothesis does not fit the other areas where the proportion of males and their abundance was higher than in the past, at least for the smaller and medium size categories (Figure 16). In these areas, a new hypothesis is proposed that egg production may be limited by the number of shelters for mating. It remains unclear whether lobsters depend on a shelter for mating in the wild but, if so, it is possible that under the current high abundance of lobsters, shelter for mating are limited and mating grounds are saturated. In crayfish, it has been observed that presence of conspecifics reduces mating opportunities (Galeotti et al. 2009) and it is possible that at high abundance, increased levels of competitive interaction among lobsters interfere with mating activity. It is also conceivable that lobster mate choice is density dependent and that at high abundance, male preference for larger females is strengthened (Debuse et al. 2003, Kokko and Rankin 2006).

As a last hypothesis to explain the difference between potential and observed egg production, it is possible that the distribution of ovigerous females has changed over time and that, with the spatially limited sampling, the reference areas did not capture this change in distribution. For instance, Seal Cove used to be a recruitment ground with low abundance of ovigerous females but this seems to have changed overtime (Figure 7). Recent sampling effort for the Lobster Node Project in Victoria Beach area have also shown that abundance of ovigerous females were high (Gaudette, unpublished data).

4.2. MATING FAILURE AND MATURITY OGIVE ESTIMATES

Because size-at-maturity is commonly estimated from cement gland development stages, mating failure could corrupt maturity ogive estimates (Gaudette, personal observation) and, therefore, affect potential egg production estimates. It is believed that uninseminated lobster do not normally resorb their ovaries but instead spawn unfertilized eggs (Aiken and Waddy 1980a, Talbot and Helluy 1995) despite the fact that lobsters have reabsorption ability and resorbed ovary recovers a year faster than spent ovary (Aiken and Waddy 1980b). If this holds true, ovigerous females with unfertilized eggs will drop them within few weeks (Aiken and Waddy 1980a) and by the following spring, these miscarried females would have undeveloped or residual cement glands. Thus, those “false immature females” would be categorized as immature based on their gland development but would indeed be mature. In addition to mating failure, false immature females may exist when females are in the alternative-year of their spawning cycle (which correspond to a year when females do not molt or neither produce a clutch (Waddy and Aiken 1986)), when female’s clutch hatched prior the sampling for maturity work (Waddy and Aiken 2005), or when the entire clutch is lost due to abrasion and/or egg parasite (Campbell and Brattey 1986). While the effect of small fall immature individuals in the maturity ogive estimate are not known, the presence of large false immature individuals in the sample may overestimate the SoM50 estimate, reduce the slope of the maturity ogives, and overestimate the proportion of small mature females (Gaudette, unpublished data). The smoother slope of the maturity ogives from 2011 and Campbell and Robinson (Figure 2) could be an effect of the presence of large false immature lobsters in the data. Furthermore, the presence of large immature individuals (>110 mm CL) in Figure 4 are likely “false immature” as at that size, the maturity ogive predict that most individual should be mature. For future maturity studies, consequently it is recommended using both, the cement gland methodology with the ovary staging to obtain an accurate estimation of size-at-maturity. Otherwise, mating ogive could be included as a scale factor to estimate the egg production potential.

4.3. INCREASED RELIANCE ON A SMALLER BROODSTOCK

Our study has shown that mating failure among small females is common. Relying on egg production from females smaller than SoM50 may therefore not be productive because of their lower mating success and represent an increasing risk for recruitment failure. Because of changes in the size structure, the relative observed contribution of small ovigerous females has increased significantly over the recent time period. For instance, it increased from 3.4% to 39% and 15% to 57% between the two time periods in group grids 4A and 2A respectively. The increase was also substantial in Alma, from 2% for the historical time period to 33% in recent years.

In addition, previous work conducted by Gosselin et al. (2003) has shown that reproductive potential of smaller males is limited. Their study showed that females inseminated by small males have smaller spermatophores, which may limit the number of eggs fertilized and thus reduce clutch size. Further, females prefer mating with larger males and multiple matings by these males may result in reduced sperm per mating event. In the Bay of Fundy, there are some signs that sperm limitation may occur (Gosselin et al. 2005, this study) and, therefore, consideration should be given to increase the protection of larger males in the future to maintain and/or increase egg production. However, whether sperm limitation is occurring remains uncertain at this stage and further research should be conducted to assess this potential issue.

While the evidence of spawner-to-recruit relationship has not been clearly shown so far for lobster (Steneck 2006, Wahle 2003), there is a general consensus in fishery science that relying on a wide size range of a broodstock is more precautious and should increase resilience potential to fishing pressure and environmental fluctuations (DFO 2009, Steneck 2006). Therefore, as a precaution it is recommended that additional measures be taken to protect large individuals. For instance, a first step may be to increase the practice of v-notching and changing the regulation so v-notched females stay protected longer. In Maine, regulation prohibit landings of v-notched females as long as a v-notch shows (Acheson and Gardner 2011). In Canada, regulation stipulates a v-notched female is protected until the reappearance of setal hairs in the scar. Because of the wide gap between current MLS and SoM50, increasing the MLS will not have a significant effect on increasing egg production unless the increase is substantial. However, such a large increase in MLS may have negative consequences on growth rates and fecundity from density-dependent processes (e.g. Grabowski et al. 2009) and additional research is recommended prior moving ahead with such an increase.

4.4. UNCERTAINTIES

1. Fecundity-size relationships need to be updated. This relationship can be impacted by sperm limitation if it is occurring and by density-dependent processes (current abundance are at all-time record high). If fecundity at size has changed from these processes, then the estimate of observed egg production may be overestimated for the recent years.
2. Mating failure impacts maturity ogive estimates by causing the presence of false immatures. This means that the divergence between the two egg production indices may be even more important. In LFA 34, data on mating success was not available.
3. This analysis has not considered the potential of consecutive spawning strategy for large females (Waddy and Aiken 1986). Again here, this would exacerbate the observed difference in contribution of large females to egg production between historical and current stocks because large lobster abundance, as indicated by lower catch rates, have declined.
4. Number of sea sampling trips has been generally low for most years and most regions and therefore, the time-series trends have uncertainty. For instance, peak of egg production potential usually happens during the same years of a peak in the observed egg production. This highlights intra-annual sampling variability as well as potential annual differences in catchability. Increased sampling intensity levels would have been preferable. However, by averaging trends among different time periods of 5-7 years, it is believed it alleviated the issue of this low sampling intensity, and therefore, the historical trend described here should described the stock trend.
5. The observed egg production indices are scaled by a CPUE-based abundance index. CPUE is affected by total fishing effort and by a host of catchability related factors. Because

of known higher fishing effort in LFA 34, the egg production indexes in LFA 34 cannot be reliably compared with those for the Bay of Fundy.

6. Although it would have been preferable, there was no historical and recent size-at-maturity information available for all the regions. Therefore, it is possible that the local egg production estimated would have been slightly different if there is a regional different in size-at-maturity. However, it is believed size-at-maturity should be relatively homogenous for LFAs 34-38. Temperature is the dominant regulator of size-at-maturity (Waddy and Aiken 1995) and because of the high mixing environment of the Bay of Fundy, it is assumed water temperature to be similar throughout the studied regions.

4.5. FUTURE NEEDS

The indices presented here combine multiple aspects of lobster biology. They integrate key information on abundance, mating success, fecundity, size structure, and size-at-maturity. These indicators would be extremely useful into the precautionary approach and some are independent to fishery performance (e.g. mating success) which can be easily obtained during sea and port sampling. Size structure and abundance is potentially dependent on fishing strategy. One of the key concepts of the precautionary approach is to ensure high level of egg production. The indices used here could provide crucial information to ensure future harvest control rules are adequate at increasing egg production.

The indices provided here have been possible because of the at-sea sampling data. The sampling program in the Bay of Fundy is currently not funded by DFO and maintaining these indices will not be possible without new sources of funds. A similar analysis could be done with trawl survey data with the limitation that the sampling is conducted in July when females started hatching and spawning, which would complicate the analysis. Another limitation of relying on groundfish trawl survey is that its sampling areas focus on deep water and a substantial fraction of the broodstock would be inshore for their seasonal migration (Campbell 1986). Enhancing existing surveys or developing new inshore surveys could provide the data necessary for these reproductive indices.

Port sampling could provide some information reproductive indices but no comparison between potential and observed egg production indices would be possible because of the prohibition of landing ovigerous females.

5. REFERENCES

Acheson, J., and Gardner, R. 2011. The evolution of the Maine lobster v-notch practice: cooperation in a prisoner's dilemma game. Ecol. Soc. 16(1): 41

Aiken, D.E., and Waddy, S.L. 1980a. Maturity and reproduction in the American lobster. Can. Tech. Rep. Fish. Aquat. Sci. 932: 60-71.

Aiken, D.E., and Waddy, S.L. 1980b. Reproductive biology. *In* The biology and management of lobsters: Physiology and behavior. *Edited by* J.S. Cobb and B.F. Phillips. Academic Press, New York. pp. 215-276.

Anthony, V.C., and Caddy, J.F. 1980. Proceeding of the Canada-U.S. workshop on status of assessment science for N.W. Atlantic lobster (*Homarus americanus*) stocks. Can. Tech. Rep. Fish. Aquat. Sci. 932: vii + 186 p.

