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BIOLOGICAL BASIS FOR THE PROTECTION OF LARGE LOBSTERS IN LOBSTER FISHING AREAS 33 TO 38

Context

In October 2007, the Regional Director-General (RDG), Maritimes Region, announced a number of priorities for the Maritimes lobster fishery, including improving conservation measures to provide better protection for large mature female lobsters in particular. At a meeting with the lobster industry in September 2008 to discuss potential new measures, industry raised questions about the biological basis for protecting large lobsters. The RDG committed Maritimes Science to a response to the questions. A meeting with industry to revisit the issue is planned for early 2009. Given the short timeframe for the response, the Science Special Response Process was used to produce this report.

While the protection for large female lobsters was recommended in the 2007 Fisheries Resource Conservation Council (FRCC) report, the biological basis for the recommendation was not fully explored. Here we review literature on *Homarus americanus* and other species to evaluate whether there is a basis for conservation measures to protect large lobsters.

Analysis

We begin by defining large lobsters and then provide a conservation rationale for their protection based on a review of existing literature. We then list some existing conservation measures and discuss the pros and cons of potential measures to protect large lobsters in Lobster Fishing areas (LFAs) 33-38.

Defining Large Lobsters as Multiple Breeders

Female lobsters are defined here as large if they are multiple breeders. Multiple breeders are those that have produced eggs at least once and will produce eggs again if protected. Multiple breeders are substantially larger than recruit sized lobsters (82.5 mm carapace length, CL) in the LFA 33-38 fisheries and have attributes (described below) that distinguish them from first-time breeders.

Size of Multiple Breeders

The minimum size of multiple breeders will depend on the size at maturity and the size of the growth increment, which are variable among areas and individuals. The 50% size of maturity (SOM50) is the size at which 50% of the females are mature. The SOM50 in the region from the south shore of Nova Scotia to the Gulf of Maine and Bay of Fundy varies from 90-105 mm CL, being smallest on the south shore of Nova Scotia (LFA 33) and largest in the Bay of Fundy. Studies have shown a progressive increase in the size of maturity between Cape Breton and the Gulf of Maine (Campbell and Robinson 1983, Miller and Watson [unpublished data], Pezzack and Duggan 1989). Campbell and Robinson (1983) indicated the SOM50 off Grand Manan was 108 mm CL; other unpublished data suggest it could be as low as 101 mm CL (personal communication, S. Waddy, St. Andrews Biological Station). A size range of 90 to 105 mm CL for the SOM50 encompasses the range within LFA 33-38.

The table below indicates the expected size at which females that produced their first clutch of eggs at 90, 95, 100 and 105 mm CL would produce their second and third clutch. The size range for second and third egg clutches is based on the range of growth increments observed in tagging studies.

		------Expected size at subsequent clutches------	
Size at which 50% mature	Size at 1st egg clutch	Size at 2nd egg clutch	Size at 3rd egg clutch
90mm	90mm	98-104mm	106-118mm
95mm	95mm	103-109mm	111-123mm
100mm	100mm	108-114mm	116-128mm
105mm	105mm	113-119mm	121-133mm

Conservation Rationale

The basis for protection of large lobsters that are multiple breeders is provided below as a series of points, which are followed by explanations with reference to the scientific literature. The first set of points relate to the increased egg production that would result from improving the level of protection for multiple breeders. The second series of points shows that lobsters live in a variable environment and that having a greater diversity of breeding strategies increases the chances for successful reproduction.

Increased Egg Production

a. Multiple breeders are larger than first time breeders and with increasing size female lobsters produce many more eggs. A 2.3 lb lobster produces close to 2.6 times more eggs in each clutch (batch or brood of eggs) than a 1 lb lobster (82.5 mm CL) and a 3.8 lb lobster, close to 4.6 times. Very large female lobsters at sizes of 153 mm CL produce close to 8 times as many eggs per clutch.

Fecundity (number of eggs per clutch) is well known for *Homarus* (Herrick 1911, Campbell and Robinson 1983, Table 4 in Fogarty 1995, Estrella and Cadrin 1995, Agnalt 2008).

b. Lobsters are long lived animals and reproduce many times over their lifetime, but in most areas, fishing has changed the size distribution such that few reach larger sizes.

