**Stomach contents and stable isotope analysis of snow crab (*Chionoecetes opilio*) in the southern Gulf of Saint Lawrence and Scotian Shelf.**

Introduction

The snow crab fishery in the southern Gulf of Saint Lawrence (sGSL) began in 1966 and is now one of the most important commercial fisheries in Atlantic Canada (Hébert et al., 1992; Sainte-Marie et al., 1995). This male-only fishery is currently regulated by quotas, a minimum legal size of 95 mm carapace width (CW) and a limited number of traps per licence (Hébert et al., 1992). Annual quotas are estimated from data gathered on post-season trawl surveys from the previous year, which provide important information on snow crab population abundance and composition (Moriyasu 2011a). Economically, the snow crab population industry is worth millions of dollars and generates thousands of jobs, either directly (fishermen, crew members) or indirectly (boat building, fish processing, tourism). Consequently, many small Atlantic coastal communities depend on and greatly benefit from this fishery. Ecologically, sGSL’s benthic community is biodiverse (DFO, 2005) and specific areas are known for high concentrations of snow crab of different life stages.

The sGSL is not immune to growing pressures on the oceans. Rising temperatures and ocean acidification can have widespread effects on marine fish and invertebrates and the ecosystems they comprise (Yao and Somero, 2014; Linares et al., 2015). Since the 1990s, mean bottom water temperatures in the sGSL have been following a general warming trend (Chassé et al., 2015). Furthermore, several studies have shown that even small changes in ocean climate can induce dramatic and persistent changes in benthic ecosystems. Stortini et al. (2015) indicated that snow crab and lower trophic levels were some of the most vulnerable populations in severe warming scenarios (increase of 3°C) which could result in shifts on the ecosystem structure and possible trophic imbalances. As such, monitoring population and trophic dynamics becomes increasingly important to assess the impact of snow crabs on benthic communities and vice versa.

In recent years, there has also been an increase in interest in offshore hydrocarbon exploration in lucrative snow crab fishing grounds. Preliminary work by Moriyasu et al. (2004) and Christian et al. (2003) studied the possible immediate and delayed impacts of seismic testing on snow crabs in the field. Moriyasu et al. (2004, 2011b) used caged snow crabs; however, baseline information on the effects of caging on snow crab has never been examined and it remains unknown if caged animals are representative of the natural population. Caging itself may create a stress response (i.e. limit food availability) in crabs, making it difficult to distinguish the effects between caging and the imposed treatment (i.e. seismic testing). Since oil and gas exploration continues to be of great interest in snow crab habitat and future caging studies are most likely, a better understanding of the possible direct or indirect effects of caging is essential.

Anthropogenic effects on marine ecosystems can result in changes to species’ distribution, behavior and diet over time. Studies on snow crab diets in the southern Gulf of Saint Lawrence have suggested highly variable diets dependent on population densities, crab size and benthic communities (Lovrich and Sainte-Marie, 1997; Brêthes et al., 1984; Squires and Dawe, 2003). However, these studies did not examine possible effects of sampling method on dietary selection and diversity. Furthermore, these studies focused solely on gut content analysis which allows stomach components to be quantified in terms of specific taxa ingested, but not necessarily assimilated. As such, ingested items can't always be identified due to their small size or advanced digestion and softer diet components may be significantly underestimated. The use of stable isotope analysis (SIA) is a technique increasingly used in combination with stomach content analyses to assess trophic relationships in a variety of ecosystems. While stomach content analyses give a snapshot view of an organism’s feeding behaviour, SIA can provide a time-integrated method of diet analysis and delineate trophic structures within a food web.

