Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*), off the Magdalen Islands

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Abstract–The natural diet of 506 American lobsters (*Homarus americanus*) ranging from instar V (4 mm cephalothorax length, CL) to the adult stage (112 mm CL) was determined by stomach content analysis for a site in the Magdalen Islands, Gulf of St. Lawrence, eastern Canada. Cluster and factor analyses determined four size groupings of lobsters based on their diet: <7.5 mm, 7.5 to <22.5 mm, 22.5 to <62.5 mm, and ≥62.5 mm CL. The ontogenetic shift in diet with increasing size of lobsters was especially apparent for the three dominant food items: the contribution of bivalves and animal tissue (flesh) to volume of stomach contents decreased from the smallest lobsters (28% and 39%, respectively) to the largest lobsters (2% and 11%, respectively), whereas the reverse trend was seen for rock crab *Cancer irroratus* (7% in smallest lobsters to 53% in largest lobsters). Large lobsters also ate larger rock crabs than did small lobsters. This study is the first to examine the natural diet of shelter-restricted juveniles (SRJs, <14.5 mm CL), which were thought to be principally suspension feeders and to a lesser degree browsers or ambush predators in or near their shelter. However, at our study site no planktonic organisms were identified from the stomachs of SRJs, whereas formaniferans, crustacean meiofauna, and macroalgal debris that could be derived by browsing, together represented only 10–14% by volume of stomach contents. We infer that SRJs obtained bivalves by predation and flesh by exploiting larger lobsters' meal scraps or food reserves. Some implications of these findings for lobster artificial reef programs and for the conservation of lobster stocks are discussed.

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American lobster, *Homarus americanus*, is a long-lived, dominant predator in temperate coastal waters of eastern North America (Elner and Campbell, 1991; Ojeda and Dearborn, 1991). After the larval phase, lobsters settle and spend much of their time in burrows or natural shelters (Cobb, 1971; Lawton, 1987; Barshaw and Bryant-Rich, 1988). However, laboratory and *in situ* observations indicate that benthic lobsters pass through successive life-history phases as they grow in size, changing from a shelter-restricted habit to a more overt lifestyle involving daily forays and seasonal migrations away from shelter (Cooper and Uzmann, 1977; Cobb and Wahle, 1994). A variety of classifications have been proposed for these successive ontogenetic phases. The latest scheme, by Lawton and Lavalli (1995), recognizes five life-history phases: shelter-restricted juvenile (SRJ, ~4–14 mm cephalothorax length, CL), emergent juvenile (~15–25 mm CL), vagile juvenile (~25 mm CL to size of physiological maturity), adolescent, and adult.

In several decapod crustaceans, diet changes as individuals grow and become more mobile and their chela size and strength increases (e.g. Lee and Seed, 1992; Freire et al., 1996). Such dietary shifts should occur in the lobster as well, especially considering this species' changing dependency on shelter which, in turn, has implications for foraging range and accessibility of prey types (Elner and Campbell, 1987; Lawton, 1987). Some studies of the natural diet of lobsters 12–125 mm CL have found little or no differences in the identity or in the frequency of food items that were ingested by different size groups (Weiss, 1970; Ennis, 1973; Hudon and Lamarche, 1987). However, other studies have pointed to changes in the identity and especially in the frequency of food items ingested by different lobster size groups. Carter and Steele (1982b), using their own results and data from nonconcomitant studies conducted at different sites in Newfoundland (Squires, 1970; Ennis, 1973), have suggested that lobsters of 12–73 mm CL consume sea urchins, ophiuroids, and mussels more frequently than larger (adult) lobsters. Scarratt (1980) reported that lobsters consumed more crabs, mussels, and fish, but fewer echinoderms, as they grew in size and approached maturity. This trend was attributed to differential accessibility of prey. Elner and Campbell (1987) indicated that the stronger chelae of larger lobsters would enable them to crush prey that are protected by heavy shells, such as gastropods and bivalves, more so than the chelae of smaller lobsters.

The natural diet of SRJ lobsters has not been examined to date (Lawton and Lavalli, 1995), excepting rare specimens of 12–14 mm CL. The feeding appendages of SRJs are capable of capturing and processing both planktonic and benthic organisms (Lavalli and Factor, 1995). From laboratory observations, several authors have proposed that SRJs may live primarily as suspension-feeders, and to a lesser degree as browsers, within the shelter or as ambush predators at the shelter's entrance (Barshaw and Bryant-Rich, 1988; Barshaw, 1989; Lavalli and Barshaw, 1989; Lawton and Lavalli, 1995). Wahle (1992) offered a conceptual model suggesting that lobsters shift from a cryptic to a wide-roaming behavior as predation risk becomes offset by the need for a high-energy diet that cannot be satisfied through shelter-restricted feeding.

Our study was conducted at the Magdalen Islands, eastern Canada, to resolve the natural diet of SRJ lobsters and to compare it with that of larger lobsters by using stomach content analysis. We found a gradual ontogenetic shift in lobster diet over the size range of 4 to 112 mm CL. SRJs were carnivorous and probably derived their meals mainly through predation and scavenging. We also determined the predator-prey size relationship for one of the lobster's preferred and most important prey, i.e. Atlantic rock crab, *Cancer irroratus* (Reddin, 1973; Evans and Mann, 1977; Carter and Steele, 1982a).

