Natural diets of lobster *Homarus americanus* from barren ground and macroalgal habitats off southwestern Nova Scotia, Canada

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ABSTRACT: Stomach contents of 1032 lobsters *Homarus americanus* from an area with dense macroalgae (n = 115) and sea urchin *(Strongylocentrotus droebachiensis)* denuded barrens (n = 917) off the southwestern coast of Nova Scotia were examined to compare natural diets. Gross dietary composition and mean stomach fullness appeared similar in these 2 habitats; the diet spectrum encompassed a broad range of plants and animals but was dominated by molluscan, crustacean, echinoderm, and polychaete remains. Mussels *(Modiolus modiolus, Mytilus edulis)* appeared the most consistently important identified prey species, in terms of frequency-of-occurrence and estimated volume (points) indexes. Patterns in prey points were investigated by discriminant analysis. Shifts in point values for gastropods, ascidians, hermit crabs and brachyuran crabs proved useful in discerning habitat. Dietary diversity (mean number of prey taxa types per stomach) was significantly less for lobsters collected on barrens in September 1979 (12.1) than for lobsters taken from the macroalgal area in August 1979 (13.9). Temporal variations in diet were investigated for the barrens. There were significant decreases in mean stomach fullness and mean number of prey taxa types per stomach for lobsters collected in February–March 1982 as opposed to July–August 1981. Concomitantly, temporal shifts in diet composition were evident from discriminant analysis, predominantly through decreased importance of sea urchins, ophiuroids, lobsters, and brachyuran crabs in February–March. Data on the dietary importance of sea urchins in relation to other prey taxa did not support the hypothesis that lobsters are a principal, 'keystone' predator on sea urchins. There is still insufficient evidence to assess whether lobster production is food limited on barrens.

INTRODUCTION

In the present paper we investigate the natural diets of American lobster *Homarus americanus* from sublittoral barren ground and macroalgal habitats off Nova Scotia, Canada. An explosion in sea urchin *Strongylocentrotus droebachiensis* densities resulted in destructive grazing of the extensive macroalgal beds along the Atlantic coast of Nova Scotia through at least the 1970's (Wharton & Mann 1981). The crustose coralline algae and microalgae on the barren grounds were estimated to be substantially less productive than the kelp communities that they replaced (Chapman 1981). On the basis of the postulated reduced food supply, as well as loss of habitat structure and a corre-

lation between declining lobster landings and the destruction of the kelp beds, Breen & Mann (1976) and Wharton & Mann (1981) concluded that lobster production suffers on the barrens. The lobster, as well as being of prime economic importance along Nova Scotia's coast (Robinson 1980, Stasko & Campbell 1980) has been purported to have a 'keystone' predator influence *(sensu* Paine 1969) on the near-shore ecosystem (Mann & Breen 1972, Breen & Mann 1976, Bernstein et al. 1983). However, hypotheses for the control of sea urchins by lobsters and the influence of the barrens on lobster feeding have, hitherto, not been examined through natural diet studies for lobsters from either Nova Scotian barren grounds or macroalgal beds.

Lobsters fragment and selectively ingest their prey (R. W. Elner & L. V. Colpitts** unpubl. data), making studies of their natural diet problematical. Identification of dietary components in the stomachs of lobsters is usually by diagnostic fragments of such relatively

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indigestible skeletal structures as gastropod operculae and crab leg tips (Weiss 1970, Elner et al. 1985). Hence, prey types that include many such fragments may appear over-represented in stomachs compared to prey that are gleaned from their skeletal structures before ingestion or are comparatively soft-bodied and lacking in persistent remnants. Notwithstanding differential selectivity, much ingested food is so masticated that even compiling a complete listing of prey is difficult and ranking prey in order of dietary importance fraught with complications (see Berg 1979, Hyslop 1980 for reviews). The frequency-of-occurrence index and the subjective, estimated volume (points) index appear the only feasible scoring methods for prey in the stomach contents of lobsters and portunid crabs; both methods have been commonly adopted (see Ennis 1973, Scarratt 1980, Carter & Steele 1982 for lobsters, and Ropes 1968, Elner 1981, Williams 1981 for portunids). While acknowledging that these indexes have their own biases (Hyslop 1980, Williams 1981), they may be used to provide a semi-quantitative ranking of food species in the diets of lobsters.

The natural diets of lobsters from barren ground and macroalgal habitats off southwestern Nova Scotia are recorded in the present paper using extensive data on stomach contents. The significance of habitat and season (for barrens) on stomach fullness, diet diversity, frequency-of-occurrence and points indexes were analyzed by direct comparison as well as by multivariate statistical techniques.

