

Survival and condition of hard shell male adult snow crabs (*Chionoectes opilio*) during fasting at different temperatures

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Abstract

There is a limited body of information on the impact of starvation in snow crab. In other species, it has been shown to negatively affect survival, protein, lipid, and carbohydrate content of tissues. This study compares survival and condition of unfed hard-shell male adult snow crabs kept at different temperatures during a holding period of 5 months. We observed 7.1–20.7% mortality according to holding temperature. Major changes were observed in tissue composition in both muscle and digestive gland. Fasting mainly resulted in an increase of water content in both tissues due to a decrease in lipid content (digestive gland) and protein content (muscle). Our results suggest that snow crabs can tolerate extended periods of starvation and that temperature has a mitigated effect on their condition. We propose the use of moisture content of digestive gland and possibly muscle as indices of the nutritional status of snow crab, on the basis of their relationship with lipid content ($R^2 = 0.67$) and protein content ($R^2 = 0.65$), respectively. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Snow crab (*Chionoectes opilio*) is the most valuable commercially exploited crab species in eastern Canada. Most of the catch has historically been exported to the US

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and Japan (Boucher, 1994). Being a small producer of snow crab however, eastern Canada has little influence on international market prices. Due to a short fishing season and high dependence on exports, local industry has pushed for the development of a regional market for *C. opilio*. This has stimulated research into long-term holding to offer live crabs off-season: snow crab landed by the fishery would be kept unfed for a short or an extended period of time under such holding conditions as to promote high survival rates and a minimum loss of quality, using similar methods as for lobster (*Homarus americanus*).

There is a limited body of information on the impact of starvation in snow crab and other crabs, most of which refers to larval stages (Kon, 1979; Anger and Dawirs, 1982; Schuh and Diesel, 1995a,b; Diesel and Schuh, 1998). Starvation of crabs during holding has been shown to negatively affect survival (Kimker, 1994; Paul et al., 1994; Provencher et al., 1995). A 60-day period of food deprivation resulted in a reduction of muscle mass, DNA content, and enzyme activity in the merus muscle, and a reduction in size of the digestive gland, while gonad weight increased in male adult snow crab following terminal moult (Mayrand et al., 2000). Digestive gland and muscle glycogen and lipids decreased during starvation in *Chasmagnathus granulata* over a similar time period (Vinagre and DaSilva, 1992). In the common shore crab (*Carcinus maenas*), Uglow (1969) found that 28 days of food deprivation significantly decreased haemolymph protein concentrations. Shorter fasting periods resulted in low digestive gland and hemolymph carbohydrate concentrations in various crab species (Dean and Vernberg, 1965; Parvathy 1971).

Snow crabs live in a fairly stable environment and are found at temperatures ranging up to 5°C (Williams, 1984). They are highly sensitive to variations of salinity but fairly tolerant to a wide range of temperatures (Hardy et al., 1994a). In the laboratory, hard-shell snow crabs tolerated temperatures up to 12–15°C (McLeese, 1968; Hardy et al., 1994b). However, all these experiments were performed on fed crabs and over short periods of time. We have little knowledge of the effects of temperature on the physiological aspects of the snow crab biology in a holding-tank environment. This study compares survival and physiological condition of unfed hard-shell adult male snow crabs kept at different temperatures during a holding period of 5 months.

2. Materials and methods

2.1. Animals

A total of 750 commercial size (carapace width > 95 mm) male snow crabs (*C. opilio*) were obtained from the St. Lawrence Estuary near Rimouski (Québec) between May 20 and May 26, 1992. They were caught using baited traps at depths ranging from 70 to 110 m.

Crabs were acclimated to holding conditions for approximately 2 weeks before the start of the experiment. The indoor holding tanks were supplied with filtered seawater pumped from the St. Lawrence Estuary. During this time, salinity and temperature followed the natural fluctuations (25.29–29.26‰, 4.0–7.0°C). Crabs were not fed during acclimation or during the experiment.

Over the acclimation period, 420 adult crabs (Sainte-Marie et al., 1995) were selected and tagged using Carlin dangler wired tags (Floy Tag, Seattle, WA, USA). The tag was fastened to the coxa of one of the pereopods. Crabs were selected to be without obvious wounds or black spots and have at most one missing leg. Carapace width (CW; ± 0.1 mm), right chela height (CH; ± 0.1 mm), total weight of the individual (TW; ± 0.1 g), and number of missing legs were recorded. The hardness of the lower surface of the chela was measured with a durometer (± 1) using a 7-lb gauge (PTC Instruments model 307HS) according to the method described by Foyle et al. (1989a).

2.2. Experimental conditions

The experiments were conducted in a system that allowed a precise control of temperature. This system included three rectangular tanks divided into two compartments measuring 122×183 and 40 cm deep each. The tanks were set up with their own temperature and recirculation systems in a semi-open design. After acclimation, the temperature of each tank was lowered to experimental conditions over a period of 24–48 h. Experimental temperatures were 1.0°C, 5.0°C and 10.0°C. Salinity was 27‰ (Table 1). Water quality (dissolved oxygen, pH and ammonia) was monitored in the first week of the experiment, to ensure that the water turnover rate (minimum flow of $1\text{--}4\text{ l min}^{-1}$ of new water) was sufficient to maintain water quality in the tanks.

Each test compartment held 70 crabs of which a certain number was sampled during the experiment ($n = 270$). The density was maintained throughout the holding period by adding unmarked hard-shell commercial size crabs to compensate for mortality and sampling. The mortality of tagged crabs was monitored on a daily basis over the course of the experiment.