Materials and methods

The study site was a narrow 2-km rocky section (47°14.5′N, 61°50.5′ to 61°51.3′W) of the south shore of Baie de Plaisance, Magdalen Islands, eastern Canada. This site corresponds to the Butte-à-la-Croix location that Hudon (1987) determined to be a settlement ground for lobster. Divers collected lobsters by hand or by suction-sampling at depths of 1 to 7 m. Lobsters were processed live usually within minutes and at most two hours after collection. The sex of collected specimens was determined and their CL was measured to the nearest 0.1 mm with a vernier caliper. Lobsters that were not berried and that were judged to be intermolt, based on criteria of shell hardness, coloration, and fouling in Aiken (1980), were dissected to remove the stomach which was preserved in buffered formalin diluted to 4% in seawater. Stomachs with calcified gastroliths were subsequently disregarded, thereby effectively eliminating from the present study all premolt lobsters from stage $D^{1.5}$ (=D_0) on (Aiken, 1980). The resulting sample consisted of 471 stomachs from lobsters of 7–112 mm cephalothorax length (CL) collected from 24 July to 31 October 1996, and of 35 stomachs from lobsters of 4–12 mm CL collected between 4 August and 13 September 1997. The 1997 lobsters were added to improve coverage of stomach contents of the early juveniles because very little settlement occurred in 1996 (Sainte-Marie et al., 2001). There was no commercial fishery during the sampling periods; therefore items in lobster stomachs were not discards or bait.

In the laboratory, stomachs were opened and their content was emptied into dishes for examination under a Wild M8 compound microscope (10–50×). Identity of food items was determined to the lowest taxonomic level possible, based on comparisons with illustrations in literature and samples of benthic and pelagic fauna from our study site. Particular care was taken when examining the stomach contents of lobsters <12 mm CL; for these stomach contents we often resorted to higher magnification (>100×) with a Leitz Dialux 20 microscope.

The contribution of each food item, exclusive of minerals and nylon debris, to the volume of stomach contents of each lobster was visually scored from 0 to 10, by 10% increments (0=0% of volume, 1=1–10%, 2=11–20%, etc.). The total for all food items could exceed 10, for example, if more than two minor food items each were scored 1 in addition to one predominant food item that was scored 8. In such cases, the corrected contribution of each food item was obtained by dividing its score by the sum of scores for all organic food items in a given stomach. Corrected volumetric contribution of each food item was expressed as a proportion of stomach content volume.

To obtain information on the size spectrum of rock crab consumed by lobsters, we established predictive (least squares) linear regressions (Sokal and Rohlf, 1995) between 30 measurements of distinctive hard body parts and cephalothorax width (CW) of 26 crabs ranging from 7 to 62 mm CW (following the approach in Lovrich and Sainte-Marie, 1997). All the predictive regressions were highly significant (r^2=0.970–0.999, P<0.001). When rock crab remains were encountered in lobster stomachs, distinctive hard body parts were measured with an eyepiece micrometer to estimate crab CW from predictive regressions. When more than one body part could be measured, the crab's CW was determined as the mean of the various estimates unless it was obvious that multiple crabs had been ingested. Such was considered to be the case when more than two similar fragments of a paired structure (e.g. eyes or claws) were found in one lobster stomach or when there was considerable divergence among crab CW estimates based on different body parts. The functional relationship between the CW of rock crab prey and the CL of lobster predators was established with a model II regression (Laws and Archie, 1981; Sokal and Rohlf, 1995).

The stomach contents, once identified and scored for volume, were transferred separately to preweighed trays, dried to constant mass at 60°C, and weighed to the nearest mg. Dry mass was not obtained for eight stomach contents because of manipulation errors. The allometric relationship between the dry mass of stomach contents and lobster CL was established by least squares linear regression, after logarithmic transformation of both variables.

Diet was described by occurrence, volumetric contribution, and the specific abundance of food items in the stomachs of lobsters grouped into 5-mm CL size classes (2.5 to <7.5 mm, 7.5 to <12.5 mm, etc.). Percent occurrence (PO) was the percentage of stomachs in one size class that contained a given food item. Volumetric contribution (VC) was the average of corrected contributions of each food item to the stomachs of all lobsters in a given size class. Specific abundance (SA) was the average volumetric contribution of a food item determined only for lobsters that had this food item in their stomach. This index is useful for food items with a low average volumetric contribution because it allows the distinction between the case when few animals consume large quantities of a given food item or when many animals consume small quantities of the same food item (Amundsen et al., 1996). The mathematical relationship of the three indices is $SA = VC \times 100/PO$.

To assess how the overall diet varied with lobster size, and thus whether or not there were size-related shifts in diet supporting the ontogenetic phases of lobster, we performed a cluster analysis (Ward's minimum variance method) on the volumetric contribution of food items per lobster size class, after standardization. A sudden increase in the joining distance of the clustering sequence represented by the dendrogram represents a natural cutting point for the determination of meaningful clusters (SAS Institute, 1995). In addition, a factor analysis (VARIMAX rotation of the first three principal components) was performed on the correlation matrix of the volumetric contribution of food items for each 5-mm-CL size class of lobsters. Cluster and factor analyses were done with JMP statistical software (SAS Institute, 1995).

Relationships between volumetric contribution and lobster CL were described by least squares linear regression for bivalves, rock crab, and flesh. Relationships between percent occurrence of bivalves and rock crab were described by locally weighted (lowess) regression with a 60% smoothing factor, and by least-squares regression for flesh.