MATERIALS AND METHODS

Lobsters were taken by SCUBA divers during daylight hours from sea urchin denuded barrens off McNutts Island, Shelburne Harbour (Fig. 1). In September 1979, July–August 1981, and February–March 1982, 117 (size range 11 to 142 mm carapace length [CL]), 400 (size range 11 to 78 mm CL), and 400 (size range 8 to 75 mm CL) lobsters respectively were captured. The site was moderately exposed, ranging in depth from 3.0 to 10.0 m with a substrate consisting of cobbles and boulders densely embedded in a shell-sand matrix. Crustose coralline algae *Corallina officianalis* covered most of the hard substrate in the sublittoral; fleshy macroalgal cover, mainly tufts of *Desmarestia* spp., was restricted to less than 3 %. The narrow infralittoral fringe provided a refuge for *Laminaria* spp., *Alaria* spp., and *Saccorhiza* spp. Sea urchins were the dominant macrofaunal organism, with densities of between 29 and 90 m^{-2}. Other grazers included periwinkles *Littorina littorea*, limpets *Acmaea testudinalis*, and chitons *Tonicella* spp. Mussels *Mytilus edulis* and *Modiolus modiolus*, and brittlestars *Ophiura* spp. were abundant suspension feeders. In addition to lobsters, common predators included seastars *Asterias* spp., rock crabs *Cancer irroratus*, Jonah crabs *Cancer borealis*, and fish.

SCUBA divers collected 115 lobsters (size range 50 to 133 mm CL) from macroalgal beds off Gull Island and Wilson Island, Lobster Bay, during daylight hours in August 1979 (Fig. 1). Substrate, exposure, and depth characteristics of the site resembled those of the barrens. However, as the area had not been destructively grazed by sea urchins, macroalgal cover approached 90 %. Irish moss *Chondrus crispus* was the dominant alga, followed by large kelps *Laminaria* spp. Sea urchins were rarely found. Gastropods, predominantly *Buccinum undatum*, bivalves *Mytilus edulis* and *Modiolus modiolus*, polychaetes, amphipods, and
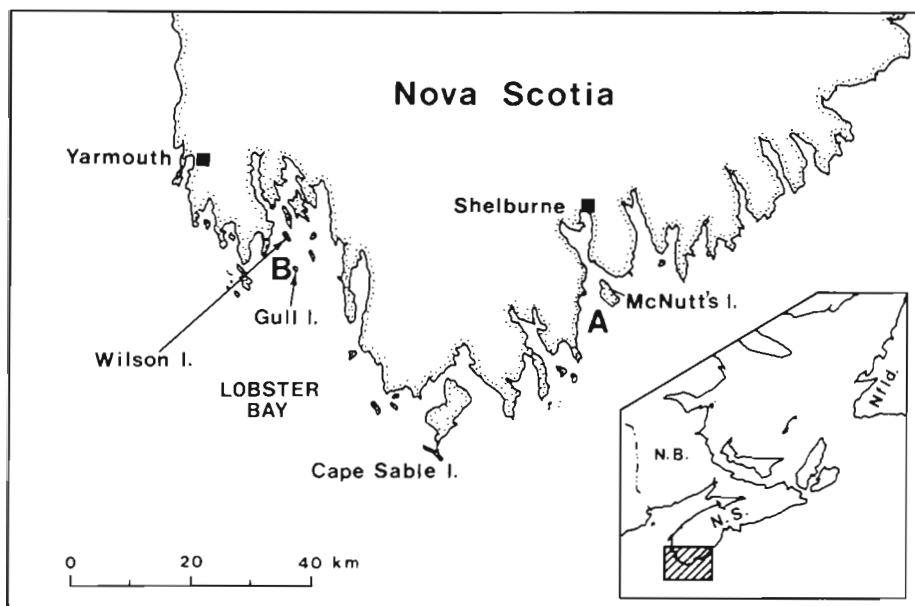

Fig. 1. Maritime provinces of Atlantic Canada (inset); collection sites for *Homarus americanus* on (A) barrens and (B) macroalgal areas off southwestern Nova Scotia

crabs *Pagurus* spp. and *Hyas* spp. were abundant. Seastars *Asterias* spp., *Cancer* crabs, green crabs *Carcinus maenas,* and lobsters were frequently encountered predators. More detailed biological data for the area are provided by Pringle & Semple (1980).

Assessments of lobster biomass were not attempted for our study; however, although standardized relative abundance estimates are impractical (given a reduced search efficiency in a kelp bed as compared to an open barrens), the actual lobster collection rates achieved by the SCUBA divers (R. W. Welsford Research Group Limited[*] unpubl. report) were similar for the barrens and macroalgal sites in 1979 (barrens: 4.6 lobsters per diver hour; macroalgal area: 4.4 lobsters per diver hour).

On collection, lobsters were sealed in individual plastic bags, together with an information slip including the date and location of capture. The lobsters were then frozen on dry ice and transported in insulated containers to the St. Andrews Biological Station where they were stored in a freezer until required for analyses. After thawing, size was determined for each lobster by measuring carapace length, from the posterior edge of an eye socket to the posterior margin of the carapace. Sex and molt stage (Aiken 1973) were also recorded. The complete stomach sac was excised from the cephalothorax, and stomach fullness was visually estimated according to a scale of 0 to 100 (empty to fully distended). After the stomach was slit open, the contents were flushed out into a Petri dish. Material from the stomach was identified under a binocular dissecting microscope to the lowest possible taxonomic level. Most food items were recognizable only by the presence of diagnostic fragments; a guide (Elner et al. 1985) to such fragments based on prey remains identified in the stomachs of *Cancer* crabs from McNutt's Island is also applicable to lobsters. The importance of each prey taxon was evaluated by 2 methods: (1) frequency-of-occurrence; and (2) the points method of Swynnerton & Worthington (1940), which considers volumetric contribution.