Crabs were of a consistent size in all experimental conditions ($F = 1.34$, $P = 0.262$) (Table 2). However, weights differed significantly ($F = 2.72$, $P = 0.044$). This was mainly attributable to the fact that almost all crabs with a missing leg at the beginning of the experiment were ascribed to one tank. When average weight of whole crabs are compared by tank temperature, the results show no significant differences ($F = 0.99$, $P = 0.398$).

The height of the chela also differed among testing conditions. Crabs in the coldest environment had a significantly smaller chela than the ones in the 10.0°C testing condition ($F = 3.69$, $P = 0.012$). This also might partly explain the difference in weight between testing conditions.

2.3. Dissection

Three or four crabs were sampled from each tank ($n = 10$) at the beginning of the experiment, on the 9th of June. Afterward, five crabs were sampled from each compartment at 14 to 18 days intervals until the 10th of November. At each sampling, the general appearance of the individuals was noted. Total weight (± 0.1 g) and gut weight (digestive gland, digestive tract, and gonads, ± 0.1 g) were taken. The right chela and samples of the digestive gland and merus muscle were weighed (± 0.01 g) and dried to constant weight at 96°C (48 h) for the determination of water content (%). Hardness

Table 1

Temperature and salinity conditions (mean \pm sd, range in parentheses) in long-term holding experiments in three tanks, each separated into two compartments. *N* indicates the number of measurements of each variable. *H* is the Kruskal–Wallis statistic testing for differences among compartments

Mean \pm sd (Min–Max) <i>N</i>	1.0°C		5.0°C		10.0°C		<i>H</i> (<i>P</i>)
	Compartment G	Compartment H	Compartment C	Compartment D	Compartment A	Compartment B	
Temperature (°C)	0.89 \pm 0.39 (0.4–2.2) 62	0.94 \pm 0.40 (0.4–2.4) 62	5.00 \pm 0.20 (4.2–5.6) 62	5.00 \pm 0.21 (4.2–5.6) 62	10.17 \pm 0.74 (8.9–14.0) 62	10.18 \pm 0.72 (8.8–13.8) 57	326.17 (≤ 0.0001) ^a
Salinity (‰)	27.35 \pm 0.83 (26.0–28.5) 13	27.31 \pm 0.83 (26.0–28.5) 13	27.31 \pm 0.75 (26.0–28.0) 13	27.23 \pm 0.73 (26.0–28.0) 13	27.33 \pm 1.27 (24.0–28.5) 13	27.27 \pm 1.27 (24.0–28.5) 13	1.07 (0.98)

^aNote: Tukey analysis revealed no significant differences ($P < 0.05$) between compartments which had the same target temperature (i.e. G–H, C–D, and A–B).

Table 2

Average size (mean \pm sd, range in parentheses) of snow crabs in long-term holding experiments in three tanks, each separated into two compartments. *N* indicates the number of crabs measured. *F* is the ANOVA statistic testing for differences among compartments

Mean \pm sd (Min–Max) <i>N</i>	1.0°C		5.0°C		10.0°C		<i>F</i> (<i>P</i>)
	Compartment G	Compartment H	Compartment C	Compartment D	Compartment A	Compartment B	
Weight (g)	736.0 \pm 152.78 (533.8–1101.6) 44	675.2 \pm 145.62 (412.8–1098.6) 45	731.5 \pm 137.58 (390.8–1018.2) 42	742.7 \pm 160.67 (461.8–1057.8) 44	753.7 \pm 138.45 (527.1–1073.7) 46	776.7 \pm 157.69 (526.8–1189.1) 45	2.323 (0.0435) ^a
Carapace width (mm)	113.7 \pm 8.52 (99.9–131.6) 44	111.8 \pm 8.08 (94.2–132.3) 46	113.8 \pm 7.55 (95.9–129.6) 40	114.0 \pm 8.02 (98.3–127.9) 42	114.4 \pm 7.21 (100.0–127.8) 45	115.2 \pm 7.77 (101.1–131.6) 45	0.929 (0.4629)
Chela height (mm)	29.78 \pm 2.74 (26.2–37.1) 46	28.90 \pm 3.08 (22.0–38.2) 46	29.55 \pm 2.44 (22.3–34.5) 42	30.20 \pm 2.73 (23.7–35.0) 44	30.36 \pm 2.78 (24.6–37.3) 46	30.82 \pm 2.91 (25.2–38.1) 45	2.642 (0.0237) ^a

^aNote: Tukey analysis reveals that *H* has significantly smaller means than *B*. All other comparisons reveal no significant differences (*P* > 0.05).

of the right chela was again measured. All crabs had a hardness index between 60 and 96 (mean \pm sd = 84.72 ± 6.10) confirming that no soft-shell crabs were present. A volume of 5–10 ml of haemolymph was sampled via the arthrodial membrane at the base of the coxa of one of the rear pereopods, using a disposable ice cold syringe fitted with a no. 21 hypodermic needle. The haemolymph was immediately transferred to an ice cold centrifuge tube and centrifuged at 10,000 rpm for 5 min. The plasma was then split into aliquots of 0.5 ml and preserved in microtubes at -20°C for plasma assays.

Variables measured included plasmatic glucose ($\text{mg} \cdot 100 \text{ ml}^{-1}$) using an enzymatic diagnostic kit (Sigma no. 315 Glucose Trinder), and plasmatic proteins ($\text{g} \cdot \text{l}^{-1}$) with a dye binding technique using Coomassie Brilliant Blue G-250 (Bio-Rad protein assay). Samples of the merus muscle and digestive gland were also used for the determination of lipid and protein contents. Lipid content was determined gravimetrically (Soxhlet extraction procedure, Soxtec unit 1043) (Bligh and Dyer, 1959). Protein content was calculated from non-protein and total nitrogen (micro-Kjeldahl determination on Kheltec system with or without protein precipitation with K_2SO_4 , followed by spectrophotometric determination using the Berthelot reaction) (Haslemore and Rougham, 1976). Non-protein nitrogen in the merus was not available for each individual where total nitrogen was measured. Since the ratio of non-protein to total nitrogen did not vary significantly across time and/or temperature ($P > 0.40$, $n = 67$), we used an average correction factor (78.75% of total nitrogen in the muscle was from the protein fraction).

