

# Niche segregation between American lobster *Homarus americanus* and rock crab *Cancer irroratus*

Christiane Hudon<sup>1</sup>, Gabriel Lamarche<sup>2</sup>

<sup>1</sup> Ministère des Pêches et des Océans, Station de Biologie Arctique, 555 boul. Saint-Pierre, Sainte Anne de Bellevue, Québec, Canada H9X 3R4

<sup>2</sup> 5467 de l'Esplanade, Montréal, Québec, Canada H2T 2Z8

**ABSTRACT:** Niche segregation of American lobster *Homarus americanus* and rock crab *Cancer irroratus* was investigated in the southern Gulf of St Lawrence using density, biomass, size structure and diet of these 2 species captured in 4 habitats. Rocky bottoms colonized with macroalgae supported the highest density and biomass of both species, but they also coexisted in lesser numbers on bare rocky bottoms. Low densities of crabs of all sizes and of large lobsters were found on eelgrass beds, and crabs only on bare sand. The proportions of size groups of lobsters and crabs differed significantly among substrate types. Small lobsters and large crabs predominated on bare rocky bottoms, while large lobsters and small crabs were mostly found between boulders with macroalgae. Examination of stomach contents of lobsters and crabs coexisting on rocky bottoms with and without algae showed the lobsters' diet to remain similar at both sites, while that of crabs differed between sites. Diets of small lobsters and small crabs were more similar than those of larger individuals, possibly because small individuals of both species remain hidden in sediment and crevices between stones. Lobsters fed principally on horse mussels, rock crabs, lobsters, gastropods and ectoprocts, while rock crabs fed on horse mussels, ectoprocts and polychaetes. Large crabs occasionally preyed upon small lobsters. At both rocky sites and for all size groups, crab diet always exhibited a lower average calorific value than that of lobster. In the bare stone habitat, supporting low densities of large lobsters, the average calorific value for large rock crab diet was consistently higher than in the large rocks with algae habitat, supporting a high density of large lobsters. While lobster diet remained similar between sites, rock crab diet was poorest on grounds where large lobsters occurred, possibly reflecting increased risk due to predation while foraging for food. The coexistence of American lobster and rock crab is made possible by their different use of the substrate and food resources with increasing size, and by the flexibility of the rock crab.

## INTRODUCTION

In North Atlantic waters, American lobsters *Homarus americanus* and rock crabs *Cancer irroratus* are frequently found in the same habitat and could be potential competitors. According to the principle of competitive exclusion, 2 species cannot occupy identical niches: ecological differentiation is the necessary condition for coexistence (Hutchinson 1957). The common need for shelter and the predatory feeding habits of lobsters and crabs suggest that their respective ecological niches are similar; yet, their coexistence on rocky bottoms indicates that fundamental differences must exist between the 2 species.

Adults of both species prefer rocky bottoms offering abundant shelter, although large crabs are also found

in low densities on bare sand (Cobb 1971, Scarratt & Lowe 1972, Shotton 1973, Winget et al. 1974). Habitat use also appears to change ontogenically: contrarily to the adults, which are commonly found in the open, small lobsters (<25 mm carapace length, CL) and small crabs (<25 mm carapace width, CW) tend to remain hidden in gravel, sand, and softer sediments between boulders (Scarratt & Lowe 1972, Pottle & Elner 1982, Hudon 1987). However, regardless of size, crabs seldom appear to excavate or maintain well-defined burrows as lobsters do (Atema & Cobb 1980).

Lobsters and crabs exhibit different behaviours and substrate use when confronted with a predator. When they are caught outside their burrow, small (<25 mm CL) lobsters often attempt to escape predators by swimming away using rapid abdomen flexing, whereas

larger lobsters tend to defend themselves with their claws (Lang et al. 1977, Hudon 1987). Although crabs occasionally respond to an aggressor by an agonistic posture, they often escape the aggressor by burying themselves in the sediment or working their way under stones (Fogarty 1976).

The diet composition of lobsters and crabs shows many similarities under natural conditions. Stomach contents generally reflect the relative abundance of prey species in the habitat (Weiss 1970, Miller et al. 1971, Ennis 1973). However, recent studies (Carter & Steele 1982a, Michaud 1986, Elner & Campbell 1987) suggest that lobster diet exhibits marked preferences for certain food items. One major dietary difference is that lobsters prey extensively on crabs (Fogarty 1976, Evans & Mann 1977, Scarratt 1980) and occasionally on other lobsters, while there is no evidence that crabs prey upon lobsters (Weiss 1970, Stewart 1971, Krouse 1971, Drummond-Davis et al. 1982). Little is known of cannibalism among rock crabs.

The above information suggests that requirements for shelter and food might differ not only between species, but also with size for each species. Since shelter and food availability also differ among substrate types, it is expected that the size distribution and abundance of each species as well as their respective diet should vary according to their use of the available resources. Such interdependence between shelter availability, standing stocks and population structure was previously shown by Howard (1980) for *Homarus gammarus*. Also, Lawton (1987) recently discussed the strong interaction between lobster size, shelter requirement and foraging behaviour. Long-term colonization of artificial reefs by lobsters has been suggested to depend on adequate food, supplied by other organisms colonizing the reef, and on the availability of shelters (Scarratt 1968).

In this study we investigated resource partitioning between *Homarus americanus* and *Cancer irroratus*, by examining population structure and diets of these species coexisting in 4 habitats. Comparisons between substrate types showed differences induced by the interactions between the species 'mode de vie' at a given size, and the characteristics associated with different habitats (shelter and food). In addition we integrated seasonal fluctuations of density and size structures of both species on 4 bottom types. The diets of lobsters and crabs belonging to 3 size groups were compared on 2 rocky bottoms offering habitats of different complexity.

## STUDY AREA

Iles de la Madeleine is a 100 km long archipelago located in the southern Gulf of St Lawrence (Fig. 1). Five of the 7 islands are linked by narrow sand dunes

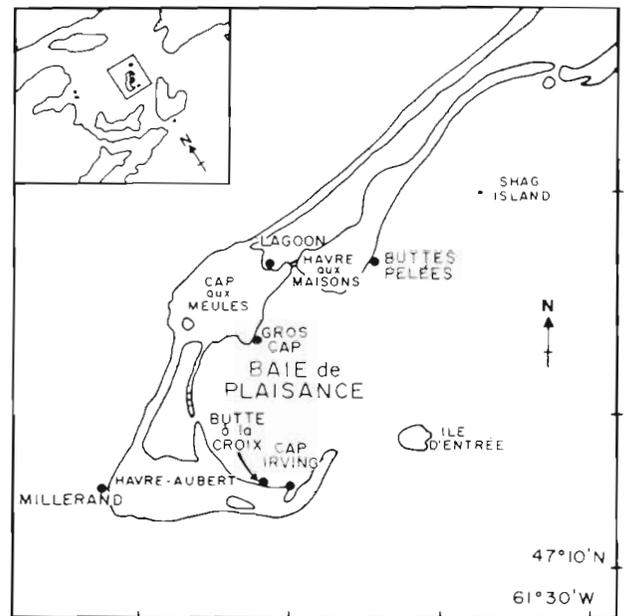


Fig. 1 Location of the Iles de la Madeleine in the Gulf of St Lawrence (inset), and of the sampling stations in the Baie de Plaisance

enclosing 3 lagoons. Sand is the most common substrate around the islands, covering 87% of the area within the 20 m isobath. The bedrock is soft red sandstone. Rocky bottoms, where lobster fishing takes place (minimum legal size: 76.2 mm CL), comprise only 9.9% of the total surface. Hard and soft bottoms are equally well represented on both sides of the islands. The open lagoons, which represent only 3.1% of the surface available to lobsters, are shallow sandy basins supporting a heavy growth of eelgrass *Zostera marina* in the summer. Fishing is prohibited in the lagoons, which harbour transient adult male lobsters attracted by the temperature gradient in early spring (Munro & Theriault 1983).