In a given stomach, the frequency-of-occurrence of each prey taxon was recorded on a presence or absence basis. Each prey taxon present was then awarded points based on its estimated volume and in proportion to the total number of points allocated for stomach fullness. For example, a three-quarters full stomach was allocated a total of 75 points; the *Cancer* spp., making up two-thirds of the bulk, would be awarded 50 points; and the remaining one-third bulk, comprising, say, unidentified plant material, would be given 25 points. Although the visual assessment of stomach

fullness is subjective and the point 'units' themselves not standardized for stomach size, we believe the method adequately ranks the various prey taxa in terms of dietary bulk. However, differences in digestion rate, feeding behavior, and relative quantity of indicator fragments may enhance the apparent importance of some taxa over others.

Data from both points and frequency-of-occurrence methods were expressed as percentages based on the total number of stomachs that contained food, rather than the total number of stomachs examined. Initially, when comparing points, data within each sample from each of the 4 area-date groups were examined according to sex, 20 mm CL size class, and molt stage. Almost all lobsters were in intermolt stage; consequently, the few lobsters at pre- or post-molt stages were not considered in our analyses. Analysis of variance (ANOVA) and the Student-Newman-Keuls test (Kim & Kohout 1975) were used to test for differences between sexes, five 20 mm CL classes and 4 area-date groups for mean stomach fullness and number of taxa per stomach after arcsine and $\log_{10}$ transformation, respectively. Since there were no significant differences ($p > 0.05$) in mean stomach fullness and number of prey taxa per stomach between sexes and size classes, the data were combined for each area-date group. Weiss (1970) and Ennis (1973) also failed to demonstrate sexual differences in lobster diet. To avoid possible biases caused by empty or near-empty stomachs, only lobsters with stomachs $\geq 10\%$ full were used in the ANOVA's and discriminant analyses; less than 5% of lobsters were excluded.

To reduce the number of variables considered, the contents of each stomach were reassigned into 26 diet categories. We selected these categories as being the most representative of the 65 taxa originally identified. Utilizing the revised diet categories, frequency-of-occurrence values were plotted against the points values to allow the relative importance of each category to be visually assessed in each area-date group. Discriminant analysis (Fisher 1936, Kelcka 1975) on points data was chosen for the analysis of variations in the diet categories of the 4 area-date groups. Discriminant analysis, or canonical variate analysis, linearly combines the diet categories in such a way as to maximize the differences between the area-date groups while minimizing the variance within each group. The point scores were arcsine transformed prior to analysis in order to approximate the condition of multinormality which the discriminant analysis assumes; however, this model is robust to some departures from the normal distribution (Legendre & Legendre 1983). Diet categories with large discriminant coefficients (≥ 0.30) within each of the first 2 canonical discriminant functions were considered important in separating the 4 groups.

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RESULTS

Individual stomach fullness varied considerably in any given lobster size class. Mean stomach fullness was not significantly different between the macroalgal 1979, barrens 1979, and barrens July–August 1981 samples (Table 1). However, mean stomach fullness for barrens in February–March 1982 was significantly lower than those of the other samples (Table 1).

Table 1. *Homarus americanus*. Mean percent stomach fullness and mean number of taxa per stomach for lobsters from the 4 area-date groups. Retransformed means followed by the same letter in each column are similar (p > 0.05); means not followed by the same letter in each column are significantly different (p > 0.01) using Student-Newman-Keuls test. Lobsters with < 10 % stomach fullness are excluded

Area-date	Mean % stomach fullness	Mean no. of taxa per stomach	N
Macroalgal:			
Aug 1979	55.5a	13.9	93
Barrens:			
Sep 1979	56.5a	12.1	110
Jul–Aug 1981	57.9a	10.8	389
Feb–Mar 1982	29.7	7.6	377

Sixty-five prey taxa were distinguished amongst all the lobster stomachs examined and most were found in both barrens and macroalgal habitats (Table 2). Except for the virtual absence of sea urchins in the sample from macroalgal habitat, the broad dietary composition, both in terms of frequency-of-occurrence and points, appeared remarkably consistent. However, compared to the macroalgal sample, significantly fewer prey taxa per lobster were identified for barren grounds (Table 1). Further, the diet on the barrens for the February–March group was, on average, less diverse than that for July–August, which in turn was less diverse than that for September 1979 (Table 1).