Atema, J., and Voigt, R. 1995. Behavior and sensory biology. *In* Biology of the lobster *Homarus americanus*. *Edited by* J.R. Factor. Academic Press. pp. 313-348.

Bushmann, P.J., and Atema, J. 1997. Shelter sharing and chemical courtship signals in the lobster *Homarus americanus*. Can. J. Fish. Aquat. Sci. 54(3): 647-654.

Campbell, A. 1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. Can. J. Fish. Aquat. Sci. 43(11): 2197-2205.

Campbell, A., and Brattey, J. 1986. Egg loss from the American lobster, *Homarus americanus*, in relation to nemertean, *Pseudocarcinonemertes homari*, infestation. Can. J. Fish. Aquat. Sci. 43(4): 772-780.

Campbell, A., and Robinson, D.G. 1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian Maritimes. Can. J. Fish. Aquat. Sci. 40(11): 1958-1967.

Cobb, J.S. 1995. Interface of ecology, behavior, and fisheries. *In* Biology of the lobster *Homarus americanus*. *Edited by* J.R. Factor. Academic Press, San Diego. pp. 139-151.

Comeau, M. 2003. Workshop on lobster (*Homarus americanus* and *H. gammarus*) reference points for fishery management held in Tracadie-Sheila, New Brunswick, 8-10 September 2003: Abstracts and proceedings. Can. Tech. Rep. Fish. Aquat. Sci. 2506: vii + 39 p.

Cowan, D.F. 2012. Maine Voices: Lobster stocks will plummet if safeguards aren't put in place soon. Portland Press Herald, Portland, Maine. Available online from: http://www.pressherald.com/opinion/lobster-stocks-will-plummet-if-safeguards-arent-put-in-place-soon_2012-06-25.html (last accessed April 1, 2014).

Debuse, V.J., Addison, J.T., and Reynolds, J.D. 2003. Effects of breeding site density on competition and sexual selection in the European lobster. Behav. Ecol. 14(3): 396-402.

Dewsbury, D.A. 1982. Ejaculate cost and male choice. Am. Nat. 119(5): 601-610.

DFO. 2009. Biological basis for the protection of large lobsters in lobster fishing areas 33 to 38. DFO Can. Sci. Advis. Sec. Sci. Resp. 2008/017.

Factor, J.R. 1995. Biology of the Lobster: *Homarus americanus*. Academic Press, San Diego. 528 p.

Fogarty, M.J. 1995. Populations, fisheries, and management. *In* Biology of the lobster *Homarus americanus*. *Edited by* J.R. Factor. Academic Press, San Diego. pp. 111-137.

Fogarty, M.J., and Idoine, J.S. 1988. Application of a yield and egg production model based on size to an offshore American lobster population. Trans. Am. Fish. Soc. 117(4): 350-362.

FRCC. 2007. Sustainability framework for Atlantic lobster 2007: Report to the Minister of Fisheries and Oceans, Ottawa, Ontario.

Galeotti, P., Rubolini, D., Pupin, F., Sacchi, R., Altobelli, E., Nardi, P.A., and Fasola, M. 2009. Presence of rivals reduces mating probability but does not affect ejaculate size in the freshwater crayfish *Austropotamobius italicus*. Behaviour 146: 45-68.

Gosselin, T., Sainte-Marie, B., and Bernatchez, L. 2003. Patterns of sexual cohabitation and female ejaculate storage in the American lobster (*Homarus americanus*). Behav. Ecol. Sociobiol. 55(2): 151-160.

Gosselin, T., Sainte-Marie, B., and Bernatchez, L. 2005. Geographic variation of multiple paternity in the American lobster, *Homarus americanus*. Mol. Ecol. 14(5): 1517-1525.

Grabowski, J.H., Gaudette, J., Clesceri, E.J., and Yund, P.O. 2009. The role of food limitation in lobster population dynamics in coastal Maine, United States, and New Brunswick, Canada. N. Z. J. Mar. Freshwat. Res. 43(1): 185-193.

Hines, A.H., Jivoff, P.R., Bushmann, P.J., van Montfrans, J., Reed, S.A., Wolcott, D.L., and Wolcott, T.G. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. Bull. Mar. Sci. 72(2): 287-310.

Jamieson, G.S. 1993. Marine invertebrate conservation: Evaluation of fisheries over-exploitation concerns. Am. Zool. 33(6): 551-567.

Kokko, H., and Rankin, D.J. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. Philosophical Transactions of the Royal Society B-Biological Sciences 361(1466): 319-334.

Krouse, J.S. 1973. Maturity, sex ratio, and size composition of the natural population of American lobster, *Homarus americanus*, along the Maine coast. Fish. Bull. 71(1): 165-173.

Landers, D.F., Keser, M., and Saila, S.B. 2001. Changes in female lobster (*Homarus americanus*) size at maturity and implications for the lobster resource in Long Island Sound, Connecticut. Mar. Freshwat. Res. 52(8): 1283-1290.

Lawton, P., Robichaud, D.A., Strong, M.B., Pezzack, D.S., and Frail, C.F. 2001. Spatial and temporal trends in the American lobster, *Homarus americanus*, Fishery in the Bay of Fundy (Lobster Fishing Areas 35, 36, and 38). DFO Can. Sci. Advis. Sec. Res. Doc. 2001/094. 70 p.

Levitan, D.R., and Petersen, C. 1995. Sperm limitation in the sea. Trends Ecol. Evol. 10(6): 228-231.

Little, S.A., and Watson, W.H. 2005. Differences in the size at maturity of female American lobsters, *Homarus americanus*, captured throughout the range of the offshore fishery. J. Crust. Biol. 25(4): 585-592.

MacDiarmid, A.B., and Butler, M.J. 1999. Sperm economy and limitation in spiny lobsters. Behav. Ecol. Sociobiol. 46(1): 14-24.

Pugh, T.L., Goldstein, J.S., Lavalli, K.L., Clancy, M., and Watson Iii, W.H. 2013. At-sea determination of female American lobster (*Homarus americanus*) mating activity: Patterns vs. expectations. Fish. Res. 147(0): 327-337.

Reeves, A., Choi, J., and Tremblay, J. 2011. Lobster size at maturity estimates in Eastern Cape Breton, Nova Scotia. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/079: vi + 18 p.

Robichaud, D.A., and Campbell, A. 1991. Annual and seasonal size-frequency changes of trap-caught lobsters (*Homarus americanus*) in the Bay of Fundy. J. Northwest Atl. Fish. Sci. 11: 29-37.

Sainte-Marie, B., Sevigny, J.M., and Carpentier, M. 2002. Interannual variability of sperm reserves and fecundity of primiparous females of the snow crab (*Chionoecetes opilio*) in relation to sex ratio. Can. J. Fish. Aquat. Sci. 59(12): 1932-1940.

Steneck, R.S. 2006. Is the american lobster, *Homarus americanus*, overfished? A review of overfishing with an ecologically based perspective. Bull. Mar. Sci. 78(3): 607-632.

Talbot, P., and Helluy, S. 1995. Reproduction and embryonic development. *In* Biology of the lobster *Homarus americanus*. *Edited by* J.R. Factor. Academic Press, San Diego. pp. 177-215.

Tremblay, M.J., Pezzack, D.S., Gaudette, J., Denton, C., Cassista-Da Ros, M., and Allard, J. 2013. Assessment of lobster off southwest Nova Scotia and in the Bay of Fundy (Lobster Fishing Areas 34-38). DFO Can. Sci. Advis. Sec. Res. Doc. 2013/078: 145 p.

Waddy, S.L., and Aiken, D.E. 1986. Multiple fertilization and consecutive spawning in large American lobsters, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43(11): 2291-2294.

Waddy, S.L., and Aiken, D.E. 1990. Intermolt insemination, an alternative mating strategy for the American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 47(12): 2402-2406.

Waddy, S.L., and Aiken, D.E. 1995. Temperature regulation of reproduction in female American lobsters (*Homarus americanus*). ICES Mar. Sci. Symp. 199: 54-60.

Waddy, S.L., and Aiken, D.E. 2005. Impact of invalid biological assumptions and misapplication of maturity criteria on size-at-maturity estimates for American lobster. Trans. Am. Fish. Soc. 134(5): 1075-1090.

Wahle, R.A. 2003. Revealing stock-recruitment relationships in lobsters and crabs: is experimental ecology the key? Fish. Res. 65(1-3): 3-32.

Wedell, N., Gage, M.J.G., and Parker, G.A. 2002. Sperm competition, male prudence and sperm-limited females. Trends Ecol. Evol. 17(7): 313-320.