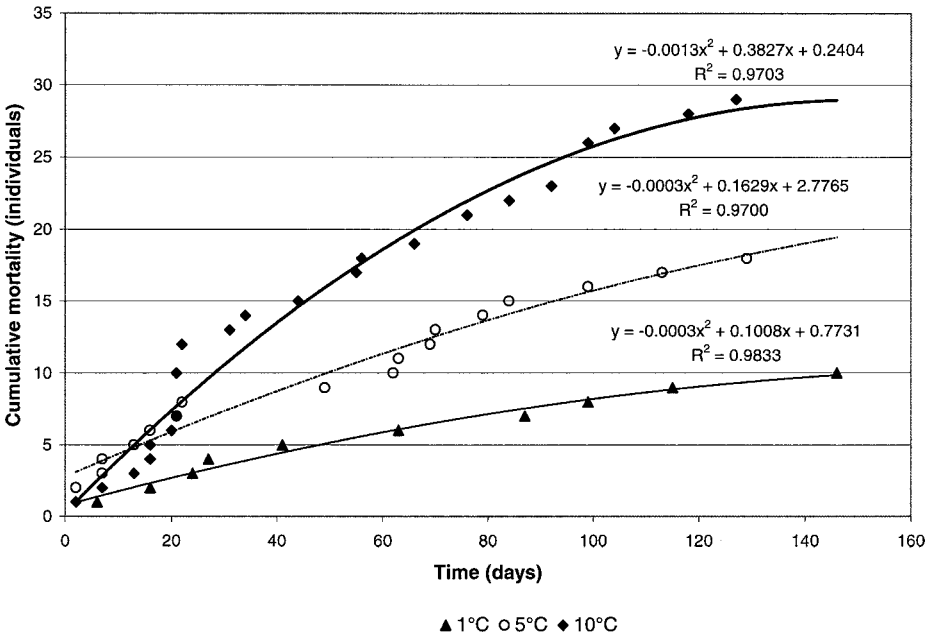


Fig. 1. Cumulative mortality of adult male snow crabs as a function of time in a long term holding experiment at three temperatures (1°C, 5°C, and 10°C). Curves shown are second degree polynomial regressions for each temperature. Each temperature group originally had 140 snow crabs.

We determined the glycogen content using the method described by Carr and Neff (1984).

2.4. Statistical analysis

Holding periods and experimental temperatures were compared with some of the variables expressed as percentages of initial fresh weight of the crab. Variables were checked for normality of distribution and homogeneity of variance using Wilks–Shapiro and Bartlett’s test, respectively. Variables with normal distribution and homogenous variances were tested by ANOVA with repeated measures, followed by a posteriori multiple comparison tests (Tukey’s test; Zar, 1984). When these conditions were not met, tests were made by the Kruskal–Wallis method followed by Tukey’s test. A posteriori tests were carried out only when the ANOVA or Kruskal–Wallis showed significant differences ($P < 0.05$). Statistical analyses were carried out using SAS software release 6.12.

Cumulative mortality of tagged crabs in relation to time for each temperature were fitted by polynomial regression. The resulting curves were then compared graphically for differences in elevation and curvature.

To evaluate the relationship between water content and lipid, protein or glycogen content of tissue, linear regression analyses were performed.

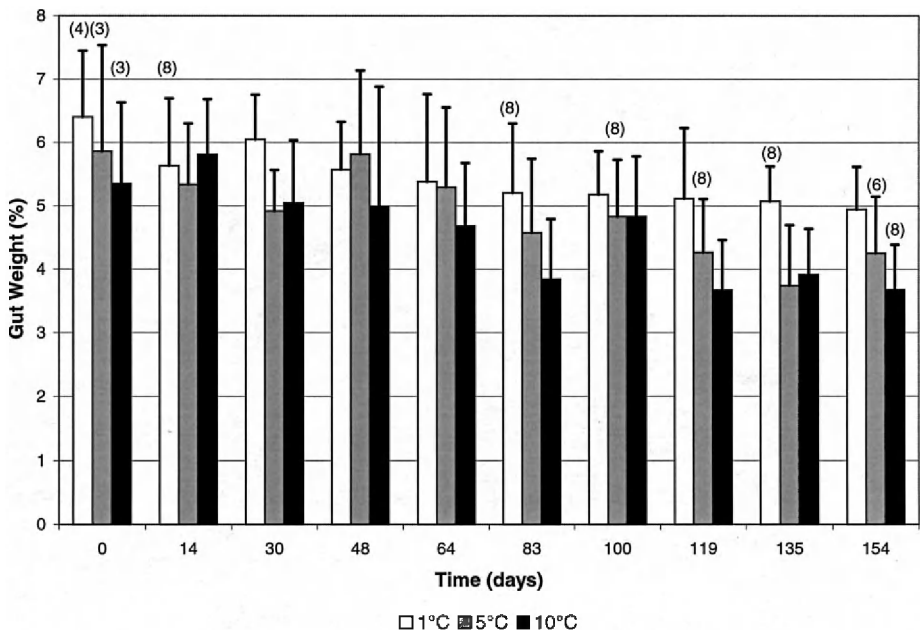


Fig. 2. Variation over time of average gut weight expressed as percentage of total weight of adult male snow crabs in a long term fasting experiment at three temperatures (1°C, 5°C, and 10°C). Error bars represent standard deviation. (n) = number of crabs sampled when smaller than 9 or 10.