Mussels were consistently one of the most important prey (Table 2). The taxon 'mussels' combined remains of the blue mussel *Mytilus edulis* and the horse mussel *Modiolus modiolus,* as the shell fragments of these 2 species were indistinguishable. Nevertheless, given that lobsters are size-selective predators on bivalves (Elner & Jamieson 1979, Elner & Lavoie 1983), we argue that *M. edulis* was the more important prey species as it occurred more commonly and in a more vulnerable size range than *M. modiolus* in either habitat.

Unidentified food remains were prominent for all area-date groups (Fig. 2) but were considered proportionately assigned to the remaining identified diet categories and thus effectively ignored. For the macroalgal site, bivalves, ascidians, brachyuran crabs, hermit crabs, gastropods, and lobsters all appeared important in terms of bulk, although unidentified algae/vascular plants were present the most frequently (Fig. 2). For the barrens in September 1979 bivalves were the dominant dietary component; brachyuran crabs, ophiuroids, lobsters, and seastars were important in terms of points, although they were surpassed by sea urchins, unidentified algae/vascular plants, polychaetes, gastropods, pebbles/foreign material, chitons, fleshy algae, and shrimp/other crustaceans in terms of frequency-of-occurrence (Fig. 2). Bivalves were also the major identified diet category for lobsters captured on the barrens in July–August 1981 and February–March 1982 (Fig. 2). However, while the patterning for most diet categories appeared similar for these latter 2 area-date groups, there were marked shifts in the relative importance of sea urchins and lobsters on both indexes.
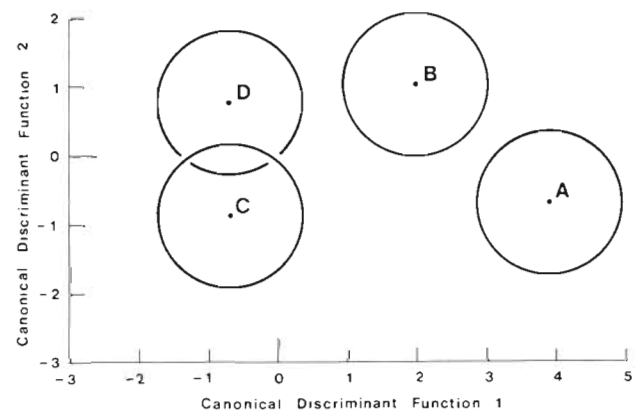

Fig. 3. *Homarus americanus*. Plot derived from a stepwise discriminant function analysis defining the canonical discriminant function centroids (dots) and ± 1 standard deviations (circles) for 26 diet categories for the 4 area-date groups (stomachs ≥ 10 % full): A, macroalgae, Aug 1979; B, barrens, Sep 1979; C, barrens, Feb–Mar 1982; D, barrens, Jul–Aug 1981. Individual data points (N = 969) were omitted, as they are too numerous

Discriminant analysis on the diet of 969 lobsters indicated significant differences between the 4 area-date groups (Fig. 3; Table 3). The first canonical discriminant function represented the largest variance (70 %) between the 4 area-date groups (Table 3). The 5 variables with the largest coefficients (≥ 0.30), giving the best discrimination between the groups (in decreasing order), were gastropods, ascidians, hermit crabs, gravel, and brachyuran crabs. The first function was generally useful in discriminating spatial (area) differences between the groups. The second canonical discriminant function (representing 21 % of variance between groups) was mostly influenced by echinoids,

Table 2. *Homarus americanus*. Occurrence of prey taxa in stomachs by percentage frequency-of-occurrence (percentage points) for the 4 area-date groups: A, macroalgal Aug 1979 (n = 115); B, barrens, Sep 1979 (n = 117); C, barrens, Jul–Aug 1981 (n = 400); D, barrens, Feb–Mar 1982 (n = 400)