The most commonly used stable isotopes for SIA are nitrogen (N) and carbon (C). Stable N isotope data have been used to delineate trophic structure in a food web since nitrogenN in tissues of consumers typically increases by 3‰ relative to their prey (Owens, 1987; Peterson and Fry, 1987). In addition to an increase between 0.0 to 0.1‰ per trophic level, C provides information of the source of carbon to the food web. More specifically, the ratio of the stable carbon isotopeC, to the more common C, is used discriminate the degree to which organisms are relying on pelagic and benthic based food sources (primary producers such as phytoplankton and microphytobenthos) within the web. The analysis of carbon and nitrogen isotopes are often used in conjunction and the measurement of both concurrently yields more information on feeding relationships and greater segregation of species than the use of a single element (Peterson and Fry, 1987).

This study was part of a larger scale report that established a wide range of biological baseline information of snow crabs in the southern Gulf of Saint Lawrence and the Scotian Shelf (Moriyasu et al., 2015). The objectives of this study were to 1) describe the diet of snow crab in the southern Gulf of Saint Lawrence and compare present results from data obtained in 2002; 2) apply stable isotope analysis, in association with stomach content analyses, to snow crabs in order to examine their dietary intake and feeding habits at different life stages; and 3) examine the effects of sampling method (trapping versus trawling) and caging on the diet of snow crabs.

**Materials and Methods**

Snow crab sampling

Snow crabs were caught by trapping and trawling in the southern Gulf of Saint Lawrence and off eastern Nova Scotia (Figure 1). Trawled catches were collected in the spring, summer and fall of 2002 and the fall of 2010 during the annual snow crab trawl surveys. A Bigouden *Nephrops* trawl net was used (mesh size of 50mm at cod end) at six tow stations. Tow durations were about 5 minutes with a vessel speed of 2 knots.

Samples of snow crab caught by trapping were collected at four stations in the spring and fall of 2012 and 2013 using three different traps types (commercial snow crab traps, modified shrimp traps and commercial rock crab traps) baited with either frozen mackerel (*Scomber scombrus*) or herring (*Clupea harengus)* and covered with a nylon mesh to prevent crabs from ingesting the bait. Traps soak times ranged from 6 to 36 hours.

* Briefly describe the spatial layout of the different types of traps in each location.
* Also, I think the type of size-based sub-sampling which was performed is not described.

At two of these trap stations, a sub-sample of crab were caged for a period 2 weeks, 6 months, and 12 months, using wire mesh cages (121 cm x 91 cm x 31 cm, 3.80 cm mesh) with a rectangular top opening (107 cm x 70 cm) and weighted with three cement bars of 121 cm x 6 cm each (total of 9kg). At each of the two cage stations, 6 lines consisting of 15 cages were set. The first 10 cages contained one mature male snow crab each while the remaining 5 cages each contained either 4 mature females or 4 small claw males (Figure 2). Each cage opening was securely closed with black UV tamper-proof 20 cm tie wraps. At each cage station, two lines of cages were lifted after two weeks, 6 months and 12 months of cage immersion.

* **How far apart were the cages, approximately? How far apart were the lines?**

On board the vessel, a modified electronic calliper was used to measure all crab caught for carapace width (CW) (both sexes), abdomen width (females) and the height of the right cheliped (males) to the nearest 0.1mm. Sexual maturity was determined morphometrically using differences in relative growth in the abdomens (females) and chelae (males). Subsamples were retained for dissection, with crab grouped by sex and maturity, while immature males were further subdivided into large (>= 50mm CW) and small (< 50mm CW) categories. Crabs were kept in chilled coolers until arrival at the dissection site.

At the dissection site, the pattern of missing appendages, carapace condition (CC), crab weight, cheliped hardness (males), hepatopancreas color and weight, ovary color and weight, and egg color were recorded for each sampled crab. Crab weight was measured to the nearest 0.1g while internal organ weights were measured to the nearest 0.1 mg. Shell hardness was determined using a durometer.