Lobsters are usually at least 8 years old before they reach minimum legal size (Gendron and Sainte-Marie 2006) and can live for another 30-50 years. Mature females can produce a clutch of eggs every 2 years, or even in successive years at larger sizes (see point c). In the absence of a fishery, females have the potential to produce up to 10-20 clutches of eggs depending on the size at which they reach maturity.

Fishing has truncated the size distribution [see point d] such that in the Gulf of Maine fisheries few females survive more than 2 years in the fishery and the result is that most females never reproduce and the majority that do only produce 1 clutch of eggs. Iteroparity (the repeated production of offspring throughout the life cycle) is an important evolutionary mechanism for coping with environmental uncertainty but in highly exploited lobster populations, we have imposed a condition approaching functional semelparity (individuals reproducing only once in their life) (Fogarty and Gendron 2004).

While the exception to this would be in the deepwater regions where larger sizes are still found, it still holds for the overall average of the various LFAs.

c. Lobsters larger than 120 mm CL have the potential to produce 2 clutches of eggs between molts.

This is based on laboratory studies of lobsters maintained at nearshore Bay of Fundy temperatures (Waddy and Aiken 1986). Below is the abstract from this paper; work since then on 50 animals substantiates this pattern (S. Waddy, pers. comm.)

> *"Large female American lobsters, Homarus americanus (> 120 mm carapace length), maintained at nearshore Bay of Fundy temperatures often spawn twice without an intervening molt (consecutive spawning). Consecutive spawning occurs in two forms: successive-year (spawning in two successive summers, a molt in the first and fourth years) and alternate-year (spawning in alternate summers, a molt in the first and fifth years). In both types, females often are able to fertilize the two successive broods with the sperm from a single insemination (multiple fertilization). Twenty of 21 large females that were held up to 13 yr displayed one of these types of consecutive spawning. Consecutive spawning and multiple fertilization enable large lobsters to spawn more frequently over the long term than their smaller counterparts. This, combined with the logarithmic relationship between body size and numbers of eggs produced, means that very large lobsters have a much greater relative fecundity than previously thought."*

Fertilization of second egg clutches can occur through stored sperm or intermolt mating (Waddy and Aiken 1990).

d. In areas where larger sizes remain, they are also under pressure as they are targeted by fishing. The numbers of large sizes have been reduced in most nearshore areas and in more recent times, we have seen the reduction of larger sizes in the USA fishery on southern Georges Bank and in some midshore areas in LFA 34.

In the early years of the lobster fishery, the size distribution was quite different than now and by the late 1800s a reduction in lobster size in U.S. and Canadian waters was evident (Herrick 1897, Venning 1873, Rathbun 1884, Wakeham 1909).

Historically large lobsters were present throughout the nearshore areas and thus spawning occurred throughout the area. In most areas, this has not been seen in many years as the first major decline in large animals occurred during the initial fishing down of the population in the late 1800s. Even with the limited gear of the time, fishermen had a major impact on the stock.

In more recent times Skud (Skud 1970) reported a progressive decline in the sizes in the newly developed offshore lobster fishery on southern Georges bank and an increased proportion of smaller lobsters. This is a trend consistent with many new fisheries that remove the larger animals that have accumulated over time and with sufficient fishing pressure reduce the bulk of the population to newly recruited animals. DFO data from the early midshore LFA 34 fishery also suggests a shift in size with a decrease in the proportion of larger sizes and an increase in the proportion of smaller lobsters (Duggan and Pezzack 1995, Pezzack et al. 1999, Pezzack et al. 2001)

Better Potential for Reproductive Success in a Variable Environment

e. Under favorable environmental conditions the population may still do well but it is a risky strategy as environmental conditions in the past have shown great variability.

In populations like lobsters where recruitment is determined during the first year of life, environment (e.g. currents, temperature, and predation) plays a crucial role. Populations may do well as long as conditions are favorable for sufficient survival of larvae and juveniles, but managing a fishery based on the need for favorable environmental conditions is risky. As breeding populations are reduced or certain components of breeders are reduced, the risk of low recruitment in any given year increases. As indicated in point b, the repeated production of offspring throughout the life cycle is an important evolutionary mechanism for coping with environmental uncertainty, but in exploited lobster populations, there is a low percentage of lobsters that breed more than once.