Prey taxa	Area-date groups			
	A	B	C	D
1. Animals	100 (94.2)	100 (92.8)	99 (97.8)	100 (97.3)
2. Protozoans/foraminiferans	1 (0.02)	5 (0.21)	45 (1.5)	31 (1.6)
3. Poriferans	1 (0.02)	1 (0.19)	0.5 (0.07)	–
4. Cnidarians	11 (0.31)	22 (0.64)	15 (0.39)	21 (1.2)
5. Bryozoans	1 (0.02)	–	1 (0.08)	–
6. Molluscs	94 (18.8)	83 (21.2)	90 (19.6)	84 (16.5)
7. Chitons	9 (0.57)	34 (1.4)	21 (1.6)	9 (1.4)
8. *Tonicella marmorea*	–	2 (0.08)	9 (0.88)	3 (0.59)
9. Gastropods	78 (6.2)	44 (2.2)	10 (0.51)	4 (0.15)
10. *Acmae testudinalis*	2 (0.16)	1 (0.02)	2 (0.04)	–
11. *Lacuna vincta*	26 (1.8)	6 (0.11)	1 (0.02)	–
12. *Skeneopsis striatum*	2 (0.16)	–	1 (0.02)	–
13. *Crucibulum striatum*	1 (0.04)	–	–	–
14. *Crepidula* sp.	2 (0.05)	–	–	–
15. *Lunatia* sp.	2 (0.16)	–	–	–
16. *Mitrella* sp.	5 (0.26)	–	–	–
17. Bivalves	63 (11.8)	71 (17.3)	87 (16.1)	78 (14.0)
18. Mussels *(Mytilus edulis, Modiolus modiolus)*	49 (9.6)	62 (16.2)	85 (15.0)	77 (13.8)
19. *Cerastoderma pinnulatum*	10 (0.57)	2 (0.03)	0.3 (0.01)	–
20. *Anomia* sp.	4 (0.27)	4 (0.08)	–	–
21. *Hiatella* sp.	–	4 (0.22)	1 (0.01)	–
22. *Mya* sp.	–	1 (0.02)	–	–
23. *Musculus* sp.	6 (0.26)	2 (0.03)	–	–
24. Polychaetes	54 (4.0)	48 (2.8)	50 (5.7)	36 (5.6)
25. *Nereis* sp.	37 (1.37)	37 (0.96)	22 (2.4)	21 (3.0)
26. Polynoids	23 (1.1)	11 (1.4)	24 (2.1)	8 (1.5)
27. *Spirorbis* sp.	2 (0.05)	–	–	–
28. *Cistena* sp.	3 (1.3)	2 (0.34)	0.5 (0.02)	–
29. Crustaceans	86 (28.2)	79 (29.1)	41 (15.5)	31 (7.5)
30. Barnacles	3 (0.09)	2 (0.03)	–	–
31. Isopods	11 (1.2)	1 (0.02)	0.3 (0.01)	–
32. *Idotea* sp.	3 (0.57)	–	–	–
33. Amphipods	23 (1.2)	3 (0.06)	2 (0.08)	0.3 (0.03)
34. *Corophium* sp.	1 (0.02)	1 (0.02)	–	–
35. *Ampithoe rubricata*	10 (0.73)	–	–	–
36. Decapods	76 (25.7)	74 (28.1)	36 (15.2)	28 (7.2)
37. *Homarus americanus*	16 (6.2)	16 (6.1)	19 (11.9)	2 (0.51)
38. *Pagurus* sp.	26 (6.7)	11 (1.8)	–	–
39. *Cancer* sp.	30 (9.5)	37 (14.9)	2 (0.53)	1 (0.49)
40. *Hyas* sp.	–	3 (1.5)	4 (0.76)	2 (0.78)
41. *Carcinus maenas*	2 (0.18)	–	–	–
42. *Caridion* sp.	1 (0.02)	1 (0.02)	–	–
43. Echinoderms	27 (6.2)	72 (19.4)	82 (27.4)	29 (14.3)
44. Holothurians	4 (2.0)	7 (2.2)	–	–
45. *Psolus* sp.	–	1 (0.03)	–	–
46. *Cucumaria* sp.	1 (0.29)	–	–	–
47. *Strongylocentrotus droebachiensis*	1 (0.04)	57 (2.6)	63 (8.1)	13 (2.5)
48. Seastars	22 (4.1)	21 (5.2)	11 (6.6)	4 (3.7)
49. Ophiuroids	3 (0.07)	24 (9.1)	15 (8.7)	6 (5.8)
50. *Ophiopholis aculeata*	–	9 (5.4)	0.3 (0.13)	–
51. *Amphiopholis squamata*	1 (0.02)	–	–	–
52. Ascidians	28 (12.1)	12 (3.1)	0.5 (0.19)	0.5 (0.28)
53. Fish	21 (1.8)	9 (2.1)	0.5 (0.11)	1 (0.27)
54. Other animals[a]	5 (0.86)	3 (0.16)	–	–
55. Unidentified animal tissue	79 (20.1)	69 (13.9)	95 (27.8)	100 (50.2)
56. Plants	83 (4.2)	49 (4.2)	44 (2.0)	37 (2.6)
57. Algae	77 (3.9)	44 (3.3)	44 (1.9)	37 (2.6)
58. Brown algae	36 (1.1)	9 (2.2)	5 (0.12)	7 (0.64)
59. Green algae	14 (0.46)	1 (0.02)	3 (0.08)	4 (0.23)
60. Red algae	23 (0.60)	21 (0.53)	33 (1.2)	27 (1.3)
61. Tufted red algae[b]	–	14 (0.26)	29 (1.0)	26 (1.2)
62. *Corallina officinalis*	36 (1.2)	15 (0.40)	9 (0.52)	2 (0.11)
63. *Zostera marina*	2 (0.04)	1 (0.03)	–	–
64. Gravel	37 (1.5)	38 (1.5)	4 (0.16)	3 (0.10)
65. Foreign material[c]	2 (0.04)	7 (1.5)	–	–

