ATTRACTION TO AND SELECTION OF PREY BY IMMATURE LOBSTERS (HOMARUS AMERICANUS)

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ATTRACTION TO AND SELECTION OF PREY
BY IMMATURE LOBSTERS (HOMARUS AMERICANUS)

by

© John Andrew Carter, B.Sc.

A thesis submitted in partial fulfillment
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ABSTRACT

Little is known of the diet of immature lobsters (Homarus americanus). Attraction to and selection of prey by immature lobsters in Newfoundland were the subject of the present study.

The relative attractiveness of extracts of Asterias vulgaris, Cancer irroratus, Mytilus edulis, and Strongylocentrotus droebachiensis were determined by observing behaviour of immature lobsters. All extracts, except that of Asterias, were attractive to immature lobsters. Cancer was preferred over Mytilus and the two echinoderm species. Immature lobsters were subjected to metabolites of prey. Most lobsters showed alert phase behaviour, regardless of the quality of the stimulus. Cancer effluent was significantly more effective than controls in eliciting food-searching behaviour. Mytilus and Strongylocentrotus effluents were less effective stimulants.

The percentage responses of immature lobsters presented with ninhydrin-positive compound (NPC) targets were determined. Proline, ammonia, arginine, and lysine were the most attractive NPCs. The NPC compositions of effluents and extracts of various prey were determined. Extracts of Nereis sp. and Cancer irroratus had the highest total concentrations of NPCs (excluding urea, unknowns, polyamines, and trace amounts). Cancer had significantly higher concentrations of glutamine, proline, and taurine compared to Asterias and Strongylocentrotus. Effluents of Nereis and Cancer had higher levels of ammonia than those of three echinoderm and two mollusc species.

Selection of intact prey by immature lobsters given a choice was determined. Brittlestars and polychaetes were the most frequently attacked, followed by Cancer, Asterias, Mytilus, and Strongylocentrotus. Consumption of polychaetes by immature lobsters was generally complete. Substantially greater proportions of the other prey species were left unconsumed. Size, morphology, and behaviour of prey appeared to influence the attack rates.

The natural diet of immature lobsters was determined by gut content analysis. Sea urchins, mussels, and crabs were frequently consumed. Cancer was the dominant item in terms of volume of gut contents. Seasonal differences in feeding behaviour of immature lobsters were observed. Electivity indices indicated a high selection of crabs and mussels by immature lobsters.

It is very cautious and cunning, capturing its prey by stealth, and with weapons which it knows how to conceal. Lying hidden in a bunch of seaweed, in a crevice among the rocks or in its burrow in the mud, it waits until its victim is within reach of its claws before striking the fatal blow.

F. H. Herrick, 1895

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INTRODUCTION

The American lobster, Homarus americanus Milne-Edwards, is one of the most important invertebrate predators of the east coast of North America. It occurs in the inshore subtidal zone and on offshore banks from North Carolina to southern Labrador (Templeman, 1940). In the middle of this range (Maine, Nova Scotia, and Gulf of St. Lawrence), the lobster is subject to an important commercial fishery. In Newfoundland, apart from the west coast, small lobster fisheries are generally concentrated in Fortune Bay, Placentia Bay, Bonavista Bay, and Notre Dame Bay (Ennis, 1974).

Because of the commercial importance of the lobster, there has been a large number of studies on the animal since Herrick (1895) described its habits and development. Most have been concerned with fishery aspects, although studies of lobster feeding behaviour and habitat relationships are becoming increasingly common (Reddin, 1973; Breen, 1974; Breen and Mann, 1976; Evans, 1976; Evans and Mann, 1977; Mann, 1977; Hirtle and Mann, 1978).

Knowledge of the feeding habits of the lobster has been enhanced considerably in the last eighty years. Herrick (1895) described the lobster as cautious and cunning, sometimes capturing its prey by stealth, although he suggested that the lobster is basically a scavenger feeding on dead fish. Later analyses of gut contents dispelled the idea that lobsters are scavengers. Squires and Ennis (1968), Squires (1970), Weiss (1970), Miller et al. (1971), and Ennis (1973) demonstrated a wide range of invertebrate prey in lobster guts and suggested that lobsters probably take prey more or less in proportion to their natural availability. This assumption is an integral part of hypotheses of lobster - sea urchin - kelp associations in eastern Canada. These hypotheses implicate the lobster as a key predator of sea urchins and a possible ultimate control of kelp beds which are grazed by urchins (Mann and Breen, 1972; Breen, 1974; Breen and Mann, 1976; Mann, 1977).

Studies of prey selection by adult lobsters suggest that the nature of lobster predation is complicated by innate food preferences (Reddin, 1973; Evans, 1976; Evans and Mann, 1977; Hirtle and Mann, 1978). Lobsters generally show a preference for crabs and a smaller attraction to mussels and sea urchins. Evans (1976) suggested that the evidence for prey preference in adult lobsters may force a re-evaluation of hypotheses of lobster - sea urchin interactions in east coast kelp beds.

The mechanisms of food attraction in the lobster have been studied by various people. Early observations by Herrick (1895) and Hadley (1912) demonstrated the importance of olfaction in food detection. McLeese (1970, 1973c) determined the olfactory responses of adult lobsters to various solutions from prey species and implicated amino acids as compounds capable of eliciting food-searching behaviour. Ache (1972) and Shepheard (1974) observed that chemoreceptors in the lateral antennular filaments of lobsters respond electrophysiologically to a variety of amino acids and that prolonged discharge may be a possible mechanism of peripheral discrimination of specific amino acids (Ache, 1972).

The stereotyped food-searching behaviour or feeding response of adult lobsters has been described by McLeese (1970) and Atema and Engstrom (1971). Observation of feeding responses has been used to detect the effects of various pollutants on lobster behaviour (McLeese, 1973a; Atema and Stein, 1974).

Immature lobsters have never been studied in terms of their attraction to and selection of prey. Studies related to the potential culture of lobsters were concerned with the nutritional requirements and agonistic behaviour of juvenile lobsters (Castell et al., 1975, 1976; Mason, 1977; Logan and Epifanio, 1978; Zeitlin-Hale and Sastry, 1978). The lobsters used in these studies generally ranged from fifth to fourteenth stage (less than one year old). Because these young lobsters moult frequently in laboratory situations, their metabolism may be in a constant flux between moult and intermoult stages. They are not particularly suited to olfaction and prey selection experiments which require individuals in a stable intermoult stage.

Larger immature lobsters (one year old to maturity), which probably moult once or twice a year in Newfoundland waters (Templeman, 1940), are amenable to laboratory studies. They are small, requiring much less space than adult lobsters for holding stock populations, and remain in stable intermoult for relatively long periods.

Apart from the practical aspects of working on immature lobsters, these animals probably comprise a numerical majority of the natural lobster population, as the adults are susceptible to an intense fishery which may take up to 90% of the available legal-sized lobsters (Squires, 1970). Immature lobsters may have a considerable effect on the biota of the shallow subtidal zone in which they occur. As food is one of the most important ecological factors controlling marine organisms (Miller et al., 1971), the present study is concerned with the attraction to and selection of prey by immature lobsters.

Because the feeding behaviour of immature lobsters had not been studied before, the approach of this study was to look at problems at various levels where attraction to and selection of prey may occur, rather than concentrate on one particular aspect. In the final analysis of prey selection, the results of the various experiments are integrated to describe the nature of feeding in immature lobsters and several factors which mediate attraction to food and affect the selection of prey.

Specifically, the purpose of this study was to determine the relative attractiveness to immature lobsters of prey effluent, prey extracts, intact prey, and the chemical components which are characteristic of particular species. Selection of prey by immature lobsters was determined in the laboratory and the natural diet of immature lobsters from Placentia Bay was determined by gut content analysis. The results of the various experiments are discussed in terms of the premises of optimal foraging hypotheses (see Pyke et al., 1977 for review) and integrated with the present knowledge of feeding behaviour of adult lobsters and their habitat relationships.

MATERIALS AND METHODS

Collection and holding conditions

Immature lobsters were collected from Arnold's Cove, Grassy Point, and Spencer's Cove in Placentia Bay (Figure 1) by SCUBA divers licensed by Environment Canada. All lobsters were obtained from nearshore talus areas in depths of water ranging from 3 to 8 metres. They were transported in coolers to the Marine Sciences Research Laboratory at Logy Bay and allowed to acclimate at ambient temperatures before recording of individual wet weight, carapace length, and sex. During the period November 1975 to December 1976, 176 individuals were collected (see APPENDIX A). Seventy-three lobsters (1.5 g - 163.8 g; mean wet weight of 64.4 g) were kept in the laboratory for experimental purposes. The remainder (1.3 g - 275.4 g; mean wet weight of 85.1 g) were analysed for gut contents.

Lobsters were kept in individual compartments of a long tank (490 cm x 75 cm x 12 cm), the compartments separated by plastic mesh on wooden frames. Compartments were labelled to allow identification of individuals. Water at 12° C. ± 1° C. was supplied continuously from an overhead heated reservoir. When the long tank was filled to capacity, additional lobsters were kept in shallow fibreglass tanks supported by A-frames and continuously supplied with water at ambient temperature. Shelter for lobsters was provided by several rocks and a scallop valve in each compartment. Natural light was available from three windows on the north side of the laboratory.

Lobsters were fed every week a ration of fresh cod and pork liver equal to 6% of the individual's wet weight. McLeese (1972b) observed

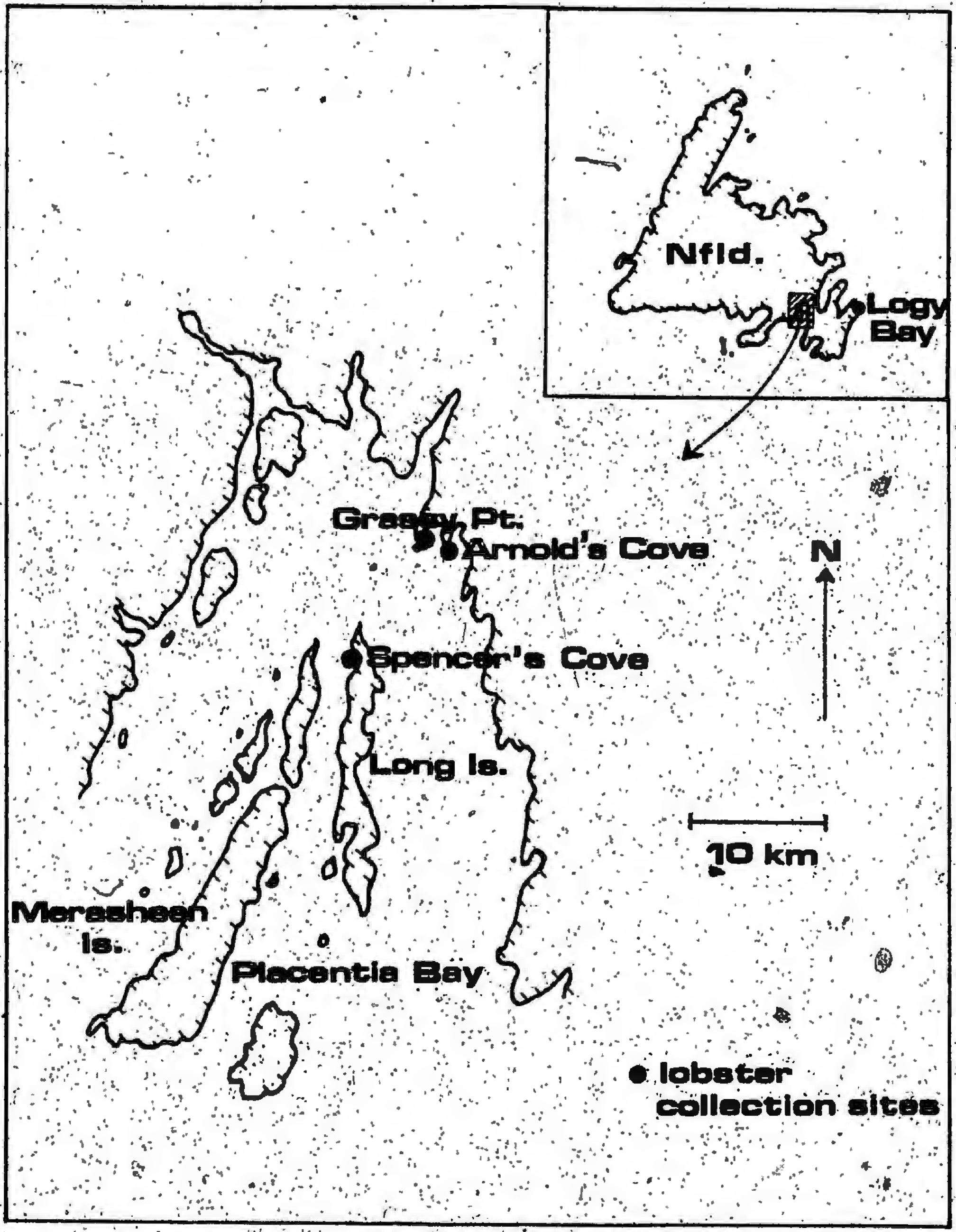

Figure 1. Placentia Bay collection sites of immature lobsters (H. americanus)

that feeding lobsters cod and liver at a rate of 6% of lobster weight per week supported healthy growth. If feeding of lobsters was delayed for any reason, the ration was adjusted accordingly to maintain the 6% feeding rate. Lobsters quickly consumed the food. Any excess was removed after two days. The tanks were periodically drained and cleaned to reduce diatom and algal fouling. The mortality rate of lobsters was approximately 10% throughout the duration of experiments, and was due mainly to cannibalism when a lobster entered another's compartment.

Prey organisms were required for many of the experiments. They were obtained by SCUBA divers while collecting lobsters and at other times from locations around the Avalon Peninsula. All prey organisms were maintained together at ambient temperature in shallow fibreglass tanks supplied with sand, rocks, and scallop valves. Densities were carefully maintained to prevent starvation of individuals.

Attraction to prey extracts

A wooden trough coated with epoxy resin (Figure 2), built approximately to the specifications of McLeese (1970), was used for all trials involving attraction of lobsters to prey extracts. The trough was 1.5 m long by 0.9 m wide with a water depth of 0.1 m. Water from the heated reservoir (12° C. ± 1° C.) was supplied to the upstream well at a rate of 3.3 l per minute. Dye tests indicated a current velocity of approximately 15 cm per minute from the upstream to the downstream baffle.

The floor of the trough was marked off into a grid of squares 10 cm by 10 cm to accommodate tracking of lobsters in the trough. A semicylinder of polyvinylchloride approximately 12 cm wide by 8 cm high was placed at right angles to the downstream baffle, in the mid-line of the trough. This shelter for the lobster was capable of telescoping such that

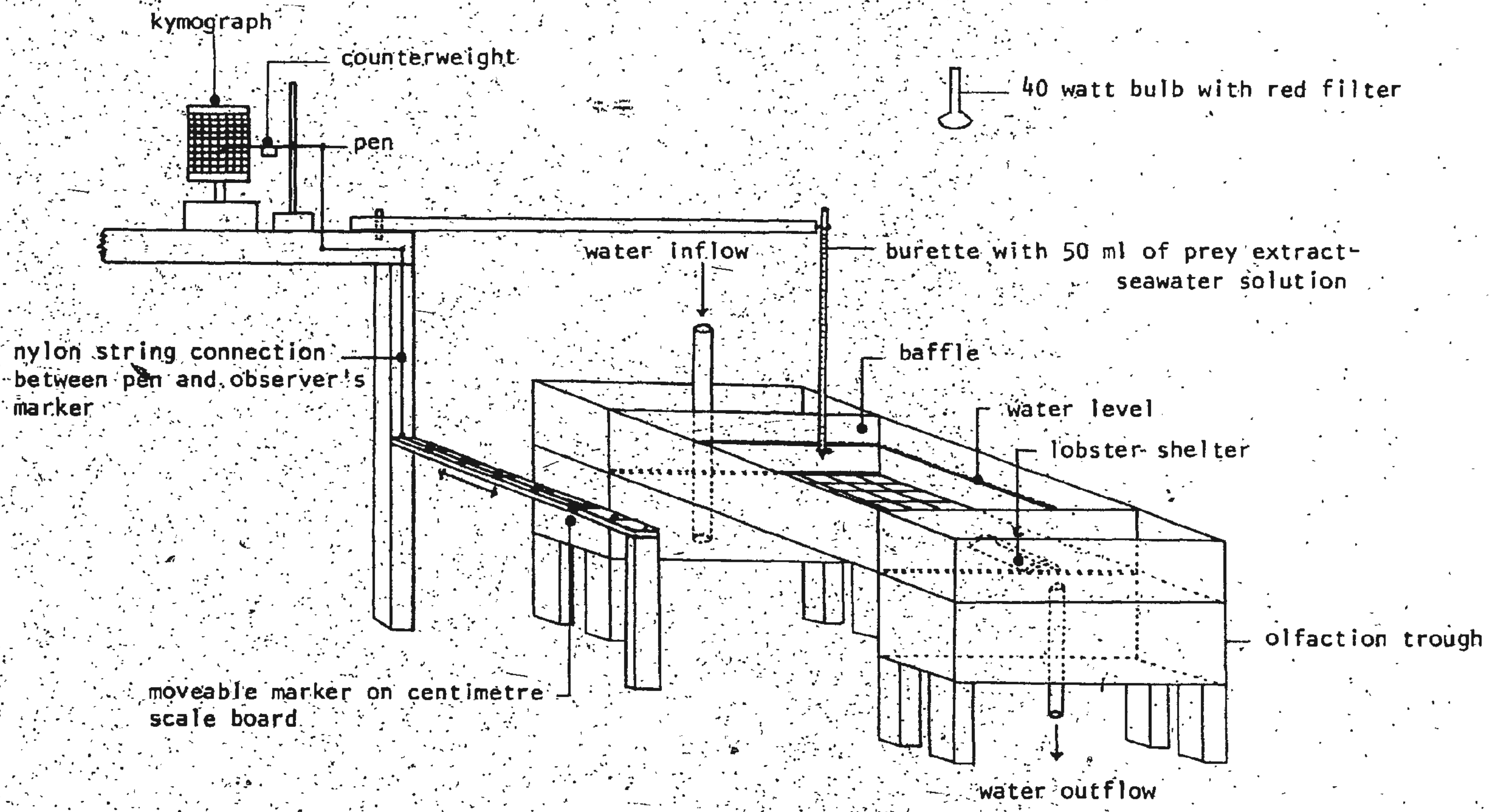

Figure 2. Schematic diagram (not to scale) of olfaction apparatus used to observe attraction of immature lobsters (H. americanus) to prey extracts.

the length of the semi-cylinder was twice the total length (excluding antennae) of the lobster.

The extract was applied to the trough from a burette hanging approximately 2 cm over the water surface at a distance of 70 cm from the proximal end of the lobster shelter. The burette was supported by a swinging rod which allowed maintenance of a 70 cm distance when the shelter length was changed.

Near the olfaction trough was a board (2 cm x 2 cm) secured to a tank frame. The board was scored with a scale marked at intervals of 2 cm, each 2 cm interval corresponding to 10 cm on the floor of the trough. A wooden marker fitted to the scale board was attached by nylon string through several eyescrews to a counterweighted kymograph pen (Figure 2). The kymograph was fitted with lined graph paper. Movement of the pen was calibrated such that a 2 cm movement of the marker would cause a pen deflection of 1 cm (i.e., 1 cm on the graph paper equaled 10 cm on the floor of the trough).

