# A plain language summary by Kate Wilke

# Adapted from:

An investigation into different sampling techniques and geographic variation in size-fecundity parameters of the American lobster, *H. americanus* 

by

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#### **Summary of MSc Thesis**

This thesis focuses on two main aspects, the first of which looks at non-invasive sampling techniques to estimate egg number on female lobsters and the second looks at a model that can predict the relationship between female size and egg number from latitude. The non-invasive sampling techniques estimate egg number for the female American lobster (Homarus americanus) based on measurements and digital image analysis. Non-invasive estimates of egg number can now be made that require the removal of only ten eggs per female instead of the entire egg mass. Applications of this technique include the evaluation of the effectiveness of conservation measures, such as v-notching or the establishment of closed areas, aimed at increasing egg production, where differences in egg production can be measured without the use of destructive sampling techniques. In order to create a model able to predict the number of eggs on a female based on her carapace length throughout the species' range, fecundity estimates for American lobster (H. americanus) from 11 different locations in the Northwest Atlantic (from the Strait of Belle Isle, Newfoundland to Buzzards Bay, Massachusetts) were obtained. The data were then analyzed for geographic variation and a distinct change with latitude was found in the model parameter b. This was then used to create a model that can predict size-egg number relationships from latitude. This model will allow for future egg number estimates to be made, utilizing size data from latitude for any population in the Northwest Atlantic.

# MSc Thesis Chapter 2 – "A non-invasive sampling technique for estimating egg number in the American lobster, *Homarus americanus"*Summary

This study presents two non-invasive sampling techniques that estimate egg number for female American lobster based on measurements and digital image analysis. These estimates are compared with egg number estimates obtained from the widely used traditional invasive technique involving the removal, drying, and weighing of eggs. The results of these comparisons show that one non-invasive technique, which requires the removal of only ten eggs per female, is capable of producing egg number estimates that are just as good as those obtained using the traditional invasive method, without having to remove all of the eggs from a female. Recent increases in conservation-oriented research makes this technique appealing for future work on the size-egg number relationships, which are used in stock assessments and scientific models to aid in fisheries management for the American lobster stocks.

#### Introduction

The number of eggs produced by female lobsters is an important characteristic of lobster populations that is often used by fisheries scientists to assess the health of the population. The number of eggs a female produces is related to her size, and typically, larger females produce more eggs.

Females in different geographic locations may produce different numbers of eggs based on differences in the environment.

There has been extensive research on the female size-egg number relationships of American lobster (*H. americanus*) for numerous locations throughout the species range. The earliest studies were carried out by Herrick (1896) in Massachusetts, which involved the collection and removal of over 4000 egg-bearing females. More recent research has focused on coastal Newfoundland (Ennis, 1981) and the Canadian Maritimes (Campbell and Robinson, 1983). The most recent study, carried out by Estrella and Cadrin (1995), involved the collection and removal of over 400 egg-bearing females from coastal Massachusetts. The ability to assess the number of eggs a female is carrying quickly, accurately, and without injury has proven difficult because current methodologies require physical removal and preservation of all eggs from females.

Female lobsters are highly fecund, meaning they can carry in excess of 80,000 eggs (Botsford, 1991), which makes counting all of the eggs impractical. Thus, estimations of egg numbers are usually made by counting the number of eggs in weighed subsamples and dividing the average weight of a single egg, as determined from the counted subsamples, into the weight of the entire egg mass (e.g. Ennis, 1981). Traditionally this involves removing, preserving with chemicals, and drying of eggs, which makes this technique for estimating egg number invasive (eggs are destroyed) and labour-intensive.

Despite the harmful effects of egg removal, egg number estimates for lobster are still measured using the traditional invasive technique requiring the removal of all the eggs from a female. This type of research directly contradicts conservation practices of fishers who must return berried females unharmed.

Recent increases in value, regulation, fishing effort, and conservation measures for lobster (Estrella and Cardin, 1995) prevents additional large scale sampling as carried out by past studies. The co-management of the species among fishers and scientists, limits the availability of permits that allow for the removal of eggs from a large number of females, and highlights the need for a reliable, non-invasive technique to estimate egg numbers. This chapter describes new, non-invasive techniques that utilize measurements and digital image analysis to estimate egg number in lobster. Estimates of egg

number were made using two new, non-invasive techniques and compared actual counts of eggs, using the traditional technique of complete egg removal to see if the new techniques were accurate.

#### Materials and methods

Lobster collection

Ten egg-bearing females, ranging in size from 69-82 mm carapace length, were collected using commercial lobster traps in May 2010 from various locations within Bonne Bay, Newfoundland (Fig. 1). Estimates of egg number were obtained using two non-invasive sampling techniques as well as the traditional invasive technique of removing and counting the eggs.

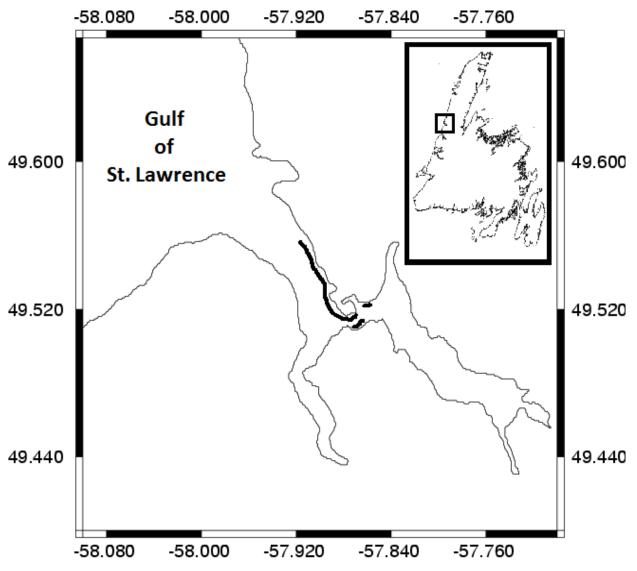


Figure 1. Map of Bonne Bay, Newfoundland depicting sampling locations within Bonne Bay. \*Note: black lines indicate location of lobster traps.