[a] Eggs, nematodes, nemertines, turbellarians
[b] Family: Ceramiaceae
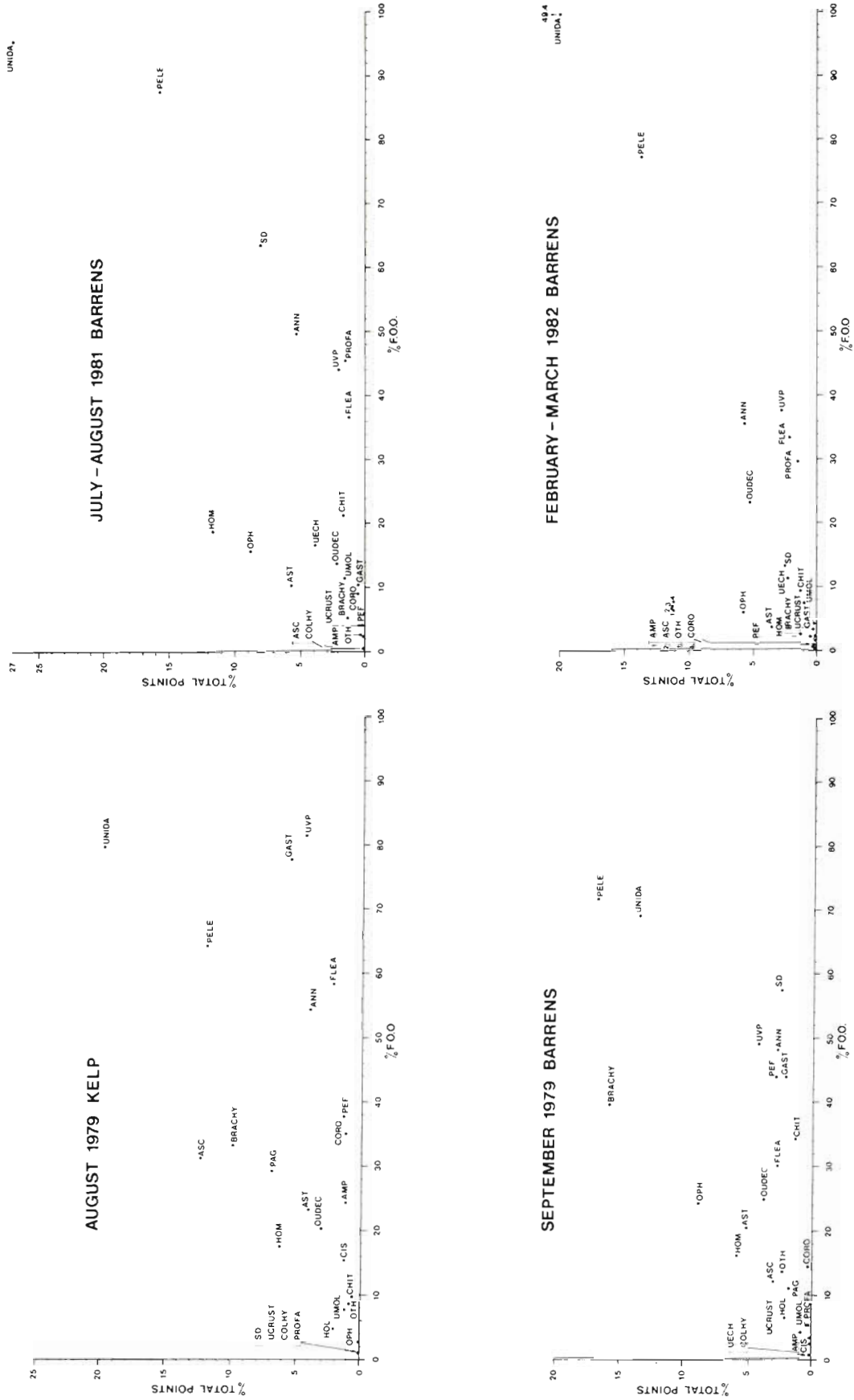[c] Plastic, rubber, wood

Fig. 2. *Homarus americanus*. Relative contribution of 26 diet categories in stomachs in terms of frequency-of-occurrence (F.O.O.) and points indexes (key to abbreviated forms in Table 3) for each of the 4 area-date groups

Table 3. *Homarus americanus.* Coefficients of the canonical discriminant functions for 26 diet categories (abbreviations for Fig. 2) from the 4 area-date groups. Coefficients have decimal places removed (e.g. −24 = −0.24). Lobsters with < 10 % stomach fullness are excluded