FIGURES

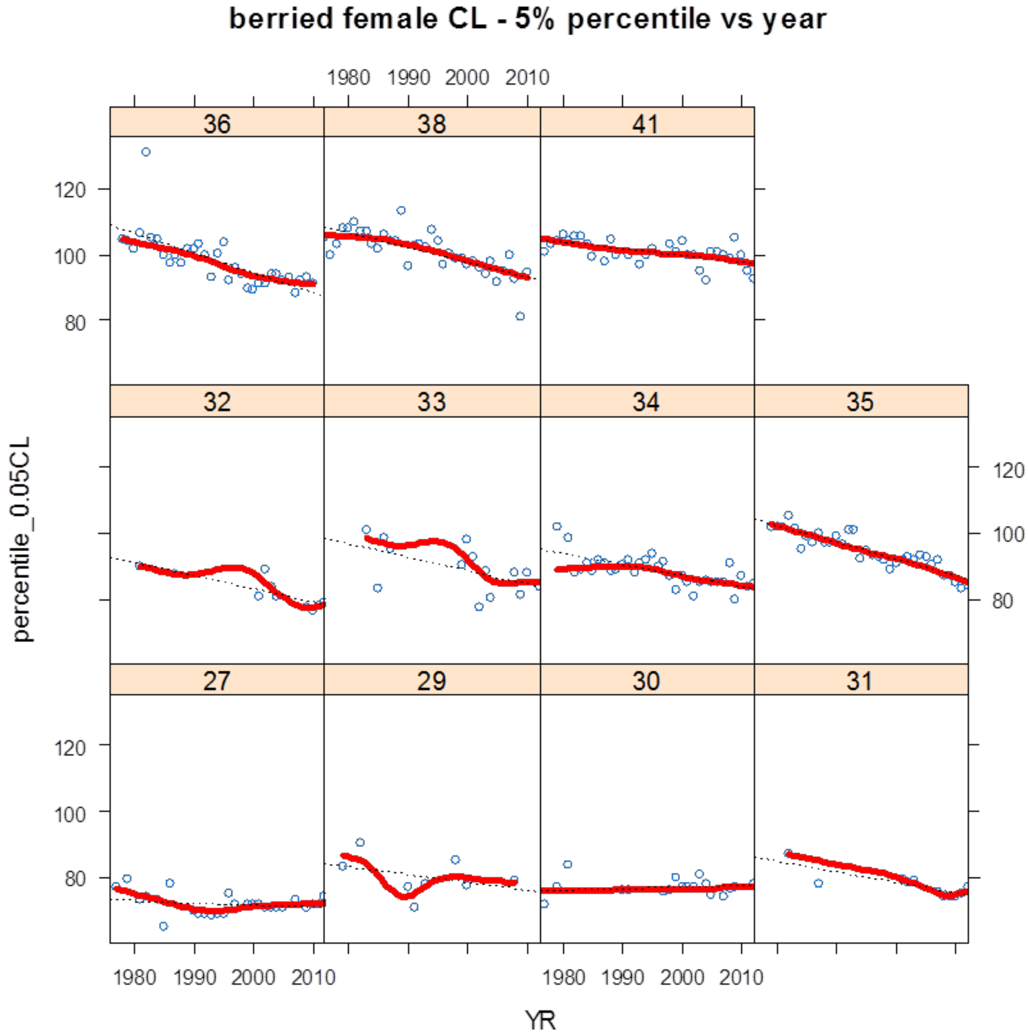

Figure 1. Size of smallest ovigerous females (5th percentile) by year (1975-2011) and LFA measured during the at-sea samples for the whole maritime region. Size corresponds to lobster carapace length (mm). Dashed line is linear fit, red line is LOESS fit.

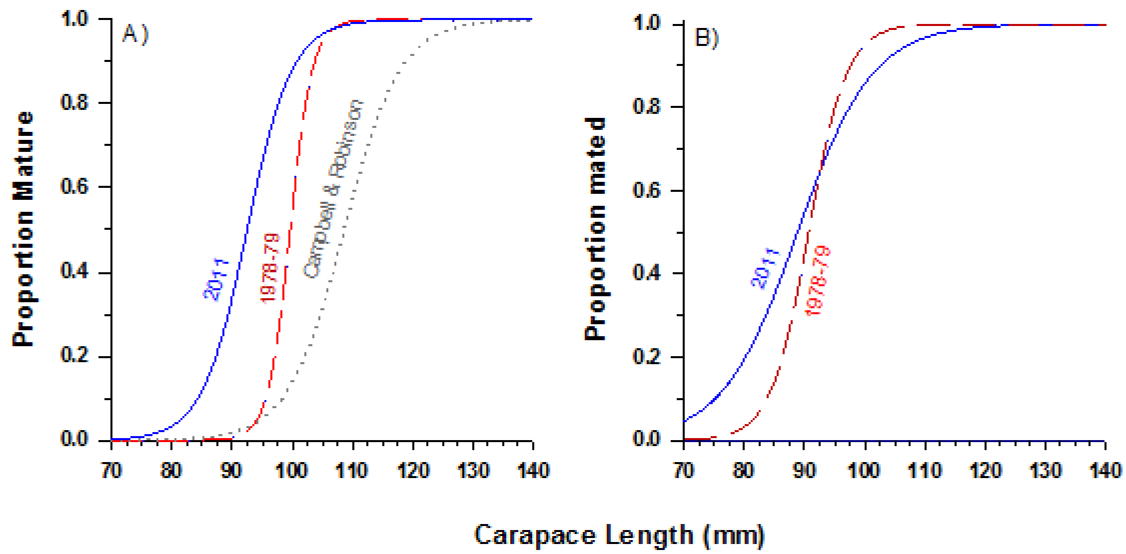

Figure 2. A) Maturity ogives in North Head, Grand Manan, in 1978-79 (red long dashes) and 2011 (blue line). Ogive from Campbell and Robinson (1983) is shown as reference (grey line). B) Mating ogives in North Head based on the presence of spermatophore in the seminal receptacle for 1978-79 (red long-dashes line) and 2011 (blue line).

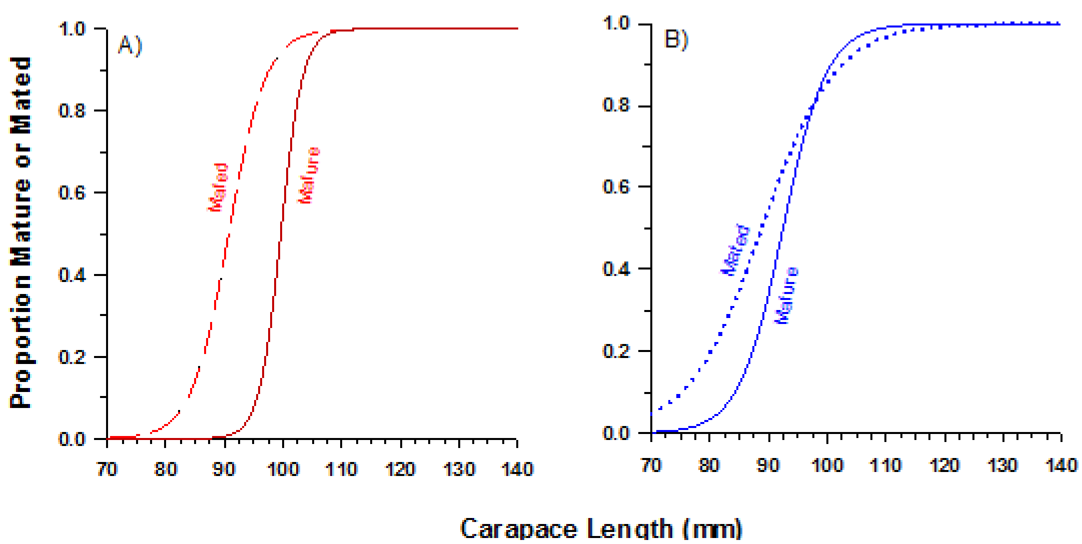

Figure 3. Comparison of maturity and mating ogives from North Head, Grand Manan in 1978-79 (left panel; A), and in 2011 (right panel, B).

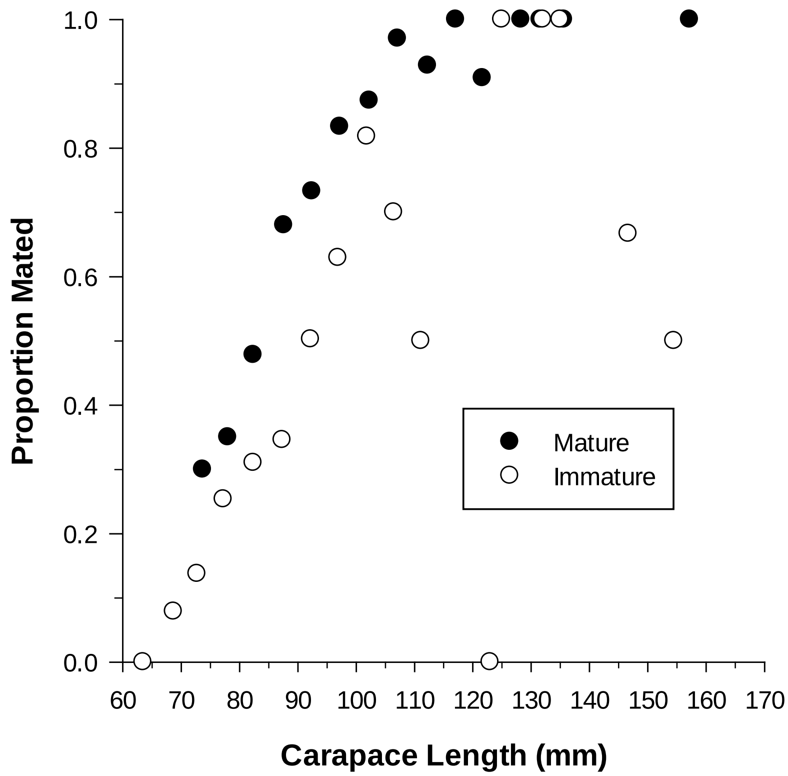

Figure 4. Proportion of mated females for different 5-mm size-classes among mature non-ovigerous females (black circles) and immature females (open circles) for the whole Bay of Fundy in 2011.