Results

Sample composition, stomach fullness, and types of food items

The 506 lobsters retained for analyses varied in size from 4.3 to 112.4 mm CL (median=35.6 mm CL). Most size classes contained more than 25 lobsters (Table 1). The smallest size class (2.5 to <7.5 mm CL) contained only 16 lobsters with a median of 7.0 mm CL; therefore we refer to this group of lobsters as the 7-mm-CL size class. The 21 lobsters ≥67.5 mm CL were pooled together into a single size class, which we refer to as the 77-mm-CL size class in reflection of their median CL. Females and males accounted respectively for 43.2% and 44.1% of all lobsters examined; the remainder were too small to determine sex. Lobsters were pooled for analyses irrespective of sex because Weiss (1970) and Ennis (1973) concluded that diet was the same for both sexes.

Only two lobsters had empty stomachs and they belonged to the 10-mm size class. With these two empty stomachs excluded, there was a highly significant relationship between the dry mass of stomach contents and lobster CL (Fig. 1). Identifiable food items included macroalgae or benthos that were grouped into broad taxonomic or ecological categories (Table 2). No planktonic organisms were identified from the stomachs, even of the smallest lobsters. However, the crustacean meiofauna group included the remains of very small crustaceans, some like the harpacticoids and ostracods, known to be bottom-dwelling, whereas unidentified minute crustacean remains may have originated from holo- or mero-planktonic forms or from juvenile amphipods, isopods, or carideans. Sand, silt, and infrequently bits of nylon rope were also found in the stomachs. "Flesh" refers to tissue bolus composed of animal soft parts that could not be attributed to a taxon, generally because no distinctive part was found in the stomach along with the tissue or less commonly because distinctive parts from several prey types were present in the stomach but none was attached to the tissue.

Table 1

Number of lobster stomachs sampled by classes of cephalothorax length (CL, in mm). Size classes represent 5-mm groupings except the smallest (7 mm CL) and largest (77 mm CL), which include all lobsters <7.5 mm CL and all lobsters ≥67.5 mm CL, respectively.

Cephalothorax length (size classes)	Number of stomachs		
	1996	1997	Total
7	1	15	16
10	17	20	37
15	28		28
20	38		38
25	56		56
30	45		45
35	52		52
40	51		51
45	45		45
50	45		45
55	31		31
60	25		25
65	16		16
77	21		21
Total	471	35	506

Ontogenetic shifts in diet

A cluster analysis on the volumetric contribution of food items to lobsters by size class yielded four groups: 7 mm, 10–20 mm, 25–60 mm, and 65–77 mm CL lobsters (Fig. 2). These same groups could be seen on a plot of the first three factors of a factor analysis of the correlation matrix of the volumetric contribution of food items (Fig. 3). The three factors explained 68.8% of the variance (39.9%, 18.2%, and 10.7% for factors 1, 2, and 3). The first factor had strong loadings for crustacean meiofauna (0.96), foraminiferans (0.96), bivalves (0.84), macroalgae (0.82), amphipods (0.78), and rock crab (–0.71). Because lobsters in the 7-mm-CL size class had little rock crab in their stomachs, but relatively high proportions of the other food items, they stood out with a very large score (3.1) on this factor. The next two size classes, 10 and 15 mm CL, scored 0.8 and 0.6, respectively. All other size classes scored between 0 and –0.6 on the first factor. The second factor had strong loadings for flesh (0.73), lobster (–0.82), and barnacles (–0.73). Lobsters of the two largest size classes (65 and 77 mm CL) had strong negative scores on this factor (–2.5 and –1.5, respectively), whereas lobsters of the 10–35 mm size classes scored between 0.5 and 1.1. The smallest size class (7 mm CL) and size classes of 40–60 mm CL had scores close to 0. Finally, the third factor had a high loading for carideans (0.74) and somewhat smaller loadings for isopods (0.67), coralline algae (–0.57), and pagurids (–0.54). This third factor separated

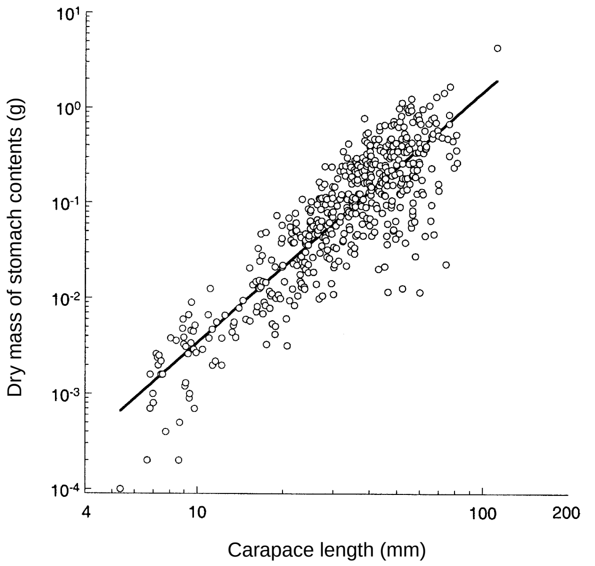

Figure 1

Relationship of dry mass of stomach contents (DM) to cephalothorax length (CL) of lobsters from the Magdalen Islands. Two lobsters of the 10-mm class had an empty stomach and are not shown. Model II regression: $DM = 7.967 \times 10^{-6} \times CL^{2.628}$ [r^2=0.51, P<0.001].

the 25- and 35-mm-CL size classes from the 10–20 mm CL size classes.