Diet category	Standardized canonical discriminant coefficients		
	Function 1	Function 2	Function 3
1. Protozoa/foraminiferans (PROFA)	−24	06	19
2. Cnidarians (COLHY)	−08	−00	09
3. Unidentified molluscs (UMOL)	−07	−03	10
4. Chitons (CHIT)	−04	08	−26
5. Gastropods (GAST)	58	02	10
6. Bivalves (PELE)	02	24	14
7. Polychaetes (ANN)	04	18	25
8. Unidentified crustaceans (UCRUST)	07	08	−11
9. Cirripeds/isopods (CIS)	15	−14	24
10. Amphipods (AMP)	18	−09	33
11. Shrimps/other crustaceans (OUDEC)	13	−08	−07
12. Lobsters (HOM)	15	30	26
13. Hermit crabs (PAG)	37	03	17
14. Brachyuran crabs (BRACHY)	32	30	−28
15. Unidentified echinoderms (UECH)	−09	24	26
16. Holothurians (HOL)	12	11	−16
17. Echinoids[a] (SD)	17	75	08
18. Asteroids (AST)	08	25	13
19. Ophiuroids (OPH)	04	34	12
20. Ascidians (ASC)	40	−01	22
21. Unidentified animal tissue (UNIDA)	−08	01	26
22. Unidentified algae/vascular plants (UVP)	18	−03	−14
23. Fleshy algae (FLEA)	−10	−03	32
24. Coraline algae (CORO)	07	−03	27
25. Gravel/foreign (PEF)	36	18	−38
26. Other (OTH)	16	10	−20
Percent variance	69.9	21.0	9.1
Eigenvalue	2.29	0.69	0.30
Canonical correlation	0.834	0.638	0.481
Wilk's λ	0.138[b]	0.456[b]	0.769[b]

[a] *Strongylocentrotus droebachiensis*
[b] $p < 0.01$

ophiuroids, lobsters, and brachyuran crabs. This second function appeared useful in discriminating temporal (date) differences between groups.

An *a posteriori* classification of individual lobster stomachs was used to estimate the discriminating power and classification accuracy of the derived canonical discriminant functions. The total percent of 'grouped' cases correctly classified into their appropriate area-date groups was 76.4 %.

DISCUSSION

Stomach contents of lobsters from barren grounds and macroalgal beds off southwestern Nova Scotia appear remarkable, not for differences but, rather, for their broad consistency. The natural diets of the lobsters studied from both habitats, although comprising a diverse spectrum of benthic prey, tended to be domi-

nated by the same major components: echinoderms, molluscs, and polychaetes. In particular, mussels were invariably the most important identified prey for all sampling areas and dates. However, notwithstanding the overall pattern, some habitat-related differences in natural diet were detected. Lobster diet diversity was higher for the macroalgal habitat than the barrens (Table 1), and area-date groups could be effectively separated by multivariate analyses (Table 3; Fig. 3). The diet categories most influential for area discrimination (gastropods, ascidians, hermit crabs, and brachyuran crabs) do change, markedly in dietary rank and abundance (B. Michaud[*] unpubl. data), between the 2 habitat-types. Nevertheless, the diet diversity differences and prey shifts responsible for group discrimination are not necessarily of dietary importance

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per se, and their functional significance remains to be tested. Indeed, 'gravel' was also a major discriminator for habitat. We, like Herrick (1895), remain nonplussed by the incidence of gravel in lobster stomachs but suggest it is probably ingested coincidentally while the lobster is feeding on more nourishing prey.

Previous studies of the natural diet of the American lobster from various parts of the western Atlantic appear in general agreement with our study in that crabs, echinoderms, mussels, and polychaetes have also been found to be dominant prey (Squires 1970, Weiss 1970, Ennis 1973, Scarratt 1980, Carter & Steele 1982). Such dietary consistency, as well as being in accord with interhabitat comparisons (above), is noteworthy given the probable geographic changes in the relative abundances of prey species over the lobsters' range. The implication is that lobsters are selective feeders with a complex foraging behavior that is capable of maintaining gross diet composition despite sharp variations in prey availability. Certainly the contentions of previous workers that lobsters are either simple opportunistic omnivores whose 'stomach contents reflect the relative abundance of prey species in the habitat' (Miller et al. 1971) or 'scavengers' (Herrick 1895) and 'most unspecialized feeders' consuming 'almost anything, regardless of its possible nutritional value' (Scarratt 1980) should now be reassessed.

Considering our results in tandem with studies by Vadas et al. (1986) on the influence of lobsters on sea urchin behavior and interpretive reviews on western Atlantic coastal ecology (Pringle et al. 1982, Miller 1985a, Sebens 1985) we argue that lobsters are unlikely agents in the transformation of macroalgal beds to barrens, and there is insufficient evidence to assess whether lobster production is adversely affected by the barren state. The initial explosion of sea urchin densities associated with destructive grazing has been accorded to a decline in a principal keystone predator, the lobster (Mann & Breen 1972, Breen & Mann 1976, Mann 1977). Sea urchins were rare in the macroalgal habitat, and their remains were found in only one out of 115 lobster stomachs examined. Although sea urchins were more prominent in the stomachs of lobsters from barrens, a habitat where urchins were the most common macrofaunal organism, they were of variable rank and always surpassed in importance by other prey, particularly mussels. Intuitively, in a keystone interaction, sea urchins should be a strongly preferred prey in both the barrens and macroalgal habitats; we contend that such a preference is not reflected by the dietary rank of sea urchins in our samples. Similarly, laboratory experiments (Evans & Mann 1977, Hirtle & Mann 1978, Elner 1980) have consistently shown that lobsters do not exhibit a preference for sea urchins when alternative prey are available. Moreover, our data do not concur with the contention by Wharton & Mann (1981) that lobsters from barren grounds experience a critical lack of food. Given that our lobster collection rate data are indicative of lobster biomass densities being similar in both habitats (see also Miller 1985a), there appear to be sufficient standing biomass and production inputs on the barrens to maintain the lobster food supply, in terms of general prey composition and bulk. Indeed, as Miller et al. (1971) determined that food production in the seaweed zone of St. Margarets Bay, Nova Scotia, was an order of magnitude greater than that needed to support the local lobster stock, we would not expect a 60 % reduction in primary productivity (Chapman 1981), in itself, to be necessarily critical.