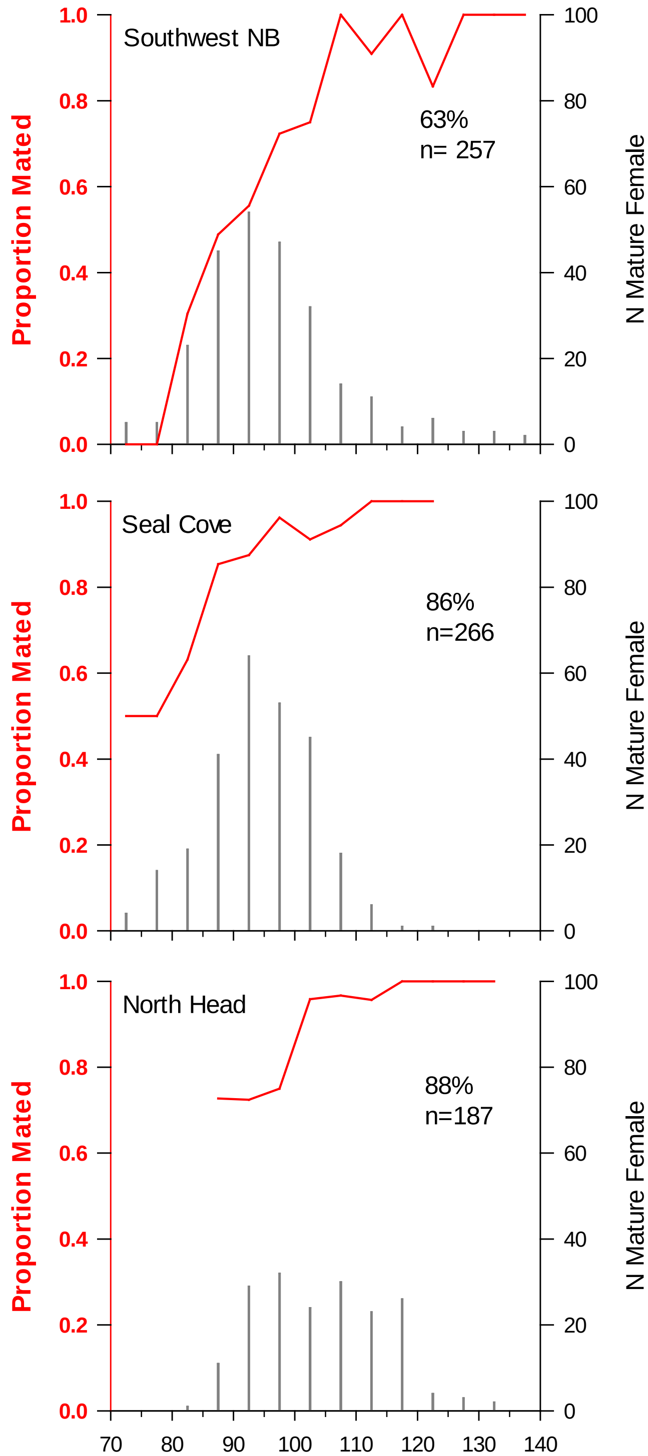

Figure 5. Proportion of mature females by 5-mm size-classes that mated in three regions of the Bay of Fundy. Thin bars correspond to the sample sizes for each size-classes (right axis). Percentage values correspond to the overall mating rates among the mature females in each region.

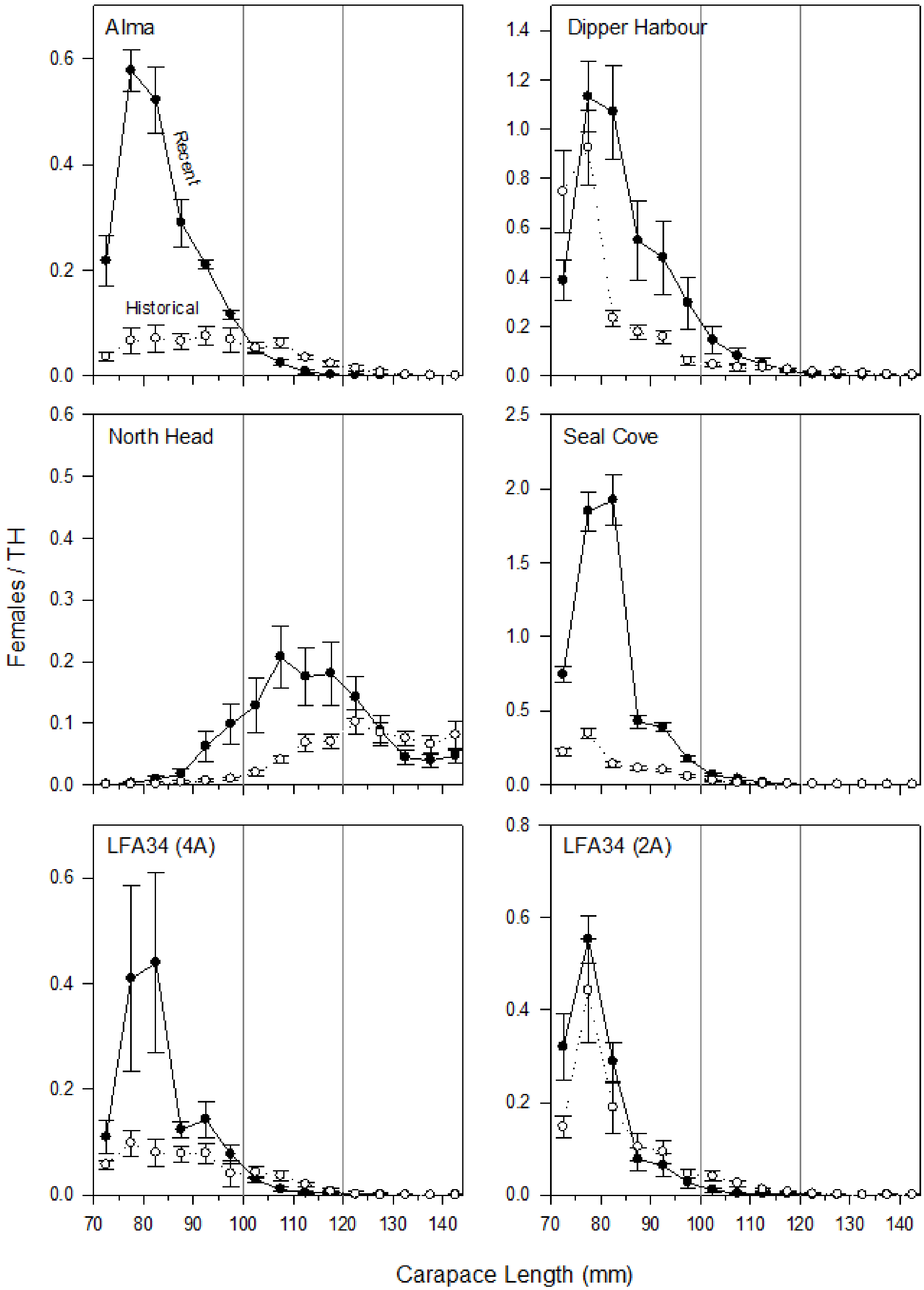

Figure 6. Female catch rates (mean ±SE) per 5-mm size-class for an historical time period (open circles) and recent years (black circles) for different regions in the Bay of Fundy and LFA 34. Vertical lines at 100 and 120 mm CL are to separate small, medium and large size categories.