## Non-invasive sampling techniques

Immediately following capture, fecundity estimates were completed using the first non-invasive sampling technique, the <u>measurement technique</u>; the length (A1) and width (A2) of the entire egg mass (Fig. 2a), was measured using a calliper (0.1mm). The height at each egg segment (A3, A4, A5, A6, and A7; Fig. 2b) was measured using a narrow ruler/depth gauge (~1 cm wide), which was inserted into the center of the egg mass between each segment until it reached the surface of the abdomen (Fig. 2c).

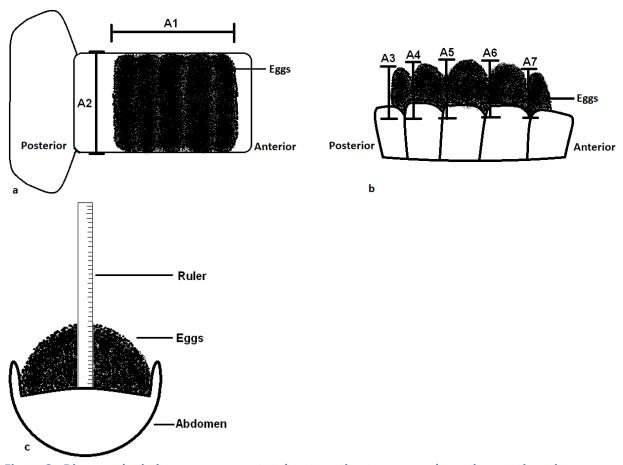


Figure 2. Diagram depicting measurements taken to estimate egg number using non-invasive sampling technique. (a) Underside view of an egg-bearing lobster tail showing length and width measurements of entire egg mass. (b) Side view of an egg-bearing lobster tail showing egg depth measurements. (c) Cross-section of an egg-bearing lobster tail showing placement of ruler for measuring egg depth.

For later egg volume calculations, a minimum of 10 eggs were removed randomly from the surface of the egg mass and preserved. Once in the lab, the volume of the entire egg mass was calculated by altering the formula for the volume of a cylinder based on height measurements and considering packing density between individual eggs. The volume for each egg was also calculated (for more details on the calculations see the actual MSc Thesis and (or) Currie *et al.*, 2010).

Additional egg-number estimates were made using the second non-invasive technique, the <a href="mage-analysis technique">image analysis technique</a>; scaled photographs of the egg mass were taken using an Olympus Stylus Tough-6000 waterproof camera. The height of the egg mass was measured at each segment (B1, B2, B3, B4, and B5) using a thin ruler/depth gauge (Fig. 3a). Once in the lab the length (B6) of the egg mass and the diameter of 10 eggs were measured using the image analysis software ImageJ® (<a href="http://rsb.info.nih.gov/ij/">http://rsb.info.nih.gov/ij/</a>; Fig. 3b). The image analysis technique did not require the removal of any eggs.

The volume of the egg mass and the eggs were calculated using the same formulas and methods as the <u>measurement technique</u>, with the exception that egg mass length (L) and egg diameters (D) were measured by analyzing the photograph (Fig. 3b) with the image analysis software.

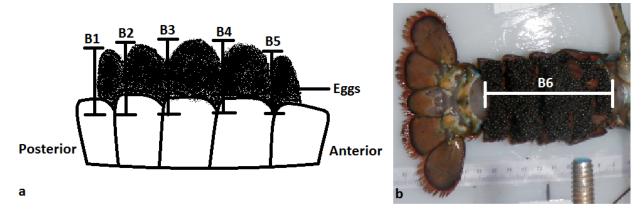


Figure 3. Diagram depicting measurements and photographs taken to estimate egg number using <a href="mage-analysis technique">image analysis technique</a>. (a) Side view of egg-bearing lobster tail showing depth measurements. (b) Under-side view of an egg-bearing lobster tail showing length measurement.

Comparison of new techniques to traditional invasive technique

After estimating egg numbers using the non-invasive techniques, all of the eggs were removed from the females using forceps and eggs were counted using the commonly practiced traditional method (e.g. Ennis, 1981; Campbell and Robinson, 1983; Attard and Hudon, 1987, Estrella and Cadrin, 1995). Steps of the traditional method included preserving eggs in chemical solution, then drying, separating, and weighing the eggs. Egg numbers were estimated by counting five weighed sub-samples

(≥30 eggs/sample) and dividing the weight of an average egg into the weight of the entire egg mass. These counts were validated by comparing them to four counted samples.

#### **Results**

The egg numbers obtained from the <u>measurement technique</u> and the traditional method were compared using statistical analysis and were found to be statistically similar. Therefore, the non-invasive <u>measurement technique</u> was deemed highly reliable for estimating egg numbers. In contrast, the <u>image analysis technique</u> showed little statistical similarity to the traditional method, consistently over-estimating egg mass length and underestimating egg diameter.

# Implications of non-invasive techniques

In addition to the potential for reducing destructive sampling effort, the measurement technique presented in this study has some desirable advantages. There have been numerous studies completed on the relationship between female size and egg number in American lobster since the first monograph on the species was published by Herrick (1896). A non-exhaustive literature search revealed that to date these studies have sampled over 7,000 lobsters, removing 138 million eggs, and potentially removing 1.3 million lobsters from the population, assuming a 1% survival rate (Herrick, 1896; Squires, 1970; Squires *et al.*, 1974; Ennis, 1981; Campbell and Robinson, 1983; Estrella and Cadrin 1995). This non-invasive method will prevent the need for future removal of eggs from egg-bearing females.