Movements of a lobster in the trough relative to the opening of the shelter were recorded by the observer by moving the marker on the scale board. The rostrum was the point of reference on the lobster. This produced a simultaneous recording (minus a very small lag due to observer reaction time) on the kymograph. The kymograph speed allowed 20 minute trials. The apparatus permitted simple, efficient recording of duration of lobster response and the number and lengths of exits from the shelter.

Prey extract - seawater solutions were prepared from healthy, well-fed prey organisms before each set of trials. Individuals of a size range naturally acceptable to lobsters were dried thoroughly with paper towels and crushed with a mortar and pestle into a reasonably uniform mixture of body fluids, tissue, and hard parts. The mixture was strained through a fine (1 mm) nylon mesh. The resultant prey extract was diluted to 10% by volume of a prey extract - seawater solution. Fifty ml of the 10% prey extract - seawater solution were applied by burette in each trial. The densities (weight per unit volume) of the prey extracts were determined on a Mettler electronic balance, and differed by no more than ± 1.5%. The water content of prey tissues was determined by drying one dozen each of Cancer, Mytilus, Strongylocentrotus, and Asterias to a stable weight in an oven at 100° C. The mean water contents of tissues ranged from approximately 55% for Mytilus with shell to approximately 70% for Cancer and the echinoderms.

Lobsters from the laboratory stock population after generally more than four days of food deprivation were tested in the olfaction trough for attraction to prey extract - seawater solutions of Asterias vulgaris, Cancer irroratus, Mytilus edulis, Strongylocentrotus droebachiensis, and a seawater control. Lobsters were allowed to acclimate to the trough and settle into the shelter for one hour at which time the extract was introduced to the trough and the kymograph turned on simultaneously.

The observer tracked the lobster for 20 minutes with movements of the scale board marker. Exits from the shelter were described as exploratory or food-searching behaviour, and noted as such on paper along with the time. Food-searching behaviour was recorded if the lobster showed vigorous motions of the maxillipeds, pereiopod scooping and lunging as it moved towards the stimulus source. These behavioural patterns have been clearly associated with food-searching (McLeese, 1970; Atema and Engstrom, 1971). Any locomotion of the lobster while not showing the above behaviour was classified as exploratory.

Preliminary trials indicated severe inhibition of lobster behaviour outside the shelter during daylight. Aluminum foil shields over the eyes of lobsters were tried (McLeese, 1970). Initial observations suggested that the shields caused erratic behaviour. Consequently, studies of attraction of immature lobsters to prey extracts and all subsequent experiments were conducted at night. The only artificial light source was a 40-watt bulb covered by a Kodak 1-A red filter hanging over the trough. Kennedy and Bruno (1961) noted that lobster vision is ineffective in the red wavelengths. With this arrangement, lobsters moved freely about the trough and were apparently not disturbed by movements of the observer. One or two lobsters were run in the trough each night. Each lobster was subjected to two or three extracts in random sequence, with forty minutes between each trial to allow the trough to flush adequately.

No lobsters were tested during their moulting periods or during the post-moult period when the natural diet appears to be calcium-rich (Weiss, 1970). Mytilus, Strongylocentrotus, and the seawater control were tested before the first moulting period of lobsters in the laboratory. Asterias and Cancer were tested with the same lobsters several months after the lobster moulting period, when these prey were more easily collected in the natural environment. In this case, the period of food deprivation of individual lobsters was the same as in the first set of trials, plus or minus one day. Ten other lobsters fed natural diets of Cancer, Mytilus, and Strongylocentrotus were tested in the fall of 1976. In all, twenty-nine lobsters (18 females and 11 males) of mean wet weight 51.8 g were tested, although not all lobsters were subjected to all prey extracts.

Several preliminary experiments indicated that individual variation in response was much smaller than population variation. The results were therefore analysed for significant differences by a paired comparison randomised block design, eliminating the effect on calculations of variance due to inherent population differences (Sokal and Rohlf, 1969).

Five response variables were analysed. These were: total duration of food-searching responses per trial; number of exits with food-searching behaviour per trial; mean maximum length of food-searching exits per trial; total duration of exploratory responses per trial; and integral of the food-searching response curve (determined with a Hruden planimeter by tracing the line of the curves (see Figure 3)). The last variable was a function of all other food-searching variables and gave an overall measure of lobster attraction to prey extracts.

Attraction to prey effluents

Individuals of <u>Cancer</u>, <u>Mytilus</u>, and <u>Strongylocentrotus</u> were maintained without food for 24 hours in tanks at 12^{0} C. with 20 ml of seawater per gram of organism wet weight to collect effluent with metabolites. All individuals had been well-fed and were of a size range naturally acceptable to immature lobsters. Individuals were carefully checked for injuries which might bias the amounts of metabolites in the seawater. At the end of the collection period the organisms were removed, the tank water was stirred and 100 ml of effluent for each trial were filtered to remove faeces.

Lobsters from the laboratory stock population, deprived of food for five days, were placed in fibreglass tanks with 1.5 l of sea-

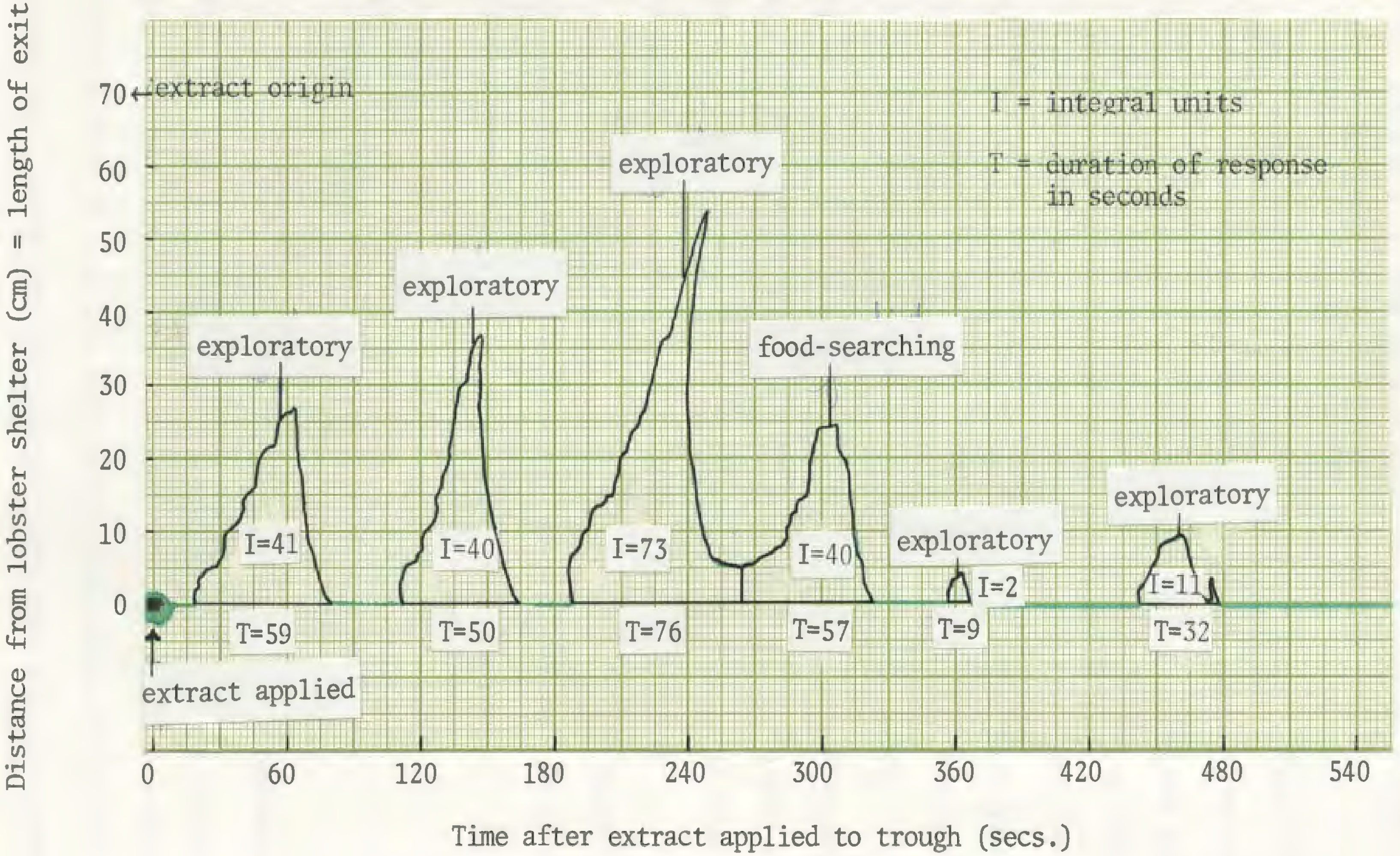

Figure 3. Portion of kymograph record of an immature lobster (H. americanus) responding to extract of Asterias.

water at 12° C. They were allowed to acclimate to the tanks for one hour. No shelter was provided.

A checklist of fifteen behaviour types (see Table 6, p. 33) which could possibly be elicited by prey effluents was made, based on previous observations and those of Atema and Engstrom (1971). One lobster was tested at a time. Prey effluent was poured very gently into the distal part of the tank, away from the corner in which the lobster had settled. Controls consisting only of seawater were applied in the same way. Behaviour types were checked off on the list as observed. At the end of five minutes the tank was drained, thoroughly rinsed and refilled with seawater. The lobster was allowed to settle for one hour before being tested again. Other lobsters were tested in the interim. Prey effluents were applied in random sequence. All tests were conducted at night.

Percentage frequencies of occurrence of behaviour types elicited by the prey effluents were tested for significant differences by G-tests of heterogeneity (Sokal and Rohlf, 1969).

Attraction to ninhydrin-positive compounds (NPCs)

The following amino acids and related compounds were obtained from Sigma Chemicals Limited, St. Louis, Missouri, U.S.A.: DL-alanine, L-arginine, L-asparagine, DL-aspartic acid, DL-glutamic acid, L-glutamine, glycine HCl, DL-leucine, DL-lysine, L-proline, DL-serine, taurine, and DL-valine. Ammonium chloride was obtained from the chemical stores of the Memorial University Biology Department.

Lobsters from the laboratory stock population, deprived of food for five days, were placed in shallow fibreglass tanks (40 cm x 30 cm x 10 cm) containing 5 l of seawater at 12° C. and allowed to acclimate for one hour. Each tank was numbered for identification of individual lobsters. Five or six lobsters were tested simultaneously in a single night.

Solutions of NPCs were prepared immediately prior to testing. The required amounts of crystals were weighed on an Oertling electronic balance. Crystals were poured into a 14.2 ml glass vial and 10 ml of distilled water added to produce a 1×10^{-1} M solution. Whatman #5 filter paper was rolled into a plug and placed in the vial to close the opening and act as a wick for the solution. One NPC target was prepared for each lobster. For DL amino acids, double the required amount of crystals was added to the vial to produce 1×10^{-1} M solutions of the L stereoisomers. D stereoisomers do not appear to be stimulatory to decapod crustaceans (Mackie, 1973). Aspartic acid, glutamic acid, and leucine were not totally dissolved. Vials containing the last three amino acids were stirred vigorously to produce a uniform mixture to accelerate dissolution in the test tanks. Solutions were not buffered as the minimum terminal concentration in the test tanks was presumed to be too low to cause pH changes. Changes of pH between 5 and 8 do not affect lobster response (Levandowsky and Hodgson, 1965).

Rubber gloves were worn throughout the preparation and application of the NPC targets as handsweat is potentially stimulatory to invertebrates (Zafiriou, 1972). NPC targets were gently placed in the corner of the tank opposite to that in which the lobster had settled. The possible minimum terminal NPC concentration in the tanks was 2×10^{-4} M.

Lobsters were observed for ten minutes. The time to seizure of the target was noted. Seizure was defined as grasping of the target with the maxillipeds. At the end of the trial the tanks were drained, rinsed and refilled with seawater. The lobsters were allowed to rest for a half hour before the next trial. All lobsters were eventually subjected to all NPCs and a seawater control. The sequence of testing was randomised each night.

Differences between percentage frequencies of NPC target seizure and control target seizure were tested for significance by Cochran's Q-test (Sokal and Rohlf, 1969).

Analysis of NPCs in prey tissue extracts and effluents

Prey tissue extracts were collected from _Asterias vulgaris_, _Cancer irroratus_, _Littorina littorea_, _Mytilus edulis_, _Nereis_ sp., _Ophiopholis aculeata_, and _Strongylocentrotus droebachiensis_ using methods described previously. Only healthy, well-fed individuals of a size susceptible to immature lobster predation were used. With _Littorina_, _Nereis_, and _Ophiopholis_, eight individuals of each genus were pooled to produce one sample of tissue extract.

Tissue extracts were centrifuged (6500 g, 4° C., 60 minutes) to remove particulate matter. For each sample, a 0.5 ml aliquot of supernatant was deproteinised by adding 30 mg of sulphosalicylic acid, and centrifugation (6500 g, 4° C., 20 minutes). The volume of the supernatant was adjusted to 2.0 ml using a 0.2 M sodium citrate buffer (pH 2.2), then analysed with a Beckman Spinco automatic amino acid analyser (Model 121) equipped for physiological analysis. Polyamine analyses were made in a similar manner except that a column containing Beckman polystyrene resin (Beckman PA-35) and two eluting concentrations of sodium citrate buffer (0.35 and 2.35 M sodium, pH 5.2) were used.

Prey effluent was collected by allowing individuals to remain in separate tanks with 7 ml of seawater per gram wet weight of individual for eight hours at 12° C. The prey were removed and the seawater - prey effluent stirred vigorously. Five ml aliquots were collected and analysed by the procedure described above. Seawater controls were also analysed.

Significant differences between individual NPC concentrations of each prey were determined by confidence interval analysis (Natrella, 1972).

Controlled prey selection

Prey selection by immature lobsters was observed by placing one each of various prey species (Asterias vulgaris, Cancer irroratus, Harmothoe sp., Littorina littorea, Mytilus edulis, Nereis sp., Ophiopholis aculeata, and Strongylocentrotus droebachiensis) in fibreglass tanks with approximately 3 l of seawater at 8° C. Prey were weighed before being placed in the tank. A rock and a scallop valve furnished shelter for the prey organisms. Air was supplied via an airstone. To each tank was added an immature lobster deprived of food for five days. The tanks were left undisturbed for 24 hours at which time observations were made.

Combinations of prey were arranged such that lobsters had a choice of at least four species. Nereis sp. and Harmothoe sp. were never offered simultaneously. On the few occasions when Cancer was offered simultaneously with a polychaete or Ophiopholis, the Cancer individuals were presumed to be too small to inflict damage on the other prey species.

In combinations with Asterias, no predation by Asterias was observed. In any case, to minimise prey interaction, all individuals were well-fed and presumably satiated. To prevent escape of prey, the water level was never beyond the reach of the claws of the lobsters. Approximately 20 lobsters were used in these experiments with replication of three or four trials per lobster. Prey organisms were of a size thought to be susceptible to predation by the lobster in each tank. They were collected at random from various locations in Placentia Bay and around the Avalon Peninsula and to some extent reflected sizes naturally available to lobster populations.

Percentage frequencies of attack of each prey were noted for all trials. Attack was defined as any visible injury to prey. The amount of individual prey presumably consumed was recorded by subtracting the weight of the remains from the original wet weight of the organism. Significant differences between percentage frequencies of attack were determined by G-tests of independence (Sokal and Rohlf, 1969). Differences between consumption rates and consumption efficiencies for each prey were analysed by Student-Newman-Keuls multiple comparison tests (Sokal and Rohlf, 1969). Confidence interval analysis (Natrella, 1972) was used to determine effects of prey size on attack rates.

Gut content analysis

Between June 4 and November 25, 1976, 103 immature lobsters were collected by SCUBA divers from three Placentia Bay collection sites (Figure 1, p.6). Lobsters were collected in the morning to reduce the influence of digestion on gut contents from feeding the night before.

collection. They were transported to the laboratory in coolers with freezer packs. In the laboratory, lobsters were weighed, measured, sex was determined, and two pleopods were clipped for moult stage determination (Aiken, 1973).

Lobsters were killed by severing the body behind the carapace. The thorax with gut intact was stored in 70% alcohol for later analysis. Guts were excised by dissection. The oesophagus was cut midway between the mouth and the cardiac stomach and the intestine cut immediately behind the pyloric stomach. Gastroliths were scraped off the gut walls if necessary. Wet weight of gut and contents was determined on a Mettler electronic balance. Gut fullness was visually estimated according to a scale of 0 to 4 (empty to full). The gut was then cut open and the contents flushed into a Petri dish. Wet weight of the empty gut was determined after it had been patted with a paper towel.

The gut contents were flooded with distilled water and observed under a dissecting microscope at 20x magnification. As much as possible, all particles were identified and pushed to the periphery of the dish. The dominant species was recorded, based on a visual estimate of relative volume. The percentage contribution of individual taxa to the total volume of gut contents was estimated in each case. All samples were observed twice to minimise errors of omission. The distilled water was drained and the contents allowed to dry by evaporation. Dry weight of contents was determined on the Mettler balance. Dry volume was determined by pouring the contents into a 10 ml cylinder and shaking vigorously to allow even settlement of the contents.

Identification of prey hard parts was confirmed by reference to various texts of invertebrate zoology and previous studies of lobster gut contents (Miner, 1950; Weiss, 1970; Meglitsch, 1972). To assist in identification of hard parts, many invertebrate species were dried, broken apart, and examined under a dissecting microscope prior to gut content analysis.

To determine the residency in the lobster gut of hard parts from natural prey consumed prior to capture, several immature lobsters were maintained in the laboratory on a diet of cod and pork liver, both of which leave no visible parts in the gut. After various periods (two to 180 days) the contents of guts of these lobsters were examined.

To estimate rate of clearance of gut contents, 14 lobsters were maintained at 8° C. and fed ad libitum diets of either Cancer irroratus, Mytilus edulis, or Strongylocentrotus droebachiensis. After periods ranging from one to eight days, the gut contents were observed and various measures of stomach fullness recorded.

Significant differences between percentage frequencies of occurrence of gut items in summer, late summer, and fall were determined by G-tests of independence (Sokal and Rohlf, 1969). The various measures of gut fullness were analysed by Model 1 analysis of variance (Sokal and Rohlf, 1969).

Prey density in Placentia Bay

During the period of collection of lobsters for gut content analysis, prey density was observed in Arnold's Cove, Grassy Point, and Spencer's Cove (Figure 1, p.6). A square metre quadrat was dropped at random to the bottom (3-8 m depths) in the collection areas by a SCUBA diver. All organisms which were readily visible to the diver (not under rocks) were counted. Approximately eight quadrats were completed in each of the three locations. As there were very few differences in prey densities between the three collection areas, the results were pooled to provide a mean organism density in the collection areas in late summer and fall.

RESULTS

Attraction to prey extracts

There were two general types of behaviour elicited by stimuli in the olfaction trough. The first, exploratory behaviour, was shown by all lobsters regardless of the quality of the stimulus. This behaviour was characterised by quick, nondirectional walking on the pereiopod tips with the antennae held in front of the lobster at an angle of approximately 120° to one another. Quite often the antennae were rubbed against the trough floor and walls (Figure 4a). During exploratory forays the flicking rate of antennules was relatively constant. Occasional movement of the third maxillipeds was observed. Scaphognathite fanning rate was relatively constant.

Exploratory behaviour was especially common within a half hour of a lobster being placed in the trough. Repeated observations indicated that this behaviour diminished considerably after a half hour. By this time lobsters generally had settled into the shelter and rarely left except when a stimulus was introduced to the trough. After one hour in the trough, lobsters were able to find and enter the shelter after exploratory forays, regardless of the light conditions.