Rock crabs are not commercially exploited off Iles de la Madeleine although they represent an abundant by-catch of the lobster fishery. Crabs caught in such a manner are generally thrown back to sea or (rarely) used as bait. Their frequent occurrence in lobster traps decreases the efficiency of lobster fishing by consuming the bait, saturating the traps and slowing shipboard operations.

## MATERIALS AND METHODS

**Sampling and measurement.** Site exploration, substrate characterization and sampling were done while SCUBA diving at 5 stations off Iles de la Madeleine (Fig. 1), from 20 May to 27 September 1985. Four major

substrate types were sampled (Table 1): (1) barren rocky bottom of stones and gravel (Butte à la Croix and Cap Irving); (2) boulder bottom heavily colonized by macroalgae (Gros Cap and Buttes Pelées); (3) bare sandy substrate adjacent to the above stations; and (4) sandy substrate with eelgrass *Zostera marina* (Hâvre aux Maisons lagoon).

Quantitative sampling of lobster and crab was carried out during daytime, using one of 2 techniques, depending on substrate type. On bare sand and eelgrass beds, 2 divers swam one each side along a 100 m long leaded line, sampling a width of 1 m on each side of the line. The eelgrass and the surface of the sand were raked (2 cm depth) for hidden or buried animals. This technique allowed survey of a large surface (200 m<sup>2</sup>) with minimal alteration to the bottom prior to sampling. The method was deemed appropriate on soft substrates since lobster and crab densities were low and animals were readily seen.

On rocky bottoms, a 2.5 m high corral, made of 7 mm mesh size seine net, was used to enclose a 10 × 4 m area. The corners of the seine were supported by 0.4 m steel rods and guy ropes driven into the substrate.

Escape of the smallest individuals was prevented by sewing a skirt of 3 mm mesh to the lower 0.45 m of the net, and by adding lead to the bottom edge, which was manually fitted to the substrate. Escape over the top was unlikely, since sampling took place in shallow water (2 to 7 m) and the seine extended over most of the water column.

The area suitable for the installation of a corral was selected by the availability of an area (10 × 4 m) with only one type of bottom material. Although this is not representative of the heterogeneity of rocky bottoms, where small patches of sand, gravel, and bedrock may be found within a few meters, it was deemed necessary to sample a bottom area as homogeneous as possible in order to allow comparison of density and size structure on different bottom types. Two divers required 30 to 60 min to locate, position, and install the corral. The bottom was usually photographed prior to sampling for reference, using a Nikonos V<sup>TM</sup> underwater camera with a 15 mm lens. Areas previously sampled were avoided.

Sampling in the corral was carried out by 3 divers moving side by side, with each diver covering a 1.3 ×

Table 1. Sample numbers, stations, substrate types (R: bare rocks, RA: rocks with algae, S: sand, SZ: sand with eelgrass), sampling method (C: corral, T: transect, F: free sampling), sampling dates, lobster and crab catches (total number per sample)

Station	Sample number	Substrate type	Sampling method	Date (1985)	Lobster catch	Crab catch
Cap Irving	1	R	C	8 Jun	112	0
	9	R	C	1 Jul	100	173
	17	R	C	1 Aug	29	87
	18	S	T	5 Aug	0	20
	21	R	C	7 Aug	64	109
	25	S	T	21 Aug	1	5
	26	R	C	21 Aug	50	142
	28	R	C	25 Sep	42	135
Gros Cap	19	RA	C	5 Aug	59	209
	8	R	C	21 Jun	18	30
	13	RA	C	5 Jul	108	288
	20	RA	C	6 Aug	43	178
	22	S	T	8 Aug	0	31
	27	RA	C	22 Aug	142	320
Butte à la Croix	29	RA	F	26 Sep	149	300
	3	R	C	12 Jun	79	34
	11	RA	C	3 Jul	49	139
	16	R	C	29 Jul	23	154
	24	R	C	19 Aug	57	76
Hâvre aux Maisons Lagoon	30	R	C	27 Sep	50	107
	5	SZ	T	17 Jun	0	59
	6	SZ	T	18 Jun	0	54
	7	SZ	T	18 Jun	0	2
	14	SZ	T	22 Jul	7	57
Millerand	15	SZ	T	23 Jul	5	7
	12	R	T	4 Jul	15	57
Buttes Pelées	23	RA	C	9 Aug	59	542

10 m corridor. All stones were overturned and crevices inspected for lobsters and crabs. The presence of other abundant animal species was noted. Lobsters and crabs were captured manually and placed in nylon mesh carrier bags filled with algae to minimize aggression between animals. After the disturbed sediment had settled for 60 to 90 min, the corral was sampled again by the same divers.

From early June to late September 1985, 17 corrals and 9 transects were sampled (Table 1). On one occasion, lobsters and crabs were collected at Gros Cap for stomach content analysis without setting up the corral (Table 1, F = free sampling). Density and size structure were therefore not available for that sampling. Replication and other technical aspects related to sampling using corrals and transects were discussed by Hudon (1987).

Following the dives, lobsters and crabs were sorted aboard the support vessel and maintained live under wet kelp. For lobsters, carapace length (CL, from the posterior edge of the eye socket to the posterior margin of the carapace, following a line parallel to the medio-dorsal suture) was measured to the nearest 0.1 mm with vernier calipers. Some individuals were retained for wet weight measurements to the nearest 0.01 g. Length-weight linear regressions calculated for males and females separately showed no significant differences. Biomass was calculated using the following length-weight relationship for both male and female lobsters:

$$\begin{aligned} \text{Log } W &= -3.172 + 3.048 \log \text{ CL}; \\ r &= 0.99, n = 199 \end{aligned} \quad (1)$$

where CL = carapace length (mm); W = fresh weight (g). The regression equation was calculated on lobsters between 6 and 60 mm CL, excluding individuals with missing appendages. For crabs, carapace width (CW) was measured at its widest point. The regressions between carapace width and fresh body weight (W) calculated for males (9.5 to 87.1 mm CW) and females (10.4 to 102.2 mm CW) had significantly different slopes ( $p < 0.001$ ). Biomass was therefore calculated separately for male and female crabs, exclusive of ovigerous females, using the following equations:

$$\begin{aligned} \text{Females : Log } W &= -3.307 + 2.669 \text{ Log CW}; \\ r &= 0.95, n = 276 \end{aligned} \quad (2)$$

$$\begin{aligned} \text{Males : Log } W &= -3.603 + 2.854 \text{ Log CW}; \\ r &= 0.98, n = 242 \end{aligned} \quad (3)$$

Biomass and density of both species were first described by scatter diagrams. The abundance of small (5.0 to 22.0 mm CL), medium (22.0 to 31.2 mm CL) and large (31.2 to 92.3 mm CL) lobsters was compared to that of small (4.0 to 26.0 mm CW), medium (26.0 to 37.1 mm CW) and large (37.1 to 124.9 mm

CW) crabs for each substrate type. Size categories were determined by the 33.3 and 66.6 percentile values of the cumulative size distribution of all samples pooled for each species. The percentile values were selected as objective criteria to divide all crabs and lobsters among 3 equal size groups. This division also roughly corresponds to an exponential increase in weight for both species ( $10^0$ ,  $10^{0.75}$ ,  $10^{1.5}$  g), which could indicate comparable changes in volumetric and energetic constraints with size for both species. Frequency tables of size groups were analysed using the BMDP-4F statistical package. The equality of frequency of all size groups was tested using a G-test of independence for 2-way tables and a log-linear model for 3-way tables.

#### Analysis of stomach contents of lobsters and crabs.

The diets of lobsters and crabs living together in 2 different habitats were characterized from examination of a large number of specimens. From Cap Irving, we examined the stomach contents of 42 lobsters (7.8 to 49.9 mm CL) and 103 crabs (8.2 to 67.5 mm CW) captured on 25 September. These were compared to the stomach contents of 136 lobsters (8.2 to 66.2 mm CL) and 59 crabs (17.2 to 124.9 mm CW) captured at Gros Cap on 26 September (Table 1). Both collections took place at midday (12:00 to 16:00 h). The wide size range of specimens and the close collection dates were chosen to investigate dietary differences among sizes within each habitat while avoiding differences due to seasonal variability.