Stomach contents analysis

Once removed, crab stomachs were and frozen immediately in sample bags and brought tothe laboratory. Stomachs were then thawed and weighed to the nearest 0.1mg. Stomach fullness was assessed visually on a scale of 1 (< 25%), 2 (26 to 50%), 3 (51 to 75%) to 4 (>75%). Stomachs were opened and rinsed with water to remove contents. Food items were observed under a dissection microscope, identified and classified to the lowest taxon possible. Food items were divided into 11 categories: polychaetes, fish, crab, non-crab crustaceans (amphipods, copepods, shrimp, barnacles), mollusks (bivalves, gastropods), echinoderms (brittle stars, starfish, sea urchins), plant/algae, eggs, man-made (twine, rope, gloves, plastic), detritus and other (insects, foraminifers, parasites, plankton). Empty stomachs and their food items were placed on separate filters (VWR filter paper with a 7.5cm diameter and grade 413) and then weighed and dried for a minimum of 24 hours at 60 °C in a drying oven. Dried stomachs and their content were weighed to the nearest 0.1 mg. Content weight percentages and frequency of occurrences were calculated for all prey items in the stomachs of each snow crab category.

Stable Isotope Analysis

For stable isotope analysis, samples of the merus muscle (2nd walking leg) were carefully dissected from the exoskeleton and tendons and immediately frozen in sample bags at -20°C. For smaller sized crabs, merus muscle from both 2nd walking legs was collected in order to have the enough tissue for analysis.

In the laboratory, snow crab muscle samples were thawed and transferred in 20 ml vials with top openings covered with aluminum foil. Muscle samples were dried in a drying oven for a minimum of 48 hours at 60 °C. Samples were then manually grinded into a fine powder with a mortar and pestle, returned in capped vials and brought to the Stable Isotopes in Nature Laboratory, Fredericton, New Brunswick for C and N isotope analysis. Dried tissue samples were weighed to the nearest 0.001mg and packed into tin capsules. Samples were flash combusted at 1100ºC using either a Carlo Erba NC2500 or Costech 4010 Elemental Analyser and resultant gases via continuous-flow were analyzed using a DELTA Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Waltham, MA, USA). Isotopic ratios were expressed in conventional delta (*δ*) notation in parts per thousand (‰) deviations from the international standards (AIR for nitrogen and V-PDB for carbon) as follows: *δ* X = [(R sample / R standard) -1] where X is 13C or 15N and R is the ratio of 13C /12C or 15N /14N. Measurements of commercially available reference material were compared across all runs for accuracy and precision. These reference materials were calibrated against the International Atomic Energy Agency (IAEA) standards. Within a given analytical run, one standard deviation of sample repeats was never greater than 0.13‰ for *δ* 13C or 0.19‰ for *δ* 15N. Analytical precision estimated as the SD of replicate analyses from laboratory standards averaged 0.13‰ and 0.14‰ for carbon and nitrogen, respectively.

Statistics

Data analysis using parametric and non-parametric tests was performed with Minitab ® (version 16.2.3.0, MINITAB Inc. State College, PA, USA) and Microsoft Excel (version 14.0., Microsoft. Redmond, Washington, DC, USA) statistical software packages. Data were examined for normality (based on the Anderson-Darling normality test), and variance homogeneity (Bartlett’s test). As data did not follow a normal distribution, or heteroscedasticity was detected and did not improve even after data transformation, non-parametric tests (Kruskal-Wallis, followed by nonparametric multiple comparison tests) were applied. All results obtained were considered significant at the significance level of 0.05.

Results

Stomach content analysis

A total of 2282 snow crab stomachs were collected and analysed for this study (Table 1). Visually, the majority of crab stomachs (70%) were less than 25% full and 1% were found to be completely empty (Figure 3). In terms of total stomach content weights, 47.9% contained less than 10 mg of food items (Figure 4). Stomach content weights by size class are summarized in Figure 5. For mature crabs, stomach contents were generally heaviest in trapped crabs and lightest in caged crabs for 2 weeks (Table 2). No trend was observed between stomach content weight and caging period. With the exception of crabs less than 50 mm CW (where sample size was considerably low for both male and female trapped crabs), the stomach content weight of trawled animals was lighter than in trapped crabs.