In Atlantic Canada, the Fisheries Resource Conservation Council (FRCC, 1995; 2007) has raised concerns about the sustainability of the fishery for American lobster. Exploitation rates are high, up to 95% in some areas, and catches consist primarily of immature animals. This practice of "fishing the measure" results in extremely low egg production and high risk of recruitment failure (FRCC, 2007), and the removal of eggs from females to create size-fecundity relationships is no longer encouraged. However, many lobster populations would benefit from the development of additional size-egg number relationships because there is known geographic variation (Estrella and Cadrin, 1995) and the relationships currently available are not applicable throughout the entire species' range. The non-invasive measurement technique presented here would allow for the continued study of the size-egg number relationships for American lobster, without the detrimental effects of egg removal, as seen in the traditional method.

MSc Thesis Chapter 3 – "Latitudinal variation in the relationships between female size and number of eggs of American lobster in the Northwest Atlantic"

Summary

Certain characteristics of lobster populations are known to vary with changes in environmental conditions and accordingly with latitude. A mathematical model to estimate these characteristics, applicable throughout the species range, has not been developed. To create such a model, egg number estimates for the American lobster, *Homarus americanus*, were obtained from 11 locations in the Northwest Atlantic (from the Strait of Belle Isle, Newfoundland to Buzzards Bay, Massachusetts). The mathematical model, *F=aCLb*, was used to describe the relationship between female carapace length *CL* and fecundity *F*, or egg number. The parameters *a* and *b* change with latitude and in this study, I define the values of *a* and *b*. This information then allows scientists to estimate of the number of eggs a female of a certain size may carry based on latitude. Establishing the relationship between female size and egg number based on latitude allows scientists to estimate egg number in locations without actually sampling adult females and removing and counting their eggs.

#### Introduction

Relationships between female carapace length and number of eggs carried on the abdomen for the American lobster, *H. americanus*, have been documented from northern Newfoundland to southern New England (Herrick, 1896; Saila *et al.*, 1969; Squires, 1970; Perkins, 1971; Squires *et al.*, 1974; Aiken and Waddy, 1980; Ennis, 1981; Campbell and Robinson, 1983; Attard and Hudon, 1987, Estrella and Cadrin, 1995). These relationships allow scientists to predict egg number from a known carapace length and provide scientists information on which to base estimates of life history patterns and population growth, and information on which to evaluate management measures (FRCC, 2007; ASMFC, 2009).

Female size and egg number relationships are different in different locations and reasons for these differences may be due to geographic location or the way the data was collected and processed. As a result, scientists have suggested that additional sampling is necessary so that methodologies can be standardized and sample sizes increased (Estrella and Cadrin, 1995; Aiken and Waddy, 1980). However, increased fishing effort and economic value has prevented such large scale sampling of egg-bearing females (Estrella and Cadrin, 1995) and the co-management of the species among fishers and researchers, limits the availability of permits that allow for the removal of eggs from a large number of females. Annual exploitation rates for American lobster are rarely below 80%, with some Lobster Fishing Areas (LFAs) exploiting 95% of the populations (FRCC, 2007; ASMFC, 2009). Fisheries managers have the

difficult task of assessing lobster populations using only a few reliable size-egg number equations that may not be applicable throughout the entire species range. A more general mathematical model that represents the size-egg number relationship throughout the lobster's entire range is needed.

The objectives of this research were: (1) to quantify geographic variation at three coastal Newfoundland regions; (2) to re-estimate past size-egg number relationships using more modern computer statistical software packages; and (3) develop a mathematical model to predict size-egg number parameters a and b from latitude (°N), which can be easily obtained for any location.

## **Materials and Methods**

Study area and data collection

Between 3 and 19 June, 2009 a total of 38 egg-bearing females were sampled from commercial lobster traps in three regions along the west coast of Newfoundland (Fig 4): Barr'd Harbour (12 lobsters), Lark Harbour (11 lobsters), and Port aux Basques (14 lobsters). Lobsters were chosen for egg number estimates if the carapace length was either greater than 110 mm or less than 82.5 mm. Intermediate sized lobsters were not selected because significant data are available for Newfoundland lobsters found within the size range 82.5 mm to 110 mm carapace length (Ennis, 1981). In order to minimize the number of eggs being removed from the population only lobsters outside this size range were sampled.

Eggs were removed from the females only if they appeared undamaged from being caught in lobster traps and subsequent handling. For every egg-bearing lobster sampled, the following attributes were measured: carapace length (mm), second segment abdomen width (mm), abdomen length (mm), and the presence/absence of a v-notch was noted. Eggs were immediately removed from females upon capture with no holding period in order to minimize egg loss due to handling. Before releasing the female, any eggs that could not be removed from the abdomen were counted to be included in the final fecundity estimate.

Eggs were then preserved in a chemical solution, for a maximum of four weeks, until all samples were collected. After preservation, eggs were rinsed in freshwater, and spread thinly over shallow glass Petri dishes to dry at  $50^{\circ}$ C for 20 hours (Attard and Hudon, 1987). The dried eggs were rubbed over a fine screen mesh netting ( $250\mu$ m) to remove any excessive connective tissue and weighed to the nearest 0.0001g. Egg number was determined by counting five weighed sub-samples (greater than or equal to 30 eggs/sample) and dividing the weight of an average egg into the weight of the entire egg

mass. These counts were validated by comparing them to four counted samples, and the error was very low (ranged from 0.09% to 0.90% (= 0.54%)).

