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The importance of rock crab (*Cancer irroratus*) for growth, condition and ovary development of adult American lobster (*Homarus americanus*)

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Abstract

The rock crab (*Cancer irroratus*) fishery is a growing industry in eastern Canada. Considering that American lobster (*Homarus americanus*) is highly dependent on the rock crab as a food source, questions have arisen as to the impacts such a fishery would have. This study examines how different rations of rock crab can affect somatic growth, condition and ovary development of mature lobster, following molt. We tested the effect of four diets containing various amounts of rock crab, blue mussel and green sea urchin. The four diets were: a reference diet where 80% of the energy was provided by rock crab (T), a diet with half the crab content of the reference diet but containing as much protein (isoproteinic) as the reference diet (E1), a diet without crab but isoproteinic with the reference diet (E2), and a diet without crab but with as much energy (isocaloric) as the reference diet (E3). In general, lobsters fed a diet without rock crab showed lower glycogen and lipid content and higher water content in the digestive gland. Growth of chela muscles was lower, although diet did not have any effect on protein concentration. Ovary development was stunted in females. Differences were mostly striking in diet E3, which contained less proteins than the reference diet. Results obtained from diet E2 were also significantly different from the reference diet and not from E3, suggesting that mussel and urchin, even if given in a greater amount, are not equivalent to crab and cannot fully compensate the absence of this essential component of the lobster's diet. The importance of rock crab for lobster may be due to its

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high protein content and presence of particular amino acids. Our results strongly suggest that the development and management of a rock crab fishery should be cautious and governed by a multi-species approach. © 2001 Published by Elsevier Science B.V.

Keywords: American lobster; *Cancer irroratus*; Condition; Diet; Growth; *Homarus americanus*; Nutrition; Rock crab

1. Introduction

American lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) are sympatric species. Juveniles and some adult crabs often share rocky habitats with juvenile and adult lobsters (Scarratt and Lowe, 1972; Hudon and Lamarche, 1989). Both species have a preference for rocky bottoms, resulting in strong interspecific competition for shelter and space, in which the lobster is clearly the winner (Wang, 1982; Cobb et al., 1986). In addition, a predator–prey relationship exists between *H. americanus* and *C. irroratus*. Although a wide diversity of food items are found in the lobster stomachs, reflecting a certain degree of feeding opportunism, rock crab is one of the main prey items found in lobster, throughout their geographic range, from Newfoundland to Long Island Sound (Squires, 1970; Weiss, 1970; Ennis, 1973; Scarratt, 1980; Carter and Steele, 1982a; Elner and Campbell, 1987; Hudon and Lamarche, 1989; Sainte-Marie and Chabot, 2001). The proportion of crab in lobster diet varies geographically and seasonally (Weiss, 1970; Carter and Steele, 1982a; Ennis, 1973; Elner and Campbell, 1987) and is influenced by benthic community composition (Carter and Steele, 1982b; Elner and Campbell, 1987). Lobster, however, do exhibit feeding preferences (Carter and Steele 1982b; Elner and Campbell 1987; Hudon and Lamarche, 1989), and rock crab is among it's most preferred preys. Observations in nature and experiments in the laboratory show that lobster will strongly select rock crab (McLeese, 1970; Reddin, 1973; Wilder, 1973; Carter and Steele, 1982b; Ojeda and Dearborn, 1991). In the laboratory, crab may contribute up to 80% of their energy intake, even when lobsters are offered a wide variety of preys (Evans and Mann, 1977). As lobsters ingest mostly the soft tissues of large preys and little of the hard parts, stomach contents most likely underestimate the true quantity of crab in their diet (Weiss, 1970; Carter and Steele, 1982a). There are also ontogenic variations in the lobster diet. As lobster grow in size, the proportion of larger, heavily armored and more mobile preys including rock crab, increases (Reddin, 1973; Scarratt, 1980; Carter and Steele, 1982a; Elner and Campbell, 1987; Sainte-Marie and Chabot, 2001).

This preference for crab is in relation to the need for lobster to feed on high-energy and protein-rich preys (Ojeda, 1987; Evans and Mann, 1977). Crab energetic content is two to three times greater than lobster's other predominant preys, such as mussels or urchins (see caloric values in Brawn et al., 1968; Duarte et al., 1980; Scarratt, 1980; Petersen, 1981). Protein content is higher in crab than in other lobster preys, and represents more than 20% of fresh weight (Vonk, 1960). This is more than four times the protein content of sea urchins, *Strongylocentrotus droebachiensis* (Giese, 1966; Breen, 1974). In captivity, growth of lobsters is directly proportional to the quantity of protein in the diet (Castell and Budson, 1974). Quality of protein may also be an

important factor, since growth of lobster postlarvae is greater when fed a crab-based diet than when fed an urchin-, mussel- or shrimp-based diet (Boghen et al., 1982).

The rock crab fishery is a growing industry in eastern Canada (Gendron et al., 1998). Considering that *H. americanus* is highly dependent on the rock crab as a food source, questions have arisen as to the impacts such a fishery would have. This study, therefore, examines how different rations of rock crab can affect somatic growth, condition and ovary development of mature lobster, following molt.

2. Materials and methods

The feeding experiment was performed on newly molted mature males and females. The assessment of the effect of the different treatments, which consisted of four different diets, was based on examination of fresh weight, water content, glycogen and lipid content of the digestive gland, muscles dry weight of the crusher chela and the abdomen, as well as their protein content and on the ovary weight of females. The experiment ran from July to November 1992. Based on previous work by Castell and Budson (1974), the experiment was planned to last a minimum of 3 months allowing for dietary differences to become apparent.

2.1. Animals

Lobsters were bought at the end of June 1992, from a commercial lobster producer located in Grande-Entrée, on the Magdalen Islands in the Gulf of Saint Lawrence (Québec). Commercial-size animals were selected to be vigorous, with intact appendices and without apparent wounds. At the time of purchase, the animals were in a hard-shell condition, but were assumed to be in a pre-molt condition, as is generally the case this time of the year. The animals were then shipped by plane to the Maurice Lamontagne Institute, in Mont-Joli, Québec, where the experiment took place. We selected animals according to size and maturity. Therefore, we kept animals ranging in pre-molt size between 76.0 and 81.0 mm (cephalothoracic length, CL). To ensure that only mature males were kept for the experiment, we selected those with a crusher propodite index (CPI) greater than 24 ($CPI = CPV/CL$, where CPV, the crusher propodite volume = length $\times$ width $\times$ thickness of propodite, in centimeters) (Aiken and Waddy, 1989). For females, only pubertal ones with an abdomen width index (AWI) ranging between 57% and 65% were kept ($AWI = AW/CL \times 100$, where AW is the abdominal width) (Aiken and Waddy, 1982). Animals were then placed in tanks and fed until molting, which started to occur approximately 4 weeks after arrival.