For each grouping, Figure 4 shows the specific abundance of each food item plotted against its percent occurrence. Bivalves and flesh accounted for a large proportion of stomach contents of the smallest lobsters (7-mm-CL size class) and were found in ≥75% of stomachs, making them the most important food items for this grouping. Rock crabs, amphipods, and polychaetes contributed 0.2 to 0.4 of stomach volume when they were ingested, but were found in fewer than 30% of the stomachs. Macroalgae and gastropods, on the other hand, were eaten by >50% of small lobsters but were ingested in small volumes. All other prey categories contributed little to stomach volume and were found in a small proportion of stomachs.

Flesh and bivalves were also the most important food items for the 10–20 mm CL lobster grouping (Fig. 4). They accounted for 0.46 and 0.22 of stomach volume, respectively, when they were ingested, and were found in 90% of stomachs. Rock crab was another important prey, with a specific abundance of 0.32 and an occurrence of 41%. Pagurids, carideans, and echinoderms had high specific abundances but were found in less than 5% of stomachs. Gastropods and polychaetes were found in about 40% of stomachs, but accounted for a small fraction of stomach volume. All other prey categories constituted a small fraction of the volume of very few stomachs.

The two main food items of lobsters measuring 25–60 mm CL were rock crab and flesh: specific abundance was high (0.34 and 0.38, respectively) and these food items

Table 2

Major categories of food items, divided into specific food items when possible, and their overall volumetric contribution (total=1) to stomach contents of all examined lobsters from Baie de Plaisance, Magdalen Islands. Abbreviations for major categories of food items are shown in brackets.

Categories of food items	Volumetric contribution
Formaniferans [For]	0.0031
Macroalgae [Alg]	0.0394
Coralline algae (*Corallina officinalis*) [Cor]	0.0178
Hydrozoans [Hyd]	0.0207
Bivalves [Biv]	0.1657
Mytilus edulis	0.0202
Modiolus modiolus	0.0992
Unidentified Pelecypoda	0.0463
Gastropods [Gas]	0.0585
Lacuna vincta	0.0028
Unidentified Gastropoda	0.0057
Polychaetes [Pol]	0.0597
Nereidae	0.0318
Polynoidae	0.0271
Unidentified Polychaeta	0.0008
Barnacles (*Balanus* sp.) [Bar]	0.0012
Crustacean meiofauna [Cru]	0.0053
Harpacticoida	0.0003
Ostracoda	0.0021
Unidentified minute Crustacea	0.0029
Amphipods [Amp]	0.0054
Corophium sp.	0.0004
Gammarus sp.	0.0003
Caprellidea	0.0004
Gammaridae	0.0016
Unidentified amphipods	0.0027
Isopods [Iso]	0.0067
Idotea sp.	0.0013
Idoteidae	0.0019
Unidentified valviferan isopods	0.0034
Carideans [Car]	0.0024
Crangon septemspinosa	0.0010
Unidentified carideans	0.0013
Pagurids [Pag]	0.0416
Pagurus acadianus	0.0051
Paguridae	0.0365
Rock crab (*Cancer irroratus*) [Cra]	0.2637
American lobster (*Homarus americanus*) [Lob]	0.0076
Echinoderms [Ech]	0.0222
Strongylocentrotus droebachiensis	0.0102
Ophiuroidea	0.0012
Unidentified echinoderms	0.0109
Fish [Fis]	0.0066
Flesh [Fle]	0.2724

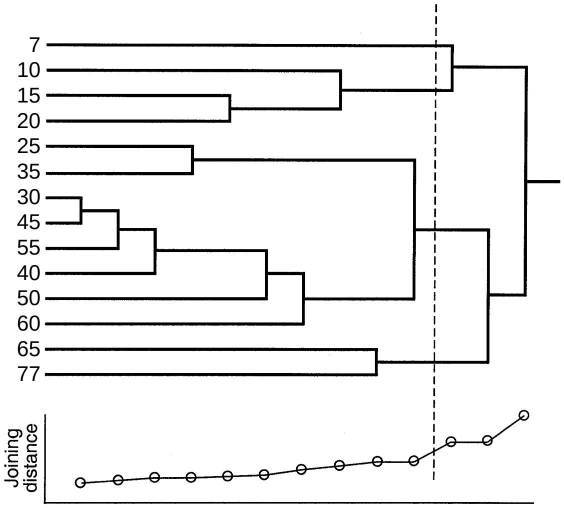

Figure 2

Dendrogram resulting from a cluster analysis on the mean volumetric contribution of major food categories by size class of lobsters from the Magdalen Islands. The bottom graph shows the joining distance at each step. The vertical dashed line indicates the cut-off value for clusters, selected because of the sudden increase in joining distance.