3. Results

Cumulative mortality increased with time and temperature (Fig. 1). At the end of the experiment, mortality was highest in the 10°C tanks (20.7%) and lowest in the 1°C tanks (7.1%). Cumulative mortality was intermediate at 5°C (12.9%).

Fasting did not result in substantial weight losses over the course of the experiment, but slight changes were observed that were significant. Crabs sacrificed at the end of the experiment had lost more weight than those sacrificed at the beginning ($H = 47.48$, $P \leq 0.0001$). Total weight loss averaged $0.73 \pm 1.73\%$ of initial weight after 64 days of starvation and had increased to $3.56 \pm 2.59\%$ by the end of the experiment. Holding temperature did not have a significant effect ($H = 0.56$, $P = 0.7552$).

Proportional gut weight varied with time ($F = 11.58$, $P \leq 0.0001$) and temperature ($F = 19.29$, $P \leq 0.0001$) with no interaction ($F = 1.26$, $P = 0.29$) (Fig. 2). The crabs held at 1°C ($5.39 \pm 0.97\%$) had significantly heavier guts than those kept at 10°C ($4.55 \pm 1.23\%$). Crabs held at 5°C showed intermediate gut weights ($4.86 \pm 1.17\%$). The weights showed no significant differences before 64 days. Proportional gut weight had decreased from $5.92 \pm 1.26\%$ before to $4.35 \pm 0.90\%$ at the end of the fasting period ($4.94 \pm 0.67\%$, $4.25 \pm 0.89\%$, and $3.68 \pm 0.71\%$ at 1°C, 5°C, and 10°C, respectively).

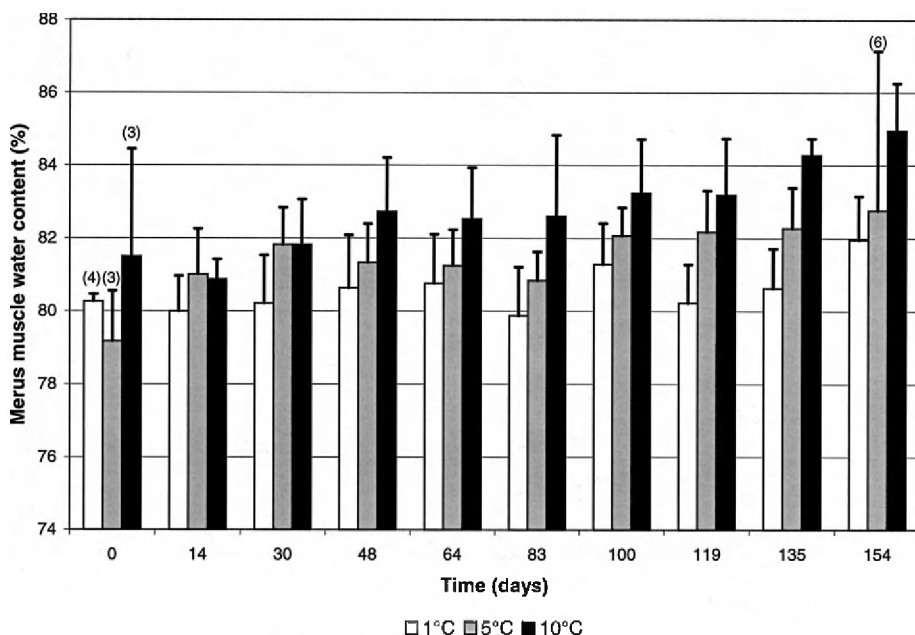


Fig. 3. Variation over time of average merus muscle water content expressed as percentage of total weight of adult male snow crabs in a long term fasting experiment at three temperatures (1°C, 5°C, and 10°C). Error bars represent standard deviation. (n) = number of crabs samples when smaller than 9 or 10.

We observed very small but significant variations of the relative fresh weight of the right chela. Temperature had no significant effect ($F = 1.39$, $P = 0.37$) on relative fresh chela weight. Sampling time in contrast had a significant effect ($F = 3.15$, $P = 0.0101$). Temporal trends were not pronounced, but in general relative chela weight was lower in the second half of the experiment. Proportional fresh weight was $4.42 \pm 0.45\%$ before fasting and $4.18 \pm 0.45\%$ after 154 days. Similar trends were observed for the relative dry weight of the right chela, but they were not significant ($H_{\text{temperature}} = 5.59$, $P = 0.06$; $H_{\text{time}} = 16.29$, $P = 0.06$).

3.1. Composition of merus muscle

Water content of merus muscle increased markedly over time ($F = 9.82$, $P \leq 0.0001$) and differed among temperatures ($F = 50.11$, $P = 0.005$), with no interaction ($F = 1.52$, $P = 0.16$; Fig. 3). Water content averaged $80.31 \pm 1.81\%$ initially and increased to an average of $83.23 \pm 2.63\%$ by the end of the experiment (day 154, treatments combined). For crabs held at 1°C , mean water content of the merus was $80.61 \pm 1.30\%$, compared to $81.59 \pm 1.60\%$ at 5°C and $82.83 \pm 1.72\%$ at 10°C , an increase by approximately 1% for every $4\text{--}5^\circ\text{C}$.