Temporal variations in the natural diet of lobsters have been detected in other investigations (Weiss 1970, Carter & Steele 1982) as well as our own. For barrens in the present study, sea urchin, ophiuroid, lobster, and brachyuran crab remains all decreased in importance between July–August 1981 and February–March 1982; indeed, these shifts were most useful in discriminating date differences between samples (Table 3). Such effects may be due to seasonal changes in both foraging activity and the availability of prey species. For example, sea urchins show seasonal variations in distribution and behavior (Bernstein et al. 1981), and crabs undergo seasonal movements and become more vulnerable during their molting period (R. W. Elner unpubl. data). Lobsters suffer an increased vulnerability during their molting period as well as demonstrating molt-related shifts in diet (Ennis 1973, Leavitt et al. 1979, Scarratt 1980). Lobster remains have also been encountered in lobster stomachs in other studies (Weiss 1970, Carter & Steele 1982); although we determined that some remains could have been from cast exuviae, others, associated with flesh, indicated that cannibalism was occurring. The significant reduction in mean stomach fullness in February–March (Table 1) could be attributed to a depression in feeding activity due to low sea temperature. A similar seasonal reduction in stomach fullness for lobsters was found by Ennis (1973), but not by Carter & Steele (1982).

The same prey types tend to be found in the stomachs of juvenile lobsters as are encountered in adults; and, although the incidence of the various types may differ (Scarratt 1980, Carter & Steele 1982), diet variations related to lobster size are claimed to be minor (Weiss 1970). However, size-related phenomena could explain the relatively high importance of brachyuran crabs and gastropods in the diet of lobsters collected on the barrens in September 1979 compared to the reduced importance of the same diet categories for the smaller barren ground lobsters in July–August

1981. These changes in diet indicate that larger lobsters have a relatively wider range of food supplies available to them: the more open foraging mode adopted by larger lobsters (Lawton 1987) is commensurate with the pursuit of mobile prey such as crabs; similarly, their stronger chelae (Elner & Campbell 1981) would enable them to crush both a wider size range of invertebrates (Elner & Jamieson 1979, Elner 1980, Elner & Lavoie 1983) and more heavily armoured species, such as gastropods, than their smaller conspecifics.

The frequency of occurrence and volume of plant material in the lobster stomachs, even those from barrens, suggest that plants are not merely ingested coincidentally with invertebrate prey but, rather, are actively sought and form a functional nutritional component. Previous authors have found plant material in the natural diet of *Homarus americanus* (Herrick 1895, Weiss 1970, Ennis 1973, Scarratt 1980, Carter & Steele 1982) as well as in other decapod crustaceans (Elner 1981, Williams 1981, Joll & Phillips 1984). Indeed, seaweeds have been reported as the major food of various spider crabs (Hartnoll 1963) and a portunid *Liocarcinus puber* (Choy 1986). Syslo & Hughes (1981) determined that seaweeds can be substituted for more expensive animal protein in diets for cultured *H. americanus* and result in comparable growth. However, the mechanism by which seaweeds contribute to lobster growth and the role of plant material in natural diets remains to be elucidated. Discussion by Joll & Phillips (1984) on the possible significance of plant material in the diet of the western rock lobster *Panulirus cygnus*, as well as the additional possibility that coralline algae contributes to calcium requirements, may be of relevance to *H. americanus.*

In conclusion, we are in agreement with Livingstone (1985) on the need to encourage and develop food habit studies. Apart from being a valuable tool, in tandem with natural history observations, in elucidating ecosystem interactions, the data provide a base to understanding relationships between prey availability and predator production. Long-term field investigations of lobster growth and population dynamics are now necessary to definitively test the effects of habitat on lobster production. To fully understand the ecological mechanisms involved, future workers will also have to consider size-specific feeding aspects and relate the biomass, density, and size distribution of lobsters with the same parameters for the prey. Studies of west coast rock lobster *Jasus lalandii* off southern Africa have suggested that food availability is probably the most important factor limiting growth rate (Pollock & Beyers 1981). Natural diet data from juvenile western rock lobsters *Panulirus longipes cygnus* off southern Western Australia failed to support the

hypothesis of Chittleborough (1976) that food supply influences growth between sex/age-class groups but did indicate that diet was the cause of growth differences between 2 sites (Joll & Phillips 1984).

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