Food-searching behaviour, elicited by all prey extracts to some extent, was quite distinct from exploratory behaviour. Once the lobster had detected the stimulus, the antennae were usually directed in front of the lobster, at an angle of less than approximately 40° to one another. The lobster assumed a position close to the trough floor and scooping of the first and second pereiopods was obvious (Figure 4b). The third max-

Figure 4a. Typical attitude of an immature lobster (H. americanus) during an exploratory foray. (x 1)

Figure 4b. Typical attitude of an immature lobster (H. americanus) showing food-searching behaviour. (x 1)
Note that the antennae are not drawn together because of the resistance of the tank wall. Pereiopods and claws are drawn into the mouth region.

4a

4b

illipeds were frequently folded into the mouth region. Flicking rate of antennules and fanning rate of scaphognathites were accelerated. The lobster proceeded towards the stimulus origin with very sudden forward movements and occasional lunges at the stimulus. This was in contrast to the fluid motion of lobsters during exploratory forays. On a few occasions the claws were raised and sometimes opened.

All prey extracts, except that of Asterias, were attractive to immature lobsters, in terms of food-searching response, relative to the control. Results are recorded in Table 1. F values of the paired comparison tests are noted in Table 2. Extracts of Cancer elicited the greatest attraction from immature lobsters, the mean integral of food-searching response curves being more than twice as great as that for Mytilus extract trials. Asterias and Strongylocentrotus extracts were relatively unattractive. Seawater controls elicited few food-searching responses. Differences between Cancer integrals and those for Asterias and Strongylocentrotus were very significant (Table 2). The difference between the Mytilus integral and that for Strongylocentrotus was significant. Integral values for all prey extracts, with the exception of Asterias, were highly significantly different from the control integrals.

The other three food-searching response variables (Table 1) showed a similar trend, with the Cancer values highest, Mytilus values somewhat lower, and the values for the echinoderm species generally lowest. For most of these variables, differences between Cancer values and others were significant. Values for the control were significantly lower than those for all prey extracts excluding Asterias.

Durations of exploratory responses were greatest in the control trials (Table 1), although only the difference between the control

Table 1. Responses of immature lobsters (*H. americanus*) to prey extracts (mean ± standard error).

Prey extracts	Integral of food-searching response curves per trial (planimeter units)	Total duration of food-searching responses per trial (seconds)	Number of exits per trial with food-searching response	Mean maximum length of food-searching exits per trial (cm)[a]	Total duration of exploratory responses per trial (seconds)
Cancer	401 ± 135 (n=25)	155 ± 36 (n=25)	2.8 ± 0.6 (n=25)	48 ± 5 (n=23)	395 ± 61 (n=25)
Mytilus	171 ± 53 (n=25)	117 ± 25 (n=25)	2.6 ± 0.5 (n=25)	35 ± 5 (n=20)	349 ± 89 (n=25)
Strongylocentrotus	117 ± 43 (n=26)	96 ± 27 (n=26)	1.7 ± 0.5 (n=26)	27 ± 5 (n=14)	244 ± 69 (n=26)
Asterias	67 ± 24 (n=15)	66 ± 16 (n=15)	1.9 ± 0.4 (n=15)	36 ± 6 (n=10)	298 ± 71 (n=15)
Control	23 ± 13 (n=26)	23 ± 13 (n=26)	0.4 ± 0.2 (n=26)	46 ± 10 (n=4)	447 ± 82 (n=26)

[a] based only on trials in which food-searching responses were detected

Table 2. Paired comparison F values for responses of immature lobsters (*H. americanus*) to prey extracts.

Prey extract: Paired comparison	Integral of food-searching response curves	Total duration of food-searching responses	Number of exits with food-searching response	Mean maximum length of food-searching exits	Total duration of exploratory responses
Cancer: *Mytilus*	3.146 (22)[a]	1.366 (22)	0.485 (22)	6.837 (15)*	1.979 (22)
Cancer: *Strongylocentrotus*	11.056 (22)**	6.761 (22)*	4.581 (22)	11.325 (10)*	5.371 (22)
Cancer: *Asterias*	12.632 (15)**	7.770 (15)*	5.146 (15)	2.231 (10)	0.526 (15)
Cancer: Control	29.235 (22)***	27.331 (22)***	17.590 (22)***	--[b]	0.014 (22)
Mytilus: *Strongylocentrotus*	6.727 (25)*	5.666 (25)	5.721 (25)*	0.136 (12)	1.536 (25)
Mytilus: *Asterias*	4.027 (12)	4.641 (12)	4.111 (12)	2.357 (6)	0.683 (12)
Mytilus: Control	36.079 (25)***	38.561 (25)***	33.061 (25)***	--	4.126 (25)
Strongylocentrotus: *Asterias*	0.629 (12)	0.814 (12)	0.844 (12)	1.487 (5)	1.396 (12)
Strongylocentrotus: Control	14.926 (26)***	17.156 (26)***	14.682 (26)***	--	6.524 (26)*
Asterias: Control	1.078 (12)	1.235 (12)	1.254 (12)	--	0.177 (12)

[a] number of paired comparisons

[b] significance not tested because of small number of food-searching exits in the control trials

* significant at $p < 0.05$; ** significant at $p < 0.01$; *** significant at $p < 0.001$

and Strongylocentrotus values was significant. The Cancer value was slightly greater than the Mytilus value. The latter was greater than either of the two echinoderm values.

The percentages of trials in which food-searching responses were elicited by the stimulus are noted in Table 3. The percentage was highest for Cancer, followed by Mytilus and the two echinoderm species. Very few trials with seawater control elicited a food-searching response in lobsters. Significant differences determined by STP G-tests are noted in Table 3.

The percentages of immature lobsters showing food-searching behaviour at the stimulus origin (70 cm from the lobster shelter) are noted in Table 4. Cancer extract elicited the highest percentage, followed by Mytilus, Asterias, and Strongylocentrotus. Only two lobsters showed food-searching behaviour at the stimulus origin during seawater control trials. Only the Cancer value was significantly greater than the control value.

An indication of preference was determined by comparing the integrals of food-searching responses for 22 immature lobsters, each of which had been subjected to extracts of Cancer, Mytilus, Strongylocentrotus, and a seawater control. There were too few trials with Asterias extract to allow comparison. The indication of preference was based on the assumption that, in nature, the greater length and duration of food-searching exits reflect greater motivation to attack and consume prey. The comparison (Table 5) indicates a significant preference for Cancer extract over other extracts, two-thirds of the lobsters showing greater integral values for Cancer extract than for other extracts. Only one-fifth of the lobsters preferred Mytilus extract over others. Strong-

Table 3. Percentage of immature lobsters (H. *americanus*) exhibiting food-searching response to prey extracts.

Prey extract	Percentage	Total number of trials
Cancer	92.0 a,s,cl[a] (23)[b]	25
Mytilus	80.0 a,cl (20)	25
Asterias	66.7 s,cl (10)	15
Strongylocentrotus	53.8 (14)	26
Seawater control	15.4 (4)	26

[a] significantly greater than:
a - *Asterias*
s - *Strongylocentrotus*
cl - control

[b] absolute number of lobsters responding

$p < 0.05$

Table 4. Percentage of immature lobsters (*H. americanus*) moving to and exhibiting food-searching response at the stimulus origin.

Prey extract	Percentage	Total number of trials
Cancer	52.0[a] (13)[b]	25
Mytilus	28.0 (7)	25
Asterias	20.0 (3)	15
Strongylocentrotus	19.2 (5)	26
Seawater control	7.7 (2)	26

[a] significantly greater than control, $p < 0.05$

[b] absolute number of lobsters responding at the stimulus origin

Table 5. Percentage of immature lobsters (*H. americanus*) in which prey extracts elicited the greatest food-searching response (integral of food-searching response curves, n=22).[a]

Prey extract	Percentage
Cancer	68.2 m,s,cl[b] (15)[c]
Mytilus	22.7 (5)
Strongylocentrotus	4.5 (1)
Seawater control	4.5 (1)

[a] each lobster was offered all extracts in random sequence; *Asterias* extract was excluded from the table because of small sample size

[b] significantly greater than:
m - *Mytilus*
s - *Strongylocentrotus*
cl - control
$p < 0.05$

[c] absolute number of lobsters showing greatest response to specific prey extract

ylocentrotus extract was rarely preferred.

Attraction to prey effluents

At least fifteen behaviour types were observed in immature lobsters subjected to effluents of various prey species (Table 6). These are noted below with a brief description of each.

Increased antennule flicking rate was observed in most lobsters immediately upon entry of the stimulus. Percentage frequency of occurrence of this behaviour was highest for control trials and lowest for trials with Strongylocentrotus effluent (Table 6). Percentage frequencies of occurrence of anchoring and raking of pereiopods, movements which tended to keep the lobster in the tank corner, were approximately equal for trials with prey effluents and greater for trials with controls. There was little difference between effluents in percentage frequencies of occurrence of directional antennule movement. This behaviour was characterised as a dipping of the antennules towards the source of the stimulus and was frequently observed immediately after the stimulus had been applied to the tank.

For behaviour such as wiping of antennules and antennae with the mouthparts, walking approach to the stimulus source, flexing of maxillipeds, and raising of the body, percentage frequencies of occurrence for control trials were generally substantially lower than for trials with prey effluents.

Several behaviour types were not observed during control trials. These were directional movement of antennae (i.e., pointing towards stimulus source), rapid lunging approach to the stimulus source, retreat,

Table 6. Percentage of immature lobsters (*H. americanus*) showing types of behaviour elicited by prey effluents.

Behaviour types	Prey effluents *Cancer* (n=30)	 *Mytilus* (n=30)	 *Strongylocentrotus* (n=30)	 Seawater control (n=15)
alert phase behaviour				
increased antennule flicking rate	53.3	53.3	30.0	60.0
raking of pereiopods	40.0	30.0	36.7	60.0
wiping of antennules and antennae	30.0	16.7	30.0	13.3
directional movement of antennae	26.7	20.0	20.0	0
directional movement of antennules	20.0	10.0	23.3	13.3
food-searching behaviour				
flexing of maxillipeds	46.7*	36.7	40.0	6.7
scooping of pereiopods	26.7*	26.7*	13.3	0
walking approach	43.3*	16.7	40.0	13.3
rapid lunging approach	13.3*	0	3.3	0
snapping and seizing with claws	23.3*	3.3	6.7	0
miscellaneous behaviour				
anchoring of pereiopods	43.3	53.3	53.3	80.0
body raised	23.3	13.3	16.7	6.7
claws raised	13.3	6.7	3.3	0
active turning	6.7	10.0	3.3	0
retreat	23.3*	3.3	10.0	0

* significantly greater than control, $p < 0.05$

active turning (constant changing of position in the tank corner), scooping of pereiopods in the mouth region, raising of claws, and snapping and seizing with claws. With the exception of active turning, percentage frequencies of occurrence of these behaviour types were highest for Cancer effluent trials. There were small differences between trials with Strongylocentrotus and Mytilus effluent in percentage frequencies of occurrence of behaviour types.

For trials with Cancer and Mytilus effluents, percentage frequencies of occurrence of scooping of pereiopods, a behaviour type characteristic of food-searching, were significantly greater than for control trials.

Walking approach, rapid lunging approach, retreat, flexing of maxillipeds, and snapping and seizing with the claws were all significantly more frequent in trials with Cancer effluent compared to controls.

Attraction to ninhydrin-positive compounds (NPCs)

Percentage frequencies of response (target capture) of immature lobsters to various NPCs are noted in Table 7. Proline was the most attractive NPC, followed by ammonia, arginine, lysine, alanine, glycine, and valine, all of which produced percentage frequencies of response significantly greater than seawater controls. All other NPCs were attractive to a lesser degree. Seawater controls elicited responses in 13% of the trials.

Almost all responses to NPCs were characterised by directed movement to the target and vigorous food-searching behaviour, lobsters grasping the lip of the target with the maxillipeds. The filter paper plug was jammed in the vial to prevent ingestion by lobsters. On some

Table 7. Percentage frequency of NPC target captures by immature lobsters (H. americanus) (n=23).

NPC	Percentage frequency of capture	Mean response time in seconds (± S.E.)
proline	56.5**	307 ± 46 (13)[a]
ammonia	52.2**	344 ± 47 (12)
arginine	47.8**	257 ± 51 (11)
lysine	47.8**	286 ± 57 (11)
alanine	43.5*	294 ± 64 (10)
glycine	43.5*	296 ± 47 (10)
valine	43.5*	277 ± 66 (10)
asparagine	39.1	266 ± 58 (9)
glutamic acid	39.1	321 ± 60 (9)
glutamine	39.1	361 ± 56 (9)
leucine	34.8	286 ± 56 (8)
serine	34.8	306 ± 61 (8)
aspartic acid	30.4	278 ± 56 (7)
taurine	30.4	290 ± 80 (7)
seawater control	13.0	304 ± 153 (3)

[a] sample size

** significantly greater than control at $p < 0.01$

* significantly greater than control at $p < 0.05$

occasions, the targets were abandoned and attacked several times.

Mean time to target capture ranged from 257 seconds for arginine to 361 seconds for glutamine. Mean time to target capture for all NPCs was 298 seconds. There was no apparent correlation between the percentage frequency of response and the mean time to target capture, indicating that a ten-minute observation period did not bias results by excluding responses to NPCs with slow diffusion rates or low solubilities.

Analysis of NPCs in prey tissue extracts and effluents

Results of NPC analysis of prey tissue extracts are noted in Table 8 (see APPENDIX B for additional details). A total of 43 NPCs were detected. Urea contributed a large and very variable amount, depending on the species, to the free NPC pool. Apart from urea, the most concentrated NPCs generally were glycine, ammonia, taurine, alanine, glutamic acid, valine, leucine, and proline.

The highest total NPC concentrations (excluding urea, unknowns, trace amounts, and polyamines) were detected in extracts of Nereis sp. and Cancer irroratus. Moderate levels were recorded for extracts of Littorina littorea and Ophiopholis aculeata. Lowest concentrations were observed in Mytilus edulis, Strongylocentrotus droebachiensis, and Asterias vulgaris.

The most concentrated NPC (excluding urea) in the echinoderms Asterias and Strongylocentrotus was glycine. Ammonia, taurine, and alanine contributed the next highest proportions to the total concentration of free NPCs in these echinoderms. In Ophiopholis tissue, the most concentrated NPCs were taurine, glycine, and ammonia. Littorina tissue had

Table 8. Mean concentrations of free ninhydrin-positive compounds (NPCs) (excluding urea, unknowns, trace amounts, and polyamines) of prey tissue extracts as a percentage of the total NPC concentration.[a]

NPC	*Asterias* (n=3)	*Ophiopholis* (n=1)[b]	*Strongylocentrotus* (n=4)	*Littorina* (n=1)[b]	*Mytilus* (n=4)	*Nereis* (n=1)[b]	*Cancer* (n=4)
alanine	3.1	1.2	7.1	6.8	6.8	10.1	9.0
ammonia	5.9	11.0	6.3	15.0	8.3	22.8	10.0
arginine	1.5	0.1	4.0	1.3	1.0	<0.1	5.2
asparagine	0.2	0.2	0.5	-[c]	0.8	unresolved	1.0
aspartic acid	0.9	0.2	0.8	0.7	4.7	<0.1	1.2
glutamic acid	1.2	1.0	2.6	12.6	4.5	3.9	5.0 a[d]
glutamine	0.3	0.1	1.2	7.3	1.6 a	1.9	2.9 a,s,m
glycine	70.1	37.3	53.3	3.3	29.1	16.8	15.8
leucine	1.2	0.1	2.1	1.7	0.9	7.4	5.4
lysine	0.7	0.4	2.8	0.3	2.3	2.2	4.9
proline	0.1	trace	0.4	12.2	1.5	2.0	5.6 a,s
serine	2.3	0.2	1.7	3.5	2.9	0.2	2.2
taurine	3.5	45.2	3.7	6.5	26.2	0.2	9.4 a,s
valine	1.5	0.2	2.6	5.5	0.8	7.0	4.6
other NPCs[a]	7.5	2.7	10.8	23.2	8.7	25.4	17.8
total concentration[e]	21.394	96.786	26.409	106.774	39.495	286.651	225.626

[a] see APPENDIX B for absolute concentrations of NPCs in prey tissue extracts

[b] one sample from eight individuals [c] not detected

[d] absolute concentration significantly greater than: a - *Asterias*; s - *Strongylocentrotus*; m - *Mytilus* $p < 0.05$

[e] µmoles/ml

high concentrations of ammonia, glutamic acid, and proline. The most concentrated NPCs in Mytilus were glycine, taurine, ammonia, and alanine. In Nereis tissue, high concentrations of ammonia, glycine, alanine, leucine, and valine were observed. The most concentrated free NPCs (excluding urea) of Cancer tissue were glycine, ammonia, taurine, alanine, and proline.

Few significant differences between individual NPC concentrations were observed because of small sample sizes. Glutamine concentration was significantly higher in Cancer extract than in extracts of Asterias, Mytilus, and Strongylocentrotus. Proline and taurine concentrations were significantly higher in Cancer extract than in Asterias and Strongylocentrotus extracts. Glutamic acid concentration was significantly higher in Cancer extract than in Asterias extract. Glutamine and urea were significantly more concentrated in Mytilus extract than in extract of Asterias.

Polyamines contributed a very small amount to the total free NPC pool of extracts. Concentrations were highest in extracts of Littorina, Strongylocentrotus, and Cancer, and lowest in Asterias and Mytilus extracts.

The common NPC in prey effluents was ammonia (Table 9). Highest concentrations were recorded for Nereis sp. and Cancer irroratus. Ammonia concentration was moderate for Asterias effluent and low for Ophiopholis, Littorina, Strongylocentrotus, and Mytilus. Only trace amounts of ammonia were detected in seawater controls.

Asterias was the only prey species to produce detectable amounts of NPCs other than ammonia in effluent. A relatively high concentration of glycine was detected compared to very low concentrations of alanine,

Table 9. Mean ninhydrin-positive compound (NPC) concentrations (μmoles/ml) of prey effluents in seawater.

NPC	*Asterias* (n=2)	*Ophiopholis* (n=1)[a]	*Strongylocentrotus* (n=2)	*Littorina* (n=1)[a]	*Mytilus* (n=2)	*Nereis* (n=1)[a]	*Cancer* (n=2)	Seawater control (n=2)
alanine	0.002	-[b]	-	-	-	-	-	-
ammonia	0.110	0.065	0.047	0.050	0.042	0.199	0.191	trace
glycine	0.121	-	-	-	-	-	-	-
histidine	0.002	-	-	-	-	-	-	-
lysine	trace	-	-	-	-	-	-	-

[a] one sample from eight individuals
[b] not detected

histidine, and lysine.

Controlled prey selection

Percentage frequencies of attack were greatest for Ophiopholis aculeata, Nereis sp., and Harmothoe sp. (Table 10). These prey were attacked significantly more often than either Strongylocentrotus droebachiensis or Littorina littorea. Moderate percentage frequencies of attack were recorded for Cancer irroratus, Asterias vulgaris, Mytilus edulis, and Strongylocentrotus droebachiensis and were significantly greater than for Littorina which was never attacked.

For all trials, the mean presumed rate of consumption of food by immature lobsters per trial was 4.69% (± 0.41%) of lobster wet weight. Ratios of weight of prey residue to the wet weight of attacked prey are noted in Table 11. Consumption of Harmothoe was apparently complete. In one trial, a few scales comprising a negligible amount of the whole mass of the worm were not ingested. Presumed consumption of attacked Nereis was comparable. Ratios of prey residue to amount attacked for the polychaetes were significantly smaller than values for all other attacked species. The ratio for Ophiopholis was significantly smaller than ratios for Strongylocentrotus and Cancer, both of which were above 0.50. Ratios of prey residue to amount attacked for Mytilus and Asterias were intermediate between Ophiopholis and Strongylocentrotus. Despite the apparently low percentage consumption of Cancer, the mean amount presumably consumed per attack was substantially greater than such values for all other prey.