Snow crab diet is quite variable, and stomachs generally had between 3-11 prey types. Overall, the most common identified prey categories observed in stomachs were polychaetes, fish, crab (almost all snow crab), crustacean (non-crab) and mollusks (Figure 5). Polychaetes were present in most crab categories regardless of sampling method. Crustaceans were more often seen in trapped and trawled crabs while crab was more often seen in caged animals. The category “insects” was only seen in trawled animals while the miscellaneous categories “other” and “human-made” were only detected in caged and trapped animals. Detritus (which included sand) was present and frequent in every crab category regardless of sampling method.

Variability by sampling method?

In terms of prey content weight, fish and crab contributed more to the total content weight even when these items were not observed as frequently (Figure 6). Weight percentages of crab as a prey item were highest in caged crab regardless of the length of caging period or number of crabs per cage. Polychaetes were also a major contributor of total content weights, especially in caged animals. Fish and crustaceans represented the majority of total content weights for crabs caught by trapping while mollusks and crustacean contributed more to the total content weights of crabs caught by trawling.

Stable isotope analysis

A total of 443 muscle samples were collected for stable isotope analysis. Crab sampling sites and seasons were combined to assess primarily the isotopic composition of sources sampled and the possible differences among crab categories and sampling method. Stable isotope analysis of C (C) and N () of snow crab are summarized in Table 3 and Figure 7. Overall, isotope values displayed a 2.7 ‰ range for C (-19.404 to -16.688) and a 4.5‰ range for N (11.610 to 16.136). Significant differences were noted among crab categories for both C and N (ANOVA, p < 0.0005). C values generally tended to be depleted in caged crab categories compared to trapped crabs. Large male categories (> 100 mm CW) were more enriched and this was significant among mature male trapped categories (Table II). When comparing males and females of similar size, mature female categories were more depleted than male categories of the same size and this was significant between crabs of 75-100mm CW (ANOVA, p < 0.0005). N values of immature crab categories were significantly depleted compared to all but one crab categories (ANOVA, p < 0.0005) (FIGURE OR TABLE). Caged crabs, especially crabs caged for 12 months, had enriched N values compared to trapped crabs. No significant differences were observed among mature trapped crab categories.

Sampling method and treatment comparison

Discussion

The main objective of applying stable isotope analyses on snow crab muscle samples for this study was to compare these results with those obtained from stomach content analyses. While stomach content analyses document feeding habits on a short-term scale, measurements of naturally occurring stable isotopes of nitrogen and carbon can provide dietary patterns and trophic relationships integrated over a period of time. Stable isotope analysis can also help alleviate the challenge of stomachs containing little content or unidentifiable prey items. In this study, since important prey items such as fish were not collected, it is difficult to accurately quantify the importance of each prey item by stable isotope analysis. Nonetheless, a general view of snow crab isotopic composition was obtained and possible differences among crab categories and sampling method were observed.

*δ13C*

Carbon isotope composition of a consumer provides information of the source of carbon. Although negligible differences occur between trophic levels for δ13C, the ratio of the stable carbon isotope 13C, to the more common 12C, is used to discriminate the degree to which organisms are relying on pelagic and benthic based food sources (primary producers such as phytoplankton and microphytobenthos) within the foodweb (Dennard *et al.* 2009). Values of δ13C for snow crab were within the range of potential food sources and were comparable to current literature (Kolts *et al.* 2013b). Females were significantly depleted in δ13C compared to males (both large and pygmy) regardless of sampling method, and values of δ13C in pygmy males usually fell between females and large males. Even though the minimum of 0.4 to 1‰ in δ13C values was small, the differences between males and females were consistent and are likely due to size differences. Bodin *et al.* (2007) found higher δ13C values in older/larger crab compared to juvenile/smaller Maja brachydactyla suggesting a change in feeding habit. As previous work on stomach content analyses have documented differences between size classes (Lovrich & Sainte-Marie 1997, Squires & Dawe 2003), it would be interesting to apply stable isotope analysis on smaller/immature snow crab.