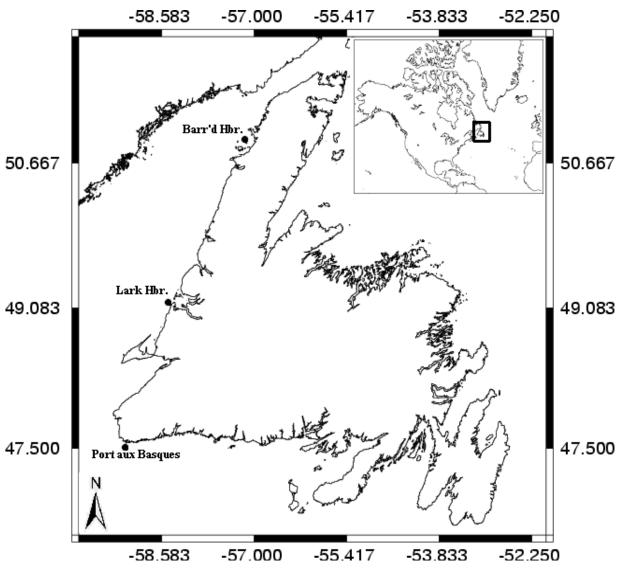


Figure 4. Map depicting the three sampling locations on the west coast of Newfoundland

Bias in fecundity estimations and data analysis

Mathematical methodologies and procedures that have been used in past studies to create size-egg number relationships may have biased estimates of egg number. The data were re-evaluated using two different methods. The bias associated with each method was recorded, and statistical analyses were conducted.

General model and data analysis

Data analysis was conducted using the using the statistical programs S-Plus® (TIBCO Software Inc., Palo Alto, California, 2010) and R $^{*}$  (R Development Core Team, 2010). A P-value  $\leq$  0.05 was considered significant.

Raw adult size-egg number data for five sites in Newfoundland waters (Ennis, 1981), three sites off Nova Scotia (Campbell and Robinson, 1983) and five sites in Massachusetts waters (Estrella and Cadrin, 1995; Herrick, 1896) were acquired from the authors of past studies. Following mathematical manipulation, two different equations to estimate female size-egg number relationships were formulated. We then tested the ability of the equations to accurately estimate egg number by comparing predicted values of egg number to observed values of egg number. The bias associated with each model was recorded, and statistical analyses were performed.

Comparisons of egg number estimates, obtained from the published equation and the second equation we developed to that of the observed egg number, were graphed for 12 locations (see Currie MSc Thesis).

#### **Results**

*Newfoundland fecundity equations* 

Statistical analysis of size-egg number relationships showed Port aux Basques to have a steeper slope then Lark Harbour and Barr'd Harbour, which displayed similar slopes (Fig. 5). Additional statistical tests were also carried out, determining that the relationship between size and egg number in Port aux Basques was significantly different from that of both Barr'd Harbour (F1,17 = 5.2572, P-value = 0.0349) and Lark Harbour (F1,17 = 4.9178, P-value = 0.0405). However, the relationship in Barr'd Harbour and Lark Harbour were not significantly different (F1,20 = 0.7071, P-value = 0.1453) and were therefore combined to produce the following equation (Fig. 6):

F = 0.049\*CL2.815

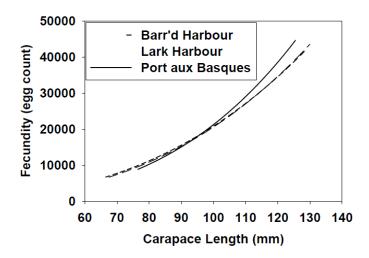


Figure 5. Size-egg number relationships for American lobster on the west coast of Newfoundland. Barr'd Harbour (n=12): R2 = 0.98, standard error (S.E.) on slope  $\pm$  0.1789. Lark Harbour (n=11): R2 = 0.98, S.E. on slope  $\pm$  0.1431, Port aux Basques (n=9): R2 = 0.95, S.E. on slope  $\pm$  0.4056.

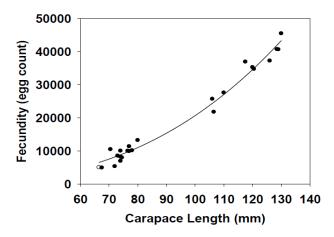


Figure 6. Combined size-egg number relationships of American lobster for Barr'd Harbour and Lark Harbour on the west coast of Newfoundland. R2 = 0.98, S.E. on slope ± 0.1092.

### General Model

To develop a general model of female size and egg number based on latitude for the entire species' range, data sets with large size ranges were needed to ensure estimates of parameters a and b were not skewed. As a result, locations with similar latitudes were tested for similarity (Fig. 7). Ship Harbour (SH) and Boswarlos (BOS), and Ship Harbour and Arnolds Cove (AC) were not included in the analysis because they all displayed narrow size ranges. The Northumberland Strait (NUS) and the Bay of Fundy (BOF), Buzzards Bay (BB) and Outer Cape Cod (OCC), and Barr'd Harbour (BH) and Lark Harbour (LH) all showed statistically similar relationships between size and egg number. These six data sets were

then combined into three and the latitudes averaged, increasing their size range for use in the analysis of geographic variation. Paradise (PAR) and the Southern Gulf of Maine (SGM) were also included in the analysis because they displayed large size ranges. Variation in size-egg number relationships over time were tested and found to be negligible.