Consumption efficiencies (ratios of amount of prey presumably

Table 10. Percentage frequency of attack of various prey organisms by immature lobsters (H. americanus).

Prey organism[a]	Mean wet weight of offered prey (g)	n	Percentage attacked[b]
Ophiopholis	1.4	46	78.3 1,s[c]
Nereis	0.7	32	75.0 1,s
Harmothoe	0.5	14	71.4 1,s
Cancer	14.0	32	65.6 1
Asterias	7.4	39	61.5 1
Mytilus	2.9	70	48.6 1
Strongylocentrotus	4.1	71	32.4 1
Littorina	5.3	46	0

[a] offered simultaneously with various other prey organisms
[b] attack is defined as visible physical injury to prey organism
[c] significantly greater than: 1 - Littorina
s - Strongylocentrotus

$p < 0.05$

Table 11. Ratios of weight of prey residues (unconsumed) to wet weight of prey attacked by immature lobsters (H. americanus).

Prey organism	Number attacked	Ratio[a]	Mean presumed consumption per attack (g)
Harmothoe	10	0.0 ± 0 a,c,m,o,s[b]	0.5
Nereis	24	0.021 ± 0 a,c,m,o,s	0.8
Ophiopholis	36	0.307 ± 0.029 c,s	1.0
Mytilus	34	0.407 ± 0.016	1.4
Asterias	24	0.434 ± 0.061	2.0
Strongylocentrotus	23	0.528 ± 0.056	1.8
Cancer	21	0.590 ± 0.102	3.6

[a] mean ± standard error

[b] significantly smaller than:
a - Asterias
c - Cancer
m - Mytilus
o - Ophiopholis
s - Strongylocentrotus

$p < 0.05$

consumed to amount offered) are noted in Table 12. Highest values were recorded for Nereis and Harmothoe, the former being significantly greater than values for all other species offered, with the exception of Harmothoe, and the latter significantly greater than values for all species except Nereis and Ophiopholis. Consumption efficiency was considerably lower for Ophiopholis compared to polychaetes, although significantly greater than values for all species with lower efficiencies. Consumption efficiency was very low for Strongylocentrotus. Despite relatively low efficiencies for Asterias and Cancer, the mean amounts of these larger species presumably consumed per trial were relatively high (Table 12).

Attacked and ignored prey individuals were classified according to percentage of lobster wet weight to obtain an indication of prey size influence on attack rate (Table 13). Lobsters attacked individuals (Cancer) up to at least 17.69% of their own mass and as small as 0.91% (Nereis). There was a significant difference in mean size between the small size class of ignored Cancer individuals and the class of attacked Cancer individuals. There were significant differences in mean sizes between the large size classes of ignored individuals of Asterias, Strongylocentrotus, and Mytilus and the respective attacked classes.

Uneaten portions of prey from all trials were observed to determine mode of consumption. Uneaten portions of Mytilus were comprised of many fragments of shell, usually stripped of tissue. A small amount of shell appeared to have been consumed (Figure 5). The sizes of shell fragments suggested that Mytilus individuals were crushed open by the claws, rather than chipped open by the mandibles.

Uneaten portions of Cancer individuals frequently included complete legs and claws broken from the main body (Figure 6), although,

Table 12. Consumption efficiency[a] of immature lobsters (*H. americanus*) offered various prey organisms.

Prey organism	Mean wet weight of offered prey (g)	Consumption efficiency[b]	Mean presumed consumption per trial (g)
Nereis	0.7 (32)[c]	0.734 ± 0.078 a,c,l,m,o,s[d]	0.59
Harmothoe	0.5 (14)	0.714 ± 0.125 a,c,l,m,s	0.37
Ophiopholis	1.4 (46)	0.542 ± 0.067 a,c,l,m,s	0.79
Asterias	7.4 (39)	0.349 ± 0.066 l,s	1.21
Mytilus	2.9 (70)	0.288 ± 0.037 l,s	0.67
Cancer	14.0 (32)	0.269 ± 0.058 l	2.36
Strongylocentrotus	4.1 (71)	0.153 ± 0.031 l	0.58
Littorina	5.3 (46)	0 ± 0	0

[a] ratio of wet weight of prey presumably consumed by immature lobsters to wet weight of prey offered

[b] mean ± standard error

[c] number of prey offered

[d] significantly greater than: a - *Asterias*; c - *Cancer*; l - *Littorina*; m - *Mytilus*; o - *Ophiopholis*; s - *Strongylocentrotus*
$p < 0.05$

Table 13. Sizes of attacked and ignored prey organisms as a percentage of immature lobster (*H. americanus*) wet weight.[a]

Prey organism	Attacked	Ignored[b] small size class	Ignored[b] large size class
Cancer	17.69 ± 2.65 (n=21)	3.86 ± 1.15* (n=8)	45.40 ± 5.80 (n=3)
Asterias	5.70 ± 0.91 (n=24)	3.48 ± 0.45 (n=5)	22.76 ± 4.60* (n=10)
Strongylocentrotus	4.64 ± 0.34 (n=23)	3.73 ± 0.12 (n=25)	8.22 ± 0.73* (n=23)
Mytilus	3.04 ± 0.28 (n=34)	2.48 ± 0.19 (n=10)	4.73 ± 0.28* (n=26)
Ophiopholis	2.00 ± 0.33 (n=36)	0.87 ± 0.23 (n=6)	3.38 ± 0.44 (n=4)
Harmothoe	0.99 ± 0.28 (n=10)	0.45 ± 0.15 (n=4)	--
Nereis	0.91 ± 0.12 (n=24)	0.54 ± 0.07 (n=7)	1.30 (n=1)

[a] mean ± standard error

[b] small size class = organisms smaller than mean size (as a % of lobster wet weight) of attacked individuals

large size class = organisms larger than mean size (as a % of lobster wet weight) of attacked individuals

* significantly different from mean size of attacked individuals $p < 0.05$

Figure 5. Remains of Mytilus edulis after feeding by an immature lobster (H. americanus) (x 2.5).

Figure 6. Remains of <u>Cancer</u> <u>irroratus</u> after feeding by an immature lobster (<u>H</u>. <u>americanus</u>) (x 2).

in most cases, several legs had been consumed. The carapace was generally fragmented and cleaned of tissue.

Uneaten portions of *Strongylocentrotus* commonly included large pieces of the test (Figure 7), most of which were stripped of tissue. Few spines appeared to have been consumed. Uneaten portions of *Ophiopholis* consistently included tips of arms. Remains of *Asterias* generally consisted of whole arms.

Gut content analysis

The remains of at least 33 taxa were observed in guts of immature lobsters collected in Placentia Bay between June and November. The most frequently occurring species were *Strongylocentrotus droebachiensis*, *Mytilus edulis*, *Cancer irroratus*, polynoids, *Nereis* sp., and *Ophiopholis aculeata* (Table 14). The number of mollusc species was fairly high, although percentage frequencies of occurrence of individual species were low. Approximately 20% of lobster guts contained unidentified hard parts of bivalves, crustaceans, gastropods, and polychaetes. Various items of questionable nutritional value, such as pebbles, sand, wood, rubber, and plastic were observed as well. Characteristic hard parts of the various consumed species are noted in APPENDIX C. Contents of individual immature lobster guts are shown in Figures 9-14.

The most abundant gut items (in terms of relative volumes of hard parts) were *Cancer irroratus*, *Ophiopholis aculeata*, *Mytilus edulis*, *Nereis* sp., polynoids, and *Strongylocentrotus droebachiensis*. Percentage frequency of occurrence of *Homarus americanus* as dominant gut item was relatively high during the moulting period from mid-August to mid-

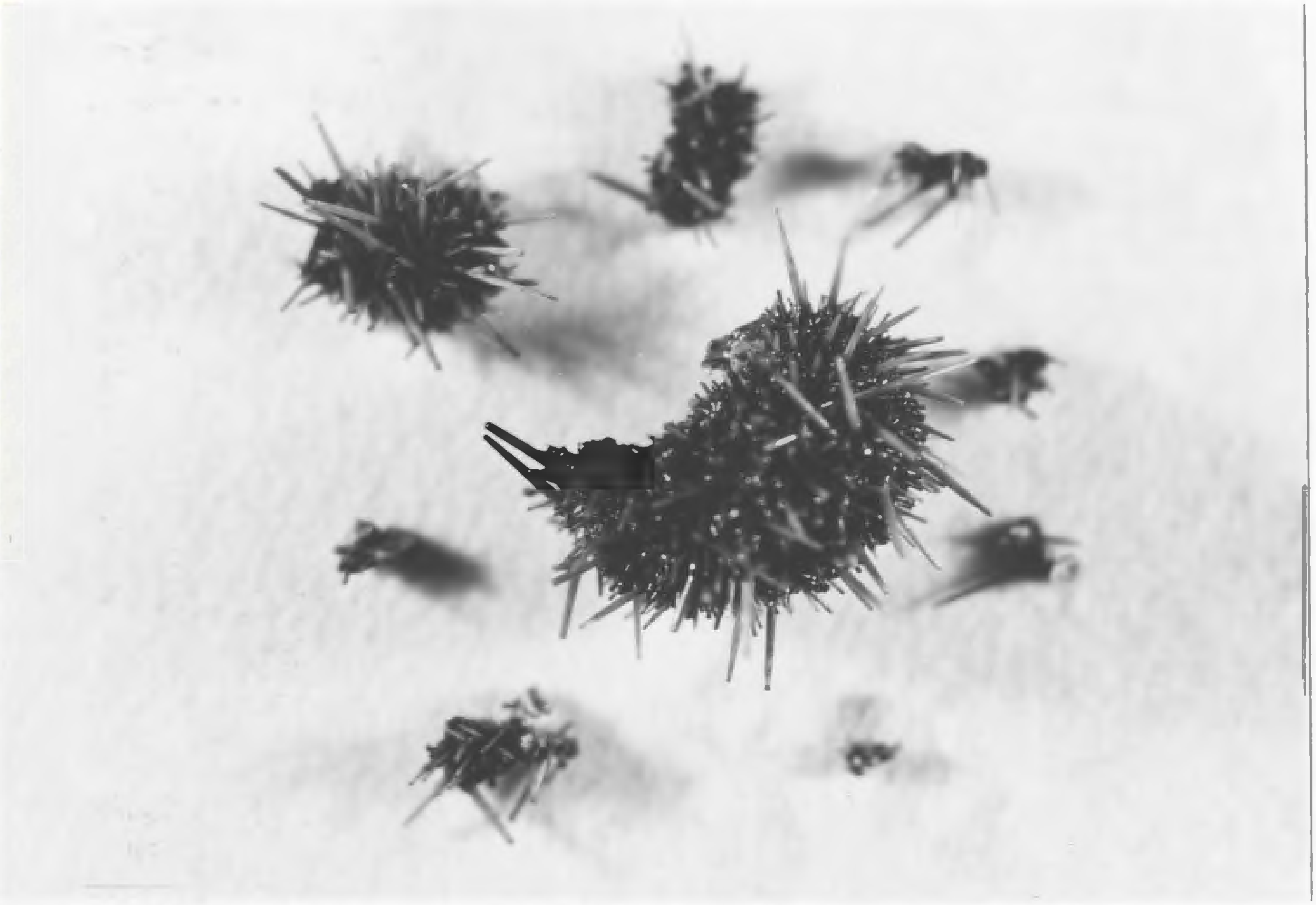

Figure 7. Remains of Strongylocentrotus droebachiensis after feeding by an immature lobster (H. americanus) (x 2.5).

Table 14. Percentage frequency of occurrence of items in guts of immature lobsters (H. americanus) from Placentia Bay in summer and fall (n=103).

Gut item	% frequency of occurrence	% frequency of occurrence as dominant gut item
Echinoderms		
Strongylocentrotus droebachiensis	71.8	5.8
Ophiopholis aculeata	34.0	14.6
Asterias vulgaris	5.8	0
Molluscs		
Mytilus edulis	66.0	11.7
Littorina littorea	31.1	1.0
unidentified chiton	22.3	1.9
Cerastoderma pinnulatum	16.5	0
Acmaea testudinalis	10.7	0
miscellaneous bivalves and gastropods	< 9.7	1.0
unidentified bivalves	17.5	0
unidentified gastropods	19.4	1.0
Decapod Crustaceans		
Cancer irroratus	53.4	18.4
Homarus americanus	15.5	7.8
Pagurus sp. and Hyas sp.	< 2.9	2.0
unidentified crustaceans	16.5	4.9
Polychaetes		
unidentified polynoids	47.6	5.8
Nereis sp.	39.8	6.8
unidentified polychaetes	13.6	0
Algae		
filamentous algae	32.0	1.9
miscellaneous algae	< 2.9	1.0
Miscellaneous		
unidentified pelagic copepod	29.1	0
unidentified hydrozoan	23.3	0
unidentified bryozoan	10.7	0
unidentified fish	2.9	1.0
miscellaneous invertebrates	< 2.9	1.0
pebbles, sand	55.3	1.0
wood fibres	21.4	1.9
tissue bolus	15.5	1.9
rubber	7.8	1.0
plastic	1.0	0

September (see APPENDIX D).

When occurring, crustacean species such as Cancer irroratus, Homarus americanus, Pagurus arcuatus, Hyas araneus, and an unidentified amphipod contributed a large percentage to the total volume of gut contents (Table 15). The same was true, although to a lesser extent, for unidentified crustacean material. Ophiopholis aculeata contributed a sizeable percentage of the total volume of gut contents when it occurred. Smaller contributions to the total volume of gut contents were made by Mytilus edulis, Asterias vulgaris, Nereis sp., chiton, Strongylocentrotus droebachiensis, and polynoid polychaetes when they occurred.

The estimated percentage contribution to the total volume of the immature lobster population diet from June to November was calculated by multiplying the percentage frequency of occurrence of individual gut items by the estimated mean percentage contribution of the item to the total volume of gut contents when occurring (Table 15). The most important items in the immature lobster diet by this reckoning are Cancer irroratus, Mytilus edulis, Ophiopholis aculeata, Strongylocentrotus droebachiensis, lobster exuviae, Nereis sp., and polynoid polychaetes. The estimated percentage contributions of various taxa to the total volume of the immature lobster population diet are shown in Figure 8.

Seasonal differences in the percentage frequencies of occurrence of gut items are noted in Table 16. Percentage frequency of occurrence of Cancer irroratus in lobster guts was significantly higher in late summer than in early summer and fall. The same was true for incidence of Homarus hard parts in guts. Elevated percentage frequencies of occurrence in late summer were recorded as well for polynoids, chitons, Lacuna vincta, Littorina littorea, unidentified bivalves, and Strongylo-

Table 15. Estimated contributions of prey items to the immature lobster (*H. americanus*) diet.

Gut item	Estimated mean % contribution to total volume of gut contents when occurring	Estimated % contribution to total volume of population diet
Echinoderms		
Strongylocentrotus droebachiensis	9.2	6.6
Ophiopholis aculeata	33.3	11.3
Asterias vulgaris	18.7	1.1
Molluscs		
Mytilus edulis	17.6	11.6
Littorina littorea	4.2	1.3
unidentified chiton	11.1	2.5
Cerastoderma pinnulatum	5.4	0.9
Acmaea testudinalis	3.7	0.4
miscellaneous bivalves and gastropods	<13.7	1.2
unidentified bivalves	8.8	1.5
unidentified gastropods	2.7	0.5
Decapod Crustaceans		
Cancer irroratus	27.8	14.8
Homarus americanus	42.6	6.6
Pagurus sp. and *Hyas* sp.	<52.5	1.8
unidentified crustaceans	21.1	3.5
Polychaetes		
unidentified polynoids	8.9	4.2
Nereis sp.	15.4	6.1
unidentified polychaetes	4.4	0.6
Algae		
filamentous algae	6.1	2.0
miscellaneous algae	<20.0	0.6
Miscellaneous		
unidentified pelagic copepod	1.1	0.3
unidentified hydrozoan	1.7	0.4
unidentified bryozoan	3.1	0.3
unidentified fish	20.0	0.6
miscellaneous invertebrates	<60.0	0.8
pebbles, sand	2.8	1.5
wood fibres	19.6	4.2
tissue bolus	20.0	3.1
rubber	10.3	0.8
plastic	1.0	0.1
amorphous material		8.8

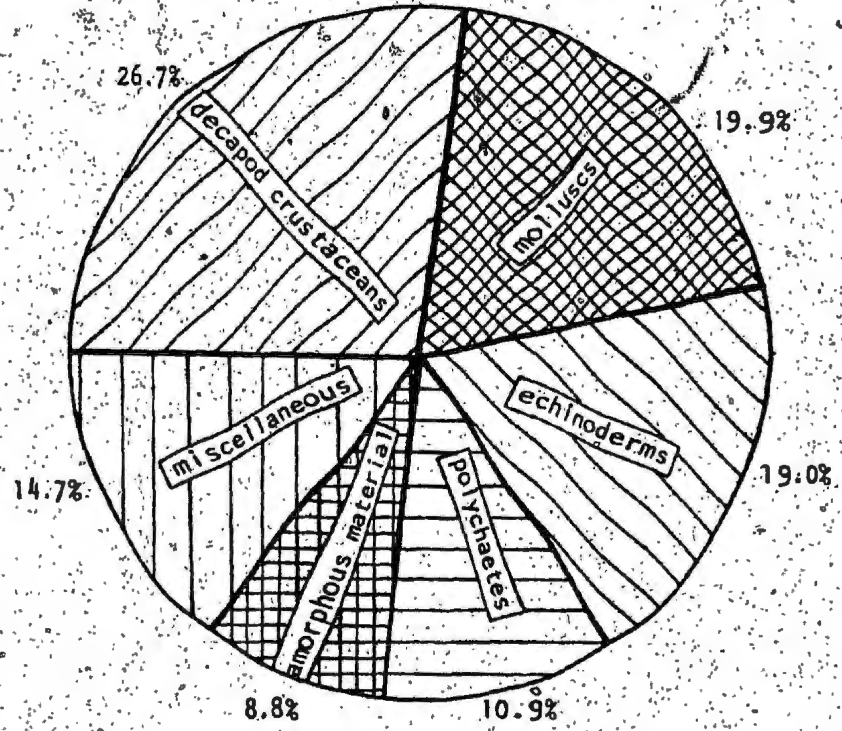

Figure 8. Estimated percentage contribution of the main taxonomic groups to the total volume of the immature lobster (H. americanus) population diet.

Table 16. Seasonal differences in percentage frequency of occurrence of gut items of immature lobsters (H. americanus) from Placentia Bay.