Less than 3 h after sampling in the field, each stomach was removed and fixed in a 4% buffered formaldehyde solution and later transferred to alcohol. In the laboratory, each stomach was given a score for fullness ranging from 0 (empty) to 4 (full) prior to examination of its content under a dissecting microscope. Prey identification was carried out to the maximum possible level of precision. Each food taxon was given an abundance score according to its volume, ranging from 1 to 10 – a score of 1 meaning that the food item was present but represented less than 10% of the total volume of gut contents, a score of 10 meaning 90 to 100% of the total volume of gut contents. Some taxa were rare or of marginal importance in the diet; others were present at only one of the 2 locations but had a taxonomically-related counterpart at the other one. We therefore grouped the original 61 taxa into 18 taxonomic groups to carry out statistical analysis of the diets (Table 2).

The compilation was also designed to account for all food items in a mutually exclusive fashion while taking into account the specimens that could not be identified to the same precision level. For instance, in Table 2, 'Polychaeta' represents those specimens of annelids that could not be identified any further and does not

Table 2. *Homarus americanus* and *Cancer irroratus*. Food items found in lobster and crab stomachs at Gros Cap and Cap Irving. Frequency of occurrence is indicated as the average abundance score

Group	Food item	Gros Cap		Cap Irving	
		Lobsters	Crabs	Lobsters	Crabs
1	Foraminifera	0.026	0.219	0.143	0.067
2	Porifera	0.000	0.000	0.000	0.010
3	Hydroida	0.155	0.082	0.405	0.029
3	Ectoprocta	0.371	1.534	0.357	0.086
4	Prosobranchiata	0.052	0.014	0.167	0.029
4	<i>Lacuna vincta</i>	0.698	0.274	0.357	0.181
4	<i>Margarites</i> sp.	0.000	0.000	0.071	0.019
4	<i>Nassarius</i> sp.	0.052	0.000	0.000	0.000
4	<i>Polinices immaculatus</i>	0.017	0.000	0.000	0.000
5	Pelecypoda	0.155	0.219	0.214	0.105
5	Mytilidae	0.060	0.014	0.000	0.038
5	<i>Modiolus modiolus</i>	2.422	4.466	1.571	2.114
5	<i>Tellina agilis</i>	0.069	0.014	0.119	0.086
6	Polychaeta	0.026	0.000	0.000	0.010
6	Nereidae	0.147	0.288	0.143	0.143
6	Polynoidae	0.069	0.027	0.119	0.210
6	<i>Lepidonotus squamatus</i>	0.052	0.000	0.381	0.810
6	<i>Harmothoe</i> sp.	0.000	0.000	0.000	0.019
6	Terebellidae	0.000	0.151	0.048	1.038
6	Glyceridae	0.000	0.000	0.000	0.048
6	<i>Spirorbis</i> sp.	0.000	0.000	0.024	0.000
7	Crustacea	0.009	0.014	0.000	0.010
7	Ostracoda	0.000	0.014	0.000	0.019
7	Copepoda, Harpacticoida	0.043	0.014	0.000	0.019
7	Isopoda <i>Idothea</i> sp.	0.017	0.055	0.000	0.038
7	Amphipoda	0.026	0.000	0.000	0.010
7	<i>Gammarus</i> sp.	0.000	0.000	0.000	0.133
7	<i>Ischyrocerus</i> sp.	0.078	0.055	0.000	0.019
7	<i>Psammonyx nobilis</i>	0.000	0.000	0.000	0.010
7	<i>Corophium</i> sp.	0.009	0.027	0.000	0.029
7	<i>Jassa falcata</i>	0.043	0.041	0.000	0.000
7	<i>Monoculodes</i> sp.	0.000	0.014	0.000	0.000
7	Caprellloidea	0.009	0.000	0.000	0.000
7	Acarina, Halacaridae	0.009	0.014	0.000	0.000
8	Cirripedia <i>Balanus</i> sp.	0.103	0.000	0.143	0.086
9	Decapoda	0.267	0.192	0.310	0.219
9	Caridea	0.000	0.000	0.024	0.000
9	Anomura <i>Pagurus</i> sp.	0.009	0.000	0.000	0.000
10	Macrura <i>Homarus</i> sp.	1.759	0.000	1.690	0.210
11	Brachiura <i>Cancer</i> sp.	1.681	0.192	0.405	0.305
12	Echinodermata	0.000	0.000	0.024	0.000
12	Asteroidea	0.216	0.000	0.000	0.000
12	Ophiuroidea	0.000	0.000	0.048	0.000
13	Echinoidea <i>Strongylocentrotus</i>	0.328	0.137	0.238	0.010
14	Ascidiacea	0.095	0.000	0.048	0.000
15	Pisces	0.086	0.000	0.071	0.343
16	Flesh	0.172	0.000	0.048	0.076
16	Flocculent matter (brown)	1.164	0.726	2.333	2.467
16	Flocculent matter (white)	1.948	0.315	1.190	0.705
17	Algae	0.621	1.000	1.571	0.590
17	Algae <i>Corallina officinalis</i>	0.009	0.000	0.024	0.000
18	Nylon	0.026	0.000	0.024	0.010
18	Unidentified	0.103	0.055	0.214	0.152

comprise specimens identified to generic level. The total representation of the polychaetes as a group can therefore be calculated by adding the values assigned to Group 6.

**Statistical analyses of diets.** Abundance scores observed for the 18 groups of food items found in the 340 stomachs were used as the initial data matrix for the analysis of diet using the asymmetrical version of

multivariate statistics. Similarity matrices were generated with Gower's (1971) index, which considers the absence of a given taxon in 2 stomach contents as an absence of information rather than as an element of similarity. For instance, 2 stomachs containing one single food item of a different type (i.e. having an identical score of zero for all food items except for one) would have a similarity value near zero with Gower's index, whereas they would have scored almost the maximum similarity value of 1.0 using symmetrical indices.

The similarity matrices thus calculated were statistically compared to hypothetical similarity matrices (model matrices) representing the expected values for a perfect segregation of diet between lobsters and crabs. Matrices were compared using the Mantel statistic, which is the sum of the products of corresponding elements of the 2 matrices to be compared (Mantel 1967, Legendre 1987). Since the frequency distribution of this statistic is unknown and differs for each particular pair of matrices (e.g. lobsters vs crabs, small vs large individuals, etc.) a reference distribution was generated for each test by randomly permuting one of the matrices and re-computing the Mantel statistic. The Mantel statistic distribution obtained after 250 random permutations was then used as a reference; this was compared with the statistic obtained from the comparison between the 2 groups being tested.

The test statistic was standardized (z-score) as described by Mantel (1967) and compared to the critical values of the standardized normal distribution. This allowed us to evaluate the probability of the null hypothesis, i.e. that there is no relation between the diet similarity matrix and the model matrix, since the second matrix represents the model of complete difference between the diets of the 2 groups considered. The test is statistically valid because the information in the model matrix is independent of that in the diet similarity matrix. This test, which has the same purpose as discriminant analysis, offers the advantage of representing dietary relationships by an ecological similarity coefficient appropriate to the data and to the nature of the problem.

Discriminant analysis was used to allocate scores of importance to the food items. Principal component analyses of the correlation matrices allowed the visual representation of the segregation of diet among species and stations.