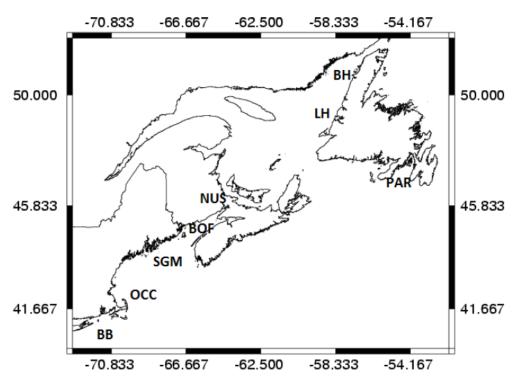


Figure 7. Map depicting locations used to graph the relationship between latitude and size-egg number parameter *b*.

# Latitude Models # 1 and # 2

Two different mathematical models were developed and tested to determine the relationship between parameter *b* and Latitude. The relation between parameter b and Latitude used in the development of both models was found to be (Fig. 8):

**Eq. 1:** b = -0.0859708305\*Lat + 7.0202045476

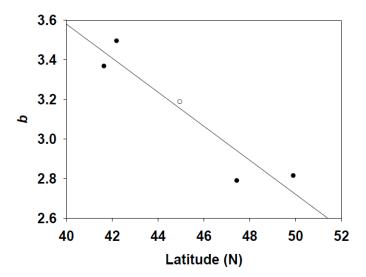


Figure 8. Relationship between parameters b (power law exponent) and Latitude. R2 = 0.8845, S.E. on slope  $\pm$  0.0179  $1/^{9}$ N.

The relation between parameter a and b used to solve for parameter a in Latitude Model # 1 was:

**Eq. 2:** 
$$a = -0.0008 + 8725.1e-4.3033* b$$

The relation between the average fecundity and Latitude used to develop Latitude Model # 2 was (Fig. 9):

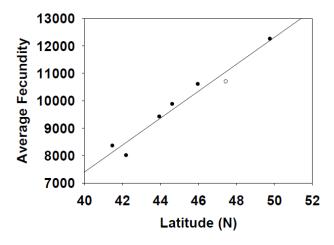


Figure 9. Relationship between the Average Fecundity (egg number) at 85 mm carapace length and Latitude. R2 = 0.96, S.E. on slope of ± 45.502 eggs/°N.

<sup>\*</sup>Only locations with large size ranges were included.

<sup>\*</sup>The average fecundity at 85 mm CL was only available for 7 locations.

#### Discussion

Geographic variation in female size-egg number relationships

An important result of this research is the latitudinal gradient in the size-egg number parameter b (Fig. 10) and the average egg number at a fixed size class (Fig. 11), which shows conclusively, regional differences exist in female size-egg number relationships of American lobster. Furthermore, these results suggest differences in the reproductive potential of female lobsters from Newfoundland to Massachusetts. Temperature is the major factor affecting size at maturity, oocyte maturation, spawning incidence, timing and synchronization, success of egg attachment and incubation, and time of hatching (Templeman, 1936, Aiken and Waddy, 1989; Waddy and Aiken, 1991), and is likely the cause for much of the observed geographic variation in the size-egg number relationships.

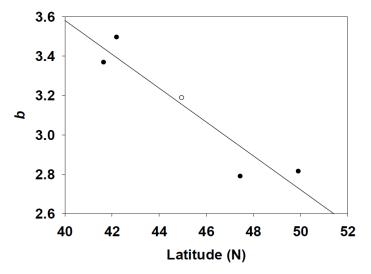


Figure 10. Relationship between parameters b (power law exponent) and Latitude. R2 = 0.8845, S.E. on slope  $\pm$  0.0179 1/ $^{\circ}$ N. Parameter b gets smaller as you go farther north. \*Only locations with large size ranges were included.

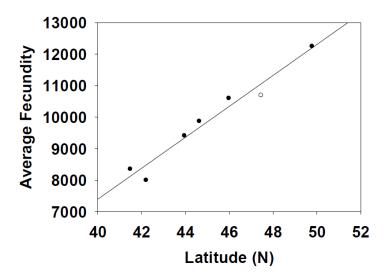


Figure 11. Relationship between the Average Fecundity (egg number) at 85 mm carapace length and Latitude. R2 = 0.96, S.E. on slope of  $\pm$  45.502 eggs/ $^{\circ}$ N. Average Fecundity, or average egg number, increases as you go farther north.

\*The average fecundity at 85 mm CL was only available for 7 locations.

The major impediments to evaluating geographic variation in size-egg number relationships to date has been the confounding effects of obtaining eggs with comparable developmental stages (Ennis, 1981), similar size ranges, and the ability to obtain high statistical relationships (Waddy and Aiken, 1991). To obtain comparisons with similar egg developmental stages, data were restricted to samples obtained during the spring (April-June), with the exception of the Bay of Fundy. Additionally, large size ranges were used to eliminate the confounding effects that small size ranges have on estimates of parameters *a* and *b*. Finally, results obtained had high goodness of fit values, ranging from 0.88 to 0.99.

Campbell and Robinson (1983) evaluated the differences in the size-fecundity relationships of lobster in three maritime regions, Eastern Nova Scotia, The Bay of Fundy, and the Northumberland Strait. Their analysis revealed no significant differences in the relationships and the data were condensed into a single equation used in Maritime stock assessments (*e.g.* Lanteigne *et al.*, 1998). However, the size ranges for each location were narrow, spanning only 40 mm carapace length, and it has been suggested that broad size ranges are needed to accurately evaluate such differences (Estrella and Cadrin, 1995). When formulating new size-egg number equations for the three maritime regions in this study, the predictive power of the equations increased substantially over those originally presented by Campbell and Robinson (1983), because the model in this study is not affected by small size ranges at

any one location. Changes in parameters a and b will alter the size-egg number relationships and have notable impacts on fecundity estimates.