Gut item		Season	
	A June to mid-Aug. (n=46)	B late Aug. to mid-Sep. (n=24)	C Oct. to Nov. (n=33)
Echinoderms			
Strongylocentrotus droebachiensis	73.9	87.5 C[a]	57.6
Ophiopholis aculeata	26.1	50.0	33.3
Asterias vulgaris	6.5	0	9.1
Molluscs			
Mytilus edulis	50.0	75.0	81.8 A
Littorina littorea	8.7	58.3 A	42.4 A
unidentified chiton	15.2	45.8 A,C	15.2
Cerastoderma pinnulatum	17.4	16.7	15.2
Acmaea testudinalis	17.4 C	12.5	0
miscellaneous bivalves/gastropods	<13.0	<16.7	< 3.0
unidentified bivalves	6.5	45.8 A	18.2
unidentified gastropods	15.2	29.2	12.1
Decapod Crustaceans			
Cancer irroratus	28.3	91.7 A,C	60.6 A
Homarus americanus	8.7	50.0 A,C	0
Pagurus sp. and Hyas sp.	4.3	0	< 3.0
unidentified crustaceans	21.7 B	8.3	15.2
Polychaetes			
unidentified polynoids	28.3	91.7 A,C	42.4
Nereis sp.	34.8	62.5	30.3
unidentified polychaetes	15.2	4.2	18.2
Algae			
filamentous algae	56.5 B,C	12.5	12.1
miscellaneous algae	< 4.3	4.2	< 3.0
Miscellaneous			
unidentified pelagic copepod	34.8	12.5	33.3
unidentified hydrozoan	19.6	16.7	33.3
unidentified bryozoan	19.6 C	8.3	0
unidentified fish	4.3	4.2	0
miscellaneous invertebrates	< 6.5	0	< 3.0
pebbles, sand	78.3 B,C	37.5	36.4
wood fibres	23.9	12.5	24.2
tissue bolus	17.4	8.3	18.2
rubber	2.2	20.8	6.1
plastic	2.2	0	0

[a] significantly greater than: A = June to mid-August; B = late August to mid-September; C = October to November $p < 0.05$

centrotus. High percentage frequencies of occurrence in immature lobster guts in early summer relative to other seasons were observed for unidentified crustaceans, Acmaea testudinalis, Lacuna vincta, bryozoans, and filamentous algae. Cancer irroratus, Littorina littorea, and Mytilus edulis were more common in lobster guts in fall than in early summer.

No immature lobster guts were completely empty, although some had only a few hard parts of animals remaining. There were no significant differences in gut fullness estimates between seasons (early summer, late summer, fall) (Table 17).

Residency of prey hard parts in guts of immature lobsters is noted in Table 18. The general indication is that prey hard parts can remain in the gut for over 90 days. Mollusc and crustacean shell, and polychaete jaws are apparently not easily digested or evacuated. Hard parts of polychaetes were observed in guts of lobsters 180 days after last natural feeding.

Clearance of gut contents of immature lobsters on single species ad libitum diets is noted in Table 19. Ratios of gut content wet weight to lobster wet weight one day after feeding were 1.7% and 1.3% for Cancer and Strongylocentrotus diets respectively. Rate of clearance is inferred from comparison of values for lobsters at different stages of food deprivation. Clearance of the gut showed an apparent negative linear relationship to duration of food deprivation. The rate of gut clearance was greater for lobsters fed a diet of Cancer than for those fed Strongylocentrotus. After three days of food deprivation, ratios of gut content dry weight to lobster wet weight for all lobsters were similar, ranging from 151.10 $\times 10^{-5}$ in lobsters fed Cancer to 181.45 $\times 10^{-5}$ in those fed Strongylocentrotus.

Table 17. Various estimates of gut fullness of immature lobsters (*H. americanus*) from Placentia Bay by season.[a]

Estimate of gut fullness		Season	
	June to mid-Aug. (n=46)	late Aug. to mid-Sep. (n=24)	Oct. to Nov. (n=33)
Ratio of gut content wet weight to lobster wet weight	0.0099 ± 0.0009	0.0101 ± 0.0013	0.0076 ± 0.0010
Ratio of gut content dry weight to lobster wet weight x 10^5	323.36 ± 37.52	316.21 ± 59.12	195.35 ± 33.54
Ratio of gut content dry volume to lobster wet weight x 10^5	968.92 ± 101.77	1011.32 ± 185.16	896.03 ± 152.05
Visual index of gut fullness[b]	1.89 ± 0.21	2.04 ± 0.29	1.73 ± 0.21

[a] mean ± standard error

[b] based on a scale of 0 to 4 (empty to full)

Table 18. Residency of prey hard parts in guts of immature lobsters (*H. americanus*).

Gut item	Number of days since capture or last natural feeding												
	2	5	6	10	12	40	60	70	80	90	100	160	180
Cancer irroratus			✓[a]	✓		✓		✓				✓	
unidentified crustacean		✓			✓	✓							
Nereis sp.	✓		✓		✓	✓			✓		✓		✓
polynoid polychaete		✓	✓					✓					✓
Littorina littorea	✓	✓				✓				✓			
unidentified gastropod		✓		✓			✓		✓		✓	✓	
Mytilus edulis	✓	✓		✓						✓		✓	
unidentified bivalve		✓	✓							✓			
Asterias vulgaris	✓												
Ophiopholis aculeata												✓	
Strongylocentrotus droebachiensis	✓	✓		✓									

[a] - ✓ indicates hard part observed in lobster gut

Table 19. Clearance of gut contents of immature lobsters (*H. americanus*) at 8° C. as indicated by various estimates of gut fullness.[a]

Estimate of gut fullness	Diet	Number of days since feeding 1	2	3	4	8
Ratio of gut content wet weight to lobster wet weight	*Cancer*	0.017 (n=1)	-[c]	0.006 ± 0.003 (n=3)	0.004 ± 0.002 (n=2)	-
	Mytilus	-	-	0.007 ± 0.003 (n=3)	-	-
	Strongylocentrotus	0.013 (n=1)	0.012 (n=1)	0.006 ± 0.004 (n=2)	-	0.004 (n=1)
Ratio of gut content dry weight to lobster wet weight x 10^5	*Cancer*	474.87 (n=1)	-	151.10 ± 91.3 (n=3)	85.42 ± 35.1 (n=2)	-
	Mytilus	-	-	170.87 ± 110.2 (n=3)	-	-
	Strongylocentrotus	271.95 (n=1)	225.00 (n=1)	181.45 ± 74.5 (n=2)	-	23.07 (n=1)
Ratio of gut content dry volume to lobster wet weight x 10^5	*Cancer*	1690.82 (n=1)	-	628.81 ± 283.0 (n=3)	505.33 ± 217.6 (n=2)	-
	Mytilus	-	-	634.04 ± 347.6 (n=3)	-	-
	Strongylocentrotus	365.85 (n=1)	416.66 (n=1)	572.41 ± 227.6 (n=2)	-	109.89 (n=1)
Visual index of gut fullness[b]	*Cancer*	4.00 (n=1)	-	1.33 ± 0.7 (n=3)	1.00 ± 0 (n=2)	-
	Mytilus	-	-	1.67 ± 0.9 (n=3)	-	-
	Strongylocentrotus	2.00 (n=1)	3.00 (n=1)	1.00 ± 1.4 (n=2)	-	0 (n=1)

[a] lobsters on *ad libitum* diets

[b] based on a scale of 0 to 4 (empty to full)

[c] no sample

Figure 9. Gut contents of an immature lobster (H. americanus) with a high incidence of remains of Ophiopholis aculeata (x 4).

a - Ophiopholis vertebra
b - sea urchin spine
c - part of bivalve shell

Figure 10. Gut contents of an immature lobster (H. americanus) with opercula of Littorina littorea and remains of Cancer (x 3).

a - operculum of Littorina littorea
b - pereiopod of Cancer irroratus

Figure 11. Gut contents of an immature lobster (H. americanus) with a high incidence of Cancer irroratus remains (x 3).

a - part of claw
b - portion of knuckle
c - tip of pereiopod

Figure 12. Gut contents of an immature lobster (H. americanus) with a high incidence of lobster exuviae (x 3).

Figure 13. Gut contents of an immature lobster (H. americanus) recently feeding on Mytilus edulis (x 3).

a - piece of shell
b - byssal threads
c - Mytilus tissue

Figure 14. Gut contents of a recently moulted immature lobster (H. americanus) with a high incidence of Cancer remains and mollusc shells (x 3).

a - tip of pereiopod of Cancer
b - bivalve shell
c - gastropod shell

Prey density in Placentia Bay

Densities of subtidal organisms, based on 24 one square metre quadrats in the Placentia Bay collection sites, are noted in Table 20. Strongylocentrotus was by far the most abundant observed organism. In Spencer's Cove, Littorina littorea was the second most abundant organism. Acmaea testudinalis, Mytilus edulis, and burrowing anemones were reasonably abundant as well. Observed densities of crustaceans were low. Observations under rocks in all areas suggested a high incidence of polychaetes and Ophiopholis aculeata, although such organisms were not counted.

Table 20. Densities of subtidal organisms in Placentia Bay (3-8 m depths) in late summer and fall, 1976.

Organism	Number of individuals per square metre - mean ± S.E. (n=24)
Strongylocentrotus droebachiensis	42.2 ± 6.4
Littorina littorea[a]	15.8 ± 4.5
Acmaea testudinalis	11.0 ± 1.4
Mytilus edulis	6.9 ± 1.5
unidentified burrowing anemone	5.0 ± 1.1
Volsella modiolus	1.9 ± 0.7
Asterias vulgaris	1.8 ± 0.9
Metridium senile	1.5 ± 0.4
unidentified chiton[b]	0.9 ± 0.4
Cancer irroratus	0.2 ± 0.1
Ophiopholis aculeata[b]	0.3 ± 0.2
Crangon septemspinosus	0.1 ± 0.1
Hiatella arctica	0.1 ± 0.1
Hyas araneus	0.1 ± 0

[a] observed only in Spencer's Cove

[b] these organisms are cryptic; therefore, the observed number of individuals per square metre is unrealistically low

Such organisms as nemerteans, polynoid polychaetes, and *Nereis* sp. were observed under rocks. No attempt was made to quantify observations of any individuals not readily visible to the diver. Data on densities of such organisms in Placentia Bay were collected by Swiss and Osborne (1976).

DISCUSSION

Attraction to prey extracts

The attraction of lobsters, Homarus americanus, to tissue extracts of various organisms has been known for at least eighty years (Herrick, 1895; Hadley, 1912; Ache, 1972; Atema and Gagosian, 1973). McLeese (1970, 1973c) observed "barrier responses" (percentage of adult lobsters reaching the upstream barrier of an olfaction trough) of 13% for tests of extracts of sea urchins and starfish, 75% for tests with mussels and clams, 84% for cod extract, and greater than 90% for tests of extracts of lobster and shrimp. The percentages of immature lobsters in the present study showing food-searching behaviour are similar to the responses of adult lobsters noted by McLeese (1970, 1973c), although his echinoderm extracts were considerably less attractive than such extracts in the present study.

Variability of response among immature lobsters was high, while individual variation was considerably lower. Similar high variability of population behaviour was observed in H. americanus by Scrivener (1971) and noted in H. gammarus by Mackie and Shelton (1972). Population response variability in the present study may have been due to differences in sex, size, and natural ingestive experience of immature lobsters prior to capture. The paired comparisons analysis avoided problems with variability in analysis while allowing statements about populations of immature lobsters in general.

The food-searching behaviour of immature lobsters, elicited to some extent by all prey extracts, appears to be a stereotyped behaviour of the species (McLeese, 1970; Atema and Engstrom, 1971; Scrivener, 1971; Atema and Stein, 1974). Atema and Engstrom (1971) indicated three levels of response to food stimuli; the alert phase; the pre-feeding phase; and active feeding. The behaviour of immature lobsters described as "food-searching" in the present study corresponds to the pre-feeding phase described by Atema and Engstrom (1971).

A few lobsters showed meral spread and opening of the claws during trials with Cancer extract, indicating aggressive behaviour as described by Atema and Engstrom (1971), Scrivener (1971), and Hoffman et al. (1975). These displays were quickly replaced by food-searching behaviour. It is suggested that this "aggressive" behaviour is very similar in appearance to the pre-feeding phase described by Atema and Engstrom (1971). While there may be some difficulty in interpretation and terminology of this behaviour, it ultimately resulted in food-searching behaviour near the stimulus origin, regardless of the motivational context (hunger, aggression) of the behaviour.

Because there were no appreciable differences in densities (weight/unit volume) of the extracts, diffusion to the downstream end of the trough where the lobsters rested was presumed similar for each extract and therefore would not have biased the reaction times of tested lobsters. Nor does it appear that the water content of tissue extracts could have influenced the potency of stimuli to any great extent as there was only a 15% difference in the mean water contents of the tested prey. As the degree of food deprivation of individual lobsters was the same for tests of each of the prey extracts, the differential attraction of individual lobsters to extracts must have been a function of types or concentrations of stimuli in the extracts themselves.

Prey preference of immature lobsters was indicated by comparing the integrals of food-searching response curves for the various extract trials of each lobster. Immature lobsters showed a significant preference for Cancer extract. Approximately 20% of the lobsters preferred Mytilus extract over other prey extracts. These observations indicate that olfactory preferences of immature lobsters are similar to actual food preferences of adult lobsters. For example, Evans and Mann (1977) noted that adult lobsters prefer Cancer over Strongylocentrotus, and Elner (personal communication) observed a preference of adult lobsters for Mytilus over Strongylocentrotus.

McLeese (1970) noted in adult lobsters a high correlation between walking and feeding responses in olfaction experiments. This is to be expected as successful feeding in nature may be dependent on movement to food. In the present study, locomotion was an important component of food-searching behaviour during tests of preferred prey. For example, Cancer extract stimulated food-searching behaviour at the stimulus source in at least 50% of the lobsters tested, while less than 30% of the lobsters showed food-searching behaviour at the stimulus source during trials with each of the other prey extracts.

Exploratory responses by immature lobsters in the olfaction trough were likely elicited by the introduction of the control or extract stimulating mechanoreceptors in the lobster and subsequent locomotion. With the exception of the difference between trials with controls and Strongylocentrotus extracts, there were no significant differences in the durations of exploratory responses during the different tests, indicating that olfaction may have had little control over mediation of exploratory response.

Attraction to prey effluents

McLeese (1973c) observed barrier responses of adult *Homarus americanus* to prey effluents of *Cancer*, *Mytilus*, and *Strongylocentrotus* of 13%, 6%, and 10% respectively. Despite differences in test procedures, the percentages of lobsters in the present study showing rapid approaches to the prey effluents are similar to the lobster barrier responses observed by McLeese, *Cancer* effluent apparently being more effective than the other prey effluents in eliciting the approach response.

Hirtle and Mann (1978) observed positive responses of adult lobsters to waterborne odour of intact living crabs (*Carcinus maenas*), sea urchins, and mussels and noted that the percentage frequency of lobster response was higher and the response time shorter to crabs than to sea urchins or mussels. While immature lobsters show a similar grading of responses, the percentage frequencies of food-searching responses were somewhat lower than those observed by Hirtle and Mann (1978).

The addition of control and prey effluents, regardless of their composition, to test containers with immature lobsters consistently elicited increased antennule flicking rate and anchoring and raking of pereiopods. To a lesser extent, all prey effluents and control elicited directional movement of antennules (pointing towards source of stimulus) and wiping of antennules and antennae. Atema and Engstrom (1971) suggested that most of these behaviour types, as well as maxilliped exopodite arrest and antennal search, are characteristic of an alert phase. The alert phase is not stimulus specific. It is a precursor for all feeding and social behaviour. Atema and Stein (1974) suggested that the alert phase is determined by the threshold perception of the chemical senses (most probably by the antennular aesthetasc hairs). However, the fact that most of the alert phase behaviour types described by Atema and Engstrom (1971) were observed after entry of seawater controls suggests a general response to entry of the stimulus rather than a specific chemoreceptor response. This general response may have been mediated by mechanoreceptors.

Mechanoreceptor capabilities are present in cuticular hair-fan and hair-peg organs of H. vulgaris (gammarus) (Laverack, 1962a,b) and in hairs of the antennal flagellum of the same animal (Tazaki, 1977). Entry of the stimulus probably caused vibrations in the tank water which were detected by similar cuticular organs of the immature lobsters in the present study. It is possible (at least in the laboratory) that detection of water movements is a precursor to increased antennule flicking rate, which is initiated in crustaceans to enhance detection of stimulatory food molecules in the water (Laverack, 1964; McLeese, 1973b,c; Price and Ache, 1977). Specifically, Snow (1973) suggested that flicking of the antennules of the hermit crab Pagurus alaskensis, for example, facilitates water circulation around the aesthetasc hairs and produces phasic sampling of dissolved chemicals in the animal's immediate environment.

Depending on the quality of the information mediated by the antennules, food-searching behaviour may be initiated. The composition or concentration of components in the prey effluents and the motivation of the lobsters were sufficient to elicit food-searching behaviour as described by Atema and Engstrom (1971). The stimulatory compounds in the prey effluents in the present study are probably excretion products. These include ammonia and other ninhydrin-positive compounds (Webb and Johannes, 1967; Hammen, 1968; Schoffeniels and Gilles, 1970; Dall, 1975; Klein Breteler, 1975; Bayne and Scullard, 1977; Propp, 1977). The composition of prey effluents is discussed later.

McLeese (1973c) suggested that lobsters are not strongly attracted from a distance to intact prey. The present results indicate that prey effluents have the capacity to elicit food-searching behaviour, although it is impossible to establish a critical distance at which these prey effluents effectively elicit responses. In the natural environment, prey effluent concentrations are probably much lower than concentrations used in the present study. This consideration, as well as the complicating factors of currents, bottom roughness, and multiple sources of stimulating compounds, probably make the critical distance at which responses by lobsters are elicited very small (perhaps within centimetres). It is possible that prey effluents may only be effective in stimulating food-searching behaviour when the lobster is practically touching the prospective prey.

Attraction to ninhydrin-positive compounds (NPCs)

Previous studies of attractiveness of food have suggested that amino acid stimulation elicits food-searching behaviour and may be a component of food attraction in natural populations of marine crustaceans (Case and Gwilliam, 1961; Levandowsky and Hodgson, 1965; Shelton and Mackie, 1971; Mackie and Shelton, 1972; Mackie, 1973; Hindley, 1975). The major attractants for most of the crustaceans studied are glutamic acid, glycine, proline, and taurine (Levandowsky and Hodgson, 1965; Crisp, 1967; Carr and Gurin, 1975; Allison and Dorsett, 1977; Hartman and Hartman, 1977; Price and Ache, 1977; Johnson and Ache, 1978).

Previous studies of chemoreception in the lobster, <u>Homarus</u> americanus, have shown that ninhydrin-positive compounds are capable of exciting antennule chemoreceptors and eliciting food-searching behaviour (McLeese, 1970; Ache, 1972; Shepheard, 1974; McLeese et al., 1977).

The present study shows greatest attraction (56.5%) of immature lobsters to proline. This agrees well with the results of McLeese (1970) who observed a feeding response to proline in 53% of the trials with adult lobsters, and with the general observations of Shepheard (1974) for the proline compound, hydroxy L-proline. McLeese et al. (1977) observed a 30% response of adult lobsters to proline in an olfaction trough. McLeese (1970) did not observe any feeding response to hydroxy L-proline, in contrast to the findings of Shepheard (1974) with respect to antennular sensitivity. Results of the present study indicate significant attraction of immature lobsters to ammonia, arginine, lysine, alanine, glycine, and valine. McLeese (1970) observed that most of these NPCs at relatively high concentrations elicited feeding responses in adult lobsters. In general, the findings of the present study agree well with the results noted by McLeese (1970) and indicate that chemosensitivity of immature lobsters does not differ significantly from that of adult lobsters.

Various studies indicate a threshold concentration at which crustaceans respond to NPCs on the order of 10^{-3} to 10^{-7} M (Levandowsky and Hodgson, 1965; Crisp, 1967; Ache, 1972; Shepheard, 1974; Carr and Gurin, 1975; Hindley, 1975; Allison and Dorsett, 1977; Hartman and Hartman, 1977). Fuzessery and Childress (1975) and Price and Ache (1977) observed electrophysiological responses of antennule nerve fibres of marine crustaceans to concentrations of compounds as low as 10^{-12} M. The effective concentrations of NPCs in the present study ranged from 1×10^{-1} M at the target to a terminal concentration of 2×10^{-4} M assuming total dissolution of the

NPC in the lobster tank. All NPCs were theoretically detectable within the limits of these concentrations.