Glycogen showed significant variations across time ($F = 8.32$, $P = 0.0058$) but not across temperatures ($F = 1.52$, $P = 0.35$). Only samples for days 48, 83, 119, and 154

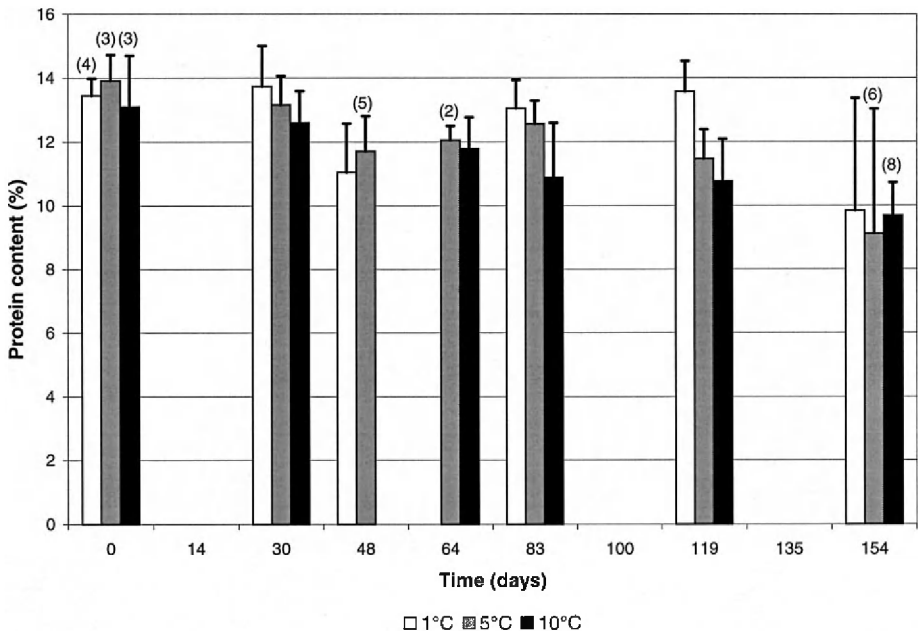


Fig. 4. Variation over time of average protein content expressed as percentage of merus muscle weight of adult male snow crabs in a long term fasting experiment at three temperatures (1°C , 5°C , and 10°C). Error bars represent standard deviation. (n) = number of crabs sampled when smaller than 9 or 10.

were assayed. During this period, glycogen concentration on a wet weight basis decreased from 3.49 ± 2.25 mg/g (48 days) to 2.38 ± 1.16 mg/g (154 days). A regression analysis of glycogen and water content did not yield any significant relationship ($P > 0.05$).

Lipid content represented less than 2% of merus composition on a fresh weight basis in all individuals measured. Only samples for days 0, 48, 83, 119, and 154 were assayed. Contents did not vary across time ($F = 2.73$, $P = 0.08$) or temperature ($F = 6.41$, $P = 0.08$).

Protein content varied across time ($F = 8.27$, $P = 0.0006$), but not across temperatures ($F = 1.86$, $P = 0.30$) (Fig. 4). Only samples for days 0, 30, 48, 64, 83, 119, and 154 were assayed. Days 48 and 64 are incomplete (10°C and 1°C measurements missing, respectively). Overall, we observed a decrease of protein content from $13.48 \pm 0.96\%$ before fasting to $9.61 \pm 2.93\%$ after 154 days. According to regression analysis, protein and water content were significantly related ($R^2 = 0.44$, $F = 115.9$, $P \leq 0.0001$) (Fig. 5). There were three outliers, determined by examining the studentized residuals, two individuals held at 1°C for 154 days and one individual held for 154 days at 5°C. We have no explanation for such low protein contents at 82% water content. The exclusion of these outliers yielded a regression which explained a much higher proportion of the variation ($R^2 = 0.65$) with only minor changes in the parameters.

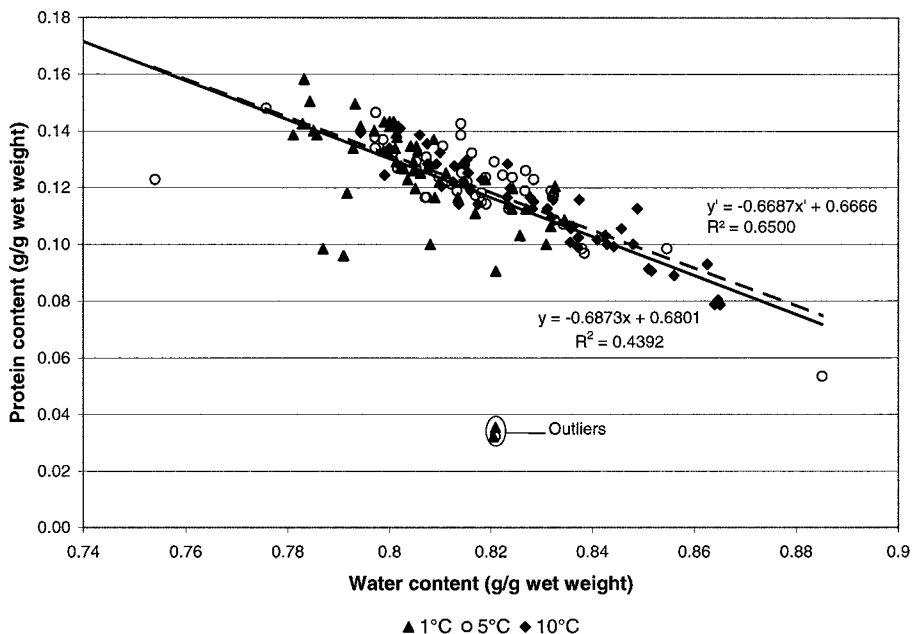


Fig. 5. Linear regression of water and protein content of muscle in the merus of adult male snow crabs held without food at three temperatures (1°C, 5°C, and 10°C) for 154 days. The linear regression was calculated with (full line) and without (dashed line) the inclusion of three outliers.