*δ15N*

N data have been used to delineate trophic structure in a food web since N in tissues of consumers typically increases by 3 to 3.4‰ relative to their prey (Owens 1987, Peterson & Fry 1987, Post 2002). In this present study, a 3‰ shift in trophic level was not observed regardless of crab category and sampling method. A trophic level shift with body size in *Maja brachdactyla* was also not observed by Bodin *et al.* (2007). Nonetheless, the significantly higher N values noted among 6 month caged females and 12 month large mature males may suggest that these crab categories may be experiencing a shift in diet composition or physiological stress. Physiological stress, such as limited food availability, has been documented to increase N values in sunfish, planarians and beetles (Colborne & Robinson 2013, Boag *et al.* 2006, Scrimgeour *et al.* 1995, respectively). The gradual increase in *δ*15N observed among wild, 6 month caged and 12 month caged large mature males suggests that long term caging may have more deleterious effects on larger crab. Caging may not meet the energetic requirements of large mature males and thus may be more detrimental for this category of crab. Interestingly, nutritional stress may not explain the higher values of N observed in females caged for 6 months as stomach contents for this category were fuller than other female crab categories. One possible explanation is the type of prey ingested. Females caged for 6 months had high levels of crab in their stomachs which could result in an increase in N values as they are eating from a higher trophic level (i.e. cannibalism).

In summary, stable isotope analysis, in combination with stomach content analysis, provide relevant information on taxonomic importance and trophic position of snow crab. The diet of snow crab, in terms of stomach content and stable isotope analysis, is composed of a wide variety of taxa and shows possible size differences and caging effects. Crab sampling by trapping may be biased towards hungry crab and other sampling methods (such as trawling) should be considered in future studies. Additionally, as previous stomach content studies suggest that differences in diet may be dependent on the size of the crab, especially between small/immature crab and large/mature crab, a wider range of crab size should be sampled. Seasonal and site-specific patterns were not consistently observed but differences could be attributed to prey abundance during sampling and should be examined in future studies. Values of C suggest a relative change in primary food source between males and females that is related to crab size. Comparable values of N for wild crab categories suggest large mature males and females share the same trophic level. Higher values of N observed in large mature males caged for 12 months and females caged for 6 months may suggest a nutritional stress and dietary shift in these crab categories, respectively.

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Table 1.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Year | Treatment | Sex | CW range (mm) | No stomachs | No isotopes samples |
| 2002 | Trawl | F | < 50 mm | 76 | 0 |
|  |  | M | < 50 mm | 20 | 0 |
|  |  | F | 50-75 mm | 442 | 0 |
|  |  | M | 50-75 mm | 122 | 0 |
|  |  | F | 75-100 mm | 24 | 0 |
|  |  | M | 75-100 mm | 399 | 0 |
|  |  | M | > 100 mm | 82 | 0 |
| 2010 | Trawl | F | < 50 mm | 0 | 11 |
|  |  | M | < 50 mm | 0 | 10 |
|  |  | F | 50-75 mm | 0 | 6 |
|  |  | M | > 100 mm | 0 | 6 |
| 2012 | Trap | M | < 50 mm | 2 | 0 |
|  |  | F | 50-75 mm | 126 | 29 |
|  |  | M | 50-75 mm | 54 | 11 |
|  |  | F | 75-100 mm | 38 | 10 |
|  |  | M | 75-100 mm | 88 | 29 |
|  |  | M | > 100 mm | 159 | 40 |
| 2012 | Cage 2 weeks | F | 50-75 mm | 33 | 0 |
|  |  | M | 50-75 mm | 4 | 0 |
|  |  | F | 75-100 mm | 7 | 0 |
|  |  | M | 75-100 mm | 35 | 0 |
|  |  | M | > 100 mm | 38 | 0 |
| 2013 | Cage 6 months | F | 50-75 mm | 27 | 13 |
|  |  | M | 50-75 mm | 9 | 3 |
|  |  | F | 75-100 mm | 10 | 7 |
|  |  | M | 75-100 mm | 27 | 15 |
|  |  | M | > 100 mm | 34 | 21 |
| 2013 | Cage 12 months | F | 50-75 mm | 25 | 15 |
|  |  | M | 50-75 mm | 14 | 7 |
|  |  | F | 75-100 mm | 8 | 5 |
|  |  | M | 75-100 mm | 15 | 13 |
|  |  | M | > 100 mm | 24 | 19 |
| 2013 | Trap | F | < 50 mm | 1 | 0 |
|  |  | F | 50-75 mm | 85 | 42 |
|  |  | M | 50-75 mm | 68 | 36 |
|  |  | F | 75-100 mm | 17 | 12 |
|  |  | M | 75-100 mm | 54 | 24 |
|  |  | M | > 100 mm | 115 | 59 |
| **TOTAL** |  |  |  | **2282** | **443** |