It was interesting to note that the most attractive NPC, proline, is the most soluble of all NPCs tested (Windholz et al., 1976). Other NPCs which were significantly attractive to immature lobsters relative to control trials are also very soluble. Despite the greater attractiveness of very soluble NPCs, there was no apparent correlation between percentage frequency of target captures and the mean time to target capture. This indicates that solubility of NPCs did not significantly affect the rate of diffusion in the lobster tank and the time to response by lobsters. Solubility may be an important factor at the chemoreceptor surface, the more soluble NPCs perhaps being more easily detected and, thus, more attractive.

Most of the attractive NPCs, with the exception of arginine and lysine, are relatively small molecules compared to those NPCs which are not attractive. Molecular size and configuration may be other important factors affecting attractiveness at the chemoreceptor surface. Lindstedt (1971) suggested that the (CH_3)-N moiety of such compounds as trimethylamine oxide and betaine is the active part of the molecule eliciting feeding responses in crustaceans. Case (1964), in his studies of dactyl chemoreceptors of <u>Cancer</u>, observed that increasing the size of the molecule reduces stimulatory capacity and that maximal stimulatory capacity occurs in straight-chain amino acids with three to five carbon atoms. Hartman and Hartman (1977) observed in the porcelain crab, <u>Petrolisthes cinctipes</u>, that amino acid stimuli become less effective in initiating feeding behaviour as the chain length is increased. The present findings are compatible with those of the studies above.

The four most attractive NPCs in the present study (proline, ammonia, arginine, and lysine), in their ionized form at normal pH, are characterised by nitrogen in the R group (Lehninger, 1975). The last three NPCs are positively charged in their ionized states. The next three most attractive NPCs (alanine, glycine, and valine) are characterised by small R groups. All the remaining relatively unattractive NPCs are characterised by large R groups. Those NPCs with large R groups containing nitrogen are uncharged. It appears that NPCs with small R groups or R groups containing charged nitrogen are potentially attractive to immature lobsters.

Analysis of NPCs in prey tissue extracts and effluents

The results of analysis of NPCs in tissue extracts indicate a relatively consistent pattern of NPC composition in marine invertebrates as noted in previous studies (see Awapara, 1962; Schoffeniels and Gilles, 1970 for reviews). Glycine generally makes the greatest contribution to the free NPC pool, with relatively large contributions from alanine, ammonia, proline, and taurine.

Taxonomically related species appear to have similar NPC compositions. For example, the echinoderms Asterias, Ophiopholis, and Strongylocentrotus all show a high concentration of glycine and a very low concentration of proline. Ophiopholis differs slightly with a high concentration of taurine relative to other NPCs.

Results of the present study agree with those of other studies of echinoderms (Kittredge et al., 1962), littorinid snails (Kittredge et al., 1962), Mytilus edulis (Wachtendonk and Käppler, 1977), Nereis virens (Ackermann, 1955; cited in Awapara, 1962), and decapod crustaceans (Camien et al., 1951; Carr, 1967; Schoffeniels and Gilles, 1970; Siebers et al., 1972; Weber and van Marrewijk, 1972; Torres, 1973; Roesijadi et al., 1976; Richard, 1977; Johnson and Ache, 1978).

There were few significant differences between individual NPC concentrations of the tissue extracts among species. However, the significantly greater concentrations of glutamic acid, glutamine, proline, and taurine in Cancer extract compared to concentrations in the extracts of most echinoderm species may reflect fundamental phylogenetic differences in NPC composition. The same may be true for the high total NPC concentrations of crustacean and polychaete tissues compared to those of echinoderms. For example, Schoffeniels and Gilles (1970) observed that the arthropods are one invertebrate phylum in which very high amino acid concentrations are found. High total NPC concentrations in tissues of crustaceans have also been observed by Camien et al. (1951), Weber and van Marrewijk (1972), Torres (1973), and Roesijadi et al. (1976).

Schoffeniels and Gilles (1970) commented that considerable variations in NPC composition of crustaceans exist in the same tissue from different species and different tissues from the same species. Kittredge et al. (1962) noted that it is necessary to consider several criteria such as ecological influences, developmental state, and sampling of individual tissues in comparative biochemistry. It is possible that all of the above factors may have influenced to some extent the NPC compositions of individual species in the present study. Despite this, and the variability inherent in small samples, the total NPC concentrations and NPC compositions of tissue extracts appear to be phylogenetically distinct.

The percentage contribution of ammonia to the total free NPC pool of tissue extracts ranged from 5.9% in Asterias to 22.8% in Nereis sp. The concentration of ammonia in the present investigation may be more apparent than real as ammonia could be produced by spontaneous release from protein prior to deproteinization and the breakdown of glutamine (Meister, 1965; Patterson, 1972). The absolute concentration of glutamine remains uncertain because of this consideration. The extremely high and variable levels of urea in tissue extracts of most of the species tested remain unexplained.

Free NPCs in invertebrates are generally implicated in osmoregulation (Awapara, 1962; Schoffeniels and Gilles, 1970). Catabolism of proteins results in many NPCs in a free state. Different concentrations of NPCs could possibly be explained by different rates of active proteolysis (Awapara, 1962). Several studies have suggested that amino acids may be used in the process of energy production (Schoffeniels and Gilles, 1970). NPCs such as amino acids, as well as ammonia and urea, are capable of being excreted by molluscs, polychaetes, crustaceans, and echinoderms (Meglitsch, 1972) and may be detectable in the vicinity of individual organisms.

The amino acid analyzer used in the present study is capable of detecting NPC concentrations as low as 2 nanomoles per ml. Analysis of seawater allowed to stand for eight hours showed only trace amounts (i.e., less than 2 nanomoles per ml) of ammonia. No other NPCs were detected. Other NPCs, however, certainly exist in seawater at very low concentrations. Daumas (1976) observed average concentrations of total dissolved amino acids varying between 0.9 and 1.2 nanomoles per ml of coastal seawater in the Gulf of Marseille. Total amino acid concentrations in other areas are generally less than one nanomole per ml (see Daumas, 1976 for review). Background levels of NPCs are mainly composed of glycine, serine, alanine, threonine, and valine (Riley and Segar, 1970; Daumas, 1976).

The sources of NPCs in seawater are generally considered to be bacterial degradation of particulate proteins and excretion by organisms (Webb and Johannes, 1967; Daumas, 1976). The fact that ammonia was the only NPC detected in the seawater control implies that ammonia is the most abundant NPC in seawater, all others being below the limit of detection.

All organisms in the present study showed excretion of ammonia, concentrations in the closed containers after eight hours ranging from 42 nanomoles per ml in the Mytilus container to 199 nanomoles per ml in the Nereis container. Only Asterias showed excretion of detectable amounts of other NPCs. It is conceivable that the other organisms excreted NPCs other than ammonia at levels below the limits of detection. For example, Webb and Johannes (1967) observed excretion of NPCs in zooplankton and noted that glycine comprised an average of 31.7% of the total NPC release. Alanine and taurine were conspicuous as well. However, most of the invertebrates in the present study, and related species, excrete nitrogen mainly in the form of ammonia (Hammen, 1968; Schoffeniels and Gilles, 1970; Bayne and Scullard, 1977; Propp, 1977) which explains why only ammonia was detected in the effluent water of most of the organisms studied.

The contribution of ammonia to the total excreted nitrogen is variable depending on season and habitat (Bayne and Scullard, 1977) and may reflect the protein content of the diet (Hammen, 1968), especially as the prime source of ammonia is deamination of amino acids after protein catabolism (Schoffeniels and Gilles, 1970).

In this regard, it was interesting to note that the greatest quantities of excreted ammonia were produced by the carnivores, Asterias, Nereis, and Cancer. The high absolute quantities of ammonia in effluent relative to that produced by the omnivores and herbivores (Ophiopholis, Strongylocentrotus, Littorina, and Mytilus) may reflect the higher protein content in the diet of the carnivores.

Passive diffusion or leakage of NPCs, as well as true excretion, may occur in Asterias, the effluent of which shows relatively high concentrations of glycine and ammonia, and lower concentrations of alanine, histidine, and lysine. Glycine and ammonia are the most concentrated NPCs in Asterias tissue extract (see Table 9, p. 39). Alanine and histidine are reasonably concentrated as well. The reason why Asterias produces detectable amounts of NPCs other than ammonia and the other organisms do not is not readily explained.

Controlled prey selection

Consumption efficiency in the present study is a function of the attack rate and the presumed consumption rate of immature lobsters. Standard errors for consumption efficiencies were relatively small, indicating that the variation of the prey population in experimental tanks probably had little influence on the attack and consumption rates. Reddin (1973) did observe some variation in the attack rates of lobsters offered various combinations of prey, although this was usually only the case when one of the two prey species offered was relatively unpalatable. Breen (1974) noted only a few differences in attack rates of lobsters offered two types of prey. He observed that sea urchins and starfish were eaten at a lower rate than usual when crabs were present, and when sea urchins and starfish were offered together, the latter were eaten at a higher rate than usual. A relatively large sample size in the present study and offerings that included generally palatable species minimised variation in data due to different combinations of prey.

Previous studies of lobster prey selection indicated a general preference for crustaceans over other prey species (Breen, 1974; Evans and Mann, 1977). Evans and Mann (1977) concluded that lobsters feed selectively and that preference for crabs (Cancer irroratus) over sea urchins reflects energetic and nutritional advantages of the crustacean diet over the urchin diet. Lobster prey selection studies by Reddin (1973) involved a greater number of species than the studies noted above. Reddin tested selection of prey by lobsters two species at a time. His data concerning selection of Strongylocentrotus and Cancer indicated an equal preference for both species. This differs considerably from the observations of Evans and Mann (1977) who showed that lobsters selected Cancer five times as much as Strongylocentrotus when the two species were offered in 1:1 ratios.

In terms of Strongylocentrotus and Cancer, results of the present study are intermediate between those of Reddin (1973) and Evans and Mann (1977) with attack frequency for Cancer approximately twice that for Strongylocentrotus. The mean percentage frequency of selection of Cancer in five of Reddin's experimental situations was 65%, which agrees well with results of the present study, although the other prey species offered in Reddin's study differed somewhat, including Mytilus, Buccinum, Strongylocentrotus, Hyas, and Pagurus. Other mean values were calculated from Reddin's data. Mean percentage frequency of selection of Mytilus was 73%, considerably higher than the attack frequency for Mytilus in the present study. The value for Strongylocentrotus was 50.3%, again higher than the attack frequency for Strongylocentrotus in the present study. These latter two high attack rates in Reddin's study are probably a function of relatively unpalatable prey being offered in combination with Mytilus and Strongylocentrotus. Elner (personal communication) found that lobsters of various sizes showed a 43:1 preference for mussels over sea urchins when offered both prey. Only 39% of the lobsters would feed on sea urchins in the first place during six-day feeding trials. In the present study, 32.4% of the immature lobsters fed on sea urchins when offered various prey.

For Asterias, Reddin (1973) found that the mean percentage frequency of selection was 10.3%, considerably lower than the attack frequency for Asterias in the present study. There are no comparable published results for selection of Ophiopholis, Nereis, and Harmothoe, although Reddin (1973) suggested that Ophiopholis and Nereis are probably only incidentally consumed by adult Homarus americanus. Reddin claimed that it was difficult for adult lobsters to obtain polychaetes. In the present study, polychaetes were obviously accessible to the small lobsters tested.

The presumed rate of consumption for immature lobsters in the present study was 4.69% of lobster weight during 24-hour tests. This agrees fairly well with studies of adult lobsters (Himmelman and Steele, 1971; Breen, 1974; Evans, 1976) and with the observations in this study of gut contents comprising 1.3% to 1.7% of immature lobster weight one day after feeding. McLeese (1972a,b) and McBurney and Wilder (1973) determined that a feeding rate of 6% of lobster weight per week (on a diet of cod, liver, and squid) was capable of sustaining healthy growth in adult lobsters.

It is recognised that some unknown proportion of food attributed to consumption by immature lobsters may have been lost during feeding in the form of body fluids and small particles. The real consumption rate of immature lobsters may, therefore, have been lower than 4.69% of lobster weight per trial. Dagg (1974) suggested that a predator's appetite affects the number of large prey particles that are discarded. If eating motivation is low, or if prey density is high, the predator can afford to eat less efficiently.

At least four factors probably influenced the attack rates and consumption efficiencies of immature lobsters offered various prey. These are prey size and morphology, behaviour of prey, and innate selectivity of prey by lobsters related to calorific and nutritional value of the various prey species. The latter is discussed later. With the exception of Littorina which possessed a thick shell, the smaller species were more frequently attacked than the larger species, and consumption efficiencies were highest for the smallest prey. Small prey may be attractive to immature lobsters because of the relative ease of capture and consumption of individuals compared to the larger species. Similar studies of various invertebrates indicate that prey size is a major limiting factor in predation success and that predator morphology and energy maximisation in feeding determine the optimal prey size (Ebling et al., 1964; Muntz et al., 1965; Himmelman and Steele, 1971; Hamilton, 1976; Holling et al., 1976; Paine, 1976; Elner and Hughes, 1978; Elner and Jamieson, 1979; Pollock, 1979). The results of Table 13 (p. 45) imply that the overall range of sizes of individuals of Ophiopholis, Nereis, and Harmothoe did not influence the attack rates as there were no significant differences between the sizes of ignored and attacked individuals. In nature, because of the low upper limit of size, probably all individuals of the above three species would be susceptible to predation by lobsters of a size used in the present study.

There was never evidence of attack of Littorina by immature lobsters. The shell of Littorina littorea is very thick and the sizes of individuals in the present study may have precluded attack.

With Asterias, Strongylocentrotus, and Mytilus, it was apparent that the large sizes of several individuals relative to the lobster may have occasionally precluded attack. In nature, some Asterias individuals may be too large for attack by the chelae of a small lobster, although it is hard to imagine that even a small lobster could not inflict some damage to a large starfish, considering its soft morphology and slow movements. Fow example, Aldrich (1976) suggested that Asterias forbesi is a cooperative prey for Libinia emarginata, which attacks sizes of Asterias out of proportion to its chela size. In his observations, he noted that autotomy of a starfish arm accommodated this out-of-proportion predation. Elner (personal communication) observed size selectivity of lobsters feeding on sea urchins and noted that smaller lobsters feed on smaller urchins. Elner and Jamieson (1979) noted size selectivity of lobsters when feeding on scallops. Large Mytilus and Strongylocentrotus can avoid predation by exceeding the extent of chela spread of immature lobsters. The same is probably true for large crabs.

Reddin (1973) stated that the largest sea urchin eaten in his experiments with adult lobsters was 16.7% of lobster weight. This is considerably larger than the mean size of attacked sea urchins in the present study. Reddin collected the data from lobsters which were offered only sea urchins. In the absence of a choice, lobsters may have attacked greater than optimally-sized urchins to avoid starvation. Reddin (1973) observed that lobsters will attack large sea urchins through the Aristotle's lantern if the claws are ineffective in immobilising the prey. He also noted that the largest attacked crab was 6.8% of lobster weight, which is considerably less than the mean size of attacked crabs in the present study. The possible reason for this disparity is that Reddin used large lobsters for Cancer consumption experiments such that even the largest attainable size of an individual crab would rarely have exceeded 6%-7% of the mass of the lobsters used in his study.

It appears that small crabs may effectively elude predation as well. In the experimental situation, smaller crabs may have been successful in hiding beneath the rocks provided or were more agile than larger crabs in their escape response. In any case, because size of prey may have been a limiting factor in predation success, percentage frequencies of attack presented in Table 10 (p. 41) are probably lower than would be the case with optimally-sized prey. On the other hand, the constrained movements of prey in the tanks probably enhanced lobster-prey encounters such that percentage frequencies of attack of prey in the laboratory do not necessarily reflect absolute attack rates in the natural environment.

Uneaten portions of _Mytilus_ almost exclusively consisted of tissue-free fragments of shells which comprised, on average, 40.7% of the total wet weight of the attacked individual. Measurements of the contribution of shell to the wet weight of live _Mytilus_ ranged from 29.8% to 35.6%. Reddin (1973) observed that little _Mytilus_ shell was consumed by adult lobsters. These observations suggest that lobsters can efficiently separate the tissue and shell of its prey. However, gut analysis revealed that immature lobsters consume small but conspicuous amounts of shell and byssus threads when feeding on _Mytilus_. Pollock (1979) observed the same thing in the rock lobster, _Jasus_ _lalandii_. Reddin (1973) inferred from remains of sea urchins after lobster feeding that little test was consumed. However, Elner (personal communication) observed that lobsters of various sizes ingest test of sea urchins while feeding on that prey. On average, approximately 50% of captured sea urchins were consumed by immature lobsters, gut analysis indicating a significant ingestion of urchin test.

The mean wet weight of _Cancer_ individuals offered to immature lobsters was approximately three times that of the next largest prey available. As a consequence, percentage consumption of crabs was relatively low. Despite this, the mean amount of crab consumed per attack was highest, almost twice the amount consumed of most of the other species, indicating relatively sustained feeding of lobsters on Cancer compared to feeding on the other species.

Gut content analysis

Gut contents of adult Homarus americanus have been examined by several people. Some results of their studies are summarised in Table 21.

Data from the present study are similar to results of previous studies, taking into account possible differences in prey availability due to location and bottom type. The percentage of immature lobster guts with crab remains is intermediate between values given for adult lobsters in other locations in Newfoundland by Squires (1970) and Ennis (1973). The relative incidence of remains of mussels and sea urchins in immature lobster guts, on the other hand, is considerably higher than such values for adult lobsters in other locations in Newfoundland. This may reflect a greater importance of such prey in the diet of immature lobsters or a difference in their availability. The adult lobsters in the study by Squires (1970) were taken by commercial fishermen from depths of water down to 18 metres. At these depths, abundance of sea urchins and mussels is probably less than in the shallow talus areas observed in the present study where food is abundant (Himmelman, 1969; Fletcher et al., 1974). On the other hand, Scarratt (personal communication) observed that sea urchin remains were more common in the guts of smaller lobsters compared to large lobsters in the Northumberland Strait. In Newfoundland, at any one point in time,

Table 21. Summary of gut content analyses of adult lobsters (H. americanus): Percentage frequencies of occurrence

Gut item	Herrick, 1895 Mass.	Weiss, 1970 N.Y.	Miller *et al*., 1971 P.E.I.	Squires and Ennis, 1968 Nfld.	Squires, 1970 Nfld.	Ennis, 1973 Nfld.
Echinoderms	✓					
Sea urchins	✓		23		4	37.0
Brittlestars					1	}24.0
Starfish		3.8	5		3	
Molluscs	✓					
Bivalves		55.0				
Mussels		38.9	67		4	28.1
Gastropods		75.0		✓		
Periwinkles			36		22	18.8
Crustaceans	✓	>90.0				
Cancer irroratus			50		}27	}81.3
Hyas araneus				✓		
Homarus americanus	✓				16	
Polychaetes			42		37	25.3
Polynoids		23.9				
Nereis sp.		42.0				
Algae	✓	3.0		✓		
Fish	✓			✓	50	
Hydroids	✓					

immature lobsters are probably more numerous than adults because of the cumulative effect of natural mortality, and, for lobsters larger than the minimum legal carapace length of 81 mm, the high rate of exploitation of the fishery (Ennis, 1974). Size selectivity of prey may reduce the degree of food requirement overlap between small and large lobsters. However, the high level of conspecific food competition which may exist between immature lobsters may result in a smaller percentage of the immature lobster population, compared to that of the adult population, feeding on preferred prey of an optimal size such as Cancer, and a greater percentage relying on sea urchins and mussels as the gut content data suggest.