2.2. Experimental conditions

Experimental lobsters were held in plastic baskets divided by wood partitions in four cells of $20 \times 24 \times 10$ cm. Each cell contained one lobster. Baskets were stackable and allowed a maximum of 144 lobsters per tank. Basket bottoms were made of mesh, which allowed water circulation.

The rearing system was comprised of four $1.2 \times 3.7 \times 0.4$ m tanks. Tanks were fed partially recirculated seawater at a rate of 110–146 l min^{-1}. New filtered seawater was added at a rate of 20–26 l min^{-1}. Outflowing water was filtered using sand beds. The tanks were cleaned once a week by suctioning. Water temperature ranged from 10.5 to 16.5 °C, which is slightly higher than waters around the Magdalen Islands in the later part of the experiment. The water temperature was kept above 10 °C to increase the metabolism and maintain growth. Upon reception of the animals, salinity oscillated between 26.8‰ and 28.5‰. Salinity in the Magdalen Islands waters is about 30‰. An osmotic shock very likely occurred. We assume, however, that animals had overcome the shock when the treatments started. For the duration of the experiment, salinity was on average 28.5‰. New and recycled water was saturated at 90% with oxygen in an adjacent water tank before flowing into the experimental tanks. Periodical measurements indicated that dissolved oxygen within the tanks remained between 62% and 68% of saturation during the experiment. It fell to 40% on one occasion, on September 8. Adjustment of flow allowed for proper saturation to be re-established and maintained until the end of the experiment.

2.3. Treatments

Animals were allowed to molt before treatment started. Once molted, animals were assigned successively to one of the four treatments (diets), allowing randomisation of the experiment. It also allowed treatments to be spread out in the four tanks. Animals were not handled until the end of the experiment, and exuviates were not removed allowing lobsters to feed on them. Males ($n = 66$) molted between July 27 and August 6, and females ($n = 39$) molted between August 10 and September 20. A second group of males ($n = 28$) that molted over a longer period (between July 24 and August 21) than the first group were added for a specific assay (water content of the digestive gland, see below). The experiment ran for a period ranging between 104 and 116 days in the case of males, and 87 and 92 days for females; 14 males and 11 females were sacrificed within 24 h after molting to serve as a base line (control group) for assessment of growth and condition.

The experimental diets were prepared based on Reddin (1973) estimation of lobster energy demand. He estimated that a commercial size lobster (~ 500 g) consumes 43.9 kJ day^{-1}. This estimate was based on a diet composed essentially of crab. Based on this data, we calculated energetic needs of 49.2 kJ day^{-1} for an average lobster weight of 560 g. Four experimental diets were prepared, composed of rock crab (*C. irroratus*), blue mussel (*Mytilus edulis*) and green sea urchin (*S. droebachiensis*). Food items were bought fresh from commercial fishers (crabs and urchins) and growers (mussels). Proportions of each food items were adjusted to satisfy the energetic demand (Table 1). Energy content of each food item was not estimated directly. Brey et al. (1988) stated that in a number of macrobenthic invertebrates, including crustaceans, bivalves and echinoderms, 1 g of ash-free dry weight (AFDW) contains, on average, 23 kJ. Based on this figure, AFDW was determined directly on a sample of crabs ($n = 20$ sections out of five whole crabs), whole mussels ($n = 49$) and whole urchins ($n = 10$) of our food batch, from which the energy content of 1 g of fresh weight was then derived. Samples

Table 1
Composition of the experimental diets in terms of fresh weight (FW) of rock crab (C), blue mussel (M), green sea urchin (U), energy and protein content provided to each lobster on an weekly basis. Composition of feed given to the pre-molt lobsters before the start of the experiment is also presented. Also presented is the average fresh weight, energy, and protein intake estimated from food remains. Each value is the mean of 3 weeks of observations

	Pre-molt	Diet T (reference)	Diet E1 (1/2 crab isoproteinic with T)	Diet E2 (no crab isoproteinic with T)	Diet E3 (no crab isocaloric with T)
Composition (g FW/lobster/week)	C: 35 M: 7 U: 42	C: 80 M: 13 U: 93	C: 40 M: 80 U: 93	C: – M: 145 U: 93	C: – M: 117 U: 93
Total (g FW/lobster/week)	84	186	213	238	210
Energy (kJ/lobster/week)	154	343	384	419	345
Protein (g/lobster/week)	0.9	15.4	15.4	15.4	12.6
Food intake					
(g FW/lobster/week)		138	142	156	134
Energy (kJ/lobster/week)		327	359	391	321
Protein (g/lobster/week)		14.8	14.5	14.5	12.0

were dried in an autoclave at 70 °C for 48 h for the determination of dry weight. Ash weight was determined after combustion at 450 °C for 24 h.

A reference diet (T) was prepared on the assumption that post-molt lobsters actively select rock crabs as their principal energy source. Therefore, the reference diet was composed of rock crab, blue mussel and green urchins in a proportion of 8:1:1 in terms of the energy content. We used three additional experimental diets: a diet with half the crab content of the reference diet but containing as much protein (isoproteinic) as the reference diet (E1), a diet without crab but isoproteinic with the reference diet (E2), and a diet without crab but with as much energy (isocaloric) as the reference diet (E3). Protein content of each diet was estimated from published data on the protein content of each of the three food items (Boghen et al., 1982).

Males were subjected to the four diets, but females were subjected only to diets T, E1 and E3. Lobsters were also fed during the pre-molt period with a diet containing approximately half the energy of the reference diet (Table 1).

Experimental lobsters were fed individually a specific diet three times a week. Diets were prepared on a weekly basis, and the weekly ratios were roughly divided into three equal parts (fresh weight). Food was offered frozen. Mussels were offered whole, urchins were opened and crabs were cut into three to four sections. Because of food preferences, urchins were never offered at the same time as crabs to avoid waste.

2.4. Food consumption

Food consumption was estimated three times during the course of the experiment. For one week in August, September and October, all uneaten food present in each basket

cell was removed, sorted by food item (crab, mussel and urchin) and weighted (fresh weight, dry weight and AFDW). Energy and protein content of the remaining food items were estimated following the same procedure described above. Energy and protein consumption was then calculated for each experimental diet by subtraction.