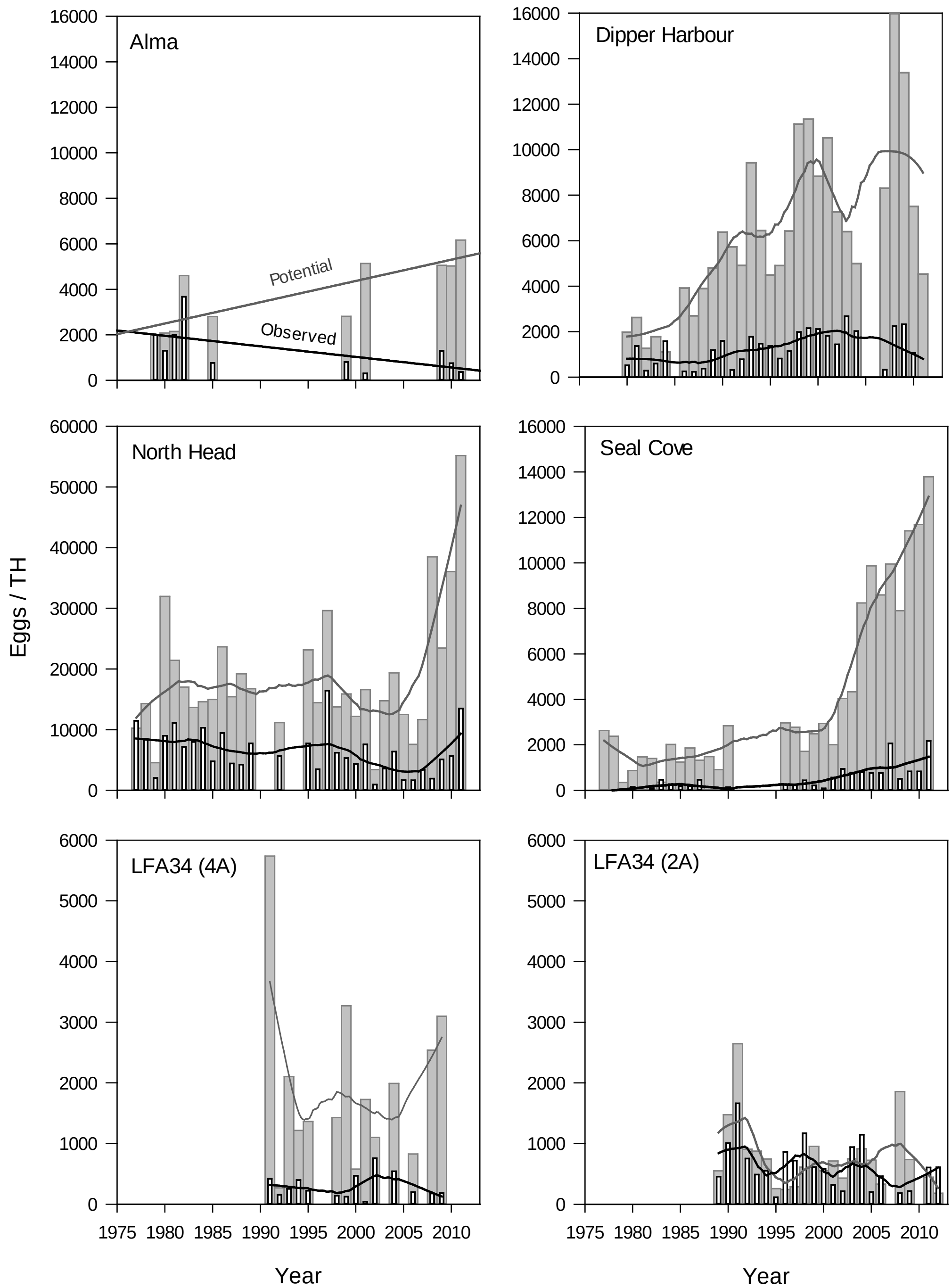

Figure 7. Time-series for the potential (grey bars and lines) and observed egg production (open bars and black lines). Lines are LOESS fit with a smoothing parameter value of 0.33 (0.5 in grid group 4A) except for Alma where it is a linear trend.

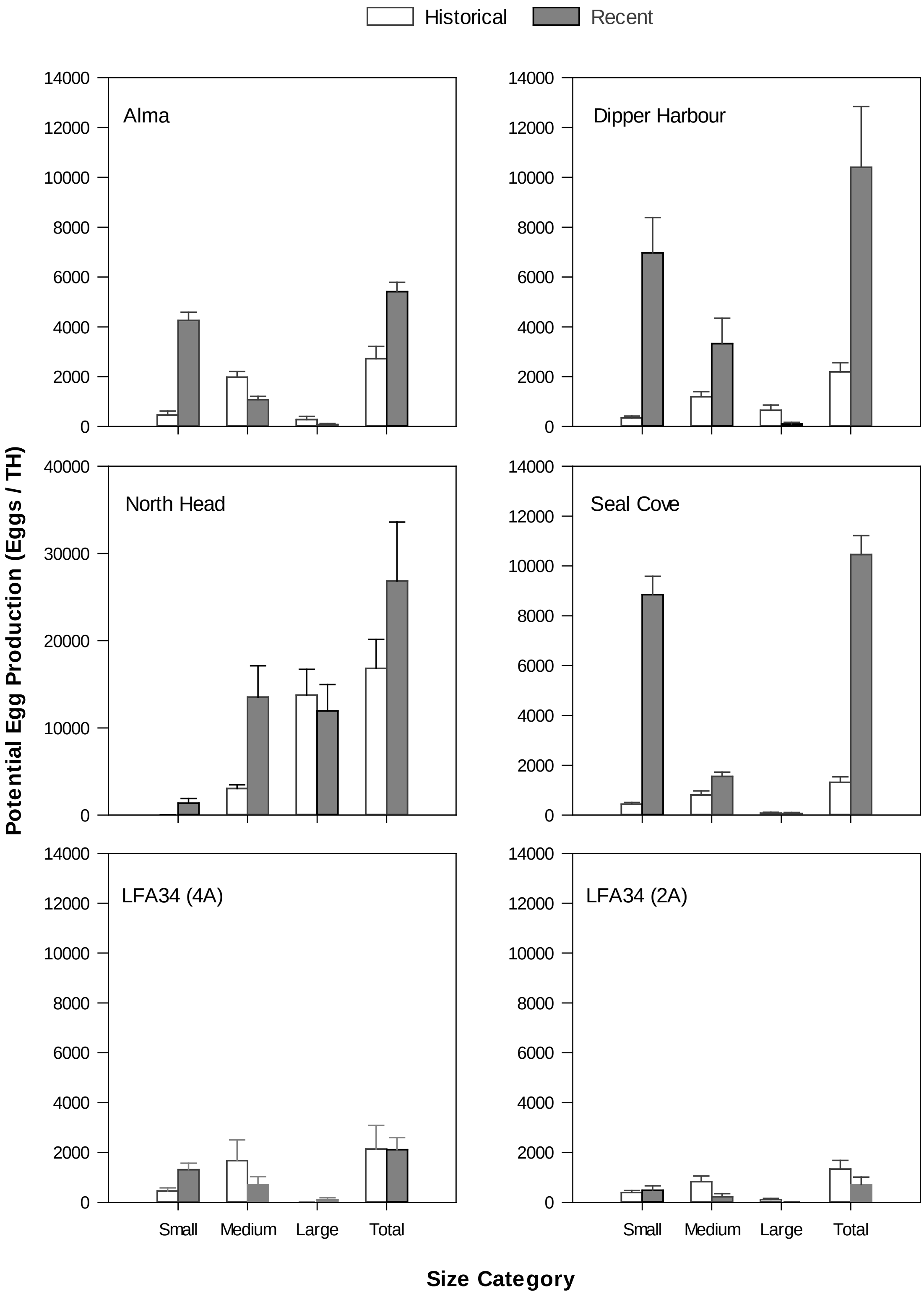

Figure 8. Egg production potential (mean ± SE) for four size categories (Small: <100; Medium: [100-120], Large: ≥120 mm CL, and Total) during two time periods (Historical and Recent) in different regions of the Bay of Fundy and grid groups of LFA 34. Note the different scale for North Head.

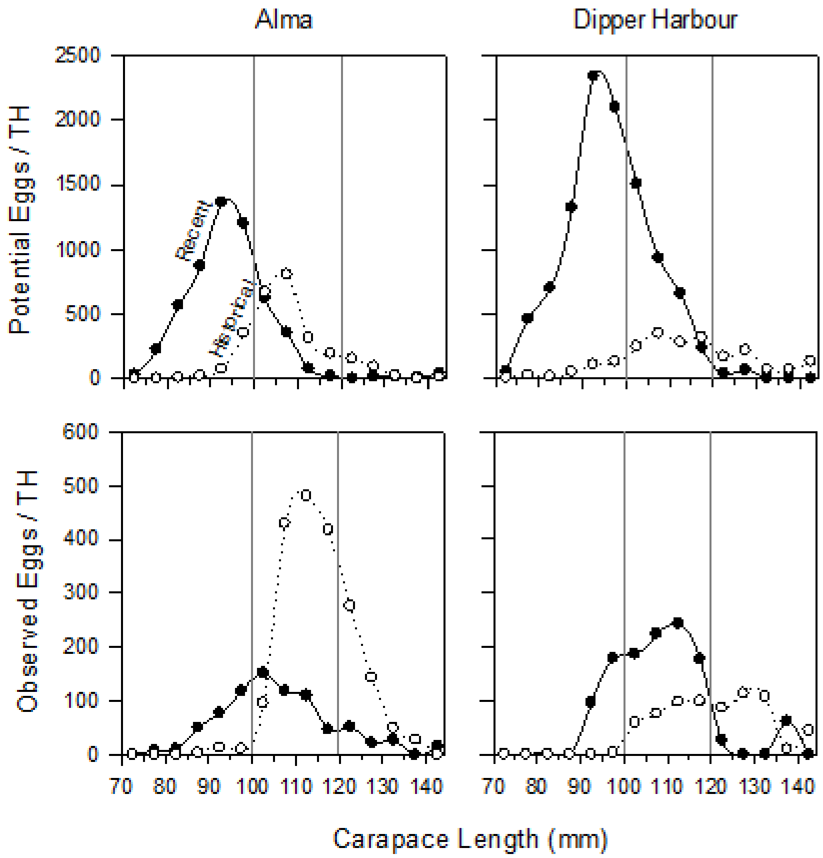

Figure 9. Historical and recent egg production estimated for Alma (left panels) and Dipper Harbour (right panels). Top panels are potential egg production and bottom panels are the observed egg production. Vertical lines at 100 and 120 mm CL separate small, medium, and large size categories.