3.2. Composition of digestive gland

Water content of the digestive gland increased significantly both with time ($F = 7.10$, $P \leq 0.0001$) and temperature ($F = 11.07$, $P = 0.0412$) (Fig. 6). There was no interaction between the two factors ($F = 1.39$, $P = 0.22$). Water made up $56.64 \pm 9.65\%$ of the fresh weight of the digestive gland at the start of the experiment and $66.55 \pm 5.25\%$ after 154 days of food deprivation. Individuals held at 1°C had an average water content of $59.69 \pm 6.64\%$ while those held at 5°C and 10°C had average water contents of $63.38 \pm 8.41\%$ (no value available for day 154) and $63.49 \pm 8.05\%$, respectively.

Glycogen concentration in the digestive gland was not significantly affected by temperature ($F = 0.05$, $P = 0.95$). It did vary according to starvation time ($F = 5.19$, $P = 0.0235$). Only samples for days 48, 83, 119, and 154 were assayed. These data suggest a decrease of glycogen concentration occurred during starvation. Average glycogen concentration was 1.95 ± 1.28 mg/g after 48 days. This value had decreased to 1.00 ± 0.95 mg/g at the end of the experiment. According to a regression analysis, glycogen concentration and water content did not exhibit a significant relationship ($P > 0.05$).

Proteins represented a small fraction of the fresh weight of the digestive gland. Average values ranged from 2.5% to 5.4% with no significant increases with time ($F = 3.12$, $P = 0.0591$) or temperature ($F = 2.11$, $P = 0.27$).

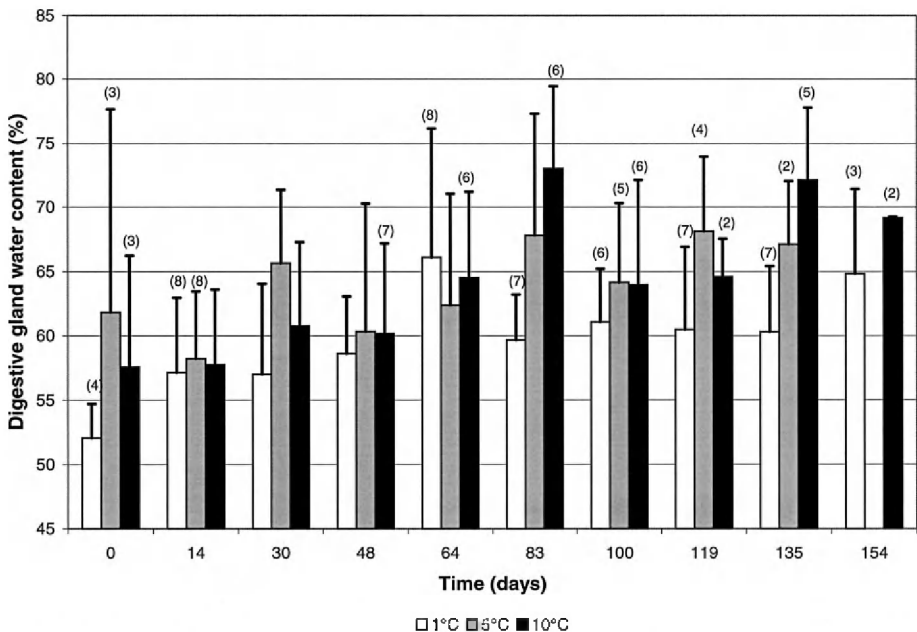


Fig. 6. Variation over time of average digestive gland water content expressed as percentage of total weight of adult male snow crabs in a long term fasting experiment at three temperatures (1°C , 5°C , and 10°C). Error bars represent standard deviation. (n) = number of crabs sampled when smaller than 9 or 10.

Lipids represented a more substantial fraction of the fresh weight of digestive gland (Fig. 7). Relations with time ($F=22.63$, $P\leq 0.0001$) and temperature ($F=25.14$, $P=0.0013$) were significant. Interaction was present ($F=4.41$, $P=0.0108$) due to the higher lipid content of one individual sampled in the 10°C tank at the beginning of the experiment. Only samples for days 0, 48, 83, 119 and 154 were assayed. Lipid content fell by 50% during the experiment but was still high at the end of the experiment. Values decreased from $30.13 \pm 12.00\%$ at the beginning of the experiment to $15.01 \pm 8.00\%$ after 154 days of starvation. Overall, higher temperatures implied a lower lipid content in the digestive gland: $25.14 \pm 7.13\%$ for individuals held at 1°C, $19.06 \pm 9.59\%$ at 5°C and $15.24 \pm 10.65\%$ at 10°C. We established a significant relationship between lipid and water using regression analysis ($R^2=0.67$, $F=145.1$, $P\leq 0.0001$) (Fig. 8).