2.5. Dissection and measurements

At the end of the experiment, lobsters were measured: CL, AW, crusher chela length, width, and thickness and fresh weight (FW). Lobsters were anesthetized by cooling for 20 min at 4 °C before being sacrificed by excision of the heart. Muscles of the abdomen and of the crusher chela, the digestive gland and the ovaries were removed, blotted and weighted (± 0.001 g). They were frozen until assays could be performed (within 4 months from the end of the experiment). Muscles and digestive gland were kept at -40 and -80 °C, respectively.

Muscles of the crusher chela and the abdomen were dried to constant weight in an autoclave at 70 °C for 72 h and weighted (± 0.001 g). Subsamples of the muscles were taken for protein content determination. Protein content was calculated from non-protein and total nitrogen content (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). Glycogen and lipid content of the digestive gland were determined. We determined the glycogen content using the method described by Carr and Neff (1984). Lipid content was determined gravimetrically (Soxtec extraction procedure, Soxtec unit 1043) (Bligh and Dyer, 1959). Since the whole digestive gland was used for the assays, males from the second group of experimental animals were also considered for the determination of water content. Digestive gland was dried at 70 °C for 48 h and then weighted.

2.6. Data analysis

Although animals did not vary much in size, weights of organs were nevertheless standardised for size. Digestive gland, abdomen muscles, female chela muscles and ovary weights were divided by CL^3 (cm). The ovarian factor (Of) was computed ($Of = \text{Ovary weight (mg)}/CL^3 \text{ (cm)} \times 10$). Because of the greater variability of the size of the crusher chela in males compared to females, male chela muscles weight was divided by the crusher propodite volume (CPV in cm^3). Values were expressed in $g/100\ mm^3$.

Means of variables describing condition for each treatment were compared using one factor ANOVA, when raw or transformed data met the conditions of normality and homocedasticity. When a significant difference ($P < 0.05$) was detected, we carried out the Tukey a posteriori multiple comparison test (Sokal and Rohlf, 1995) to contrast the impact of the various diets (T, E1, E2 and E3). A Dunnett's test was used to compare the condition of the experimental individuals with that of control lobsters, sacrificed at the start of the experiment (C). When the assumptions of normality and homocedasticity could not be satisfied, we used a Kruskal–Wallis analysis. If significant, it was followed by a Tukey-like non-parametric multiple comparison procedure for comparisons among treatments and a Dunn test for comparisons with the control group (Zar, 1984).

3. Results

3.1. Food consumption

On a weekly basis, lobsters from all diets consumed over 60% of the food (fresh weight) offered. Remains consisted mainly of hard parts (carapace, shell and test). Consumption ranged from 134 to 142 g FW/lobster/week for diets T, E1 and E3. It was generally higher for diet E2, reaching an average of 156 g FW/lobster/week (Table 1). Consumption was, on the whole, constant during the course of the experiment, although a slight decrease was observed in October. Over 90% of the energy contained in the food was taken up by lobster irrespective of the diet. Values of energy intake ranged from 321 to 391 kJ/lobster/week. Energy intake was higher in the half (E1) and no-crab diets (E2), while E3 was equivalent to T. In all diets, protein intake was between 93.9% and 96.3% of the proteins initially provided. Protein intake was similar for diets T, E1 and E2 (14.5–14.8 g/lobster/week), but lower for diet E3 (12.0 g/lobster/week), which originally contained less. In general, consumption was proportional to what was provided, regardless of the species composition of the diet, although slightly more urchin was left over (16.8% FW) by lobsters fed diet T, compared to lobsters fed the other three diets (11.5%, 12.2%, and 11.6% urchin FW, for diets E1, E2 and E3, respectively).

3.2. Size, weight and maturity of experimental animals

3.2.1. Males

Size and maturity of males were comparable among groups, including the control group. There were no significant differences in mean length of males ($F = 1.40$, $P = 0.248$). Mean CL varied from 86.7 to 89.0 mm in all treatments, including the control group (Table 2). The maturity index did not vary significantly among treatments ($F = 0.58$, $P = 0.678$) and average CPIs ranged from 27.9 to 31.5 (Table 2). At the time of sacrifice, fresh weight of fed lobsters was similar among treatments ($F = 0.18$, $P = 0.910$) and means ranged between 550.8 and 562.8 g (Table 2). Males in the control group showed a smaller mean weight (516.9 g).

3.2.2. Females

Average size of females did not vary significantly among groups, including the control group (Table 2). Average CL ranged from 83.5 to 85.8 ($F = 2.46$, $P = 0.079$). At the time of sacrifice, the mean abdomen width in females from C was lower (64.9%) and differed significantly from T (67.6%) ($F = 3.04$, $P = 0.042$) (Table 2). The lower value for C can be attributed to the fact that measurements were taken while lobster were in soft-shell condition. The abdomen may have been slightly compressed by the caliper. At the end of the experiment, fresh weight of fed females ranged between 456.2 and 485.5 g and were not significantly different. Females of the control group had a significantly smaller fresh weight, compared to fed lobsters ($F = 4.01$, $P = 0.041$). Mean fresh weight of control post-molt lobsters was 445.6 g.

Table 2
Characteristics of adult male lobsters and pubertal females assigned to four experimental diets. Averages and standard deviations are presented with sample size in parenthesis. CL indicates length of cephalothorax, FW indicates the total fresh weight, CPI indicates the male crusher propodite index, and AWI is the female abdomen width index. Control lobsters were sacrificed immediately after molt to serve as a baseline for assessment of changes in condition

		Control (C, post-molt)	Diet T (reference)	Diet E1 (1/2 crab isoproteinic with T)	Diet E2 (no crab isoproteinic with T)	Diet E3 (no crab isocaloric with T)
Males	CL (mm)	87.3 ± 2.3 (14)	86.7 ± 2.9 (14)	88.0 ± 2.1 (14)	87.3 ± 2.2 (14)	89.0 ± 2.3 (10)
	FW (g)	516.9 ± 40.0 (14)	551.3 ± 65.9 (14)	562.8 ± 51.3 (14)	550.8 ± 45.5 (14)	561.0 ± 51.5 (10)
	CPI (CPV/CL^3)	31.5 ± 5.0 (14)	30.2 ± 3.8 (14)	30.6 ± 3.8 (14)	28.9 ± 5.6 (14)	27.9 ± 3.6 (10)
Females	CL (mm)	84.7 ± 1.0 (11)	84.8 ± 1.7 (9)	83.5 ± 2.4 (9)	Not measured	85.8 ± 2.1 (10)
	FW (g)	445.6 ± 14.3 (11)	483.6 ± 38.6 (9)	456.2 ± 29.4 (9)	Not measured	485.5 ± 39.4 (10)
	AWI (%, AW/CL)	64.9 ± 2.5 (11)	67.6 ± 2.6 (9)	66.3 ± 2.0 (9)	Not measured	65.2 ± 1.5 (10)