The incidence of polychaetes in guts of immature lobsters is very similar to values obtained in previous studies (Squires, 1970; Weiss, 1970; Miller et al., 1971; Ennis, 1973). For both immature and adult lobsters, the frequency of Asterias in guts is relatively low. Brittlestars may form a more important part of the diet of immature lobsters than adult lobsters, as previous studies show a low incidence of Ophiopholis (Squires, 1970; Miller et al., 1971; Ennis, 1973). Alternatively, the difference between immature and adult lobsters in the incidence of Ophiopholis in the guts may reflect differences in the availability of this prey. Incidence of periwinkles in the guts of immature lobsters is very similar to values recorded for adult lobsters from various locations (Squires, 1970; Miller et al., 1971; Ennis, 1973).

In the present study, Cancer occurred in a greater percentage of guts examined in late summer than in early summer and fall. Scarratt (personal communication) observed that crabs are more important in the diet of lobsters in the Northumberland Strait at the end of summer compared to other times of the year when samples were taken. The seasonality of crab incidence in immature lobster guts may have been due to the increased vulnerability of crabs during their moulting period. Weiss (1970) noted that increased ingestion of <u>Cancer</u> spp. in New York coincided with moulting of those animals.

The higher incidence of lobster shell in late August and early September coincided with the lobster moulting period and may indicate consumption of cast exuviae (Herrick, 1895; Reddin, 1973). A greater incidence of mollusc shells was noted in post-moult immature lobsters than in lobsters taken at times other than the moulting period. Similar feeding habits in adult lobsters were recorded by Herrick (1895), Weiss (1970), and Reddin (1973). It has been suggested that this shift to a calcium-rich diet aids shell hardening after moulting.

The apparent feeding rate of immature lobsters based on estimates of gut fullness changed little throughout the study period, with only a slight decrease by October/November. These results are very similar to those of Ennis (1973) for adult male lobsters. The feeding level coincided roughly with seawater temperature until the end of September. Feeding rate appears to remain fairly high after that period and may indicate the need for food for physiological recovery after moulting in late summer (Ennis, 1973). Scarratt (personal communication) observed that gut contents comprised approximately 1% to 2.5% of lobster weight. Values for immature lobsters in the present study are similar.

The high incidence of polychaetes in immature lobster guts in late summer may indicate increased availability of these prey at this time of year. Pettibone (1963) stated that <u>Nereis virens</u>, for example, swarms during the reproductive season in New England from March to August. Weiss (1970) noted that nereids in Long Island Sound swarmed in late spring and that incidence of nereids in lobster guts coincided with this swarming period. Nearly all nereid polychaetes die after spawning (Pettibone, 1963) and may be more accessible to lobsters when in a degenerated condition. Apart from the spawning period, polychaetes are probably available to lobsters foraging at night, as both polynoids and nereids are active night predators, especially in mussel beds (Pettibone, 1963).

Figure 15 elaborates the ways in which individual prey species may contribute to the immature lobster population diet and permits speculation about the mode of feeding of individual lobsters. It is an adaptation of the graphic portrayal of gut content analysis of Burukovskiy and Froyerman (1974). Point A indicates the theoretical situation of a single-prey diet, assuming that detection of hard parts in the immature lobster gut is possible within a period longer than the tolerable interfeeding period. Both the percentage frequency of occurrence of A in guts of the lobster population and the percentage contribution to the volume of gut items when A occurs are 100%. Theoretical species B and C are presumed to have equal importance (in terms of volume, not calorific or nutritional value) in the immature lobster population diet and are equidistant from A. A greater proportion of the theoretical population feeds on B; but when it does so, B forms a small proportion of the total volume of gut items. Species C is opposite. It is not consumed by the population as frequently as species B, but when consumed, large quantities are ingested relative to the volume of other items in the gut.

In terms of the overall volume of food consumed by immature lobsters, it appears that Cancer is the most important prey. Cancer occurs relatively frequently in immature lobster guts and contributes a relatively large proportion to the total volume of gut contents, compared to other

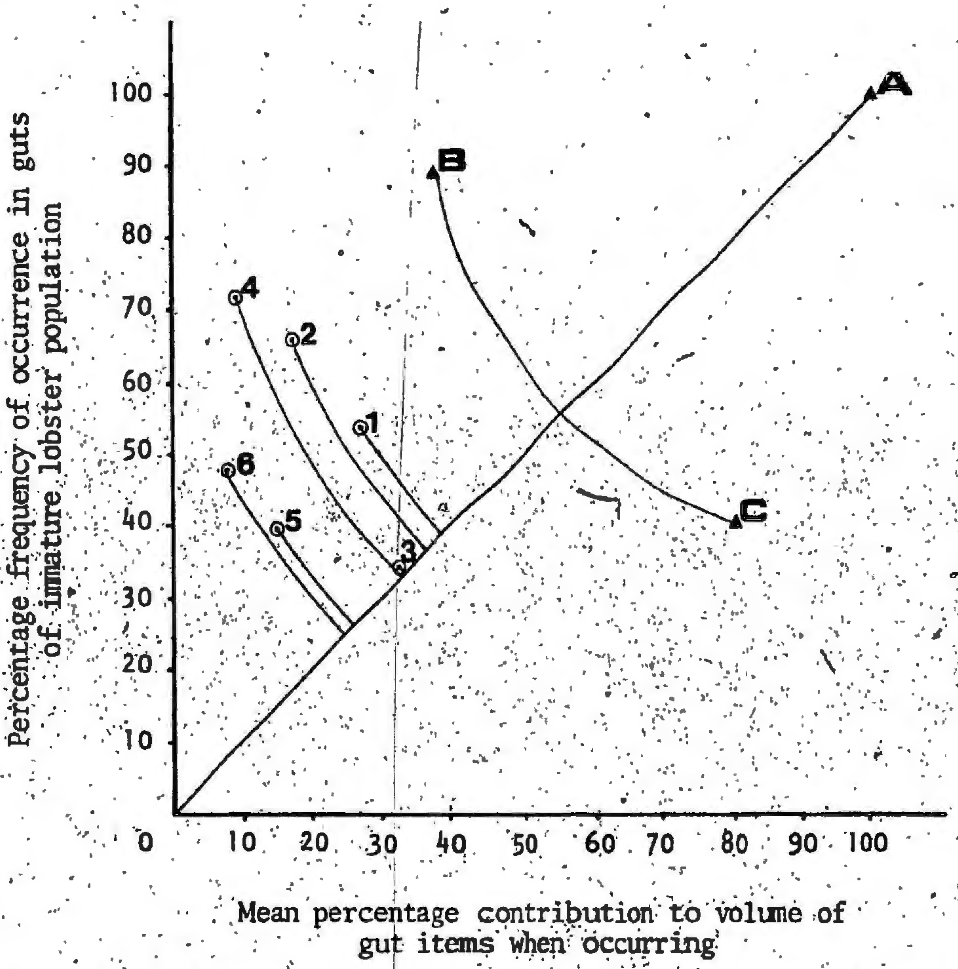

Figure 15. Relative volume contributions of prey species to the immature lobster (*H. americanus*) population diet. (see explanation in text, p. 89)

1 - *Cancer*
2 - *Mytilus*
3 - *Ophiopholis*
4 - *Strongylocentrotus*
5 - *Nereis*
6 - polynoids

items in the gut. This may indicate that Cancer is preferred by immature lobsters over other species. An individual lobster eats more of Cancer during a single feeding than it does of most other species (as shown in the controlled prey selection experiment), either because more crab is available (the crab is larger than other species), or more hard parts are ingested at a single feeding than other species (see APPENDIX E). In either case, it appears that the lobster feeds uninterrupted to satiation, ignoring other prey species which may be available. Mytilus is preferred second to Cancer by this reasoning. It occurs more frequently than Cancer in lobster guts, but contributes a smaller proportion to the total volume of gut contents. Strongylocentrotus is preferred less than either Cancer or Mytilus, being frequently ingested but contributing little to the total volume of gut contents. It is interesting that Ophiopholis, another echinoderm, is equally as important as Strongylocentrotus, but reflects a different lobster feeding strategy. It occurs much less frequently in lobster guts than urchins, but when it does, contributes a large proportion to the total volume of gut contents. This may indicate that Ophiopholis is only consumed in extreme situations (when the gut is virtually empty) such that Ophiopholis contributes a large portion to the total volume of gut contents. On the other hand, these values may indicate the mode of consumption. Ingestion of hard parts of Ophiopholis is inevitable (as confirmed by the controlled prey selection experiment) considering the morphology of brittlestars and their size. Sea urchin consumption may involve less ingestion of hard parts as the soft tissue is more easily separated from the test. Polynoids and Nereis sp. are almost equally preferred. They are less frequently consumed than the other prey species and contribute a fairly small portion to the total volume of gut contents. The small size of these polychaetes relative to the other prey species is probably the reason for these values considering that ingestion of polychaetes is virtually 100% of the prey individual when it does occur.

Consideration of the density of prey in Placentia Bay further elucidates the degree of preference of immature lobsters for certain species. While Figure 15 shows a certain preference of immature lobsters for species in terms of volume contributions to total gut contents, it is not directly related to accessibility of those species in the natural environment.

The present study shows a numerical dominance of sea urchins over mussels and crabs in the shallow subtidal zone of Placentia Bay. Density of mussels is 16% that of urchins, and crab density is approximately 0.5% that of urchin density. These data are in general agreement with other studies in eastern Canada (Himmelman, 1969; Miller et al., 1971; Scarratt and Lowe, 1972; Fletcher et al., 1974; Swiss and Osborne, 1976; Drummond-Davis, 1978; Wharton, personal communication). Swiss and Osborne (1976) conducted subtidal sampling in Placentia Bay around the Come By Chance refinery location. Their subtidal transects 5, 6, and 8 were very close to collection sites in the present investigation. They noted that polychaete worms were the dominant subtidal organisms (in terms of numbers). Mean abundance of polynoids ranged from 18.6 to 78.5 per square metre for Harmothoe imbricata and was approximately 22.1 per square metre for Lepidonotus squamatus. Mean abundance of Nereis pelagica ranged from 23.1 to 35.6 per square metre. Mean abundance of Ophiopholis ranged from 43.4 to 59.6 per square metre. These prey density data are incorporated into electivity indices discussed below.

Ivlev (1961), in his experimental study of the feeding ecology of fish, suggested that the fundamental concepts of selective feeding include the accessibility of an item of food and a degree of preference for it. He stated that the degree of success in hunting must be proportional to the degree of concentration of prey. To accommodate the variables which influence selection of food, Ivlev suggested use of an 'electivity' index:

$$E = (r_i - p_i)/(r_i + p_i)$$

where:

r_i = relative content of any ingredient in the ration (as a percentage of the whole ration)

p_i = relative value of the same ingredient in the food complex of the environment

Chesson (1978) and Cock (1978) observed that consideration of a value of Ivlev's E in isolation can be misleading as it suggests that a predator's behaviour towards a single prey type is unchanged, regardless of the percentage contribution that prey makes to the total available food. Preference values calculated using this index for different prey densities are not directly comparable. Cock (1978), however, pointed out that Ivlev's index, unlike others (see Cock, 1978 for review), does have a more functional scale of preference (it is finite) which is more sensitive to slight preference, and the index does have the advantage that more than two prey types can be included. Ivlev's electivity index was used on data from the present study, because of its simplicity and because there are no comparisons of E among experiments with varied prey densities. It provides a very useful indication of selective predation in immature lobsters.

Ivlev's electivity index was calculated for the natural situation by considering accessibility of prey in terms of their numbers (Table 22) and their biomass (Table 23). The parameter p_i was based on values from the present study and means of values reported by Swiss and Osborne (1976)

Table 22. Electivity index based on natural availability (in terms of numbers) of prey species and the percentage of immature lobster (*H. americanus*) guts in which those species were dominant.

Prey organism	Number/m^2	Percentage numerical ratio[a]	Percentage of population feeding on prey (last meal)[b]	Index
polynoids	70.7[c]	11.74	5.8	-0.34
Ophiopholis	51.5[c]	8.55	14.6	+0.26
Strongylocentrotus	42.2	7.01	5.8	-0.09
Nereis sp.	29.4[c]	4.88	6.8	+0.16
Littorina	15.8	2.62	1.0	-0.45
Acmaea	11.0	1.83	0	-1.00
Mytilus	6.9	1.15	11.7	+0.82
Asterias	1.8	0.30	0	-1.00
Cancer	0.2	0.03	18.4	+1.00

[a] as a percentage of 602.4 organisms/m^2 (110 species) of potential prey in Placentia Bay (Swiss and Osborne, 1976)

[b] equivalent to percentage of immature lobster guts in which dominant ("feeding proportions") (Peterson and Bradley, 1978)

[c] mean of values recorded by Swiss and Osborne (1976)

Table 23. Electivity index based on natural availability (in terms of biomass) of prey species and the percentage contributions of those species to the total volume of the immature lobster (*H. americanus*) population diet.

Prey organism	Number/m^2	Mean weight[a] g	Weight/m^2 g	Percentage of biomass[b]	Percentage contribution to total volume (= biomass) of diet[c]	Index
polynoids	70.7[d]	0.5	35.4	8.2	4.2	-0.32
Ophiopholis	51.5[d]	1.4	72.1	16.7	11.3	-0.19
Strongylocentrotus	42.2	4.1	173.0	40.1	6.6	-0.72
Nereis sp.	29.4[d]	0.7	20.6	4.8	6.1	+0.12
Littorina	15.8	5.3	83.7	19.4	1.3	-0.87
Acmaea	11.0	1.0	11.0	2.5	0.4	-0.72
Mytilus	6.9	2.9	20.0	4.6	11.6	+0.44
Asterias	1.8	7.4	13.3	3.1	1.1	-0.48
Cancer	0.2	14.0	2.8	0.6	14.8	+0.92

[a] based on mean weight of individuals used in controlled prey selection experiment (mean weight of *Acmaea* estimated conservatively)

[b] total weight of all organisms/m^2 is unknown; assumed negligible biomass for species other than those on the list (Miller *et al.*, 1971)

[c] relative volumes used as an estimate of relative weight contributions of prey, assuming negligible differences in specific gravities of prey

[d] mean of values recorded by Swiss and Osborne (1976)

for species not counted in the lobster collection areas. In the case considering accessibility of prey in terms of their numbers, the parameter r_i was expressed in terms of the percentage of guts in which a species was dominant, implying that the last meal was the dominant item in the gut (see APPENDIX E) and that if no preference were exhibited by lobsters, E would be 0 because of the equality of r_i and p_i. If dominance in the gut can be considered attributable to the last meal, this variable is equivalent to the proportion of all individuals found feeding on a given prey type ("feeding proportion") (Peterson and Bradley, 1978), and is a reasonable measure of r_i. The parameter r_i in the case considering accessibility of prey in terms of their biomass was based on the relative contributions of prey species to the total volume of the immature lobster diet, considered equivalent to weight contributions if there are negligible differences in specific gravities of prey.

Application of Ivlev's electivity index to the gut content data indicates a high degree of selectivity for Cancer and Mytilus (Tables 22 and 23). These two species comprise only a small percentage of the available prey species population in terms of numbers and biomass. Nereis sp., as well, is apparently selected out of proportion to its natural availability in terms of both numbers and biomass. Brittlestars are selected by immature lobsters more frequently than would be the case if predation occurred randomly, but do not comprise a disproportionate weight of the total volume of gut contents (Table 23). The negative indices suggest that most of the more numerous prey species are frequently ignored or not encountered by lobsters at a rate proportional to their abundance. They may only be consumed by immature lobsters when the more preferred prey species are not available. While the electivity indices are based on several estimates, rather than absolute values, they do provide a useful comparison of gut content data and natural relative abundance of prey.

Considerations of immature lobster feeding behaviour in terms of optimal foraging

It is important to consider the results of the present study in terms of various discussions of feeding strategies and optimal foraging (see Schoener, 1971; Pyke et al., 1977 for reviews). Most considerations of optimal feeding are of a theoretical nature, concerned with development of foraging models with predictive capabilites (Emlen, 1966; Schoener, 1969; Rapport and Turner, 1970; Rapport, 1971; Marten, 1973; Katz, 1974; Nakamura, 1974; Pulliam, 1974, 1975; Griffiths, 1975; Covich, 1976; Norberg, 1977; Hughes, 1979; Stenseth and Hansson, 1979). A few studies of actual feeding strategies of arthropod predators, fish, and echinoderm foragers exist as well (Werner and Hall, 1974; Charnov, 1976; Vadas, 1977; Cook and Cockrell, 1978; Elner and Hughes, 1978). Several studies are concerned with switching behaviour and functional responses of predators to prey density (Holling, 1965, 1966; Murdoch, 1969, 1973; Oaten and Murdoch, 1975; Cornell, 1976).

One of the main premises of optimal foraging theories is energy maximisation whereby a predator chooses its diet to maximise net energy intake per unit foraging time. An alternative premise, not exclusive of the latter, is minimisation of time in the foraging process. The parameters which are integral to theories of energy maximisation are searching time, handling time, and calorific value of the prey. Generally, the theoretical optimal diets are determined by beginning with the highest value of the ratios of food value to handling time and then adding food types to the diet in rank order. The optimal diet includes all items for which the ratio above is positive.

Several factors are important to the development of optimal foraging theories. One of the assumptions of feeding models is that predators forage efficiently, yet this requires an ability of the predator to assess energy value of individual food items. Emlen and Emlen (1975) suggested that predators are not capable of this perfect decision making. Charnov (1976) and Norberg (1977), on the other hand, suggested that energy efficiency is only one ultimate factor in feeding strategy, and Marten (1973) and Westoby (1978) suggested that sampling of food may be an important component of foraging behaviour such that variety is maintained even when food is superabundant. Maintenance of food variety may be especially important when maximum fitness of the predator is defined not only by calories but also by other nutrient factors as well (Pulliam, 1974). One of the manifestations of nutrient constraints in available diets is establishment of partial preferences whereby some prey types are consumed on some encounters but not all encounters (Pulliam, 1975). Finally, one of the main suppositions with considerable empirical proof is that predator selectivity of diet decreases as the total abundance of food decreases (Holling, 1966; Werner and Hall, 1974; Charnov, 1976; Vadas, 1977; Cook and Cockrell, 1978; Elner and Hughes, 1978).

Elner and Hughes (1978) explored optimal foraging in the shore crab, Carcinus maenas, incorporating the concept of a finite recognition time as the predator evaluates the prey by chemical and tactile clues. They suggested that, because the crabs are not visual hunters, they cannot scan large areas to estimate overall prey availability. As they crawl over the bottom, crabs encounter prey one or several at a time. Prey acceptance/rejection sequences suggested to Elner and Hughes that crabs have very short-term memories causing suboptimal prey to be rejected at first but accepted if optimal prey are not soon encountered. They suggested that this flexible mechanism rapidly adjusts the feeding response to small-scale changes in prey availability. Holling (1965) hypothesised a similar effect; extinction of learned responses in the absence of reinforcement.

Assuming that energy maximisation _is_ a maxim of optimal foraging and that there are additional nutrient requirements in excess of calories alone, it is important to assess each potential prey of immature lobsters. Available data for the prey used in the present study or for related species are summarised in Table 24.

In general, dry weight calorific values are highest for molluscs, followed by polychaetes, crustaceans, _Asterias vulgaris_, and sea urchins. Varying contributions of water and shell alter the ranking of calorific values of live animals. Wet weight calorific values (of more relevance to natural predation) are high for crustaceans, moderately high for polychaetes, and moderate for _Asterias vulgaris_ and molluscs. Wet weight calorific values are very low for _Strongylocentrotus_ sp. In terms of other nutrient values, molluscs and brittlestars are high in carbonate. Both crustaceans and molluscs have relatively high levels of protein. Echinoderms, on the other hand, are low in proteins.