3.3. Composition of haemolymph

Though significant differences in glucose concentration occurred among samplings ($H=43.74$, $P<0.0001$), no clear pattern emerged. Average glucose concentration ranged from 4.44 to 12.86 mg/100 ml over the course of the experiment. Some extreme values outside that range were observed at 14 days in the 10°C tanks and at 119 days in all tanks. Except for those two samples, glucose concentration decreased steadily from

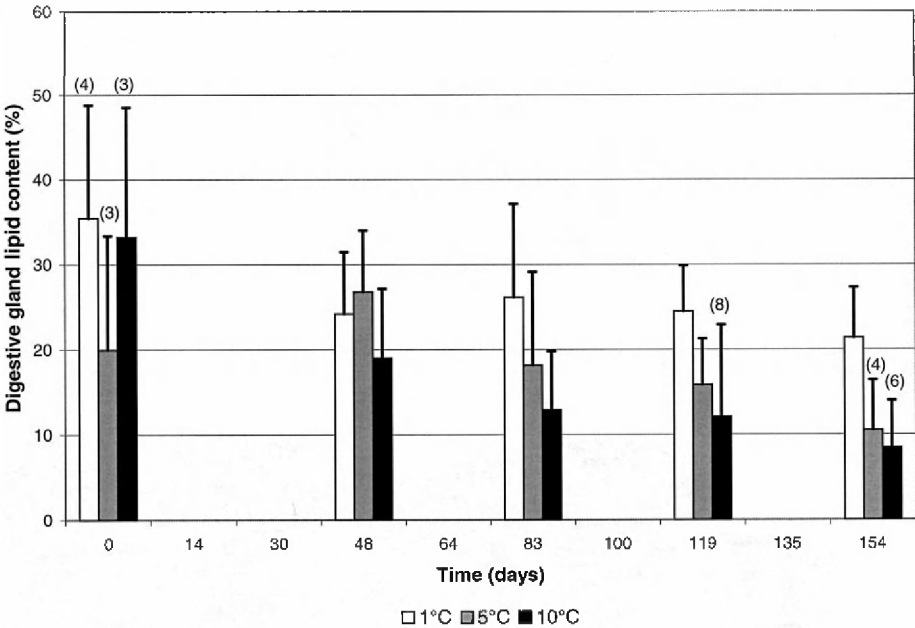


Fig. 7. Variation over time of average lipid content expressed as percentage of digestive gland weight of adult male snow crabs in a long term fasting experiment at three temperatures (1°C, 5°C, and 10°C). Error bars represent standard deviation. (n) = number of crabs sampled when smaller than 9 or 10.

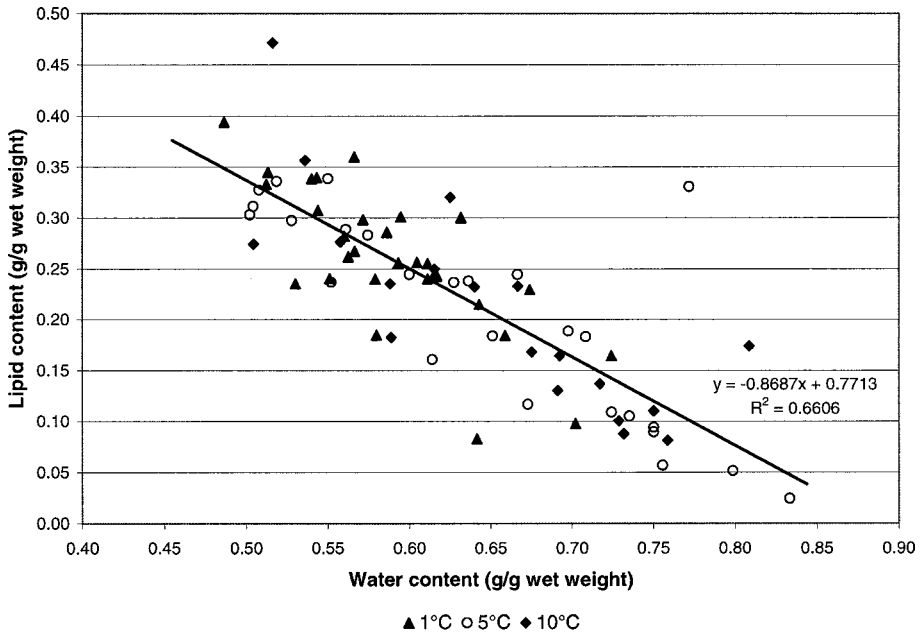


Fig. 8. Linear regression of water and lipid content of digestive gland in adult male snow crabs held without food at three temperatures (1°C, 5°C, and 10°C) for 154 days. The least-square fit is shown.

12.86 ± 3.96 to a low of 5.40 ± 1.47 mg/100 ml on day 100. Concentrations then increased until the end of the experiment (8.16 ± 1.92 mg/100 ml). Temperature had no effect on glucose concentrations ($H = 3.4862$, $P = 0.18$).

Protein content of haemolymph showed significant differences with time ($F = 29.72$, $P \leq 0.0001$) and among temperatures ($F = 10.77$, $P = 0.0427$), with no interaction ($F = 1.25$, $P = 0.29$). We observed a sharp increase in protein content after 83 days (38.80 ± 8.75 g/l) up from 22.25 ± 6.38 g/l at 64 days. This represented a 74% increase. In general, individuals held at 1°C generally had higher concentrations of protein (31.73 ± 11.16 g/l) than those held at 10°C (26.67 ± 9.41 g/l) with intermediate concentrations at 5°C (29.33 ± 12.13 g/l).

4. Discussion

Starvation has been shown to adversely affect survival in crabs of the genus *Chionoecetes*. Forty percent of Tanner crabs (*Chionoecetes bairdi*) held for 119 days in closed pots without nourishment died (Kimker, 1994). Mortalities also occurred once feeding was resumed in Tanner crab; mortalities ranged from 40% to 100% in crabs fed ad libitum following a starvation period of 30–90 days (Paul et al. 1994). Provencher et al. (1995) measured mortality of snow crab held in cages at sea to measure the feasibility and optimal stocking density for in situ storage. Percent mortality varied from 12.5% to 28.3% according to time spent in cages (21–91 days) and type of cage used.