Research on regional differences in abdomen area, carapace length, and chelae length has been carried out in Nova Scotia coastal regions (MacCormack and DeMont, 2003). Results of this study showed that the scaling factor of abdomen area with carapace length varied with region. During spawning, female lobster release their eggs onto the underside of their abdomen, and it has been shown that a larger abdomen area allows for higher egg masses (Templemen, 1935, Atema and Voigt, 1995). This is in accordance with our results, which show distinct differences in the size-egg number equations with region. The differences observed are thought to be the result of varying temperatures. The northern and southern limits of lobster experience extreme differences in the range and duration of cold and warm water temperatures and these differences are known to effect egg production (Waddy and Aiken, 1991).

The observed trend in egg number estimates throughout the species' range may be explained by differences in growth rates. Newfoundland lobsters are known to grow at slow rates when compared to lobsters found in more southern locations such as Southern Gulf of Maine (Ennis, 1980). In this study, lobsters occurring in colder waters tended to have higher egg counts at smaller sizes up to 110 mm CL. This could be explained by a slower growth rate which would require the lobsters to produce more eggs at smaller sizes, since they would require a longer time period to reach larger sizes. Further research and variations in egg size with latitude could help explain the observed trend.

The observed latitudinal trend in size-egg number relationships may also be due to differences in size at first maturity. It is well-accepted that lobsters reproduce at smaller sizes in warm waters (Aiken and Waddy, 1976). The results suggest that smaller lobsters from southern locations would have fewer eggs; however, this may not be the case. The relationships may be influenced by the earlier maturation of lobster in the southern locations when compared to northern location giving the impression of fewer eggs at smaller size. Further research on comparisons of egg number estimates of lobsters at sizes just above their ages at maturity is needed and would aid in the explanation of the observed trends.

#### Latitude models

The fishery for American lobster in the United States and Canada has a total of 48 different management zones (DFO, 2009). A total of thirteen size-egg number relationships have been developed (Factor, 1995) and are available for use in the management of these 48 different zones. As a result of geographic variation, potential differences in the size-egg number relationships of lobster in these zones

may exist. As a result, research using equations from different regions may produce inaccurate estimates of fecundity. Of the two latitude models developed and presented in this study, through statistical analysis it was found that Latitude Model # 2 was the best to predict egg number based on latitude (better than Latitude Model # 1). The development of Latitude Model # 2 will allow data poor locations to formulate size-egg number equations from latitudes. Fisheries scientists can now use customized size-egg number relationships in stock assessments and yield- and egg-per-recruit models, which can be developed for any site from latitude, as first and best approximations of egg number.

#### References

- Aiken, D.E. and Waddy, S.L. 1976. Controlling growth and reproduction in the American lobster. Proceedings of the World Mariculture Society 7: 415–430.
- Aiken, D.E. and Waddy, S.L. 1989. Interactions of temperature and photoperiod in the regulation of spawning by American lobster, *Homarus americanus*. Canadian Journal of Fisheries and Aquatic Sciences 46: 145-148.
- Aiken, D.E. and Waddy, S.L. 1980. Maturity and Reproduction in the American lobster. Canadian Technical Report of Fisheries and Aquatic Sciences 932: 60-71.
- Annala, J.H. 1991. Factors influencing fecundity and population egg production of *Jasus* species. Wenner, A.M. and Kuris, A. (eds). In: Crustacean Egg Production. Crustacean Issues 7th ed. Rotterdam: A.A. Balkema. pp. 301-315.
- Atema, J. and Voigt, R. 1995. Behaviour and sensory biology. Factor, J.R. (ed). In: Biology of The Lobster *Homarus americanus*. San Diego, California: Academic Press. pp. 313-348.
- Atlantic States Marine Fisheries Commission (ASMFC). 2009. American lobster stock assessment report for peer review. Report # 09-01. 316 pp.
- Attard, J. and Hudon, C. 1987. Embryonic development and energetic investment in egg production in relation to size of female lobster (*Homarus americanus*). Canadian Journal of Fisheries and Aquatic Sciences 44: 1157-1164.
- Botsford, L.W. 1991. Crustacean egg production and fisheries management. Wenner, A.M. and Kuris, A. (eds). In: Crustacean Egg Production. Crustacean Issues 7th ed. Rotterdam: A.A. Balkema. pp. 379-394.
- Bryan, J.L., Wildhaber, M.L., Papoulias, D.M., DeLonay, A.J., Tillitt, D.E., and Annis, M.L. 2007. Estimation of gonad volume, fecundity, and reproductive stage of shovelnose sturgeon using sonography and endoscopy with application to the endangered pallid sturgeon. Journal of Applied Ichthyology 23(4): 411-419.
- Caddy, J.F. 1977. Approaches to a simplified yield-per-recruit model for crustacea, with particular reference to the American lobster, *Homarus americanus*. Canadian Fisheries and Marine Service Manuscript Report 1445: 1-14.
- Caddy, J.F. 1979. Notes on a more generalized yield per recruit analysis for crustaceans, using size-specific inputs. Canadian Fisheries and Marine Service Manuscript Report 1525: 1-7.
- Campbell, A. and Robinson, D.G. 1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian Maritimes. Canadian Journal of Fisheries and Aquatic Sciences 40(11): 1958-1967.
- Cobb, J.S., Booth, J.D., and Clancy, M. 1997. Recruitment strategies in lobsters and crabs: a comparison. Marine and Freshwater Research 48: 797-806.
- Costa, T.M. and Negreiros-Fransozo, M.L. 2002. Population biology of *Uca thayeri* Rathbun, 1900 (Brachyura, Ocypodidae) in a subtropical South American mangrove area: results from transect and catch-per-unit-effort techniques. Crustaceana, 75: 1201-1218.
- Department of Fisheries and Oceans Canada. 2009. Canada's lobster fisheries. Available online at <a href="http://www.dfo-mpo.gc.ca/fm-gp/sustainable-durable/lobster-homard-eng.htm">http://www.dfo-mpo.gc.ca/fm-gp/sustainable-durable/lobster-homard-eng.htm</a>. Accessed March, 2010.
- Dover, C.L.V. and Williams, A.B. 1991. Egg size in squat lobsters (Galatheoidea): Constraint and freedom. Wenner, A.M. and Kuris. A. (eds). In: Crustacean Egg Production. Crustacean Issues 7th ed. Rotterdam: A.A. Balkema. pp. 143-156.
- Ennis, G.P. 1981. Fecundity of the American lobster, *Homarus americanus,* in Newfoundland waters. Fishery Bulletin 79(4): 796-800.
- Ennis, G.P. 1980. Recent and current research on lobster growth in the wild. Canadian Technical Report of Fisheries and Aquatic Sciences. 932: 10-15.