The Gulf of Maine and surrounding area are variable physical environments, exhibiting considerable seasonal and annual variation. There have been warm and cold periods (Frank et al. 1990, Drinkwater 2006), and year-to-year changes in temperature on the Scotian Shelf and in the Gulf of Maine are among the most significant in the North Atlantic Ocean (DFO 2005). Currents vary seasonally (Han et al. 2002, Brown and Irish 1992) and annually (Bisagni and Smith 1998). Climate change has already been observed in the U.S. Northeast and changes associated with warming (e.g. seasonal warming patterns, advances in high-spring streamflow, decreases in snow depth, extended growing seasons, earlier bloom dates) are expected to continue into the future (Hayhoe et al. 2007). Climate change has the potential to have a wide range of biological effects including modifying larval dispersal via potential changes in currents and timing of hatching in relation to their food source (Fields et al. 1993). Climate extremes are expected to increase in the future. Atlantic storms are getting stronger, with a 30-y trend that has been related to an increase in temperatures over the Atlantic Ocean (Elsner et al. 2008). In addition to variation in the physical environment, there have been profound changes in the biological environment of some areas of the Northwest Atlantic over the last few decades (Choi et al. 2004).

Although the last 10-15 years in the Bay of Fundy and LFA 34 have seen high landings and presumably a high number of breeders, it is uncertain how long this pattern will remain.

f. Different sized females undertake different movement patterns, hatch eggs at slightly different times and in different locations, increasing the chances that enough larvae will survive in the face of variability in the environment (e.g. temperature, storms and currents) adding the potential for reduced variability in recruitment.

Recent work by Gendron and Ouellet (2007) indicates that multiple breeders hatch their eggs earlier in the season than first time breeders. Hatching at different times exposes the larvae to different conditions resulting in different growth and settlement time and possibly different settlement locations.

Lobster movement studies in the Gulf of Maine (Cowan et al. 2007), showed that larger and smaller berried females were exposed to different temperature regimens during egg incubation as a result of different movement patterns with larger lobsters experiencing more stable and less extreme temperatures. Having females in a range of temperature conditions minimizes the vulnerability to extreme conditions in either the shallower nearshore or deep basins (i.e. extremely cold winters or springs inshore, or cold water extrusions in the deep basins).

Reproductive strategies that spread the risk (“bet-hedge”) are widely accepted to be important for organisms in variable environments (Stearns 1976, Flowers et al. 2002, Stevens 2006, Hsieh et al. 2006, Stevens and Swiney 2007). Lobsters live in a variable environment (see point e), and increasing the proportion of multiple breeders in the lobster population should reduce the risk of low larval survival in any given year.

g. Lobsters are migratory animals and their larvae can drift considerable distance. Some reserves of larger animals remain outside of the main fishing areas and the larvae from these animals may play a role in population stability.

Lobsters in the Bay of Fundy and Gulf of Maine can move 10s to 100s of kilometers on a seasonal basis and movement tends to be greater in larger lobsters (Campbell 1983, 1986; Campbell and Stasko 1985, 1986; Robichaud and Lawton 1997)

From their hatching locations, lobster larvae can drift to and settle in locations that range from a few kilometers to 100s of kilometers (Xue et al. 2008). Settlement areas can vary from year to year depending on wind and water movements. Local retention may also be high in nearshore coastal waters (Xue et al. 2008). Having a mix of hatching areas increases the changes of successful larval delivery to more areas.

While reserves of large lobsters are uncommon in the existing fisheries there is no indication that large lobsters have any reduced reproductive ability due to aging (Klapper et al. 1998). In fact their high fecundity and ability to produce consecutive clutches without molting means they produce eggs out of proportion to their actual numbers in the population

h. Reducing exploitation on multiple breeders reduces variability in populations by reducing risk of recruitment failure

There are numerous papers that have looked at the implications of truncated size and age structures in fisheries (Birkeland and Dayton 2005, Hsieh et al. 2006, Anderson et al. 2008, Hsieh et al. 2008). They conclude that a lack of large mature animals increases the population’s susceptibility to environmental variability resulting in greater variability in recruitment levels and population size, and susceptibility of the populations to downturns.

i. Worldwide there is growing recognition that fisheries management has been concentrating predominantly on protecting smaller sized animals and not giving sufficient consideration to the importance of the larger mature animals.