Table 2.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Crab category | Treatment | Sex | n | Mean dry content weight (mg) | St. dev. |
| < 50 mm | Trap | F | 1 | 14.0 | - |
|  | Trawl |  | 76 | 21.30 | 31.76 |
|  | Trap | M | 2 | 1.55 | 1.63 |
|  | Trawl |  | 20 | 16.36 | 22.00 |
| 50-75 mm | Trap | F | 211 | 60.07 | 87.85 |
|  | Trawl |  | 442 | 23.33 | 35.95 |
|  | Cage 2 weeks |  | 33 | 6.48 | 10.68 |
|  | Cage 6 months |  | 27 | 57.6 | 74.7 |
|  | Cage 12 months |  | 25 | 12.82 | 19.91 |
|  | Trap | M | 122 | 47.32 | 96.26 |
|  | Trawl |  | 122 | 32.89 | 54.71 |
|  | Cage 2 weeks |  | 4 | 1.625 | 1.982 |
|  | Cage 6 months |  | 9 | 45.7 | 85.3 |
|  | Cage 12 months |  | 14 | 27.96 | 36.99 |
| 75-100 mm | Trap | F | 55 | 62.9 | 95.8 |
|  | Trawl |  | 24 | 30.8 | 64.2 |
|  | Cage 2 weeks |  | 7 | 3.83 | 5.30 |
|  | Cage 6 months |  | 10 | 94.1 | 118.1 |
|  | Cage 12 months |  | 8 | 45.9 | 80.9 |
|  | Trap | M | 142 | 70.35 | 114.28 |
|  | Trawl |  | 399 | 32.13 | 53.00 |
|  | Cage 2 weeks |  | 35 | 8.73 | 31.12 |
|  | Cage 6 months |  | 27 | 10.89 | 39.48 |
|  | Cage 12 months |  | 15 | 13.67 | 34.44 |
| > 100 mm | Trap | M | 274 | 215.0 | 39.09 |
|  | Trawl |  | 82 | 82.8 | 129.7 |
|  | Cage 2 weeks |  | 38 | 10.33 | 12.38 |
|  | Cage 6 months |  | 34 | 9.28 | 18.63 |
|  | Cage 12 months |  | 24 | 78.1 | 245.1 |



Figure 1. Visual estimation of stomach fullness by crab category for trawled crabs (A), trapped crabs (B), crabs caged for 2 weeks (C), crabs caged for 6 months (D), and crabs caged for 12 months (E). (light grey bars: less than 25% full, white bars: 25-50% full; dark grey bars: 50-75% full; black bars: 75-100% full.



Figure 2.