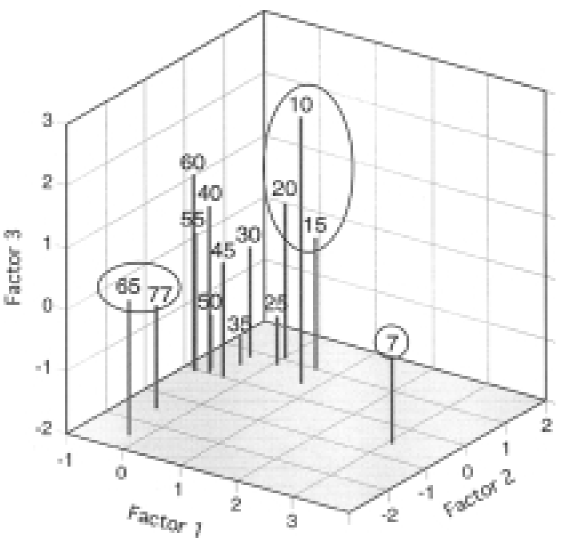

Figure 3

Results of the factor analysis on the correlation matrix of volumetric contribution of major food categories by size class of lobsters from the Magdalen Islands. See text for factor loadings. Three clusters identified in Figure 2 are shown inside ellipses; the other size classes constitute the fourth cluster.

were found in more than 70% of stomachs (Fig. 4). Bivalves were still found in a large proportion of stomachs (87%) but accounted for a low proportion (0.18) of volume. Gastropods, polychaetes, and macroalgae also occurred frequently but accounted for only a small fraction of stomach volume. Pagurids and lobsters were found in few stomachs but contributed >0.2 of stomach volume.

The grouping of the largest lobsters, 65–77 mm CL, had rock crab as the most important food item (specific abundance=0.55; occurrence=86%). Lobsters, pagurids and fish contributed a large proportion of stomach volume when they were eaten, but these prey were ingested by <20% of lobsters. Gastropods, flesh, bivalves, polychaetes, and macroalgae were found in a large proportion of stomachs but occupied a small proportion of the volume of these stomachs.

Overall, bivalves, rock crab, and flesh were the only food items that each accounted for >0.1 of stomach volume for the whole sample (Table 2). For these food items, a significant linear relationship existed between volumetric contribution and lobster CL, the latter explaining 68% to 92% of the variability in volume (Fig. 5). Regression of volumetric contribution on lobster CL produced a negative slope for bivalves and flesh, and a positive slope for rock crab. Similarly, strong linear or nonlinear relationships existed between percent occurrence of these three food items and lobster CL (Fig. 5). Furthermore, large lobsters tended to eat larger rock crabs than small lobsters, as evidenced by the significant positive linear relationship between the CW of rock crabs found in lobster stomachs and lobster CL (Fig. 6).

Discussion

Data

Stomach content analysis is a useful method for the investigation of the natural diet of animals, even though the lack of distinctive hard parts in some prey and differential digestibility of soft and hard body parts limits the spectrum of food items that can be recognized and can lead to biased perception of the relative importance of the food items. We took care to process lobsters as quickly as possible after collection, thus attenuating the effects of differential digestibility, and we examined only intermolt and nonovigerous lobsters, thus reducing sources of diet variability associated with molt cycle and female reproductive status (e.g. Weiss, 1970; Ennis, 1973). In addition, our study was conducted over a small area where the various lobster size classes were evenly distributed; therefore all lobsters potentially could access the same food. We recognize that our volumetric contribution index underestimates the importance of predominant food items, owing to correction for stomachs with multiple food items and total scores >10. However, this was a minor problem because analyses using uncorrected values revealed that the volumetric contribution of the three main food items was underestimated by no more than 2–5% and that relationships to lobster size class were unchanged. Therefore, we are confident that the dietary differences among the lobster size classes that we detected are real and that they