These results are much closer to the mortality observed in our experiment (Fig. 1). We observed 7.1–20.7% mortality according to holding temperature. Numbers reported in our study are percentages of initial numbers in the tanks however, and not all crabs were fasted for 154 days. Food deprivation lasted 54 days on average. Mortalities may have been more frequent had all crabs been unfed for a period of 154 days. Alternately, lower mortalities in our study may be due in part to a better control of holding conditions than in studies conducted at sea (Kimker, 1994; Provencher et al., 1995). Furthermore, latent mortalities, i.e., mortalities that occur once feeding is resumed (Paul et al., 1994), were not measured since crabs were never fed during our experiments.

Fasting resulted in only minor changes in the gut (Fig. 2) and total weight of crabs, but major changes were observed in tissue composition in both muscle and digestive gland. Mayrand et al. (2000) observed a reduction in the dry mass of muscle in the merus and a reduction of the dry mass of the digestive gland in snow crab deprived of food in the first 60 days following ecdysis. The reduction in muscle mass resulted from a reduction in the number of cells with the remaining muscle fibres maintaining a high protein/DNA ratio. Muscle glycogen decreased and was estimated to be a major source of energy in fasting *C. granulata* (Vinagre and DaSilva, 1992). In the present study, snow crabs also mobilised muscle glycogen during fasting, but more energy was derived from protein catabolism (Figs. 3 and 4). Vinagre and DaSilva (1992) found a non-significant effect of fasting on muscle lipids. Our results concur, with lipids representing only 1% of fresh muscle. In contrast, lipids made up a large proportion of the wet mass of the digestive gland and this proportion decreased markedly in fasting *Cha. granulata* (Vinagre and DaSilva, 1992) previously fed with a carbohydrate-rich diet. Heath and Barnes (1970) also observed a substantial reduction of neutral fat in the digestive gland of intermoult *Car. maenas* following 28 days of starvation. The present study shows that changes in size of the digestive gland in fasting snow crab (Mayrand et al., 2000) mainly result from the catabolism of lipids (Fig. 7), although some energy may be derived from glycogen as well. On the other hand, the stepwise increase in protein content of haemolymph after 80 days is puzzling. Haemolymph proteins decreased by 20% in fasting *Car. maenas* (Uglow, 1969). Haemolymph protein concentrations were higher in hard-shell than soft-shell snow crabs (Hardy et al., 1994a), with hard-shell snow crabs having similar protein concentrations as snow crabs after starvation in the present study.

Condition indices may be used to provide a crude assessment of nutritional status and provide information on the quality of the environment. They are widely used in the study of fish species and have been used with success to monitor seasonal and long-term trends in condition (e.g. Lambert and Dutil, 1997) and to assess natural mortality (e.g. Dutil and Lambert, 2000). In cod (*Gadus morhua*), Fulton's condition factor (K), a ratio of somatic weight to length, and the liver-somatic index, a ratio of liver to somatic weight, have been proposed as being reliable indices of condition (Lambert and Dutil, 1997). Furthermore, muscle proteins and liver lipids were closely related to water content, energetic value, and the above-mentioned condition indices. The use of condition indices is not as common in crustacean research. Digestive gland thickness and cell disintegration were readily identifiable in juvenile lobsters (Niles et al., 1993) and prawns (Vogt et al., 1985) and have been proposed as indices of condition. We propose moisture content of digestive gland as an index of the nutritional status in snow

crabs, on the basis of its relationship with lipids (Fig. 8). In the same manner, moisture content of the muscle could be used (Fig. 5) although protein content variability is less pronounced (Fig. 4). More information is required, particularly with regards to moult cycle, before these indices are used in field studies or in holding facilities to monitor condition.

Temperature did not have a major impact on any of the tissues examined. The rate of energy utilisation in ectotherms is controlled by ambient temperature and we expected marked differences among treatments. According to Foyle et al. (1989b), the energy budget of snow crab fed *ad libitum* is negative when temperature rises above 6°C. Furthermore, McLeese (1968) observed that hard-shell snow crabs did not tolerate temperatures above 12–15°C in the laboratory. Fifty percent of the crabs died within 30 days in his experiment. Thus, we assumed physiological condition would deteriorate faster at high temperature. Cumulative mortality did show a significant increase with temperature (Fig. 1). Differences in tissue composition among temperatures were however generally small compared to the ones created by starvation time.

Our results suggest that snow crab can tolerate extended periods of starvation. This is relevant to aquaculture scenarios (Hardy et al., 1994b). Because low temperatures and short periods of fasting resulted in fewer mortalities and changes in condition, short term holding at low temperatures (several weeks, 1–5°C) should be favoured. Holding crabs for longer periods of time requires near 0°C temperatures. High temperatures (5–10°C range) would be acceptable only if crabs were held for very short periods of time. Temperatures above 15°C and salinity below 22‰ are lethal and must be avoided (Hardy et al., 1994a). Snow crab in the St. Lawrence Estuary live at temperatures below 3°C. While higher temperatures should promote faster growth rates, near 0°C temperatures should promote survival in situations of low food abundance. Snow crabs in our study were sampled in the spring period. Based on their tolerance to fasting during the experiment and on the high lipid content of the digestive gland at the start of the experiment, large male adult snow crabs were presumably able to face a period of low prey availability.

In conclusion, duration of starvation has a clear impact on the physiological condition of crabs. Our study shows that, in the merus muscle, average protein and glycogen stores became depleted (~30% decrease) over time during fasting. In the same manner, in the digestive gland, average lipid and glycogen stores decreased by approximately 50%. Fasting caused a progressive water content increase in both the merus muscle (4%) and the digestive gland (17%). These variations indicate an overall decrease in condition over time during fasting. Furthermore, similar tendencies were observed with respect to temperature, which would indicate that as the temperature increases, so do the effects of starvation. However, the variations related to temperature were less marked than those related to starvation time.

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