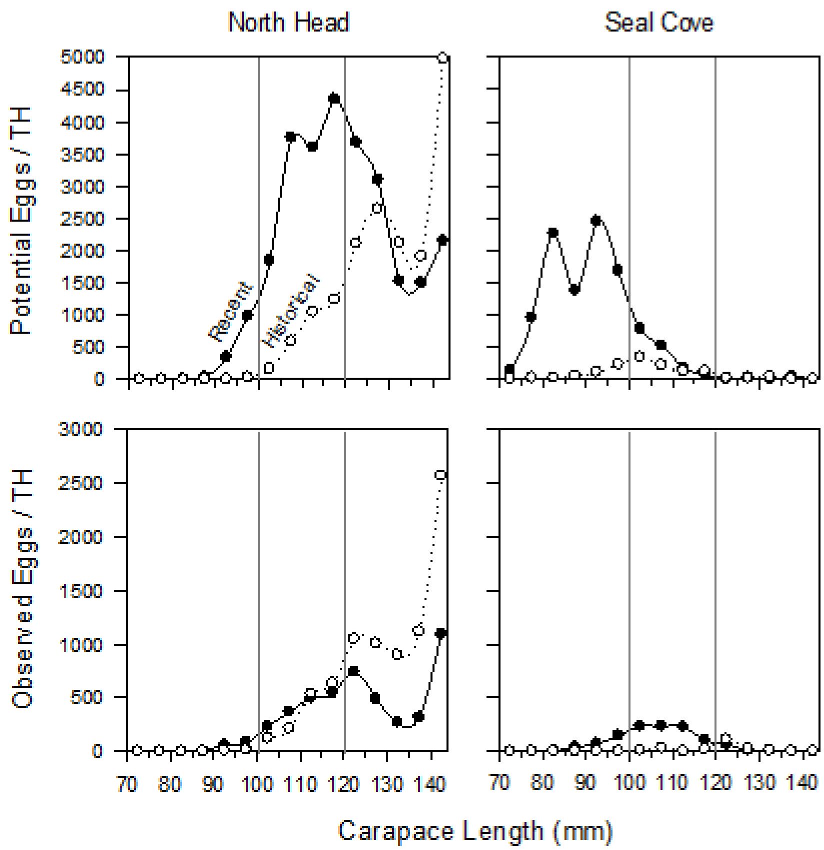

Figure 10. Historical and recent egg production estimated for North Head (left panels) and Seal Cove (right panels). Top panels are potential egg production bottom panels are the observed egg production. Vertical lines at 100 and 120 mm CL separate small, medium, and large size categories.

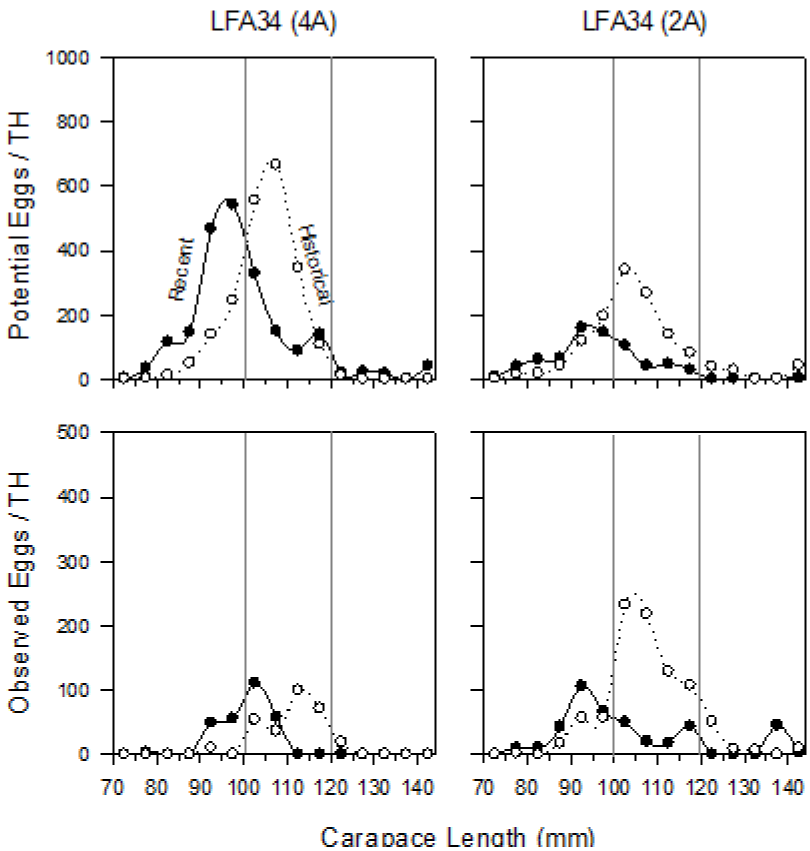

Figure 11. Historical and recent egg production estimated for LFA 34 in grid groups 4A (left panels) and 2A (right panels). Top panels are potential egg production and bottom panels are the observed egg production. Vertical lines at 100 and 120 mm CL separate small, medium, and large size categories.

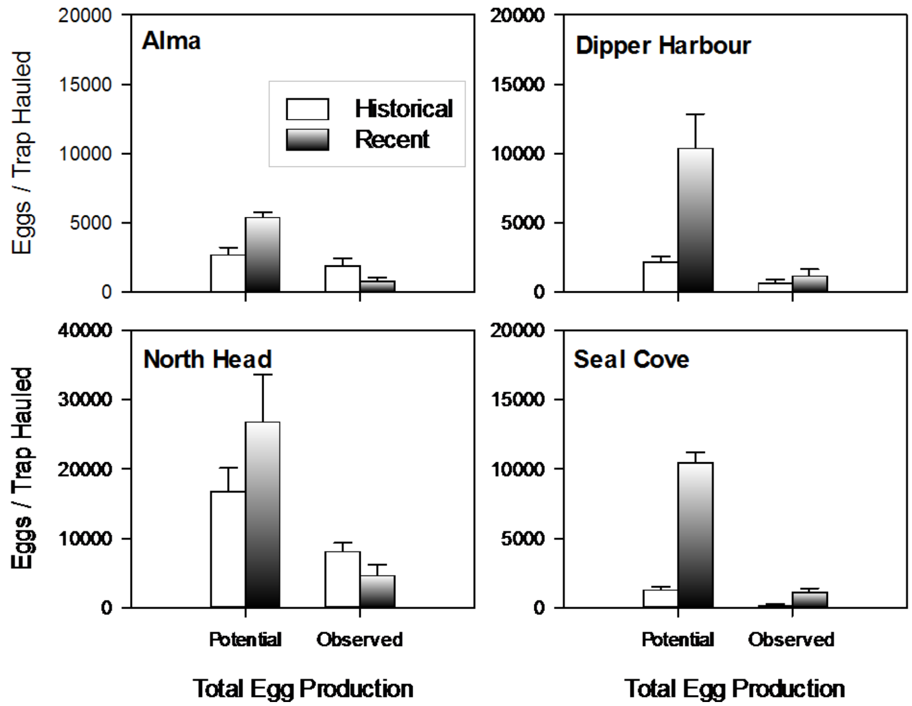

Figure 12. Lobster egg production for four locations within the Bay of Fundy for historical (1980s) and recent time (past 5-7 years) periods. Potential egg production (based on non-ovigerous females) and observed egg production (based on ovigerous females) are shown.