The weighted calorific value of individual stomach contents was computed using calorimetric values ( $\text{cal g}^{-1}$  of fresh weight) available from the literature (Brawn et al. 1968, Thayer et al. 1973, Atkinson & Wacasey 1979). The number of calories per g fresh weight was selected because lobsters and crabs generally ingested at least some hard body parts. In the

absence of data for a particular species, we used the average calorific content measured for other species of the same group. For each stomach (s), the weighted calorific value ( $E_s$ ) equalled the sum of the products of the abundance scores of each food item ( $Y_{ps}$ ) and its energetic value ( $c_p$ ), divided by the sum of the abundance scores:

$$E_s = \frac{\sum_1^p (Y_{ps} \cdot c_p)}{\sum_1^p Y_{ps}} \quad (4)$$

The mean and standard deviation of weighted calorific values were then calculated for each group of species, station and size, to allow statistical comparisons.

## RESULTS

### Description of sampling stations

Cap Irving and Butte à la Croix stations were characterized by small stones imbedded in soft sediments interspersed with patches of gravel and sandstone. Small crevices were available and burrowing was possible in the soft sediments present between stones (5 to 20 cm diameter). Scattered tufts of short (*Ptilota serrata*, *Chordaria tomentosa*) and encrusting algae (*Corallina officinalis*) offered very limited surface cover. Mussels (*Mytilus edulis*, *Modiolus modiolus*) were imbedded between stones and polychaetes (especially *Lepidonotus squamatus*) were abundant in the soft sediments. The underside of stones was colonized by littorinid gastropods, hydroids, barnacles and brittle stars. Water temperature of the shallow coastal stations varied from 11°C in early June to 15°C in late September, with a maximum of 19°C in late August.

The station located at Millerand and one corral off Gros Cap were characterized by a bedrock bottom (sandstone) on which stones were scattered. Some cover was available under stones and in small holes (10 to 60 mm diameter) bored in the bedrock by the bivalve *Zyrrhaea crispata*. Scattered algae were also present, and the associated macrofauna appeared similar to that observed in Butte à la Croix and Cap Irving, although less abundant.

At Gros Cap and Buttes Pelées, the bottom was comprised of piles of large rocks (20 cm diameter and more) on a sand base. The rocks were abundantly colonized by macroalgae (*Laminaria* spp., *Ulva* sp., *Chondrus crispus*, *Chordaria tomentosa*, *Rhodimena palmata*, etc.), which provided excellent surface cover in addition to numerous crevices of many sizes. The macrofauna was richest at this station, comprising

caprellid amphipods, sea urchins (*Strongylocentrotus droebachiensis*) and gastropods (*Lacuna vincta*, *Nassarius* sp.). Mussels (*Mytilus edulis*, *Modiolus modiolus*) were abundant on rocks. Hydroids, ascidians and sponges were found on rocks, on the larger mussels and on the stipes of laminarian algae. In contrast to the assemblages found at Butte à la Croix and Cap Irving, this community hosted conspicuous predatory species such as nereid polychaetes, seastars, and fish (*Tautoglabrus adspersus*, *Myoxocephalus* sp.).

Sandy areas adjacent to the rocky stations described above were sampled concurrently. Macrofauna was scarce on sandy bottoms devoid of macroflora. The most common organisms were the sand dollar (*Echinarachnius parma*), polychaetes and burrowing pelecypods (*Venus mercenaria*, *Ensis directus*, *Mya arenaria*). Large fish (*Raja radiata*, *Hypoglossoides platessoides*, *Myoxocephalus* sp.) were occasionally seen. Sandy bottom colonized by eelgrass (*Zostera marina*) and *Ulothryx* spp. supported a richer fauna, with the additional presence of the grey shrimp (*Cragon septemspinus*) and small fishes such as sticklebacks (*Gasterosteus aculeatus*). Water temperature was cooler in the lagoon than off the shallow coastal stations, varying from 12°C in June to 10°C in late September, with a maximum of 16°C in late August.

**Abundance and population size structure on different bottom types**

Rock crabs were found on all bottom types, whereas lobsters were most abundant on rocky bottoms, absent on sand and rare on sand with eelgrass. Density and biomass varied widely (Figs. 2 and 3). Density and biomass of lobsters and crabs were lowest on bare sand and highest on rock with algae. In nearly all samples and on all bottom types, crabs outnumbered lobsters per surface unit (Fig. 3, Table 3). However, the higher

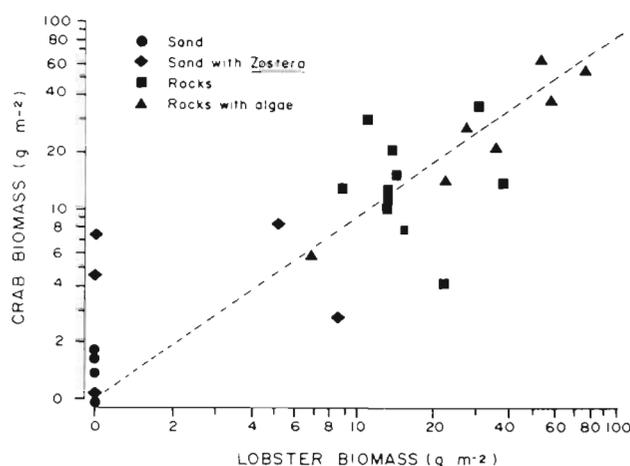


Fig. 2. *Homarus americanus* and *Cancer irroratus*. Correspondence between the biomass of lobsters and crabs cohabiting on different bottom types. The dotted line indicates equivalent values of biomass of lobsters and crabs and is drawn for reference only

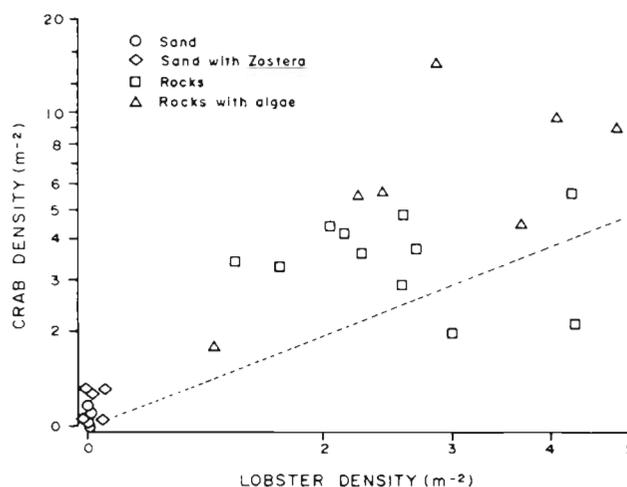


Fig. 3. *Homarus americanus* and *Cancer irroratus*. Correspondence between the density of lobsters and crabs cohabiting on different bottom types. Legend as Fig. 2

Table 3. *Homarus americanus* and *Cancer irroratus*. Total number of lobsters (L) and crabs (C) of each size group captured on the different bottom types. Average density (m<sup>-2</sup>) is shown in brackets. Proportion of lobsters and crabs belonging to the 3 size groups differed significantly among substrate types ( $p < 0.00001$ , log-linear model)

Substrate type	Species	Size category		
		Small	Medium	Large
Sand	L	0	0	0
	C	20 (0.034)	17 (0.029)	17 (0.029)
Sand and eelgrass	L	0	0	12 (0.018)
	C	8 (0.008)	31 (0.035)	139 (0.163)
Bare rocks	L	342 (0.919)	196 (0.462)	111 (0.269)
	C	335 (0.834)	345 (0.846)	440 (1.119)
Rocks with algae	L	84 (0.426)	226 (0.873)	299 (0.975)
	C	725 (3.358)	696 (2.807)	486 (1.893)

density of crabs was not reflected in larger crab biomass (Figs. 2 and 3). Analyses of contingency tables showed that the proportion of lobsters and crabs belonging to the 3 size groups differed significantly among substrate types ( $p = 0.0$ , log-linear model) (Table 3).