To address the recognition that large mature animals are important for reducing variability in exploited marine populations, the European states have instituted a plan to increase the numbers of large fish in all areas. This has been achieved through the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR). OSPAR is the mechanism by which fifteen Governments of the western coasts and catchments of Europe, together with the European Community, cooperate to protect the marine environment of the North-East Atlantic), using advice from the International Council for the Exploration of the Sea (ICES).

Other areas have proposed increasing the proportion of large animals in the populations through the establishment of Marine Protected Areas (MPA). These would protect large spawners and allow them to contribute to reproduction (Roberts et al. 2005, Davidson et al. 2002, Cox and Hunt 2005)

Existing Large Lobster Protection

A list of existing management measures for protection of large lobsters in the Maritimes Region, the Gulf Region and some relevant areas of the USA are provided below:

Maritimes Region:

-152 mm (6”) Maximum Hoop Size (Females/Males):	LFA 28 & 29
-132mm (5 ¼”) Maximum Size Females:	LFA 30
-114-124mm Window/Slot Size Females:	LFA 31A
-Fixed Amount V-notching Females:	LFA 31B & 32
-Voluntary V-notching Females:	LFA 33-38
-Voluntarily Restrict Landing Males/Females >6lb:	LFA 41

Gulf Region

- 115-129mm Window/Slot Size Females:	LFA 23-26B
- 114mm Maximum Size Females:	LFA 25

USA

Maximum Size (Males and Females):

-127mm (5”) Maine
-133mm (5 ¼”) southern New England
-175mm (6 ¾) offshore

The window measure in the Gulf Region was put in place in 2003 and there is evidence that it has increased egg production as expected. The contribution of window sized females to total egg production was estimated to have increased from 4% in 2003 to 23% in 2007 (MacMillan et al. 2008).

Possible Options for Protection of Larger Lobsters

The advantages and disadvantages of potential management measures in LFA 33-38 are provided below. Note that Maximum Size refers to an upper size limit that protects all lobsters above that size. Window Size refers to a size range in which all females are protected and allowed to reproduce. Females below and above the window size range can be harvested as they are now.

Pros and Cons of a Maximum Size

Pros

- Will reduce population variability over current situation
- Is a simple measure that is enforceable and will stand up in court
- Produces a large return in egg production with 6 or more extras clutches of eggs
- Targets lobsters that are in lower market demand
- Provides immediate protection to breeding animals larger than the maximum size
- Provides a buffer to periodic declines in recruitment

Cons

- Lobsters are permanently removed from the fishery (some loss in yield)

- Eliminates a size group from the market
- Takes a long time for full benefits of more eggs (>10 years)
- Will have larger impact on some sectors of the fishery that are at present more dependent on larger sizes

Window Measure

The window size range should be selected so that (i) all females are mature within the window and (ii) there are a sufficient number of females in the window to provide a measurable increase in egg production. All females in the protected or closed size range should be able to produce eggs before molting to a larger size. Females remain in this size range for one molt or 2 years, and then they are available again to the fishery. Some may remain in the closed size range for 3-4 years and produce 2 clutches of eggs

Pros
- Will reduce population variability over current situation
- Is a simple measure that is enforceable and will stand up in court
- Allows lobsters available again to the fishery at larger sizes
- Provides immediate protection to breeding animals
- Allows 1 extra clutch of eggs (some will produce 2 extra clutches)
- Egg benefits occur quickly
- Results in an increase in numbers of larger females some of which will reproduce again before capture by the fishery

Cons
- Requires three measures (minimum legal, lower window, upper window)
- Produces only one extra clutch, though some will produce two extra clutches
- Reduces the availability of a middle size group in the market
- Will have larger impact on some sectors of the fishery that are at present more dependent on window sizes
- Provides little long-term buffer if recruitment declines because it only protects 1-2 molt groups