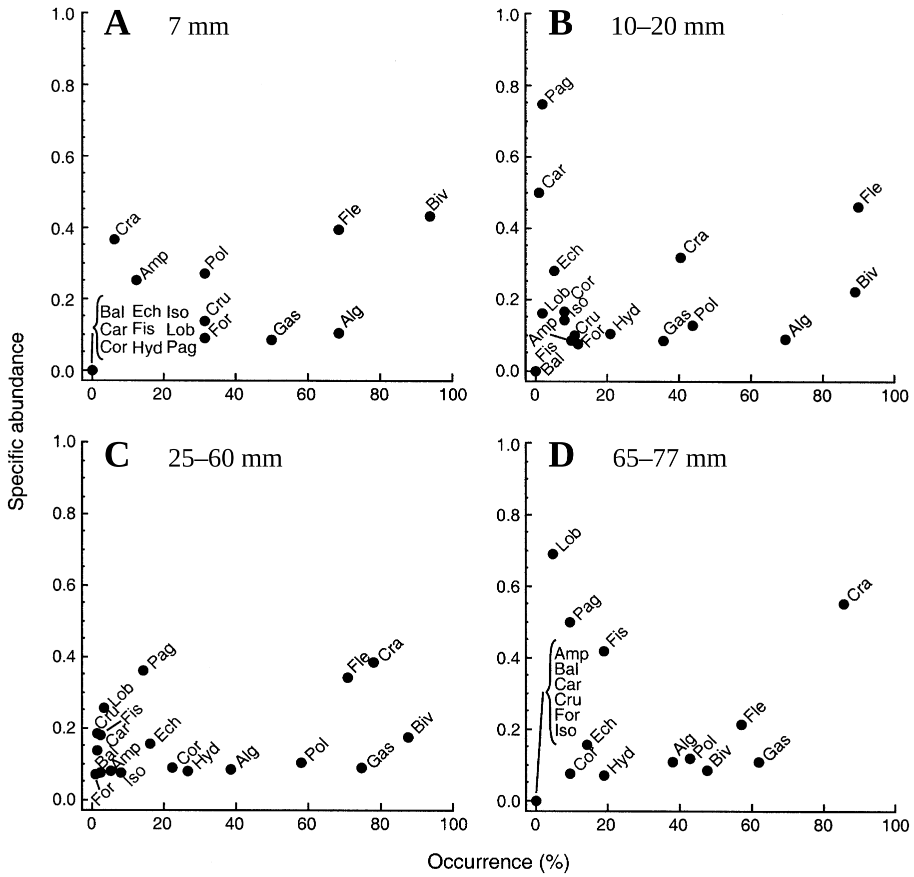

Figure 4

Relationship between specific abundance and percent occurrence for the major food categories in relation to clusters for size classes of the (**A**) 7 mm, (**B**) 10–20 mm, (**C**) 25–60 mm, and (**D**) 65–77 mm CL (see Fig. 2) for lobsters from the Magdalen Islands. Refer to Table 2 for abbreviations of major food categories.

reflect mainly changing lobster preferences and differential accessibility of prey types.

Ontogenetic shifts in diet

There was clear evidence of a progressive dietary shift with increasing lobster size at our study site. Smaller lobsters relied to a greater extent than larger lobsters on soft or easily acquired food items (flesh, sessile juvenile bivalves, macroalgae, meiobenthic crustaceans, and foraminiferans). Larger lobsters fed on bigger, more mobile and also more nutritious prey, including crustaceans that were protected by heavy shells, and fish. Fishes were probably taken by predation (see Weiss, 1970) because there was no fishing activity at or near our study site that might have provided lobsters with fish bait or discards.

The most striking ontogenetic changes in volumetric contribution of prey types occurred for rock crab and bivalves, the former increasing from 0.07 to 0.53 and the latter decreasing from 0.28 to 0.02 from the smallest to the largest lobster size class, respectively (Fig. 5). Only limited comparisons with other studies are possible, given the differences in methods and in the size range of lobsters examined. However, the observed trends of increasing importance of rock crab and of decreasing importance of bivalves with increasing lobster size were consistent with the analyses of Scarratt (1980) and of Carter and Steele (1982b), and they suggest that lobsters are not simply opportunistic or unspecialized feeders (see Elner and Campbell, 1987).

Multivariate analysis of lobster diet resulted in size groupings that are quite consistent with Lawton and Lavalli's (1995) size classification of the early life-history phases based on a broad set of behavioral and ecological criteria. Major shifts in diet in the present study occurred at about 7.5, 22.5, and 62.5 mm CL (Fig. 2). The two classifications differ in the smaller size for the transition from the first to second group (7.5 mm in our diet-based classification compared with 14.5 mm CL in Lawton and Lavalli's scheme), but the size for transition from the second to the

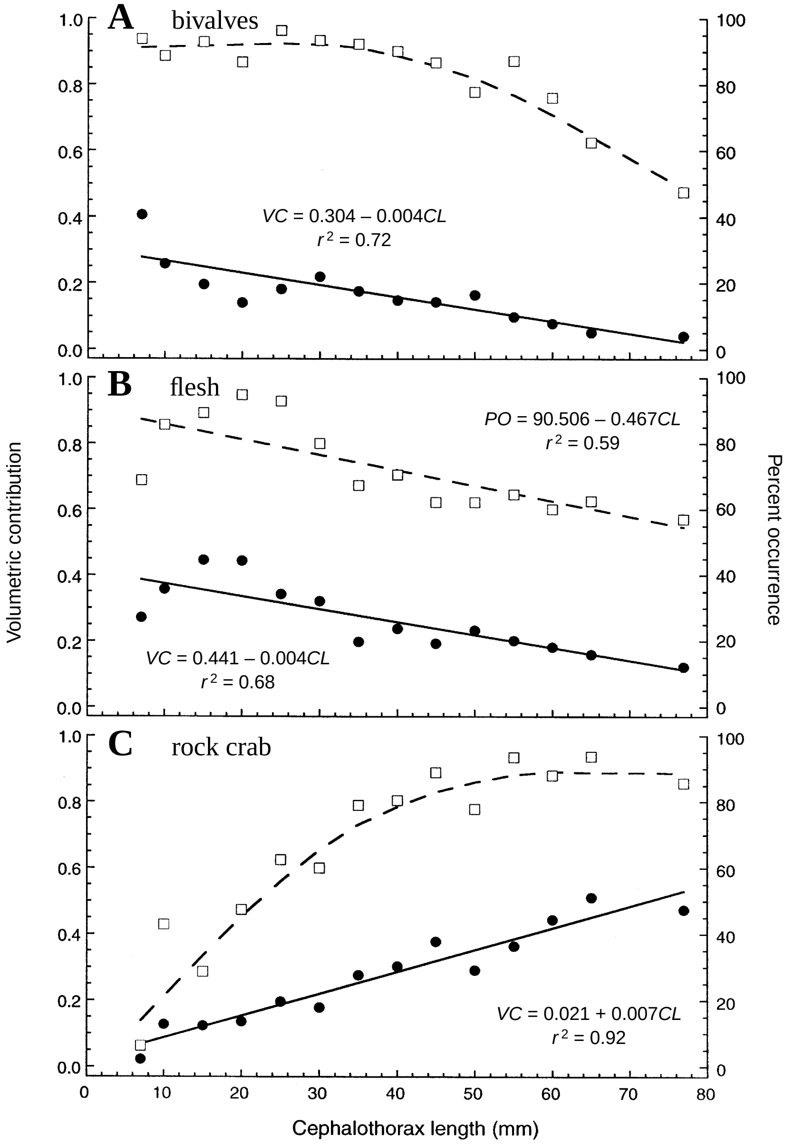

Figure 5

Relation between percent occurrence (PO, □) or volumetric contribution (VC, •) and lobster cephalothorax length for the three main food items of lobsters from Magdalen Islands: (**A**) bivalves, (**B**) flesh bolus, and (**C**) rock crab. All linear regressions are highly significant ($P<0.001$).