Sand supported no lobsters, although crabs of all sizes were present in low densities. Sand with eelgrass was inhabited by large lobsters only, and large crabs (74 %) predominated over medium and small crabs. On bare rocks, the highest proportion and densities were achieved by lobsters of the small size group, with decreasing proportions and densities for medium and large lobsters. Crabs followed the opposite trend on bare rocks, with a predominance of large crabs, in proportion as well as in density. Rocks with algae hosted mostly large and medium lobsters in the presence of very high densities of small and medium size crabs (Table 3).

Significant differences in the proportions of lobsters and crabs of different sizes were found among corals sampled at different dates for a given type of substrate, indicating temporal changes in population size structure.

#### Analysis of lobster and crab diets

Only 3 of the 178 lobster stomachs and 14 of the 162 crab stomachs were empty. Mean fullness scores were 2.60 for lobsters and 2.31 for crabs, indicating that on average, stomachs were more than half-full. The list of taxa found in all stomachs analysed (Table 2) shows the occurrence of 53 food items, later grouped into 18 categories for multivariate analysis. Seventeen food items occurred exclusively in stomachs from one station, indicating differences of availability among sites.

The diet of lobsters remained the same at both stations, but differed consistently from that of crabs (Table 4). The absence of difference in lobster diet between stations allowed us to rule out the possibility of differences among size groups of lobsters since the initial similarity matrix contained lobsters of all size categories. At both Gros Cap and Cap Irving, the 5 most abundant species found in lobster diet were, in order of decreasing importance: *Modiolus modiolus*, *Homarus americanus*, *Cancer irroratus*, *Lacuna vincta*, and ectoprocts (Table 2). Algae were frequently eaten in small quantities at both stations. Lobsters consumed 24 other occasional prey organisms at Gros Cap, and only 17 alternate prey at Cap Irving.

In contrast, crab diet differed significantly between Gros Cap and Cap Irving (Table 4). At Gros Cap, *Modiolus modiolus* and ectoprocts were major food items for crabs, being found together with 18 other

Table 4. *Homarus americanus* and *Cancer irroratus*. Diet comparison using the z-statistic calculated from the Mantel permutation test. Level of significance of the difference is determined as: ns: non significant; \*  $p < 0.05$ , significant; \*\*  $p < 0.01$ , highly significant; \*\*\*  $p < 0.001$ , very highly significant

Comparison		Probability	
Cap Irving:	lobsters vs crabs	0.000	***
Gros Cap:	lobsters vs crabs	0.000	***
Lobsters:	Gros Cap vs Cap Irving	0.303	ns
Crabs:	Gros Cap vs Cap Irving	0.000	***
Crabs, Cap Irving:	small vs medium	0.040	*
	small vs large	0.004	**
	medium vs large	0.036	*
Crabs, Gros Cap:	small vs medium	0.744	ns
	small vs large	0.664	ns
	medium vs large	0.532	ns

occasional species. At Cap Irving, *M. modiolus* also predominated in crab diet, but to a lesser extent than at Gros Cap. The diet was often complemented at Cap Irving by 2 types of polychaetes (*Terebellidae* and *Lepidonotus squamatus*), in addition to 24 other occasional species (Table 2).

The overall differences between species, stations and size groups are best visualized in the projection of the diet on the 2 first principal axes of a principal component analysis (Fig. 4). As previously described by the results of the Mantel statistic, lobsters from Gros Cap and Cap Irving appear similar in terms of diet but crabs constitute 2 distinct groups separated from each other and from lobsters. The overall shape of the projected samples (Fig. 4) resembles an arrowhead, with the lobsters of the 2 stations constituting the tip and central part of the pattern. Crabs from Gros Cap were mostly located in the upper posterior angle of the arrow, while crabs from Cap Irving were found in the lower posterior angle.

Diet differences among crabs of different sizes were found at Cap Irving, while no significant differences among sizes were found at Gros Cap (Table 4). This is also visible in Fig. 4. Large crabs from Cap Irving are mostly found at the outer edge of the diagram (lower right), in the most distant position from the central group representing the lobsters, while medium and small crabs are generally found closer to the center.

Discriminant analysis (Table 5) was then used to examine which food groups were most responsible for the segregation between species and stations as previously shown by the Mantel statistic and the principal component analysis. At Cap Irving, lobsters ate more hydroids, ectoprocts and algae than crabs did, while crabs selected them more often at Gros Cap (Tables 2 and 5).

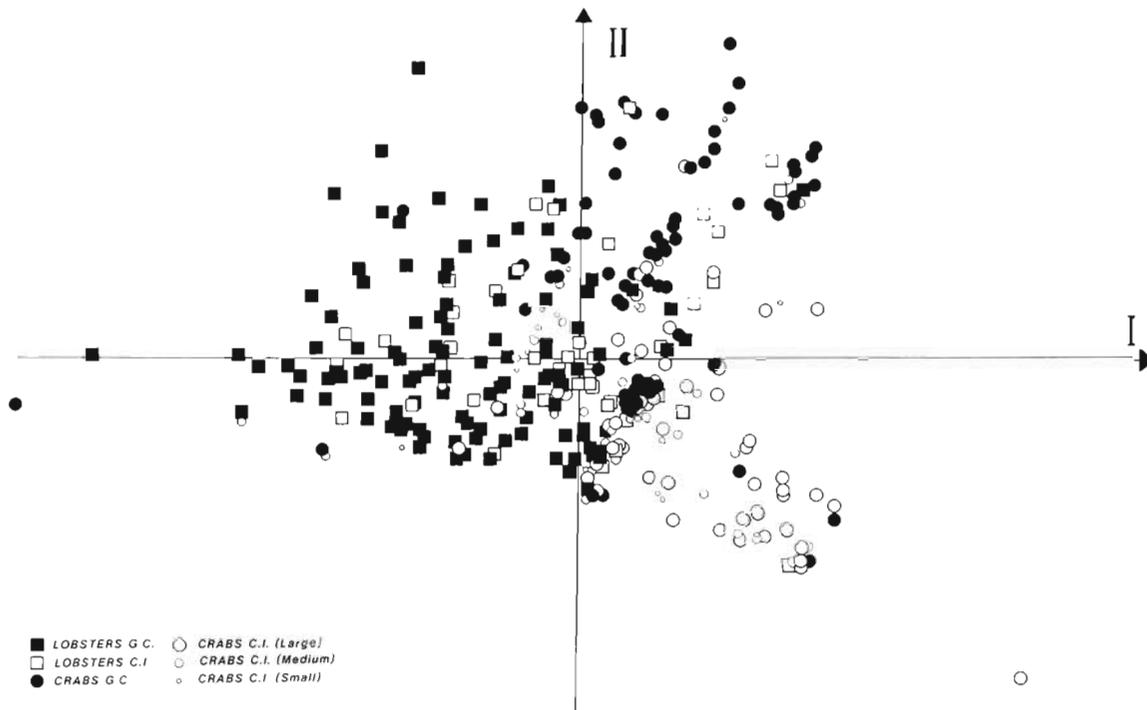


Fig. 4. *Homarus americanus* and *Cancer irroratus*. Principal component analysis of the diet of lobsters and crabs captured at Gros Cap (G.C.) and Cap Irving (C. I.)