3.3. Digestive gland

3.3.1. Males

The standardised fresh weight of the digestive gland did not vary much among treatments, except for E3 (Fig. 1a). The mean for E3 (2.75 g/100 cm^3) was significantly less ($F = 8.65$, $P < 0.001$) than for T, E1 and E2, which had an overall mean of 3.16 g/100 cm^3. There was no significant difference in digestive gland fresh weight among diets E1, E2 and T. There were differences among treatments in water content of the digestive gland ($H = 16.3$, $P = 0.001$) (Fig. 1b). Besides a lower fresh weight, the digestive gland in E3 had a higher water content (71.8%). Water content was high also in E2 (68.6%), and not significantly different from E3. In general, digestive gland of lobsters from diets containing crab (E1 and T) showed lower water content, at about 60%, than diets without crab (E2 and E3) (Fig. 1b).

Energy reserves in the tissue (Fig. 1c,d) were significantly different among treatments with respect to both glycogen content ($F_{\log10(\text{glycogen})} = 4.94$, $P = 0.006$) and lipid content ($F_{\text{lipid}} = 3.18$, $P = 0.036$). In both instances, the Tukey test revealed that lobsters fed the E3 diet had significantly lower glycogen (1.35 g/100 g FW) and lipid reserves (9.5%) than the lobsters fed the T diet (2.41 g glycogen/100 g FW and 14.9% lipids). Glycogen content in E2 individuals was also low (1.61 g/100 g FW) and not significantly different from that of E3. Although glycogen values in the digestive gland of lobsters from E2 were lower than what was observed in lobsters from T and E1 (2.47 g/100 g FW), differences were not significant. Lipid reserves of lobsters from T, E1 and E2 were significantly different from those of E3, but not from each other.

Significant differences were noted when comparing the results obtained from the experimental lobsters to those obtained from the control lobsters (Fig. 1). By the end of the experiment, fresh weight of the digestive gland had decreased by 8.4% in T and by as much as 20.1% in E3 ($F = 10.04$, $P < 0.001$). Average fresh weight in E2 decreased by 5.2%, but this was not significant. The water content of the digestive gland showed also significant differences ($H = 19.7$, $P < 0.001$). Water content was significantly higher in the E3 treatments than in C (Fig. 1). The difference was not significant between C and T, E1 and E2, although very marginally in the case of the latter. The absence of crab in the diet during treatment seemed to increase the amount of water contained in the digestive gland compared to the initial state, while its presence seemed to maintain the water content level at approximately 60%.

A difference between control and experimental animals was again visible in energy reserves. Glycogen content of lobsters subjected to all experimental diets was shown to be lower than the one found in post-molt individuals ($F_{\log10(\text{glycogen})} = 20.52$, $P < 0.001$). In post-molt animals, glycogen concentration reached 6.6 mg/g FW. Similarly, lipid reserves in the control group were almost twice as high (23.5%) as those of the experimental animals ($F = 16.08$, $P < 0.001$).

3.3.2. Females

Fresh weight of the digestive gland remained constant, regardless of the treatment (Fig. 2a). No significant differences were detected by ANOVA ($F = 0.70$, $P = 0.508$). However, glycogen content differed significantly between lobsters fed diet T (3.4 mg/g FW) and E3 (1.1 mg/g FW) ($F = 8.53$, $P = 0.005$) (Fig. 2b). A significant difference

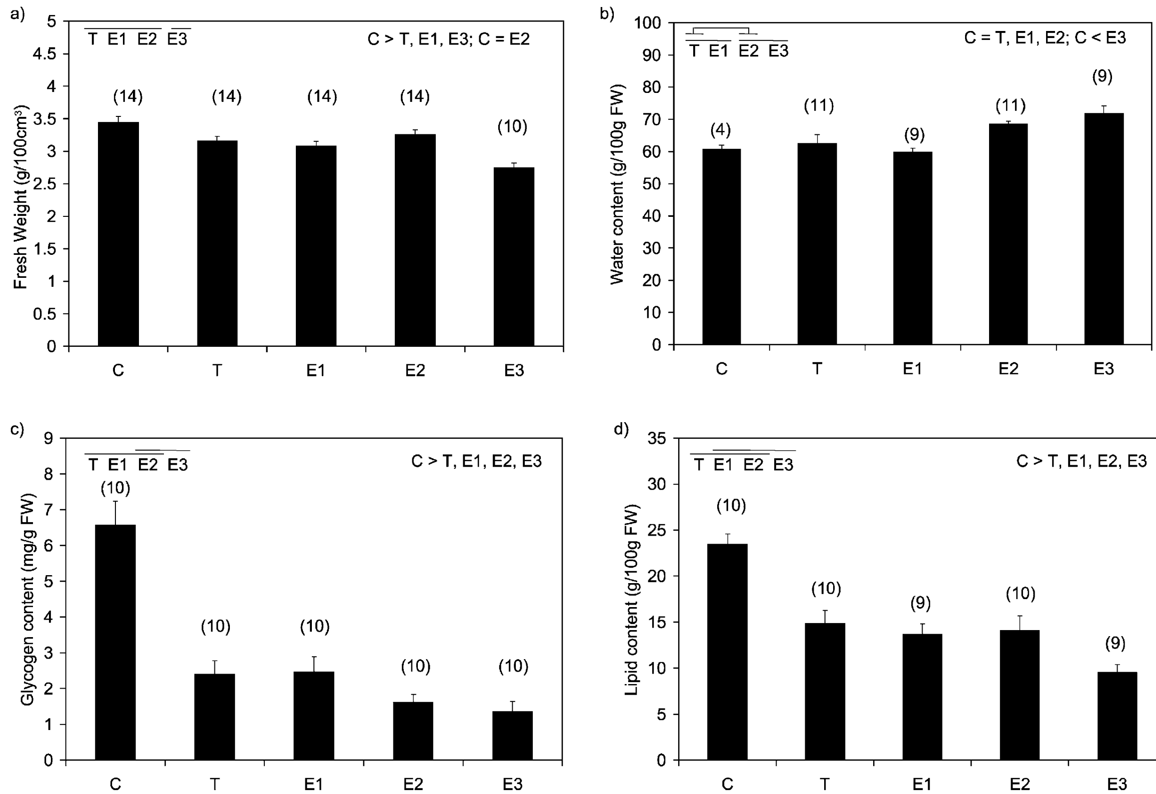

Fig. 1. Digestive gland size and composition of adult male lobsters assigned to four diets: reference (T), half-crab and isoproteinic with T (E1), no crab and isoproteinic with T (E2), no crab and isocaloric with T (E3), and of post-molt lobsters sacrificed at the beginning of the trials (C). (a) Average fresh weight (FW) standardised by CL^3, in g/100 cm^3, (b) average water content in g/100 g FW, (c) average glycogen content in mg/g FW and (d) mean lipid content in g/100 g FW. Error bars illustrate the standard error on the mean. (n) indicates sample size. Treatments showing no significant differences ($P > 0.05$) share a common line.