- Ennis, G.P. and Akenhead, S.A. 1978. A model and computer program used to assess yield per recruit in Newfoundland lobster stocks. Canadian Atlantic Fisheries Science Advisory Committee Research Document (78/30): 1-13.
- Estrella, B.T. and Cadrin, S.X. 1995. Fecundity of the American lobster (*Homarus americanus*) in Massachusetts coastal waters. ICES Marine Science Symposia 199: 61-72.
- Factor, J.R. 1995. Biology of The Lobster Homarus americanus. San Diego: Academic Press, INC. 528 pp.
- Faulk, C.K. and Holt, G.J. 2008. Biochemical composition and quality of captive-spawned *Cobia rachycentron* canadum eggs. Aquaculture 279(1): 70-76.
- Fisheries Resource Conservation Council (FRCC). 1995. A Conservation Framework for Atlantic Lobster 1995. Report to the Ministers of Fisheries and Oceans. 100 pp.
- Fisheries Resource Conservation Council (FRCC). 2007. Sustainability framework for Atlantic lobster 2007. Report to the Ministers of Fisheries and Oceans. 68 pp.
- Forster, G.R. 1951. The biology of the common prawn, *Leander serratus* pennant. Journal of the Marine Biological Association of the United Kingdom (30): 333-360.
- Ganias, K., Vavalidis, T., Nunes, C., Stratoudakis, Y. 2008. Automating batch fecundity measurements using digital image analysis systems: A case study in the Iberian sardine. In: Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in ICES areas VIII and IX, Nantes. pp. 1-8.
- Hartley, H.O. 1961. The modified gauss-newton method for the fitting of non-linear regression functions by least squares. Technometrics 3(2): 269-280.
- Hartnoll, R.G. and Gould, P. 1988. Brachyuran life history strategies and the optimization of egg production. Fincham, A.A. and Rainbow, P.S. (eds). In: Aspects of Decapod Crustacean Biology: Symposia of the Zoological Society of London. pp. 1-9
- Herrick, F.H. 1896. The American lobster: A study of its habits and development. Bulletin of the United States Fish Commission 15: 1-252.
- Hunner, J.V. and Lindqvist, O.V. 1991. Special problems in freshwater crayfish egg production. Wenner, A.M. and Kuris, A. (eds). In: Crustacean Egg Production. Crustacean Issues 7th ed. Rotterdam: A.A. Balkema. pp. 235-246.
- Jensen, J.P. 1958. The relationship between body size and number of eggs in marine malacostrakes. Meddel Danmarks Fisk-Og Havundersog New York Series 2: 1-25.
- Kennedy, J., Geffen, A.J., Nash, R.D.M. 2007. Maternal influences on egg and larval characteristics of plaice (*Pleuronectes platessa*). Journal of Sea Research 58(1): 65-77.
- Kennelly, S.T. and Watkins, D. 1994. Fecundity and reproduction and their relationship to catch rates of spanner crab, *Ranina ranina*, off the coast of the Australia. Journal of Crustacean Biology 14: 146-150.
- Klibansky, N. and Juanes, F. 2008. Procedures for efficiently producing high-quality fecundity data on a small budget. Fisheries Research 89(1): 84-89.
- Klaoudatos, S.D. and Klaoudatos, D.S. 2008. Phylogeny biology and ecology of Crustaceans (Phylum Arthropoda; Subphylum Crusacea). In: Mente, E. (eds). Reproductive Biology of Crustaceans, Case studies of Decapod Crustaceans. Science Publishers, New Hampshire, USA. pp. 13-90.
- Lanteigne, M., Comeau, M., Mallet, M., Robichaud, G., and Savoie, F. 1998. The American lobster, Homarus americanus in the southern Gulf of St. Lawrence (lobster fishing areas 23, 24, 25, 26A, and 26B). Report no. 98/123.
- Lizarraga-Cubedo, H.A., Pierce, G.J., and Santos, M.B. 2008. Reproduction of Crustaceans in relation to fisheries. In: Mente, E. (eds). Reproductive Biology of Crustaceans, Case studies of Decapod Crustaceans. Science Publishers, New Hampshire, USA. pp. 169-222.
- Lizarraga-Cubedo, H.A., Tuck, I., Bailey, N., Pierce, G.J., and Kinnear, J.A.M. 2003. Comparisons of size at maturity and fecundity of two Scottish populations of European lobster. *Homarus gammarus*. Fisheries Research (65): 137-152.