Table 5. *Homarus americanus* and *Cancer irroratus*. Results of discriminant analyses between diets of lobsters and crabs from different stations, and between the crabs captured at Cap Irving and Gros Cap. The types of prey with the highest values of discrimination (underlined) are the ones accounting for most of the difference between the groups

Prey type	Prey group	Cap Irving lobsters vs crabs	Gros Cap lobsters vs crabs	Crabs Gros Cap vs Cap Irving
Foraminifera	1	0.01133	0.07413	0.03655
Porifera	2	0.00384	0.00000	0.00440
Hydroida	3	<u>0.29875</u>	0.11426	<u>0.25424</u>
Gastropoda	4	0.07504	0.18253	<u>0.01326</u>
Pelecypoda	5	0.13931	<u>0.24789</u>	<u>0.19100</u>
Polychaeta	6	0.11574	0.07797	<u>0.17867</u>
Small Crustacea	7	0.06997	0.00002	0.02161
Cirripedia	8	0.03999	0.04011	0.01329
Decapoda (misc.)	9	0.10157	0.02632	0.01699
<i>Homarus</i>	10	<u>0.18116</u>	<u>0.26752</u>	0.01799
<i>Cancer</i>	11	0.03732	<u>0.32041</u>	0.01002
Asteroidea	12	0.02888	0.01570	0.00000
Echinoidea	13	0.11818	0.14596	0.01178
Ascidiacea	14	0.01434	0.03185	0.00000
Pisces	15	0.02606	0.03185	0.03613
Detritus	16	0.06816	0.23837	0.16921
Algae	17	<u>0.17079</u>	0.03295	0.04247
Unidentified	18	0.07493	0.01179	0.01183

At both stations, the second most important difference in the diet of lobsters and crabs was their degree of mutual consumption (cannibalism, necrophagy or predation) (Table 5). Lobsters ate their congeners consistently more often than crabs did (Table 2). Also,

lobsters commonly ate crabs whereas only large crabs from Cap Irving appeared to eat lobsters. Although this pattern is likely to result from aggressive interaction, necrophagy could take place as well as active predation.

In order to provide more evidence of food resource partitioning at Cap Irving (bare stones) and at Gros Cap (boulders colonized with macroalgae), the weighted average calorific value ( $\bar{E}_s$ ) of stomach contents was calculated (Table 6). At Gros Cap, lobsters of each size category ingested food of a significantly higher average calorific value than crabs did. This difference between the 2 species was not significant at Cap Irving.

The diet of lobsters from Gros Cap exhibited a marginally higher weighted average calorific value than lobsters from Cap Irving. However, large crabs from Gros Cap had a lower  $\bar{E}_s$  value than at Cap Irving, although values for medium and small crabs did not differ significantly among stations. It also appeared that food of a higher calorific value was selected as crabs and lobsters grew larger. However, that trend was significant ( $p < 0.05$ , Kruskal-Wallis) only for crabs captured at Cap Irving.

## DISCUSSION

### Habitat preferences

Lobsters lack the ability to rapidly bury themselves in sand. They seek the protection of natural shelters such as crevices or excavate burrows in soft sediments under rocks or boulders (Cobb 1971, Aiken 1980, Richards & Cobb 1986). Up to a size of about 25 mm CL, lobsters generally attempt to escape predators by rapid abdomen flexing. As they increase in size, flight is progressively replaced by confrontation, during which the lobster extends its claws in a menacing stance (Lang et al. 1977). *Cancer irroratus* also prefers to seek protection under natural shelters (Fogarty 1976) when pre-

sent in abundance such as at Gros Cap, or to burrow into sediment next to rocks but without excavating permanent burrows like lobsters do. When natural shelters are absent, *C. irroratus* attempts to protect itself by quickly burying itself into the sediment. Its defensive behaviour involves lateral merus display with an extension of the pereopods, raising the body high off the substratum, a behaviour also hypothesized to be a valuable strategy against predatory fishes which swallow their prey whole (Fogarty 1976). Off Iles de la Madeleine, predation of lobster and crab by the cunner *Tautoglabrus adspersus* was observed, but was not documented for other potentially important species.

*Cancer irroratus* appears confined to sandy areas and excluded from rocky substrata where lobsters coexist together with the Jonah crab *Cancer borealis* (Jeffries 1966, Weiss 1970, Haefner & Terretta 1971, Stewart 1971, Winget et al. 1974). This was attributed to the lighter, less massive claws of *C. irroratus* (Jeffries 1966), which presumably disadvantages the rock crab in aggressive confrontations. *C. borealis* is also dominated by *Homarus americanus* (Fogarty 1976). However, its larger size and typical behaviour of crouching down when threatened makes it less vulnerable to lobster aggression than rock crab. Jeffries' (1966) study suggested that were *C. borealis*, and possibly, *H. americanus* be removed from Narragansett Bay, *C. irroratus* would extend its range into the rocky areas. When lobsters occur with Jonah and rock crabs on a rocky bottom, Jonah crabs could therefore contribute to the exclusion of rock crabs by monopolizing shelters not used by lobsters.

The overall higher densities of lobsters and crabs found at Gros Cap suggest that boulders colonized by

Table 6. *Homarus americanus* and *Cancer irroratus*. Weighted average calorific value of ingested prey items ( $\bar{E}_s$ , average calories per g fresh weight), standard deviation (SD), number of observations ( $n$ ). Probability of difference between species at each station and between stations for each species was tested using the Mann-Whitney  $U$ -test. ns: non significant difference; \* significant ( $p < 0.05$ ); \*\* highly significant ( $p < 0.01$ ); \*\*\* very highly significant ( $p < 0.001$ )

Site/species	Size category		
	Small $\bar{E}_s$ (SD, $n$ )	Medium $\bar{E}_s$ (SD, $n$ )	Large $\bar{E}_s$ (SD, $n$ )
Gros Cap			
Lobsters	649.9 (181.3, 3)	729.4 (195.6, 15)	712.7 (205.4, 64)
	.	***	***
Crabs	405.7 (35.3, 7)	473.3 (127.4, 15)	494.3 (226.3, 36)
Cap Irving			
Lobsters	588.4 (221.1, 18)	647.7 (197.4, 13)	681.6 (230.8, 11)
	ns	ns	ns
Crabs	576.0 (232.5, 10)	612.8 (250.8, 23)	726.4 (233.4, 42)
Between stations			
Lobsters	.	.	.
Crabs	ns	ns	***

algae provide a complex habitat bearing a high carrying capacity. Cobb (1971), Aiken (1980) and Hudon (1987) found a relationship between the occurrence of crevices of adequate size and size structure of lobster populations on a given bottom type. At Cap Irving, small stones imbedded in the sediment supported mostly small lobsters, co-occurring with relatively equal proportions of all sizes of crabs (Table 3). Small lobsters and small crabs can presumably easily find shelter and coexist among the stones; lobsters utilize crevices while crabs also burrow in the sediment. Combined densities of small and medium size individuals indicated that an average of 1.4 lobsters and 1.7 crabs could coexist on 1 m<sup>2</sup> of stony bottom such as that found at Cap Irving. However, the low representation (17 %) of large lobsters suggested they are more dependent on the occurrence of natural shelters than large rock crabs. For rock crabs, large individuals represented 39 % of the total on bottoms made of small stones.

Sandy bottoms were less utilized than rocky bottoms by rock crabs and were seldom used by lobsters (Fig. 3, Table 3). The occurrence of small and medium size crabs in eelgrass (in the lagoon) likely resulted from the importation of planktonic crab larvae to the lagoon by currents, as was previously observed for lobster larvae (Hudon et al. 1986). The lower densities of small crabs on soft bottoms (Table 3) could result from differential habitat selection at settlement and/or a heavier post-settlement predation than on rocky bottoms. Small and medium size crabs possibly escaped predation by their ability to bury themselves in the sand. No small or medium lobsters were found on sand, irrespective of the presence of eelgrass, which suggests a higher bottom selectivity and/or lower survival than crabs. On eelgrass beds, all lobsters and 74 % of the crabs were large. The predominance of large individuals could be attributed to their active migration into the lagoon, as previously reported for large lobsters (Munro & Theriault 1983).

Significant differences in the size proportions of lobsters and crabs were found among corrals sampled at different times on each type of substrate. Temporal differences in density have been previously attributed to seasonal migrations of large lobsters (Cooper et al. 1975) and crabs (Scarratt & Lowe 1972) to and from shore, in relation with moulting activity or egg maturation and hatching. The density of small individuals also fluctuated seasonally, due to the benthic settlement of planktonic lobsters and crabs in the latter part of the summer (Hudon 1987, Hudon et al. unpubl.), and their rapid early benthic growth. The cumulative sampling over a long time interval (June to September) used in this study de-emphasized the finer temporal fluctuations of size structure to concentrate on the larger differences among types of substrata.