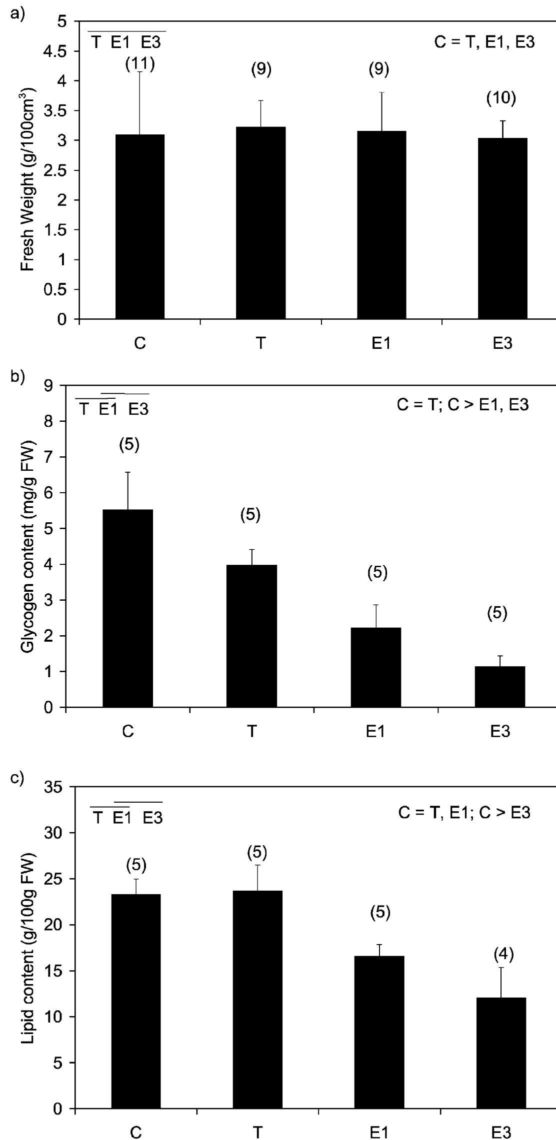

Fig. 2. Digestive gland size and composition of pubertal female lobsters assigned to three diets: reference (T), half-crab and isoproteinic with T (E1), no crab and isocaloric with T (E3), and of post-molt lobsters sacrificed at the beginning of the trials (C). (a) Average fresh weight (FW) standardised by CL^3 in g/100 cm^3, (b) average glycogen content in mg/g FW, and (c) mean lipid content in g/100 g FW . Error bars illustrate the standard error on the mean. (n) indicates sample size. Treatments showing no significant differences ($P > 0.05$) share a common line.

in lipid content was also noted between T and E3 ($F = 5.35$, $P = 0.024$), where levels reached 23.7% and 12.0%, respectively (Fig. 2c). In both cases, values from E1 were intermediate and not significantly different from either T or E3.

When compared to the post-molt lobsters (Fig. 2), again, fresh weight was stable ($F = 0.58$, $P = 0.632$), but glycogen and lipid content varied ($F_{glycogen} = 8.13$, $P = 0.002$; $F_{lipids} = 5.59$, $P = 0.009$). Glycogen content of lobsters fed diet E1 (2.2 mg/g FW) and E3 (1.1 mg/g FW) were both significantly lower than the initial state of 5.5 mg/g FW. In lipid content, however, only E3, at 12.0%, showed a significant difference from C at 23.3%.

3.4. Muscles

3.4.1. Males

There was a variation of chela muscles dry weight with variation of diet composition in males (Fig. 3a). The dry weight of the crusher chela muscles decreased gradually from 4.95 g/100 cm^3 in diet T to 3.65 g/100 cm^3 in E3 ($F = 14.63$, $P < 0.001$). Weight was 26.3% lower in E3 compared to T. Chela muscles weight in E3 was significantly different from all other treatments. Lobsters from the other diet without crab (E2) also differed significantly from those of the reference diet (T), although these two diets were isoproteinic. Lobsters fed diets containing crab, either a full or a half portion (T and E1), did not differ significantly from each other, although the weight was smaller in E1 (4.58 g/100 cm^3) compared to T.

A decrease in the weight of the abdominal muscles was also observed as the proportion of crab and the amount of proteins in the diet decreased (Fig. 3b). The weight of the muscles of the abdomen went from 1.93 g/100 cm^3 in T to 1.62 g/100 cm^3 in E3 ($F = 8.33$, $P < 0.001$), a 16.1% drop. Diets without crab (E2 and E3) were significantly different from the reference diet (T).

Variations in muscles weight did not translate, however, into variations in protein concentration (Fig. 3c,d). In the chela muscles, values ranged from 0.48 and 0.53 g/g DW ($F_{chela} = 0.78$, $P = 0.519$), and in the abdomen muscles, they ranged between 0.54 and 0.56 g/g DW ($H_{abdomen} = 1.63$, $P = 0.653$).

When compared to the post-molt lobsters of the control group, the fed individuals did show some progression in chela muscles weight (Fig. 3). Over the ≈ 110 days of treatment, chela muscles weight was significantly higher in all four diets than in the control group ($F = 69.95$, $P < 0.001$). The situation was, however, different in the case of the abdomen muscles, as a decrease in weight was observed ($F = 13.98$, $P < 0.001$). Protein concentration did not change significantly as a result of the treatments, either in the crusher chela ($F = 0.81$, $P = 0.533$) or in the abdomen ($H = 8.48$, $P = 0.076$), although abdomen protein concentration was always higher in experimental animals compared to control animals.