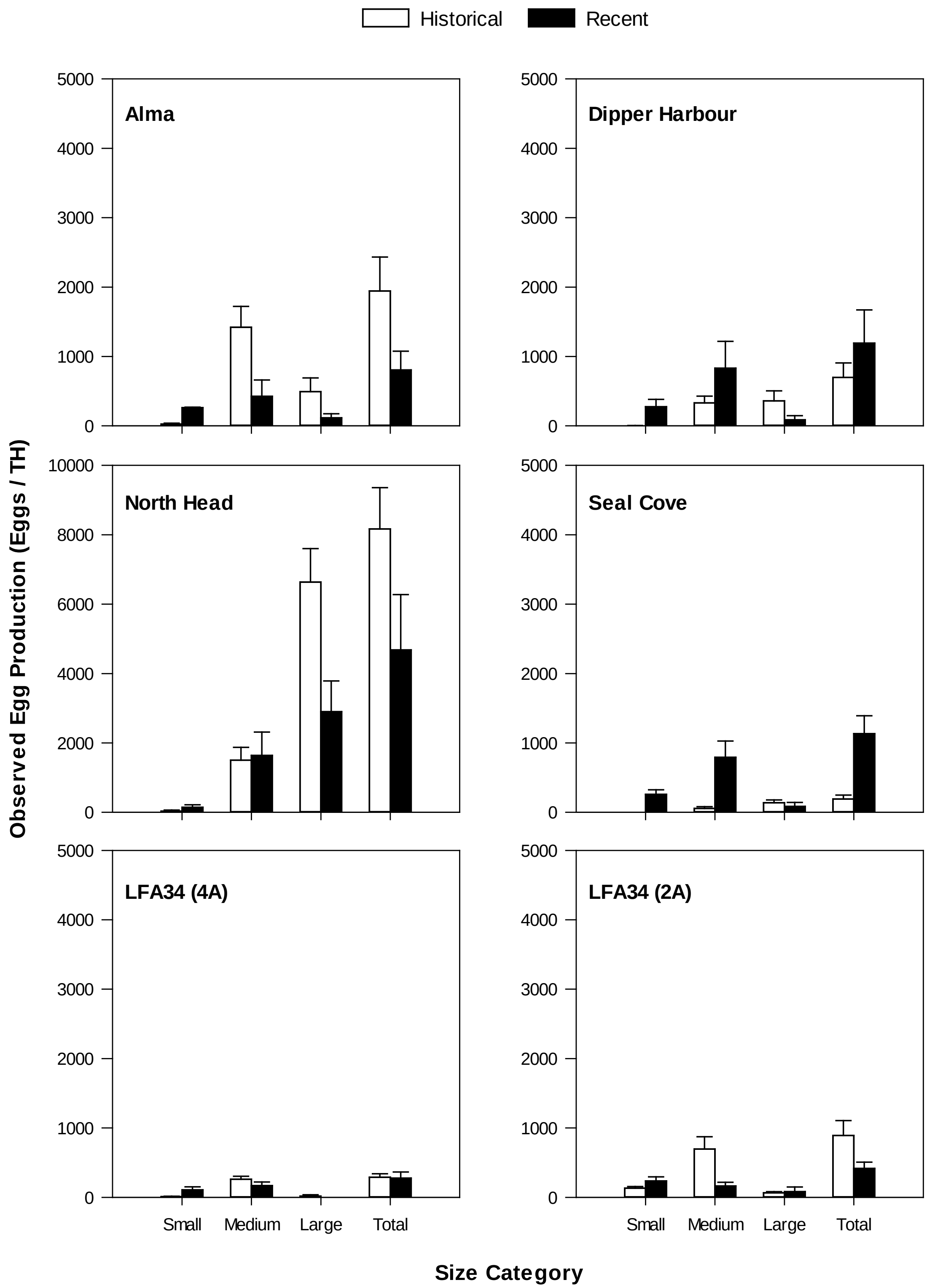

Figure 13. Observed egg production (mean ± SE) for four size categories (Small: <100; Medium: [100-120], Large: ≥120 mm CL, and Total) during two time periods (historical and recent) in different regions of the Bay of Fundy and grid groups of LFA 34. Note the different scale for North Head.

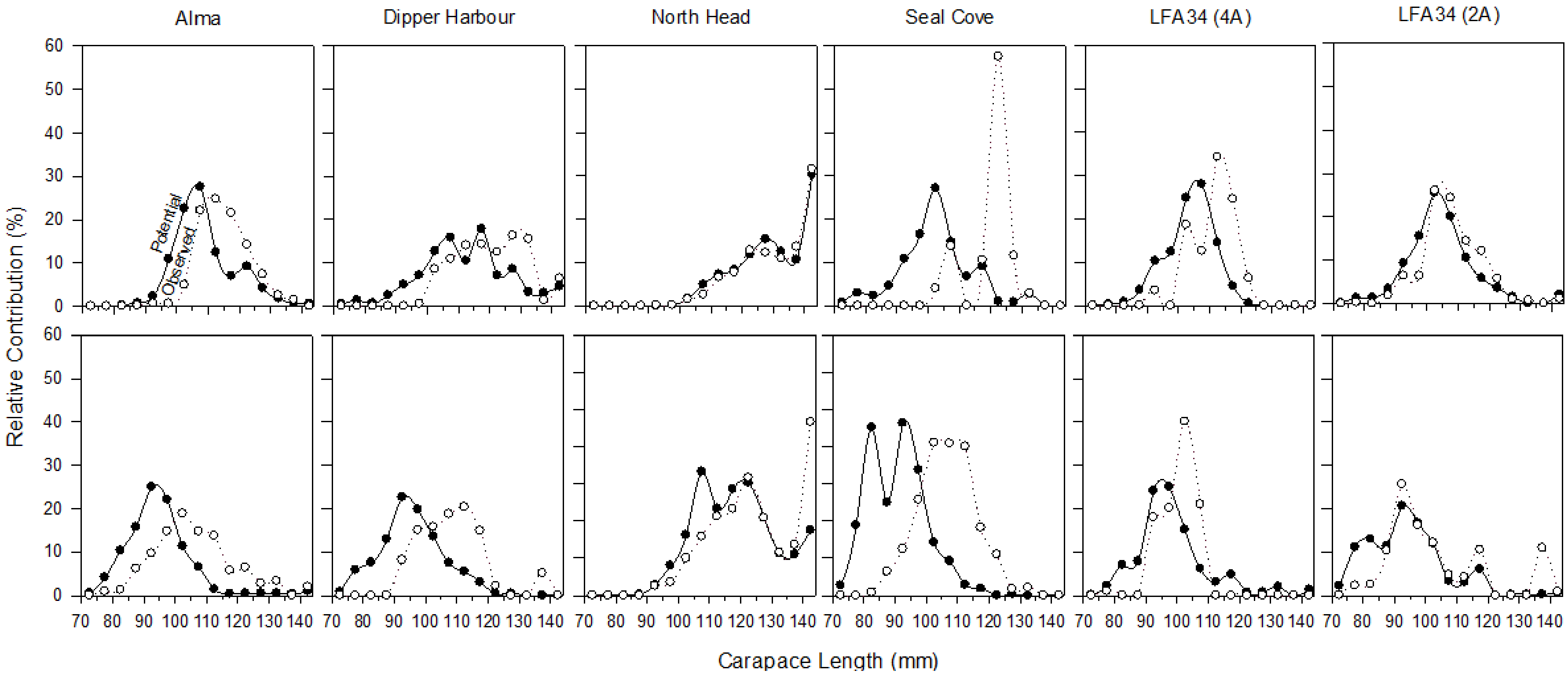

Figure 14. Relative 5-mm size-class contribution to egg production potential (black dots) and observed egg production (open circles) for two time periods: historical (top panels) and recent (bottom panels).

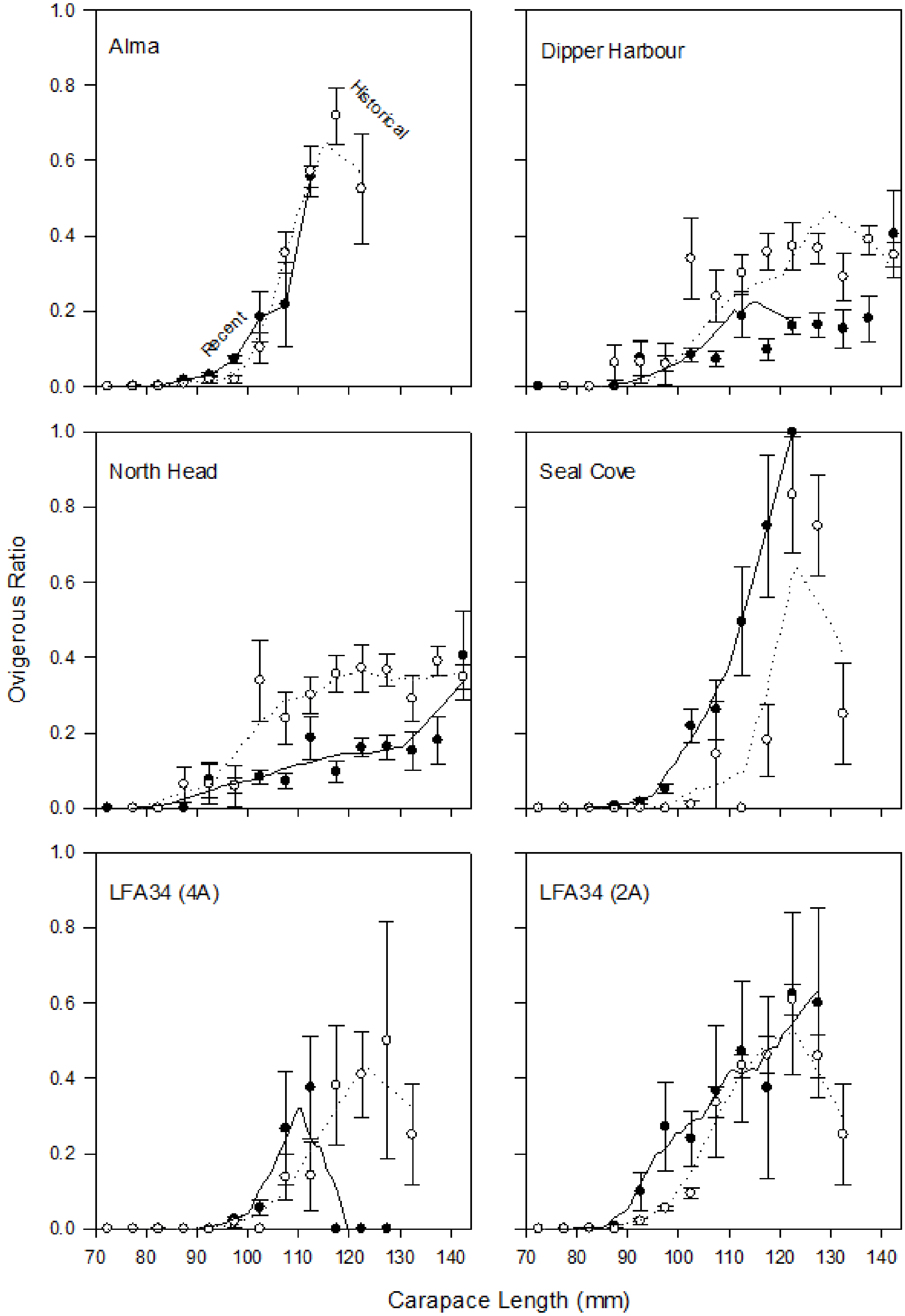

Figure 15. Proportion of ovigerous females among females across 5-mm size-classes during two time periods (historical and recent). Lines are LOESS 1st degree fit with smoothing parameter value of 0.4.