Therefore, our characterization of size structure for each bottom type probably underestimates the inherent dynamism of habitat partitioning between lobsters and crabs through time. However, the differences among substrata documented here should be reliable since they encompass the major part of the seasonal migratory, settlement and growth activity for both species.

We deliberately avoided dealing with seasonal diet fluctuations by sampling stomach contents on 2 consecutive days at the 2 sites. It is expected that temporal fluctuations of habitat partitioning should be less than for food partitioning. Whereas the number of shelters remains constant through time, food abundance varies seasonally and is superimposed onto the effects of moult cycle on feeding behaviour.

#### Food availability versus selection

Stomach content analysis of individuals captured in each environment is the most reliable way to assess their respective diets, although the method suffers from a number of possible biases (see discussion by Elner & Campbell 1987). Alteration of food fragments by digestion makes quantitative estimates difficult. Also, food items differ in their digestion time, calorific value and residence time, and this causes underestimation of highly digestible and possibly energy-rich food. Carter & Steele (1982b) showed that sea urchin remains could stay in lobster stomachs for as long as 180 d. In the case of lobsters, ingestion of the exuviae after moulting could unduly increase the estimate of cannibalism (Aiken 1980), and at least partly explain the high abundance of congeneric remains in lobster stomach contents observed at both stations. Also, movements between neighbouring but distinct habitat types may distort between-habitat diet comparison.

The feeding regime of the lobster (Herrick 1895, Squires 1970, Weiss 1970, Ennis 1973, Scarratt 1980, Carter & Steele 1982b, Elner & Campbell 1987) and of the rock crab (Scarratt & Lowe 1972, Drummond-Davis et al. 1982) are well documented. Scarratt & Lowe (1972) reported that stomach contents of lobsters show some similarity with those of crabs in the occurrence, for example, of polychaetes, starfish, sea urchins, mussels, and tunicates. The most common food of lobsters includes mussels, rock crabs, periwinkles, polychaetes, sea urchins, starfish and brittle stars (Squires 1970, Ennis 1973, Scarratt 1980, Carter & Steele 1982b). Periwinkles, starfish and brittle stars were not abundant in the stomach contents that we examined and this confirms that lobsters would prefer food of a high calorific value such as mussels and polychaetes if they are available. These studies suggested that lobsters

and rock crabs were 'opportunistic', as their diet reflects local and seasonal availability of food items. In our study, the wide range in the diet of lobsters and crabs was apparent from the diversity of food items found in the stomach contents (Table 2).

Although it is beyond the scope of this study to compare food availability at each station, the presence of certain food items in the diet of both species at one station and its absence at the other station suggest differences in local abundance. In spite of this, lobsters maintained a nearly identical diet at both sites. Immature lobsters have a diet similar to that of adults, although the proportions of food items may differ (Scarrott 1980, Carter & Steele 1982b). The consistency of lobster diet among size classes and sites indicates selectivity on the part of the lobster, resulting from the preferential ingestion of particular food items if they occur at a site. The preference of lobster for certain food items was recently shown (Carter & Steele 1982a, Michaud 1986, Elner & Campbell 1987). In contrast, crab diet differed among sites and among size groups, which suggests that they are truly opportunistic. These differences in lobster and crab diet could be further accentuated by within-habitat spatial and temporal partitioning of food resources, or perhaps differential ability of lobsters and crabs to handle different prey types. More detailed studies on the fine-scale spatio-temporal fluctuations of resource partitioning are needed to shed light on this aspect.

### Niche segregation

Results suggest that lobsters and crabs were able to cohabit because they used the substrate and the food resources in different ways. We also showed that the diets of both species were significantly different although diets of small crabs and small lobsters were somewhat similar. The diets of small lobsters and crabs tended to reflect their sedentary and cryptic habit, hiding among stones where food could be found within a small foraging range. This observation is consistent with laboratory observations by Lawton (1987). At Cap Irving, large densities of small lobsters and small crabs coexisted on a stony bottom (Hudon 1987, Hudon et al. unpubl.). At this station, the diet of crabs differed among size groups with respect to both species composition and weighted average calorific value. This leads us to hypothesize that ontogenetic changes in food preferences and/or foraging behaviour are more pronounced for crabs than for lobsters.

Abundance of large lobsters appeared limited on bare stone bottoms by the absence of large shelters, but large crabs did not appear to be so affected as their density was high at Cap Irving. Interactions between

large crabs and large lobsters were thus reduced at that station. The weighted average calorific value of rock crab diet was much higher at Cap Irving than at Gros Cap. In addition, large crabs from Cap Irving ingested significantly more energy-rich food items than any other crabs. It is notable that large crabs from Cap Irving represented the only instance in which lobster remains were found in crabs stomachs, thus indicating that crabs can occasionally prey upon lobsters or their exuviae under certain conditions.

Highest densities of medium and large lobsters were found at Gros Cap, on rocks and boulders covered with macroalgae (Table 2). The occurrence of large lobsters presumably increased predation pressure on large crabs (37 to 125 mm CW), which are more easily visible than smaller crabs living in the sediment or between stones. High densities of small crabs were also observed, with decreasing proportions of medium and large crabs. In terms of density, however, medium and large crabs were as abundant as on bare rocks. In this most heterogeneous habitat, crabs of all sizes could presumably find a profusion of shelters not readily accessible to lobsters. The low values of the average weighted calorific content for crab stomachs suggested that predation pressure from large lobsters affected crab foraging behaviour at Gros Cap. In order to minimize predation risks, medium and large crabs would benefit from remaining in their shelters and using food items available at close range. Coexistence of carnivorous species might also be facilitated if different predators utilize different prey sizes and/or types. An example of this type of niche segregation was given for lobsters and rock crabs preying on sea urchins (Elner 1980), on mussels *Mytilus edulis* (Lawton 1987), and on sea scallops *Placopecten magellanicus* (Elner & Jamieson 1979, Jamieson et al. 1982) in which prey size was shown to be a function of predator size.

Niche segregation between lobster and rock crab appears to take place through specific adaptations allowing these 2 decapods to partition the resources of their environment. Size structure is related to substrate coarseness and species' ability to use the substrate for shelter, either by using rock crevices or by burrowing in soft sediments. The similarities in the diet of small lobsters and crabs could result from their smaller foraging areas. As both species grow in size, lobster dominance over crab is reflected both by active predation and the composition of lobsters' diet throughout their size range and among different sites. The rock crab appears more opportunistic in its feeding, as its diet differs in presence or absence of large lobsters. The complexity of the habitat and the risks involved in foraging thus appear to influence the feeding regime of rock crabs.

**Acknowledgements.** The help of Jean Attard, Daniel Gauthier, François Hazel, Lucie D'amours, Paul Boudreault, Mario Poirier and Michel Papageorges was much appreciated in the field and laboratory. The help of Pierre Brunel, Marie Desroches and Bernard Sainte-Marie with the sorting and identification of stomach contents is gratefully acknowledged. Pierre Legendre and Alain Vaudor were very helpful in planning and carrying out the statistical analyses of data. The comments of Alex Bielak, Bernard Sainte-Marie, Ted Grainger and 2 anonymous reviewers on early versions of the manuscript are acknowledged with thanks.