third group is the same in both studies (22.5 and ~25.0 mm CL). Comparison of the size threshold for transition from the third to the fourth group is less appropriate because Lawton and Lavalli (1995) considered this threshold to be determined by physiological maturity, which is a temperature-dependent trait that varies among regions.

Natural diet of shelter-restricted juveniles

This first investigation of the diet of SRJ lobsters does not support the view that these juveniles derive a substantial portion of their diet by suspension feeding and browsing in their shelters, at least at our study site and during the two years we sampled. With respect to suspension feeding, there was no evidence of planktonic organisms in stomachs, although some of the unidentified prey of the crustacean meiofauna category may have been planktonic. Foraminiferans, harpacticoids, ostracods, and macroalgal debris represented food items that potentially could be browsed within shelters. However, these taxa together contributed relatively little to stomach volume of lobsters in the 7-mm size class (0.14 for the combined categories,

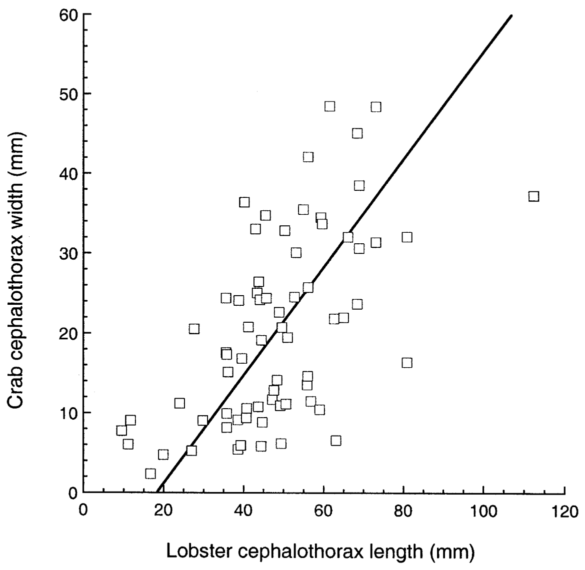

Figure 6

Relationship of predator (lobster) size to prey (rock crab) size, based on rock crab cephalothorax width (CW) estimated from measurements of indicator fragments and lobster cephalothorax length (CL), for the Magdalen Islands. Model II regression: $CW = -12.341 + 0.677CL$ [$r^2=0.34$, $P<0.001$].

in spite of the fact that one or the other category occurred in 88% of stomachs) and even less to stomach volume of lobsters in the 10-mm size class (0.10, 86%). During our study, lobsters settled in August at sizes of 4.3–5.2 mm CL and grew to 12–14.5 mm CL by October (Sainte-Marie et al., 2001). Thus, we sampled the lobster population during the only period of time when SRJs were present and seasonal sampling bias cannot be invoked to explain the lack of plankton in their diet.

The other food items in the stomachs of SRJs, and especially the predominant bivalves and flesh (Figs. 4 and 5), probably were derived by predation and scavenging. Bivalves in the stomachs of SRJ lobsters were represented by recently settled *Modiolus* and *Mytilus*. Mussel spat may settle aggregatively and quite synchronously, forming dense patches that can provide a short-term prey pool requiring little or no search time (e.g. Auster, 1988). Furthermore, because mussel spat often settle in crevices or under rocks (e.g. Nair et al., 1975), SRJs could access them with little or no risk of exposure to predators. Lawton (1987) argued that dominance and territoriality were likely to exist early in the ontogeny of lobsters, as demonstrated subsequently (James-Pirri and Cobb, 1999; Paille and Sainte-Marie, 2001), and that prolonged occupation and defense of shelters located close to a food patch would be advantageous for juveniles. Exploitation of mussel patches, inferred from the present study, is consistent with that hypothesis.

Flesh (tissue boluses) that could not be attributed to a particular animal for lack of indicator fragments was a very important food item in the diet of SRJs, both in terms of percent occurrence and of volumetric contribution (Figs. 4 and 5). Elner and Campbell (1987) also found that unidentified animal tissue was one of the most frequent and most volumetrically important foods in the stomachs, however, of larger lobsters. Weiss (1970) observed that adolescent and adult lobsters often captured crabs or other shelled prey, cracked them open, and then selectively ingested only soft tissue. Interestingly, the percent occurrence and volumetric contribution of flesh to diet was greater in lobsters of size classes ≤30 mm CL (i.e. SRJs and emergent juveniles) than in larger lobsters (Fig. 2). It is unlikely that the smallest of lobsters could find (within the confines of their shelter) and subdue prey sufficiently large to provide tissue boluses devoid of hard parts. Furthermore, claws are not differentiated into cutter and crusher forms in SRJs (Govind and Lang, 1978; Costello and Govind, 1984) and early juveniles may be incapable of breaking open shelled prey (Costello and Lang, 1979; Lawton and Lavalli, 1995). Therefore, flesh ingested by SRJs and emergent juveniles probably was obtained by scavenging animal remains. Considering that larger lobsters may hoard and bury food in or nearby their dens (Herrick, 1895; Smith, 1976; Lawton, 1987; Wickins et al., 1996), we propose that early juveniles exploit the meal scraps or food reserves of larger lobsters. Indeed, we observed that small lobsters often occupied galeries beneath, or in rock pilings nearby, the dens of larger lobsters. This is consistent with reports that odor from conspecific adults is a proximate cue for lobster settlement (Boudreau et al., 1993). Cohabitation of small lobsters with large lobsters would offer the former protection from predators and a potentially abundant, high-quality, sheltered food source, and would therefore represent a form of commensalism. The risk of cannibalism for small lobsters living in the vicinity of larger lobsters probably does not offset the benefits. Few lobster remains were found in lobster stomachs in this (Fig. 4) as in other studies (Weiss, 1970; Carter and Steele, 1982b; Elner and Campbell, 1987), and an unknown proportion of those remains may have been exuviae.