3.4.2. Females

Muscles taken from females after ≈ 90 days of feeding showed some differences. The muscles of the crusher chela were lighter in females from E3 (0.92 g/100 cm^3) than from T (1.11 g/100 cm^3) ($H = 6.81$, $P = 0.033$) (Fig. 4a). Values observed in E1 were intermediate (1.05 g/100 cm^3) and not different from either T or E3. However, the

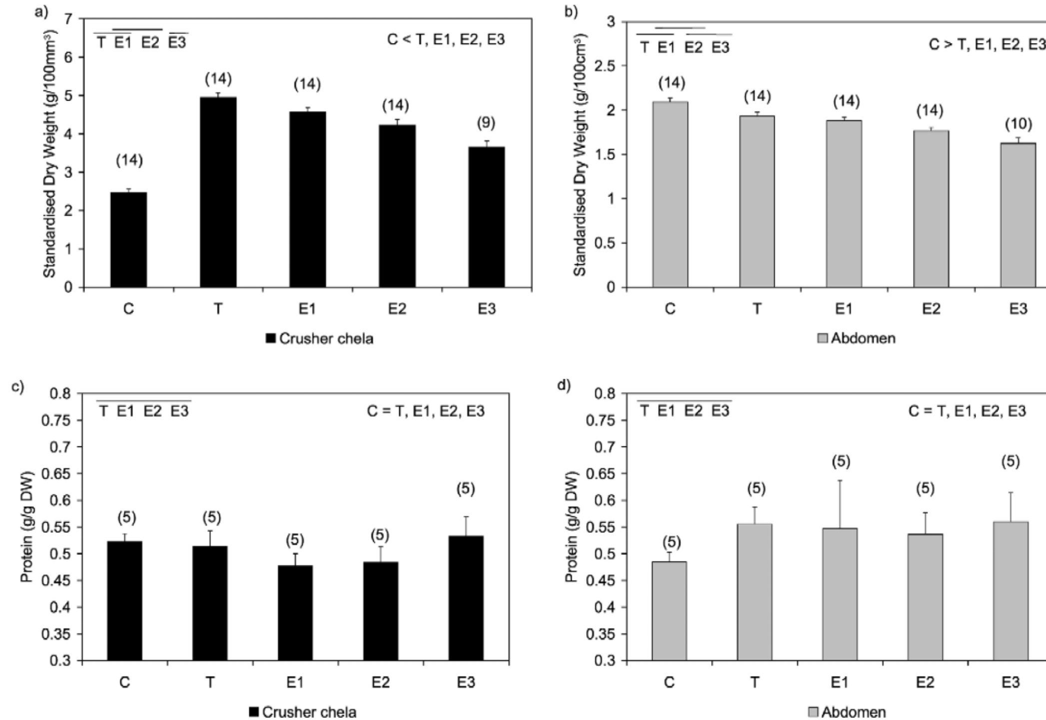

Fig. 3. Weight and protein content of crusher chela and abdomen muscles of adult male lobsters assigned to four diets: reference (T), half-crab and isoproteinic with T (E1), no crab and isoproteinic with T (E2), no crab and isocaloric with T (E3), and of post-molt lobsters sacrificed at the beginning of the trials (C). (a) Average standardised dry weight (DW) of the crusher chela muscles in g/100 mm^3. The weight was standardised for size using the volume of the crusher chela (CPV, see text). (b) Average dry weight of the abdomen muscles standardised by CL^3, in g/100 cm^3, (c, d) mean protein content in g/g DW in the crusher chela and the abdomen muscles, respectively. Error bars illustrate the standard error on the mean. (n) indicates sample size. Treatments showing no significant differences ($P > 0.05$) share a common line.

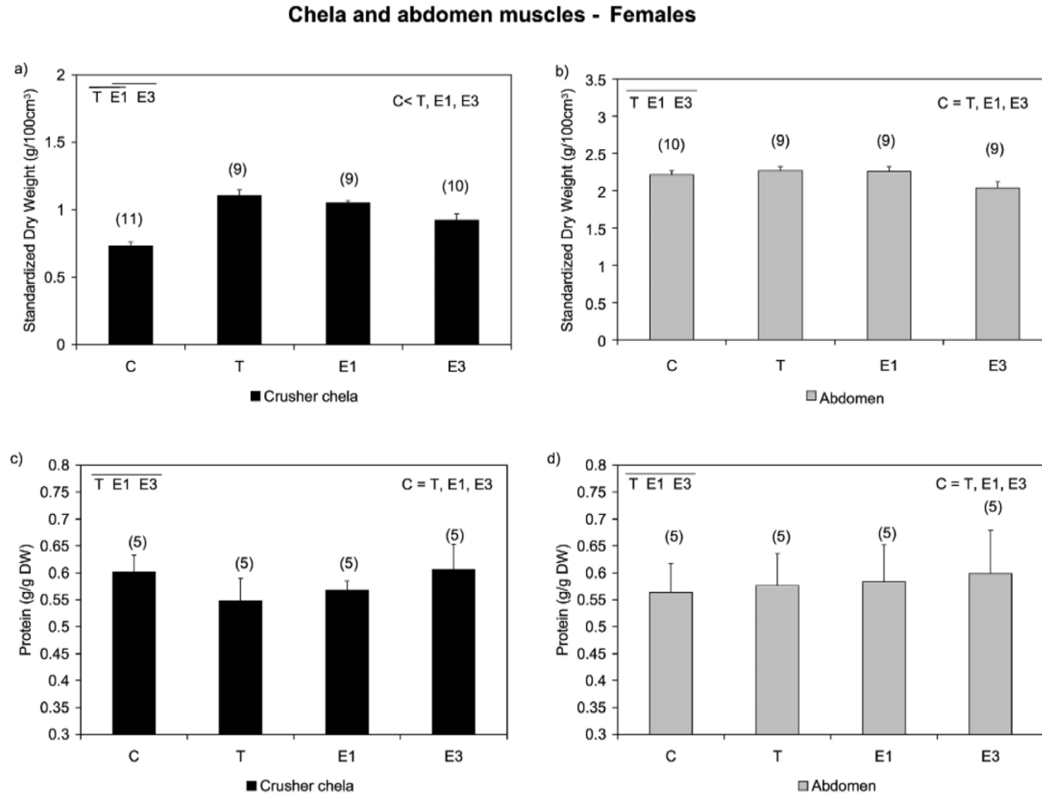

Fig. 4. Weight and protein content of the crusher chela and abdomen muscles of adult female lobsters assigned to three diets: reference (T), half-crab and isoproteinic with T (E1), no crab and isocaloric with T (E3), and of post-molt lobsters sacrificed at the beginning of the trials (C). (a) Average standardised dry weight (DW) of the crusher chela muscles in g/100 cm^3. The weight was standardised with CL^3. (b) Average dry weight of the abdomen muscles standardised by CL^3, in g/100 cm^3, (c, d) mean protein content in g/g DW in the crusher chela and the abdomen muscles, respectively. Error bars illustrate the standard error on the mean. (n) indicates sample size. Treatments showing no significant differences ($P > 0.05$) share a common line.