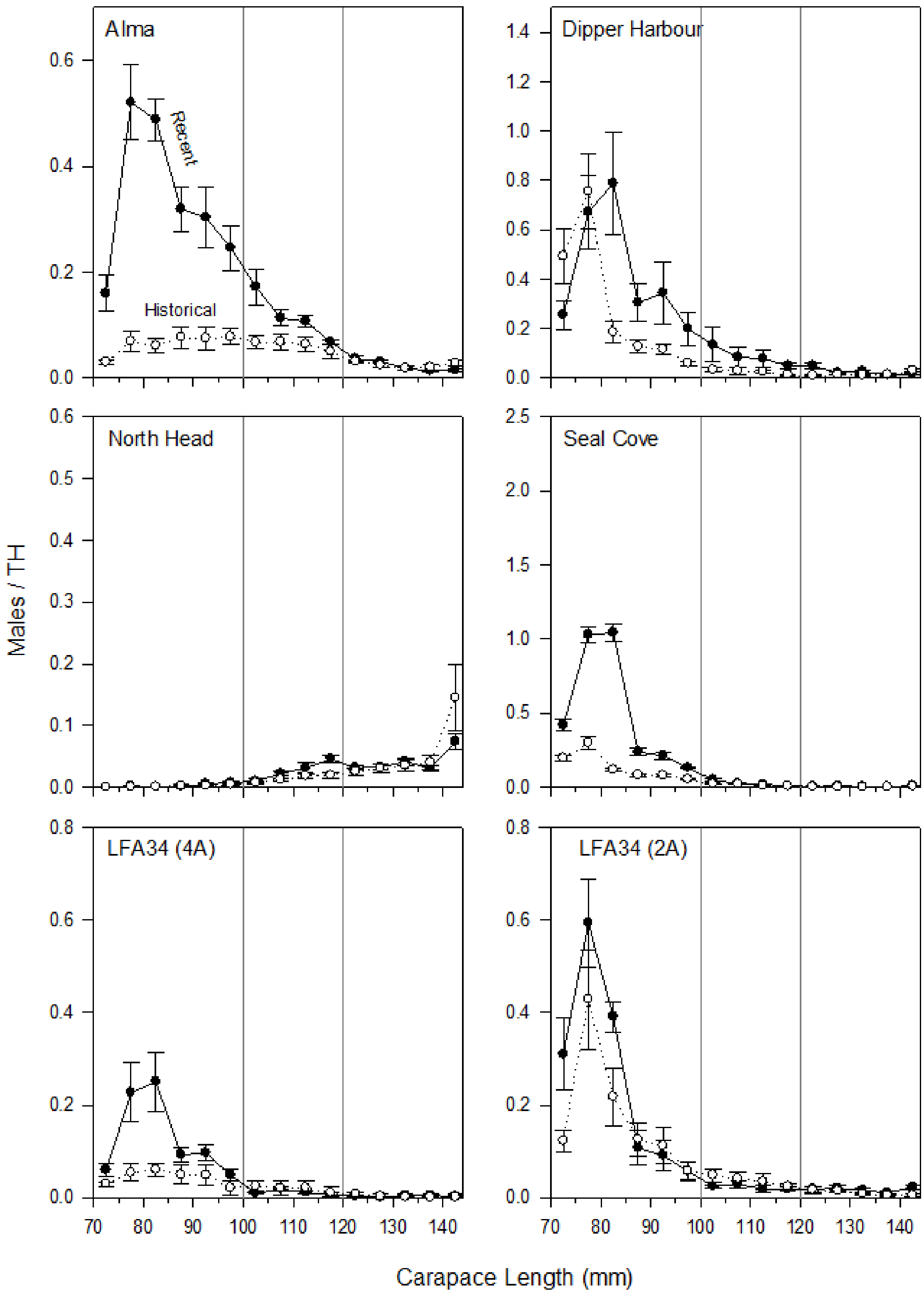

Figure 16. Male catch rates (mean ±SE) per 5-mm size-class for an historical time period (open circles) and recent years (black circles) for different regions in the Bay of Fundy and LFA 34. Vertical lines at 100 and 120 mm CL are to separate small, medium and large size categories.

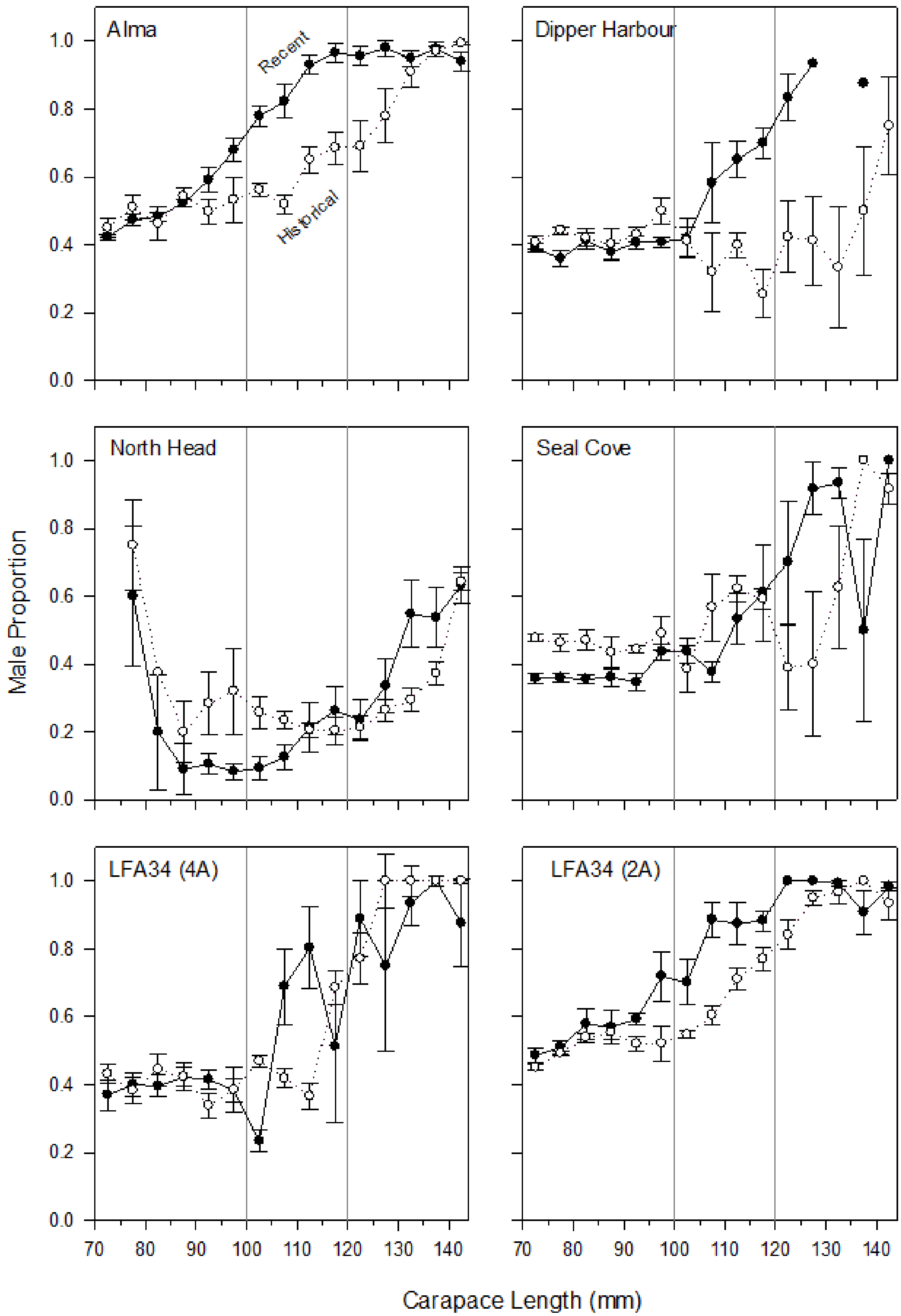

Figure 17. Proportion of male in 5-mm size-class during two time periods (historical: open circles; and recent: black dots). Lines are LOESS 1st degree fit with smoothing parameter value of 0.4.