- MacCormack, T.J. and DeMont, M.E. 2003. Regional differences in allometric growth in Atlantic Canadian lobster (*Homarus americanus*). Journal of Crustacean Biology: 258-264.
- MacDiarmid, A.B. 1989. Size at onset of maturity and size dependant reproductive output of female and male spiny lobster *Jasus edwarsii* (Hutton) (Decapoda, Palinuridae) in Northern New Zealand. Journal of Experimental Marine Biology and Ecology 127: 229-243.
- Mente, E. (ed). 2008. Reproductive Biology of Crustaceans: Case Studies of Decapod Crustaceans. Science Publishers. New Hampshire, USA. 549 pp.
- Mente, E. and Neofitou, C. 2008. An overview. Mente E, editor. In: Reproductive Biology of Crustaceans: Case Studies of Decapod Crustaceans. Science Publishers. New Hampshire, USA. 1-12.
- Motulsky, H.J. and Christopoulos, A. 2004. Fitting models to biological data using linear and nonlinear regression: A practical guide to curve fitting. Oxford University Press. Oxford, U.S.A. 351 pp.
- Packard, G.C. and Boardman, T.J. 2008a. Model selection and logarithmic transformation in allometric analysis. Physiological and Biochemical Zoology 81(4): 496-507.
- Packard, G.C. and Boardman, T.J. 2008b. A comparison of methods for fitting allometric equations to field metabolic rates of animals. Journal of Comparative Physiology 179(2): 175-182.
- Packard, G.C. 2009. On the use of logarithmic transformations in allometric analyses. Journal of Theoretical Biology 257(3): 515-518.
- Paul, A.J. and Paul, J.M. 2000. Changes in chelae heights and carapace lengths in male and female golden king crabs *Lithodes aequispinus* after moulting in the laboratory. Alaska Fishery Research Bulletin 6: 70-77.
- Perkins, H.C. 1971. Egg loss during incubation from offshore northern lobsters (decapoda: *Homaridae*). Fishery Bulletin 69(2): 451-453.
- Peters, R.H. 1983. The ecological implications of body size. Beck, E., Birks, H.J.B., and Connor E.F. (eds). Cambridge University Press. Cambridge, U.K. 329 pp.
- Polluck, D.E. 1997. Egg production and life-history strategies in some clawed and spiny lobster populations. Bulletin of Marine Science 67: 97-109.
- Russell, H. 1980. The determination of growth rates for American lobsters. Canadian Technical Report of Fisheries and Aquatic Sciences 932. 1-7.
- Saila, S.B., Flowers, J.M., and Hughes, J.T. 1969. Fecundity of the American lobster, *Homarus americanus*. Transactions of the American Fisheries Society 98(3): 537-539.
- Smith, J.R. 1993. Logarithmic transformation bias in allometry. American Journal of Physical Anthropology 90: 215-228.
- Smith, R.J. 1984. Allometric scaling in comparative biology: Problems of concept and method. American Journal of Physiology Regulatory Integrative and Comparative Physiology 246(2): 152-160.
- Smith, R.J. 1980. Rethink allometry. Journal of Theoretical Biology 87: 97-111.
- Somers, K.M. 1991. Characterizing size-specific fecundity in crustaceans. Wenner, A.M. and Kuris, A. (eds). In: Crustacean Egg Production. Crustacean Issues 7th ed. Rotterdam: A.A. Balkema. 357-378.
- Song, C., Wang, P., and Makse, H.A. 2008. A phase diagram for jammed matter. Nature 453: 629-632.
- Sprugel, D.G. 1983. Correcting for bias in log-transformed allometric equations. Ecology 64(1): 209-210.
- Squires, H.J. 1970. Lobster (*Homarus americanus*) fishery and ecology in Port au Port Bay, Newfoundland, 1960-65. Proceedings of the National Shellfisheries Association 60: 22-39.
- Squires, H.J., Ennis, G.P., and Tucker, G.E. 1974. Lobsters of the northwest coast of Newfoundland, 1964-67. Proceedings of the National Shellfisheries Association 64: 16-27.
- Tack, P.I. 1941. The life history and ecology of the crayfish *Cambarus immunis* Hagen. The American Midland Naturalist (25): 420-446.
- Templeman, W. 1936. Local differences in the life history of the lobster *Homarus americanus*) on the coast of the maritime provinces of Canada. Journal of Biological Board of Canada 2: 41-87.

- Torquato, S., Truskett, T.M., and Debenedetti, P.G. 2000. Is random close packing of spheres well defined? The American Physical Society 84(10): 2064-2067.
- Tully, O., Roantree, V., and Robinson, M. 2001. Maturity, fecundity and reproductive potential of the European lobster (*Homarus gammarus*) in Ireland. Journal of the Marine Biological Association of the United Kingdom (81): 61-68.
- Waddy, S.L. and Aiken, D.E. 1991. Egg production in the American lobster, *Homarus americanus*. Wenner, A. and Kuris, A. (eds). In: Crustacean Egg Production. Crustaceans Issue 7th ed. Brookfield: A.A. Balkema. 267-290.
- Wenner, A. and Kuris, A. (Eds). 1991. Crustacean Egg Production. Brookfield. A.A. Balkema. 401 pp. Witthames, P.R. and Greer Walker, M. 1987. An automated method for counting and sizing fish eggs. Journal of Fish Biology 30: 225-235.53
- Wootton, R.J. 1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. Miller P.J. (ed). Fish Phenology: Anabolic Adaptiveness in Teleosts Academic Press London, U.K. 133-159.
- Zar, J.H. 1968. Calculation and miscalculation of the allometric equation as a model in biological data. BioScience 18: 1118-1120.