At the September 12, 2008, meeting with industry concern was raised that there could be cannibalism by larger lobsters left on the bottom. Our review indicates cannibalism has not been observed to be significant. While lobsters can be cannibalistic when reared in close proximity, long-term observations of captive lobsters indicate that when provided with shelter and fed to excess with high quality food (lots of shrimp and mollusks), cannibalism ceases to be an issue (S. Waddy, pers. comm.). In nature, cannibalism does not appear to be important. In fact Saint-Marie and Chabot (2002) reported that smaller lobsters are often associated with larger lobsters and may benefit from excess food the large lobsters have hoarded:

> *"Indeed, we observed that small lobsters often occupied galleries beneath, or in rock pilings nearby, the dens of larger lobsters. This is consistent with reports that odour from conspecific adults is a proximate cue for lobster settlement (Boudreau et al., 1993). Cohabitation of small lobsters with large lobsters would offer the former protection from predators and a potentially abundant, high-quality, sheltered food source, and would therefore represent a form of commensalism. The risk of cannibalism for small lobsters living in the vicinity of larger lobsters probably does not offset the benefits. Few lobster remains were found in lobster stomachs in this study as in other studies (Weiss, 1970; Carter*

and Steele, 1982; Elner and Campbell, 1987), and an unknown proportion of those remains may have been exuviae."

With regard to potential interactions in traps, we note that unlike most other lobster fishing areas, the Bay of Fundy and offshore still have a high proportion of large lobsters in their catch. In these areas there are no reports that cannibalism in traps is any greater than elsewhere.

Mature Males under Maximum Size and Window Measures

If females are protected by a maximum size, large mature males will require protection for the following reasons:

- To mate, males must be either similarly sized to the female or larger. Larger males can mate with a wider range size of females, but males can be too large to mate with a small female
- While males grow faster than females, males also have a higher exploitation rate because females are protected when they are berried.
- One male can mate with a number of females; however there is a limit to the number of females a male can mate
- In the Bay of Fundy mature males do not necessarily mate every year. Nearly all of their mating is in years that they do not molt (Waddy and Aiken 1991)
- A shortage of males could affect the success of female insemination (DFO 2006). This could result in failure of some females to mate, unfertilized eggs and incomplete egg clutches. There is some evidence for sperm limitation in lobsters (Gosselin et al. 2003, 2005).

Under a window measure no protection of males is thought to be required because there should be a sufficient number of males to mate with the window-size females. To ensure this is the case, reproductive success of window-sized females should be monitored.

Quantifying the Benefits from Protecting Large Lobsters

The benefits of protecting large lobsters have been quantified with a lobster growth and reproduction model (egg-per-recruit) (Lawton et al. 1999, Pezzack et al. 1999). These analyses showed that egg production would increase under various maximum sizes for females, with the level of increase depending upon the size adopted, the area of the fishery and the exploitation rate. For example in the analysis done at that time a maximum size of 127 mm CL would increase egg production by 30-120% depending on the LFA and estimates of exploitation rates. At larger maximum sizes the benefits dropped off. Compared to a maximum size of 127 mm CL the egg-per-recruit increases were less than half for a maximum size of 133 mm CL and about 1/10th for a maximum size of 140mm.

Given some candidate scenarios for protection of large lobsters, their relative value can be compared by revisiting the lobster growth and reproduction model previously used to estimate egg-per-recruit levels. If measures for protection for large lobsters are adopted, benefits can be quantified by monitoring reproduction indicators such as berried female abundance, egg production by primi- and multiparous females, female insemination, and sex ratios.

Conclusions

There is a firm biological basis for providing additional protection for large female lobsters that are multiple breeders. Additional protection reduces the risk to the long-term sustainability of lobster populations and is consistent with the precautionary approach.

The evidence presented comes from experiences with other species and other fisheries, and in what is known about the reproductive biology and life history of *Homarus americanus*, and the variable environment in which *Homarus* lives. Protection of large females that are multiple breeders results in increased egg production and a greater diversity of breeders that will lead to more successful egg production under a variety of environmental conditions.