#### LITERATURE CITED

- Aiken, D. E. (1980). Molting and growth. In: Cobb, J. S., Phillips, B. F. (eds.) The biology and management of lobsters. Vol. I. Academic Press, New York, p. 91–163
- Atema, J., Cobb, J. S. (1980). Social behavior. In: Cobb, J. S., Phillips, B. F. (ed.) The biology and management of lobsters, Vol. I. Academic Press, New York, p. 409–450
- Atkinson, E. G., Wacasey, J. W. (1979). Caloric values of zoobenthos and phytobenthos from the Canadian Arctic. Tech. Rep. Fish. Res. Bd Can. 632: 1–24 + v
- Brawn, V. M., Peer, D. L., Bentley, R. J. (1968). Caloric content of the standing crop of benthic and epibenthic invertebrates of St. Margaret's Bay, Nova Scotia. J. Fish. Res. Bd Can. 25: 1803–1811
- Carter, J. A., Steele, D. H. (1982a). Attraction to and selection of prey by immature lobsters (*Homarus americanus*). Can. J. Zool. 60: 326–336
- Carter, J. A., Steele, D. H. (1982b). Stomach contents of immature lobsters (*Homarus americanus*) from Placentia Bay, Newfoundland. Can. J. Zool. 60: 337–347
- Cobb, J. S. (1971). The shelter-related behavior of the lobster, *Homarus americanus*. Ecology 52: 108–115
- Cooper, R. A., Clifford, R. A., Newell, C. D. (1975). Seasonal abundance of the American lobster, *Homarus americanus*, in the Boothbay region of Maine. Trans. Am. Fish. Soc. 10: 669–674
- Drummond-Davis, N. C., Mann, K. H., Pottle, R. A. (1982). Some estimates of population density and feeding habits of the rock crab, *Cancer irroratus*, in a kelp bed in Nova Scotia. Can. J. Fish. Aquat. Sci. 39: 636–639
- Elnor, R. W. (1980). Predation on the sea urchin (*Strongylocentrotus droebachiensis*) by the American lobster (*Homarus americanus*) and the rock crab (*Cancer irroratus*). In: Pringle, J. D., Sharp, G. J., Caddy, J. F. (eds.) Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can. Tech. Rept. Fish. Aquat. Sci. 954: 46–65
- Elnor, R. W., Campbell, A. (1987). Natural diets of lobster *Homarus americanus* from barren grounds and macroalgal habitats off southwestern Nova Scotia, Canada. Mar. Ecol. Prog. Ser. 37: 131–140
- Elnor, R. W., Jamieson, G. S. (1979). Predation of sea scallops, *Placopecten magellanicus*, by the rock crab, *Cancer irroratus*, and the American lobster, *Homarus americanus*. J. Fish. Res. Bd Can. 36: 537–543
- Ennis, G. P. (1973). Food, feeding and condition of lobsters, *Homarus americanus*, throughout the seasonal cycle in Bonavista Bay, Newfoundland. J. Fish. Res. Bd Can. 30: 1905–1909
- Evans, P. D., Mann, K. H. (1977). Selection of prey by American lobsters (*Homarus americanus*) when offered a choice between sea urchins and crabs. J. Fish. Res. Bd Can. 34: 2203–2207
- Fogarty, M. J. (1976). Competition and resource partitioning in two species of *Cancer* (Crustacea, Brachyura), M.Sc. thesis, Univ. Rhode Island, Kingston
- Gower, J. C. (1971). A general coefficient of similarity and some of its properties. Biometrics 27: 857–871
- Haefner, P. A., Terretta, R. T. (1971). The Chesapeake Bay rock crab. Comm. Fish. Rev. 33: 16–17
- Herrick, F. H. (1895). The American lobster: a study of its habits and development. Bull. Fish. Comm. 15: 1–252
- Howard, A. E. (1980). Substrate controls on the size composition of lobster (*Homarus gammarus*) populations. J. Cons. int. Explor. Mer 39: 130–133
- Hudon, C. (1987). The ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Iles de la Madeleine (Quebec). Can. J. Fish. Aquat. Sci. 44: 1855–1869
- Hudon, C., Fradette, P., Legendre, P. (1986). La répartition horizontale et verticale des larves de homard (*Homarus americanus*) autour des Iles de la Madeleine, golfe du Saint-Laurent. Can. J. Fish. Aquat. Sci. 43: 2164–2176
- Hutchinson, G. E. (1957). Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415–427
- Jamieson, G. S., Stone, H., Ether, M. (1982). Predation on sea scallops (*Placopecten magellanicus*) by lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) in underwater cage enclosures. Can. J. Fish. Aquat. Sci. 39: 499–505
- Jeffries, H. P. (1966). Partitioning of the estuarine environment by two species of *Cancer*. Ecology 47: 477–481
- Krouse, J. S. (1972). Some life history aspects of the rock crab, *Cancer irroratus* in the Gulf of Maine. J. Fish. Res. Bd Can. 29: 1479–1482
- Lang, F., Govind, C. K., Costello, W. J. (1977). Developmental neuroethology: changes in the escape and defense behavior during growth of the lobster. Science 19: 682–685
- Lawton, P. (1987). Diel activity and foraging behavior of juvenile American lobsters, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 44: 1195–1205
- Legendre, P. (1987). Organisation spatiale des communautés biologiques: importance pour les théories de gestion des écosystèmes. In: Compte-rendu de la Conférence européenne 'Diversité biologique-Un défi pour la Science, l'Economie et la Société', Dublin, Irlande, 4–6 Mars 1987. Programme FAST, Commission des Communautés Européennes, Bruxelles, p. 1–26
- Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. Cancer Res. 27: 209–220
- Michaud, B. J. (1986). Composition and production of macrobenthic invertebrate communities and food resources of the American lobster *Homarus americanus* along the Atlantic coast of Nova Scotia. Ph.D. thesis, Dalhousie University, Halifax
- Miller, R. J., Mann, K. H., Scarratt, D. J. (1971). Production potential of a seaweed-lobster community in eastern Canada. J. Fish. Res. Bd Can. 28: 1733–1738
- Munro, J., Therriault, J. C. (1983). Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des Iles-de-la-Madeleine. Can. J. Fish. Aquat. Sci. 40: 905–918
- Pottle, R. A., Elnor, R. W. (1982). Substrate preference behaviour of juvenile American lobster *Homarus americanus*, in gravel and silt clay sediments. Can. J. Fish. Aquat. Sci. 39: 928–932
- Richards, R. A., Cobb, J. S. (1986). Competition for shelter between lobsters (*Homarus americanus*) and Jonah crabs

- (*Cancer borealis*): effect of relative size. Can. J. Fish. Aquat. Sci. 43: 2250-2255
- Scarratt, D. J. (1968). An artificial reef for lobsters (*Homarus americanus*). J. Fish. Res. Bd Can. 25: 2683-2690
- Scarratt, D. J. (1980). The food of lobsters. In: Pringle, J. D., Sharp, G. J., Caddy, J. F. (eds.) Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can. Tech. Rept. Fish. Aquat. Sci. 954: 66-91
- Scarratt, D. J., Lowe, R. (1972). Biology of the rock crab (*Cancer irroratus*) in Northumberland Strait. J. Fish. Res. Bd Can. 29: 161-166
- Shotton, L. R. (1973). Biology of the rock crab, *Cancer irroratus* Say, in the coastal waters of Virginia. M.A. thesis, Univ. Virginia, Charlottesville
- Squires, H. J. (1970). Lobster (*Homarus americanus*) fishery and ecology in Port au Port Bay, Newfoundland, 1960-65. Proc. natl. Shellfish. Ass. 60: 22-39
- Stewart, L. L. (1971). The seasonal movements, population dynamics, and ecology of the lobster, *Homarus americanus*, off Rand Island, Conn. Ph.D. thesis, University of Connecticut, Storrs
- Thayer, G. W., Schaaf, W. E., Angelovic, J. W., LaCroix, M. W. (1973). Caloric measurements of some estuarine organisms. Fish. Bull. U.S. 71: 289-296
- Weiss, H. M. (1970). The diet and feeding behavior of the lobster, *Homarus americanus* in Long Island Sound. Ph.D. thesis, University of Connecticut, Storrs
- Winget, R. R., Maurer, D., Seymour, H. (1974). Occurrence, size composition and sex ratio of the rock crab, *Cancer irroratus* Say and the spider crab, *Libinia emarginata* Leach in Delaware Bay. J. nat. Hist. 8: 199-205

This article was presented by Dr G. C. Harding, Dartmouth, Nova Scotia, Canada

Revised version accepted: November 17, 1988