< 10 mg

10-25 mg

25-50 mg

50-75 mg

75-100 mg

100-200 mg

200-300 mg

300-400 mg

400-500 mg

500-1000 mg

1000-1500 mg



Figure 2. Content weight by category. AA: sexe and treatments combined; A: females by sampling treatment and, B: Males by sampling treatment

< 10 mg

10-25 mg

25-50 mg

50-75 mg

75-100 mg

100-200 mg

200-300 mg

300-400 mg

400-500 mg

500-1000 mg

1000-1500 mg















Polycheates

Fish

Crab

Crustacean

Mollusks

Echinoderm

Plant

Eggs

Human-made

Detritus

Insect

Other

Table 3.Summary of mean carapace width (CW), weight andC and N values (with standard deviation in parentheses) of snow crab by size category. Data are separated to show the three sampling treatment: free (caught by trap), caging for 6 months and caging for 12 months (IM = Immature male; IF = Immature female; MM = Mature male; MF = Mature female).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Sampling type | Crab size category (in mm) | Sexe | n | CW (mm) | Weight (g) | C | N |
|  | < 50 | IM | 10 | 35.14 (2.43) | 15.67 (3.30) | -17.810 (0.235) | 11.900 (0.194) |
|  |  | IF | 11 | 36.31 (3.33) | 16.56 (4.11) | -17.980 (0.128) | 11.954 (0.238) |
|  | 50-75 | MM | 47 | 69.11 (4.27) | 135.42 (24.41) | -17.963 (0.467) | 13.037 (0.422) |
| Free |  | MF | 77 | 66.64 (5.17) | 107.57 (23.24) | -18.152 (0.376) | 13.00 (0.399) |
|  | 75-100 | MM | 53 | 82.25 (5.07) | 218.47 (47.96) | -17.958 (0.434) | 12.99 (0.428) |
|  |  | MF | 22 | 79.41 (4.84) | 160.95 (24.24) | -18.275 (0.428) | 13.260 (0.536) |
|  | > 100 | MM | 105 | 120.33 (8.96) | 756.1 (174.7) | -17.634 (0.347) | 12.979 (0.451) |
|  | 50-75 | MM | 3 | 64.24 (3.92) | 104.30 (9.27) | -18.065 (0.417) | 12.610 (0.329) |
|  |  | MF | 13 | 69.15 (3.79) | 119.75 (17.74) | -18.529 (0.288) | 13.533 (0.509) |
| 6 months caged | 75-100 | MM | 15 | 87.87 (6.66) | 282.9 (58.0) | -17.910 (0.491) | 13.248 (0.572) |
|  |  | MF | 7 | 81.30 (3.90) | 177.96 (19.51) | -18.513 (0.304) | 13.599 (0.146) |
|  | > 100 | MM | 21 | 124.09 (6.66) | 841.7 (155.1) | -17.807 (0.380) | 13.216 (0.384) |
|  | 50-75 | MM | 7 | 65.94 (3.15) | 116.5 (20.07) | -18.523 (0.579) | 13.891 (0.923) |
|  |  | MF | 15 | 67.92 (4.96) | 109.31 (23.09) | -18.677 (0.326) | 13.356 (0.486) |
| 12 months caged | 75-100 | MM | 13 | 85.52 (6.85) | 253.7 (66.3) | -18.140 (0.642) | 13.376 (0.884) |
|  |  | MF | 5 | 79.24 (3.27) | 167.3 (31.7) | -18.749 (0.349) | 13.954 (0.579) |
|  | > 100 | MM | 19 | 123.91 (6.79) | 835.5 (128.8) | -17.660 (0.554) | 14.279 (0.874) |



Figure 5

Figure 6

Table 4

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  |  | DF | Sum of Squares | Mean Square | F | p-value |
|  | Between Groups | 16 | 38.278 | 2.392 | 14.52 | < 0.0005 |
| C | Within Groups | 426 | 70.200 | 0.165 |  |  |
|  | Total | 442 | 108.478 |  |  |  |
|  | Between Groups | 16 | 74.490 | 4.656 | 19.48 | < 0.0005 |
| N | Within Groups | 426 | 101.823 | 0.239 |  |  |
|  | Total | 442 | 176.313 |  |  |  |