The two main approaches for protecting large female lobsters are a maximum size and a closed window size. There are advantages and disadvantages of each approach.

Previous analyses indicated that additional protection of large lobsters could result in considerable increases in egg production. These analyses only considered the added value of the increased fecundity associated with larger sizes. This document presents evidence that protecting large lobsters increases not only fecundity, but also potentially the overall survival rates of larvae. By increasing the duration and number of locations of hatching, the chances that larvae will survive under variable environmental conditions is increased.

Egg production will increase under various levels of protection for large females but the level of increase will depend on the exact measure adopted. Given some candidate scenarios for protection of large lobsters, their relative value can be compared by revisiting a lobster growth and reproduction model. If measures for protection of large lobsters are adopted, reproduction indicators can and should be monitored.

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Appendix - Notes on issue of multiple breeders and egg size.

Egg size has implications for survival of planktonic larvae. It has generally been thought that larvae hatched from larger eggs survive better (e.g. Giméneza and Anger, 2001; Rideout et al. 2005), although this has not been demonstrated for *Homarus*.

In a review of the literature for a number of lobster species on the relationship between female size and egg size and subsequent survival, there is a mixture of patterns. There is some evidence that smaller and first time breeding females produce smaller eggs and the size increases in subsequent breedings. The evidence for *Homarus* is mixed and does not appear to extend to all areas.

A 2001 report on *Homarus americanus* indicated that egg size increased with increasing maternal size (Plante et al. 2001). Later work by Ouellet and Plante (2004) indicated that egg size does not continue to increase as lobsters grow but eventually levels off. They suggested that the difference in egg size is more related to whether the females are first time breeders (primiparous) or multiple breeders (multiparous).

In the plots of egg size or Stage I larvae size versus female size from Ouellet and Plante (2004), there is an increase in egg or larval size over the adult female size range of 80-110 mm CL. Other studies on the closely related European lobster, *Homarus gammarus* show a similar pattern of smaller eggs in smaller females and a non-linear increasing egg size reaching a maximum size in multiple breeders (Jorstad et al. 2005, Agnalt 2008)

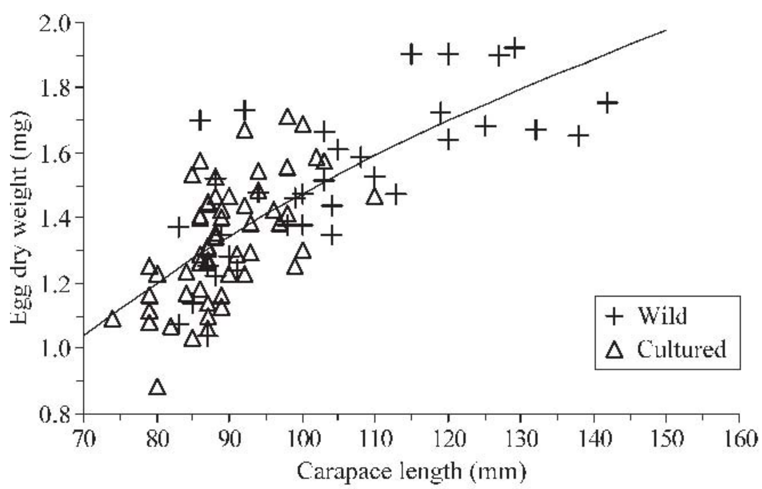

Figure 5. Relationship between egg dry weight (mg) and CL (mm) for wild and cultured European lobster (*Homarus gammarus*), seasons combined. The solid line is a natural logarithm-fitted model fitted to all data combined ($y = 1.2286 \ln CL - 4.1827$, $r^2 = 0.56$, $n = 93$).

Figure from Agnalt 2008.

Studies by Ouellet, Plante and Annis (2003) did not detect an increase in egg size among multiple breeders in the Gulf of Maine. They reported that in two populations of the Gulf of St. Lawrence the small females (first-time spawners) tended to produce small eggs, and hatching larvae that are smaller relative to larger (multiple spawners) females. However, this effect was not observed in lobster populations where size at maturity is larger; e.g., Bay of

Fundy, Gulf of Maine. For each year and population, there was high variability in egg size within individual females.

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