Some other rarer food items found in the stomachs of SRJ lobsters were probably taken by predation, possibly within, but more likely in the neighborhood of, the lobsters' shelters. The most important of these prey by volumetric contribution were polychaetes, comprising juvenile nereids and polynoids that are frequently found in soft sediment or on the underside of rocks, and recently settled rock crab. Similarly, amphipods and gastropods found in the stomachs of SRJs were juveniles or small species that may abound in crevices and in spaces beneath rocks.

A carnivorous, high-energy diet such as the one demonstrated for SRJs in our study would promote growth from settlement time. By contrast, Lavalli (1991) demonstrated that a diet of only diatomous algae was insufficient for extended growth and survival of early juvenile lobster. A diet of mesozooplankton sustained growth of juvenile lobsters, at least for some time after settlement (e.g. Daniel et al., 1985; Barshaw, 1989; Lavalli, 1991). However, Lawton and Lavalli (1995) pointed out that intermolt periods tended to be longer and molt increments smaller in laboratory-held, juvenile lobsters reared on mesozooplankton than in wild lobsters, suggesting that the latter incorporated more nutritious foods into their diet.

The finding that early juvenile lobsters are primarily predators or scavengers, if confirmed by studies at other sites, has implications for the development and implementation of artificial reefs. Such structures are increasingly being considered as a means to enhance lobster productivity on traditional grounds or to expand lobster habitat onto less hospitable grounds (e.g. Gendron, 1998). The carnivorous benthic feeding mode of SRJs and of emergent juveniles at our site implies that successful reefs will have to be designed, localized, and weathered so that they are initially well colonized and subsequently regularly colonized by benthic prey that are easily accessible and of high nutritional value to juvenile lobsters. Additionally, if SRJs and emergent juveniles derive some protective and nutritional benefits from the presence of larger conspecifics, reefs designed to offer shelter to a full suite of lobster sizes may prove to be more productive in the long term than reefs offering shelter only to small lobsters.

Importance of rock crab to lobster

Several previous studies have noted the importance of rock crab in the diet of lobster (Reddin, 1973; Evans and Mann, 1977; Carter and Steele, 1982a). Boghen et al. (1982) found that juvenile lobsters survived and grew better on a diet containing crab protein alone than on a diet of live brine shrimp (*Artemia salina*) or of protein extracts from urchin (*Strongylocentrotus droebachiensis*), mussel (*Mytilus edulis*), or shrimp (*Penaeus* sp.). Gendron et al. (2001) found that condition, somatic growth, and gonadal development of lobster increased with increasing amount of rock crab in diet. In nature, even SRJs may benefit from a diet including large amounts of rock crab protein because they preyed directly on very small rock crabs (Figs. 4 and 5), and the tissue boluses they contained may have been that of rock crab (see above).

We were able to establish a positive size relationship for lobster preying on rock crab (Fig. 6). The smallest rock crab prey were 2–6 mm CW and belonged to the first benthic instars of this species. In our study, apparently no rock crabs larger than 50 mm CW were consumed by lobsters, and the maximum ratio of crab CW over lobster CL was 0.90, even though rock crabs up to 120 mm CW were seen (own personal diving observations). In the laboratory, Weiss (1970) observed that lobsters of 60–80 mm CL attacked crabs offered in the size range of 62–78 mm CW. Lawton and Lavalli (1995) reported that juvenile lobsters can subdue juvenile intermolt rock crabs up to approximately 0.40 times their own body size. Their observation was based on the comparison of predator and prey wet masses; when expressed in terms of crab CW over lobster CL, the maximum ratio was equivalent to about 1.27.[1] This ratio of prey CW to predator CL is somewhat larger than that derived from our stomach analyses. Because lobsters probably ingest only soft tissue when the prey-predator size ratio is sufficiently high (Weiss, 1970; and see above), our analysis of rock crab prey-size frequencies may correctly estimate the minimum prey size but underestimate the maximum prey size and the volumetric contribution and occurrence of rock crab in the diet of any given lobster size class. Nevertheless, the present study clearly shows that all lobster size classes rely on rock crab as food and that the size spectrum of rock crab that is used by lobsters is broad and includes even those at the settlement stage. Given the much greater economic value of lobster in relation to rock crab, and the trophic dependency of the former on the latter, caution should be exercised in developing rock crab fisheries (Gendron and Fradette, 1995).

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