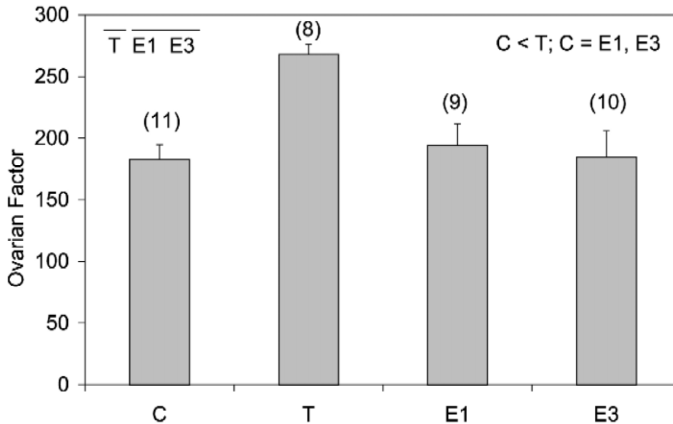

Fig. 5. Average ovarian factor (Of) of pubertal female lobsters assigned to three diets: reference (T), half-crab and isoproteinic with T (E1), no crab and isocaloric with T (E3), and of post-molt lobsters sacrificed at the beginning of the trials (C). Of = Ovary weight (mg)/CL^3 (cm) $\times$ 10. Error bars illustrate the standard error on the mean. (n) indicates sample size. Treatments showing no significant differences ($P > 0.05$) share a common line.

abdomen muscles weight did not vary significantly among treatments ($F = 3.02$, $P = 0.068$), although muscles weight of E3 lobsters was slightly lower (Fig. 4b). In both tissues, the protein content ($F_{chela} = 0.73$, $P = 0.504$; $F_{abdomen} = 0.12$, $P = 0.885$) apparently remained constant (Fig. 4c,d).

When compared to post-molt females of the control group (Fig. 4), the muscles of the chela increased in weight in all treatments ($F = 21.25$, $P < 0.001$), while the muscles of the abdomen remained unchanged ($F = 2.31$, $P = 0.095$). Protein content of both tissues was apparently stable ($F_{chela} = 0.81$, $P = 0.507$; $F_{abdomen} = 0.24$, $P = 0.868$).

3.5. *Ovary*

One female from the reference diet T had light-green ovaries instead of the expected medium- to dark-green color characterising pubertal females. This female was assigned to a pre-pubertal condition and, therefore, was not considered in the following computations. Ovarian factor was significantly higher in females fed the reference diet T ($F = 6.38$, $P = 0.006$) (Fig. 5). Mean ovarian factor reached 267.7 in diet T, compared to 194.0 and 184.4 in diets E1 and E3, respectively.

The ovarian factor of females of the control group was lower compared to fed animals (182.6 ± 40.31), but differed significantly only from diet T ($F = 5.79$, $P = 0.003$) (Fig. 5).

4. Discussion

This experiment was undertaken to examine how different rations of rock crab could affect condition, somatic growth and ovary development of mature lobster, following molt. The half- and no-crab diets (E1 and E2) were adjusted so that the protein content

would be equivalent to a reference diet (T), in which crab was the dominant food item. This allowed us to examine the effect of the quality of the prey. An additional diet containing no crab (E3) was prepared, in which energy content was equivalent to that of the reference diet. Consequently, it had a lower protein content, and this allowed us to examine the effect of protein quantity. Observations on food remains, which consisted mainly of inorganic material (carapace, shell and test), suggest that lobsters ate most of the organic matter, assuming that organic matter was not lost in the tanks. Lobsters took up a great part (over 90%) of the energy and protein available, regardless of the diet composition. It can, therefore, be reasonably assumed that the results obtained reflect the nature of the diet offered.

Our results show that the absence of rock crab in the diet of lobster has an important effect on energy reserves and muscular development, although total fresh weight did not vary significantly among treatments. The effects are generally more obvious in the case of males, as treatments were extended over a longer period of time than for females. Figs. 1–4 illustrate that energy reserves and muscle growth is better when crab is present in the diet. Total absence of crab seemed to lower the overall condition of the lobster. This is striking in diet E3, in which alternative food items (mussel and urchin) were not increased to compensate for the reduction in protein content caused by the absence of crab. In the case of males, results from E3 were always significantly different from the reference diet T. This was the case also in females for glycogen and lipid reserves in the digestive gland, as well as chela muscles dry weight. In most cases, results obtained from diet E2, a diet with no crab but isoproteinic with T, were significantly different from T, but not from E3, suggesting that mussel and urchin, even if given in a greater amount, are not equivalent to crab. Diet E1 gave results similar to the reference diet, even if crab content was reduced by half. In general, animals in E1 were slightly less in condition than those in diet T, although differences were rarely significant. This could suggest that only a strong depletion in crab availability could affect lobster growth and condition. On the other hand, it is reasonable to think that the differences observed in our experiment would have been greater had the treatments lasted longer. Our results show the benefits of consuming crab in a context where animals were confined in space. The actual benefits in the natural environment could be less considering the energetic cost associated to the capture of this mobile species.

Knowledge of the nutrition needs of *H. americanus* is limited. The majority of information available comes from studies based on larvae and juveniles (age: < 120 days) (Conklin, 1995). We do know, however, from the experiments of Castell and Budson (1974), that muscle growth is directly proportional to the amount of protein in the diet. Furthermore, they showed that organ weight and size were dependent on the protein content of the diet. Our results show the same trend for mature lobster. In the diet with a lower protein content (E3), male chela muscles weight was significantly less than with the other diets. It was lower also for females. Fresh weight of the digestive gland was lower also for males and moreover, contained more water. Size and fresh weight of tissue can be misleading indicators of condition since metabolised tissues are replaced with water (Heath and Barnes, 1970; Dall, 1974).

Castell and Budson (1974) also mention that digestive gland glycogen content increased with protein content of the diet. Our results do support Castell and Budson's

assertion. The dependence of *H. americanus* on protein for growth has also been observed in a natural environment (Weiss, 1970; Ennis, 1973). This dependence may be due in part to the fact that lobsters derive most of their energy from proteins. Proteases form the majority of gastric enzymes (Brockerhoff et al., 1970) and their exact amount is proportional to the diet, while amylases tend to remain constant (Hoyle, 1973). This fact may explain the relatively lower performance of the diet E3, with a lower protein content, compared to the three others. The total amount of protein required by lobsters is not precisely known (Conklin, 1995), although many attempts have been made to estimate the required levels (Castell and Budson, 1974; Leavitt et al.,1979; Boghen et al.,1982).

Our experiments further show that even when crab is substituted by blue mussel and urchin, in quantities sufficient to maintain the amount of proteins in the diet (E2), growth and energy reserves are not maintained. It would seem that a diet solely based on sea urchin and blue mussel is in no way equivalent to a diet containing crab. This leads us to speculate that rock crab provides certain benefits to *H. americanus*, while these other species do not. Tank experiments have demonstrated that a diet based on proteins extracted from rock crabs was superior to others based on mussels, urchins, or shrimps (Boghen et al., 1982). Crab is rich in certain amino acids, such as arginine, lysine and methionine, which might explain its superiority as an element of the lobster's diet (Boghen et al., 1982). Conklin (1995) does mention that certain amino acids are essential to lobster, but not much more is known. Alternatively, it could be that despite the abundant provision of sea urchins and blue mussels, lobsters are less attracted to these prey species and ingest smaller amounts of them compared to rock crab. However, in our experiments, lobsters apparently consumed most of the organic matter, regardless of its identity. There is evidence reported in the literature of the presence of specific chemical attractants in crabs that lobster can detect and react to (Derby and Atema, 1982), which could stimulate ingestion of crabs as suggested by McLeese (1970). Also, Carter and Steele's (1982b) laboratory studies found that lobsters show a stronger food-searching response in the presence of metabolites from rock crab compared to metabolites from sea urchins or starfish. It is suggested that the significant attractiveness of rock crab metabolites, coupled with visual cues (Hirtle and Mann, 1978) could enhance lobster–crab encounter rate. The benefits of preying on rock crab could, therefore, result not only from a potential increase in the quality of proteins ingested, but also from an increase in the quantity ingested.

The presence of crab in the diet helped maintain lipidic reserves. We did not distinguish between different types of lipids in our assays. D'Abramo et al. (1980) demonstrated that polyunsaturated lipids were important for growth of juveniles. It is also interesting to note that when crabmeat is added to the diet of juvenile lobsters, there is no need to add lecithin to the food to maintain good growth rates (Kean et al., 1985). Lecithin is an essential phospholipid in the transport of cholesterol from the digestive gland to hemolymph (Kean et al., 1985; Conklin, 1995). The presence in crab, of lecithin or of another substance acting as lecithin, could be another key element in the role of rock crab in the lobster's diet. Moreover, lipids are known to be important for the development of ovaries, egg fertilisation and hatching (Castell and Kean, 1986). Our experiments did show that lipidic reserves were lower in the absence of crab in the diet.

Also, there was a significant increase in ovarian development when females were offered a full ration of crab. No significant differences were observed between the other treatments, although the ovarian factor was smaller in the diet containing no crab and less protein (E3), compared to the diet with a half portion of crab (E1). Complete ovary maturation from molt (pubertal female) to the time of spawning (adult female) is a process that lasts for 9–11 months. We can imagine that the small differences observed over the short-term of our experiment would have been emphasised if treatments had lasted during the whole process of ovary maturation.

The lobsters from the control group were sacrificed within 24 h after molt. They were, therefore, in molt stage A (Aiken, 1973). We know very little on the biochemical constituents of the lobster in relation to its molt cycle. An accumulation of glycogen and lipids in the digestive gland has been reported for *Cancer* species during the pre-molt period, which would then be quickly metabolised after exuviation (Heath and Barnes, 1970). This is consistent with our results. After molting, in both males and females, a decrease in lipid and glycogen content can be observed (Figs. 1 and 2). Glycogen would be transformed into chitin, while lipids may play the role of energy source during the fasting period following molt (Heath and Barnes, 1970). Lobsters also exhibit a period of fasting after molt, which lasts a few days (personal observations).

In our experiment, muscle growth in males was mainly observed in the crusher chela (Fig. 3), often at the expense of the abdomen muscles, which even slightly regressed. This may be to insure a feeding capacity. In *Panulirus longipes*, leg and chela muscles are not metabolised as quickly as abdomen muscles during fasting to maintain mobility (Dall, 1974). In both males and females, chela muscles weight was rather small at the time of the molt. This may be due to the fact that proteins from the chelipeds and muscle mass can be reduced by 30–60% right before the molt, to aid in the exuviation of the old shell (Mykles, 1980). It is likely that muscle restoration of the chelipeds is a top priority after molt, as this is where the growth was concentrated. It is also interesting to note that the regression in abdomen muscles weight was not as pronounced in females compared to males. This can be associated to the duration of the experiment that was shorter for females. On the other hand, it could reflect some investment in abdomen muscles growth by females for reproductive functions.

Lobster feed abundantly on rock crab from postlarval to adult stage (see review by Gendron and Fradette, 1995; Sainte-Marie and Chabot, 2001), as well as during larval stages (Juinio and Cobb, 1992; Gendron and Fradette, 1995). Lobster are known to select rock crab, and very few other prey species seem to attract lobster as crab does. We demonstrated that rock crab plays an important role in the diet of the American lobster, and that its absence can have significant effects on lobster condition and development. Even large amounts of blue mussel and sea urchin cannot fully compensate the absence of this essential component of the lobster's diet. Even if no other brachyuran crabs were found in the stomachs of lobsters off the Magdalen Islands (Hudon and Lamarche, 1989; Sainte-Marie and Chabot, 2001), it seems a priori improbable, given its diversified diet base in the natural environment, that lobster could suffer from a nutritional imbalance or deficiency as a result of low crab consumption. There are many other species not tested in our experiments that could have good nutritional value in terms of energy and proteins, such as amphipods and isopods or

hermit crabs, although these species are rarely dominant preys in the lobster stomachs. In certain areas, such as Newfoundland, the brachyuran spider crab *Hyas araneus* is abundant (Ennis 1973) and could be an interesting alternative prey for lobster. Also, high exploitation of rock crab could release competition or predation pressure on a number of interesting species that could become more available to the lobster. On the other hand, if alternative preys do not compensate the absence of crab in the diet, either by their quality or abundance, the ensuing reduction in muscle growth and depletion of energy reserves could slow the molt cycle or even inconvenience the actual molt. Moreover, effects on ovary development could eventually affect egg and larval condition or spawning and hatching periods. This may play a role in lobster recruitment. Many details of the nutritive quality of the rock crab and the energetic cost associated to its capture are still unknown, and our results warrant further examination in this area. Finally, our results strongly suggest that the development and management of a rock crab fishery should be cautious and governed by a multi-species approach.

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