There is an apparent correlation between the calorific value and protein content of prey and the degree of preference of prey by immature lobsters, suggesting that energy maximisation is a characteristic of lobster foraging behaviour. Reddin (1973) observed capture, immobilisation and opening, and consumption of three species of prey by adult lobsters. He determined that, while capture times were fairly variable, times of immobilisation, opening, and consumption of prey were quite similar, such that total handling time was approximately 100 minutes for each of _Cancer_,

Table 24. Summary of available data on prey calorific values and miscellaneous nutrient components.

Phylum	Taxon	Calorific value[a]	Other value	Reference
Annelida	4 marine polychaetes	$\bar{X}$ = 3388 (not ash-free) (674)	∿ 80% water	Tyler, 1973
	2 errant polychaetes	$\bar{X}$ = 4459 (903)	∿ 80% water	Brawn *et al*., 1968
	nereid polychaetes	$\bar{X}$ = 4857		Cummins and Wuycheck, 1971
	Nereis virens	4691		Chesney and Estevez, 1976
Mollusca	2 marine gastropods	$\bar{X}$ = 4494 (617)	82% water	Brawn *et al*., 1968
	Colus stimpsoni	4587 (471)	68% shell by weight	Tyler, 1973
	5 marine bivalves	$\bar{X}$ = 4069 (not ash-free) (284)	80% water shell-free	Tyler, 1973
	3 marine bivalves	$\bar{X}$ = 4671 (524)	89% water	Brawn *et al*., 1968
	Mytilus edulis	4448		Reddin, 1973
	"	5272 (mantle only)		Klein Breteler, 1975
	"	4657 (flesh only)		Elner and Hughes, 1978

[a] calories/gram dry weight; calories/gram wet weight indicated in brackets

.... cont'd.

Table 24 cont'd.

Phylum	Taxon	Calorific value[a]	Other value	Reference
	Mytilus edulis		> 90% protein and carbohydrates in mantle - late summer and fall	Gabbot and Bayne, 1973
	"		protein - 60% of dry weight	Adelung and Ponat, 1977
Arthropoda (crustaceans)	2 marine decapods	$\bar{X}$ = 4645 (1201)	74% water	Brawn *et al.*, 1968
	4 marine decapods	$\bar{X}$ = 4403 (1019)	75.7% water	Tyler, 1973
	juvenile *Homarus americanus*	3125		Logan and Epifanio, 1978
	Carcinus maenas (recently moulted)	4265		Klein Breteler, 1975
	Carcinus sp.		inorganics (mostly calcium) 50% of dry weight	"
	Cancer irroratus	4211		Reddin, 1973
	Cancer pagurus		protein - 22.4% of fresh weight	Vonk, 1960

[a] calories/gram dry weight; calories/gram wet weight indicated in brackets

.... cont'd.

Table 24 cont'd.

Phylum	Taxon	Calorific value[a]	Other value	Reference
	Cancer magister		high proteins in gonads and skeletal muscle; lipids in ovaries and hepatopancreas; shell - 33% of weight; haemolymph - 37% of weight; skeletal muscle - 20%; shell - 32% of weight	Allen, 1971
	Hyas		shell - 32%	
Echinodermata	Ophiopholis aculeata		81% carbonate	Brawn et al., 1968
	Asterias vulgaris	2551 (calcium carbonate correction) (633)	75% water	"
	Strongylocentrotus droebachiensis	883 (287)	68% water	"
	"	3448		Reddin, 1973
	"	770 (5800 for gonads)	65%-70% water	Propp, 1977
	Strongylocentrotus sp.		protein - ~ 4% of fresh weight	Giese, 1966

[a] calories/gram dry weight; calories/gram wet weight indicated in brackets

Strongylocentrotus, and Mytilus prey. A relatively long capture period for Strongylocentrotus was compensated for by a shorter consumption period. In nature, energy expense of capture of crabs may be greater than suggested by laboratory studies in which the mobility of crabs is ultimately restrained by tank walls. The relatively sessile nature of mussels and sea urchins probably makes the energy expense of capture of these prey small relative to that of crabs.

These considerations of capture expense are further complicated in nature by relative abundances of prey. If capture expense includes searching time, the cost of capture of crabs may further increase, given their infrequency in nature relative to mussels and urchins, although enhancement of the lobster-crab encounter rate is possible (this is discussed later). Evans (1976) suggested that the calorific superiority of Cancer over other prey more than offsets the greater energy expense required to pursue and subdue this more active prey.

The actual calorific expenditure associated with handling time of prey by lobsters has not been calculated. Assuming that Reddin's (1973) handling times are realistic, there is probably little difference in handling expense between species of a large size such as crabs, mussels, and sea urchins. Feeding on Asterias would probably involve a much smaller expense in handling, but the concomitant benefit in terms of calories is relatively low. Consumption of polychaetes probably involves little expense and, although the total volume of food at each capture is small, the calorific value of polychaetes is high. Perhaps the most productive foraging technique is capture of large prey (such as Cancer and Mytilus) with high calorific value and other nutrient attributes. For example, Elner (personal communication) observed that mussels contributed approximately seven times more energy to the diet than sea urchins when lobsters were given a choice of mussels and urchins.

Apart from the calorific value of prey, the apparent preference of lobsters for crustaceans has additional significance when the dietary requirements of lobsters are considered. For example, Castell and Budson (1974) demonstrated that adult lobsters have a requirement for high levels of dietary protein, and Logan and Epifanio (1978) suggested that the minimum calculated percentage of protein in food to maintain small lobsters is 17.4%. The actual minimum is probably higher because of loss of nitrogen in forms other than ammonia and the loss of nitrogen as glucosamine (in chitin) at each moult. Table 24 (p. 101) indicates that crabs can meet this protein requirement. Mason (1977) found that methionine and phenylalanine were essential in the diet of juvenile lobsters. NPC analysis of prey tissue extracts in the present study indicated greater than 10x higher levels of these amino acids in <u>Cancer</u> compared to levels in <u>Mytilus edulis</u> and three echinoderm species. <u>Nereis</u> sp. had very high levels of methionine and phenylalanine as well. Evans (1976) stated that lobsters have requirements for the pigment, astaxanthin, and glucosamine, and that these may be satisfied by ingestion of crustacean material.

Considering the results of the studies above, it appears that crustaceans are the most beneficial prey for immature lobsters in terms of their calorific value and other nutrient levels.

It is apparent that the prey preferences of immature lobsters have considerable adaptive value in terms of meeting food requirements. Emlen and Emlen (1975) suggested, however, that predators must have an ability to judge energy value of individual food items in order to feed in a maximally efficient way. It seems possible that olfactory messages in the form of NPCs from prey provide lobsters with information reflecting food value. As olfactory preference is apparently correlated to the food value of prey, natural selective pressure on the feeding behaviour of lobsters has resulted in their attraction to items with high NPC concentrations. This is an important adaptation, given that the NPC compositions of prey to some extent reflect their own feeding modes, and, thus, their composition: i.e., carnivores such as crabs have high levels of protein and NPCs, and are attractive to immature lobsters. This adaptation is also important considering that the best prey (crabs) are the least abundant of prey acceptable to lobsters.

Hunger must have an important influence on the degree to which immature lobsters respond to prey effluents. An 'olfactory threshold' - the concentration of NPC stimulus above which the lobster will initiate food-searching behaviour - may operate. Prey such as Cancer may consistently produce NPC concentrations above the threshold, assuring their attractiveness to lobsters. Echinoderms probably produce NPC concentrations in their effluent below the threshold of satiated lobsters. As the degree of food deprivation increases, the olfactory threshold is lowered such that more inferior prey may elicit food-searching responses in immature lobsters. This threshold control of feeding behaviour may be equivalent to the short-term memory effect on foraging behaviour of crabs described by Elner and Hughes (1978). Regardless of whether the hunger effect on optimal foraging is accommodated by a short-term memory or a flexible olfactory threshold, the ultimate result is the same; inclusion of suboptimal prey in the lobster diet with increasing hunger.

NPCs released from prey during feeding by immature lobsters appear to be important, as well, in reinforcement of feeding behaviour as suggested by results of experiments in the olfaction trough. A strong reinforcement of feeding is likely in the case of immature lobsters feeding on crabs, as shown by the large volumes consumed relative to other prey (see Table 11, p. 42; Figure 15, p. 90). There appears to be little reinforcement of feeding behaviour during feeding of immature lobsters on sea urchins. Hunger would probably influence the degree of feeding reinforcement of immature lobsters, as it would the olfactory threshold which determines the initiation of food-searching behaviour in the first place.

Evans (1976) did not see switching behaviour in lobsters when relative proportions of sea urchins and crabs were altered. This was probably because lobster food preferences are strong as shown in the present study. As long as some crabs are available to lobsters, preference for crabs can be maintained. Murdoch (1969) observed that switching behaviour was not evident in snails with strong preferences and that these preferences could not be altered by training. In the case of the lobster, prey preferences assure that an individual will feed on optimal prey whenever the opportunity exists. Suboptimal prey are probably only taken as a contingency against starvation in the absence of optimal prey (Hughes, 1979). Evans (1976) suggested that by increasing the proportion of urchins in the diet, a lobster could decrease the total time spent searching for prey. This may in fact be a net result of including sea urchins in the diet, given the greater abundance of urchins in the natural environment, but probably is not the reason for the phenomenon that Evans observed. It is likely that sea urchins are an alternative food in the absence of better prey.

It is possible to develop a scenario of the natural feeding sequences of immature lobsters, in consideration of the results of the present study and the premises of optimal foraging theory. Several predator-prey interactions are hypothesised, assuming that other decapod predators such as Cancer irroratus possess olfactory abilities and feeding motivations similar to lobsters (Case, 1964; Pecci et al., 1978).

It is assumed that immature lobsters feed only on preferred prey when close to satiation, if they feed at all. If hunger is not a strong motivation, it may be advantageous for individuals to remain in their shelters and avoid predation, at the same time waiting for fortuitous passing of palatable prey, which are identified by NPCs in their effluents. The scenario of immature lobster feeding behaviour is summarised in Table 25.

If a lobster is completely satiated it does not feed. If the gut is not completely full, a lobster may start foraging. Foraging commences at sunset and extends throughout the night with varying intensity (Scarratt, personal communication). Selectivity of prey is high at the beginning of the foraging period. Lobsters frequently encounter sea urchins but, initially, do not feed on them. Similarly, brittlestars are extremely common, but are generally cryptic and unattractive in terms of NPCs in effluent, and are ignored. Most polychaetes such as nereids and polynoids are cryptic and may be difficult to capture, but considerable numbers may be moving about at night (Pettibone, 1963). Lobster encounters with polychaetes are probably common but successful captures less so. However, the handling cost of polychaetes is low and the calorific value per unit weight is relatively high and lobsters probably attempt capture of polychaetes on every encounter unless very close to satiation. Mussels are not as common as polychaetes, brittlestars, and urchins. Encounters with mussels are therefore less common; but, because of high food value of mussels, their capture and consumption is attempted at each encounter by a less-than-sat-

Table 25. Scenario of natural foraging of immature lobsters (H. americanus) with various degrees of hunger.

Prey	Number for each crab	Distribution	Degree of hunger		
			empty gut	gut half-full	gut nearly full
polynoid	354	cryptic - uniform ?	occasional encounters; attempts capture of prey	occasional encounters; attempts capture of prey	occasional encounters; may ignore prey
brittlestar	258	cryptic - uniform ?	occasional encounters; may partially consume prey	occasional encounters; may ignore prey	occasional encounters; ignores prey
sea urchin	211	uniform, some clumping	many encounters; consumes optimal size of prey	many encounters; ignores prey	many encounters; ignores prey
nereid	147	relatively uniform, natatorial	occasional encounters; attempts capture of prey	occasional encounters; attempts capture of prey	occasional encounters; may ignore prey
mussel	35	tends to be patchy	infrequent encounters; consumes optimal size of prey	infrequent encounters; consumes optimal size of prey	infrequent encounters; may ignore prey
starfish	9	generally uniform, some clumping	infrequent encounters; may consume small amounts of prey	infrequent encounters; may ignore prey	infrequent encounters; ignores prey
crab	1	scattered	enhanced encounter rate; attempts consumption of smaller prey	enhanced encounter rate; attempts consumption of smaller prey	enhanced encounter rate; attempts consumption of smaller prey

iated lobster. Lobsters feed to satiation unless disturbed or a better prey becomes available. Lobsters attempt capture of crabs on all encounters with this prey.

If the initial foraging period does not result in successful capture and consumption of preferred prey, the lobster is more likely to feed on less preferred prey as Table 25 indicates. Percentage frequencies of remains of less preferred prey, such as sea urchin, in immature lobster guts are high, indicating that preferred prey species are not encountered frequently enough to preclude sea urchins from the diet.

The percentage frequency of occurrence of crabs in immature lobster guts is totally disparate with crab abundance in nature (Tables 22 and 23). Random encounters of lobsters and crabs alone cannot account for the high incidence of crabs in immature lobster guts. It is suggested that lobster feeding behaviour may enhance the lobster-crab encounter rate. As crabs have olfactory capabilities similar to lobsters (Case, 1964), the act of a lobster feeding on a sea urchin or a mussel, which releases prey extracts, may attract crabs to the feeding site. Presumably, lobsters can also be attracted to crabs feeding on prey. There is evidence for this prey extract reinforcement of lobster-crab encounters in nature. For example, Pecci _et al_. (1978) determined that bait in lobster traps consistently attracted high numbers of _Cancer irroratus_, _C. borealis_, and lobsters to the same traps. In the event of lobster-crab encounters, a lobster may cease feeding on the inferior prey and attempt to capture the crab. The energetic advantage of feeding on crab instead of sea urchin may be 15 times as great (Evans, 1976). Hirtle and Mann (1978) suggested that visual stimulus of food-searching behaviour through prey movement may reinforce the naturally greater attraction of lobsters to crabs over other prey, especially considering the high mobility of crabs compared to all other available prey. This, as well, may enhance the lobster-crab encounter rate.

If olfactory and visual enhancement of lobster-crab encounters does occur, much food in the form of uneaten urchins and mussels may be available to other lobsters. Apart from this, considering that lobsters feed at a rate of 1%-2% of their weight per day, most prey are probably only partially consumed in any case. Immature lobsters may be attracted to these partially consumed prey by olfactory information. On three occasions during the collection period, very small immature lobsters were observed cohabiting a shelter with an adult. Such observations have been made elsewhere in Newfoundland (Ennis, personal communication). If a dominance hierarchy is established such that the adult ignores the immature lobster, and lobsters consume captured prey in their shelters as Scarratt (personal communication) suggests, much food may be available to the immature lobster. The benefits to the small lobster in terms of avoiding exposure to predation associated with foraging are considerable.

Considerations of lobster habitat relationships

Lobsters are considered a key predator of the subtidal kelp zone of the rocky shores of eastern Canada (Miller et al., 1971). These authors suggested that production rates of prey species exceed the lobster ingestion rates by a factor of more than 10 and concluded that lobster production in the seaweed zone could be increased by reducing predation and competition for food and increasing suitable shelter. One of the main premises of their hypothesis was that the estimated consumption by lobsters of each prey species is proportional to the production of those species. This clearly may not be the case, given the evidence of the present study and others (Evans and Mann, 1977; Hirtle and Mann, 1978) for strong prey preferences in lobsters. As well, the production model of Miller et al. (1971) does not adequately consider the importance of Cancer in the diet of lobsters.

Mann and Breen (1972) suggested that heavy exploitation of lobsters may lead to overgrazing of seaweeds by sea urchins, with resultant loss of primary productivity. Breen and Mann (1976) tested this hypothesis. Their model showed that sea urchins were controlled except when lobster abundance was very low. Some changes in the model results were observed when crabs and wolffish were added. Evans (1976) stated that this model is probably too simple to predict the threshold abundance of lobsters necessary to keep urchins in check. Mann (1977) further suggested that the urchin-dominated barren grounds of St. Margaret's Bay, Nova Scotia are a new, stable configuration of the ecosystem and that a long-term decrease in primary and secondary productivity of coastal waters can be expected. He suggested that destruction of the kelp beds by sea urchins leads to destruction of the habitat for young lobsters. Mann also suggested that, given the dietary preference for crabs shown by lobsters, crabs may have a greater importance in the ecosystem dynamics than previously thought, although Hirtle and Mann (1978) suggested that urchins outnumber crabs in the diet of lobsters despite a preference for crabs.

The general concensus of most of these studies is that, while lobsters may exert a control over the sea urchin population, the degree to which this happens is difficult to determine because of lobster food preferences and predator interactions. There are no published results of gut content analyses of lobsters from the coast of Nova Scotia to corroborate speculations about lobster diets there (although such studies are planned; Michaud, personal communication). As well, the influence of immature lobsters on the kelp ecosystem has been ignored.

Results of the present study indicate that immature lobsters, while having a high incidence of small quantities of urchins in the gut, selectively feed on crabs and mussels, and possibly polychaetes, if the opportunity exists. The head of Placentia Bay is similar to St. Margaret's Bay in that kelp beds are depleted (not necessarily because of sea urchins) and urchin abundance is high; yet, substantial quantities of prey other than sea urchins exist and form an important component of the lobster diet. Electivity indices are consistently negative for sea urchins. Therefore, it appears unlikely that immature lobsters will exert a great control over sea urchin populations as long as immature lobster numbers are relatively low and better value prey remain in the area in sufficient quantity. However, if the population of immature lobsters is increased, competition for preferred food such as crabs and mussels will be greater, and a greater number of sea urchins will be killed by lobsters.

Most of the studies of lobster-urchin dynamics have suggested a rather direct effect of lobster fishing; that is, lobsters taken from the natural environment can no longer feed on urchins. When the effect of fishing is considered not only in terms of the predation pressure taken from the system, but also in terms of the effect on the remaining lobster population, the significance of the optimal foraging aspect of lobster feeding on the urchin population is considerably greater. Specifically, it is suggested that intensive lobster fishing in Nova Scotia in particular has had the net effect of reducing the competition between adults for food. Adult lobsters which are not trapped can therefore feed in an optimal way, selecting crabs and mussels to the general exclusion of sea urchins from the diet, and allowing an explosion of the sea urchin population.

SUMMARY AND CONCLUSIONS

Results of the present study indicate that immature lobsters are more attracted to and prefer intact individuals and effluent of Cancer irroratus compared to Mytilus edulis and Strongylocentrotus droebachiensis. Ammonia and probably other ninhydrin-positive compounds released as metabolites from intact prey can stimulate food-searching behaviour within an undefined range. Rate of capture of ammonia targets by immature lobsters was significantly greater than capture rates of all other target types except proline. These observations, as well as the results of ninhydrin analysis showing higher concentrations of ammonia in Cancer effluent than in Mytilus and Strongylocentrotus, may explain the greater attraction of immature lobsters to Cancer irroratus compared to other prey species.

Fidelity of attraction was maintained in tests of immature lobster behaviour elicited by prey extracts (simulating olfactory reinforcement during feeding), with ranking of behaviour variables showing the following order of apparent preference by immature lobsters: Cancer irroratus, Mytilus edulis, Strongylocentrotus droebachiensis, Asterias vulgaris, and control. The ninhydrin-positive compound compositions of the extracts may explain the various degrees of food-searching responses to the extracts. Cancer extract contained a much higher total NPC concentration compared to the other prey extracts and had significantly higher levels of proline. NPC target experiments showed that proline targets were captured more frequently than any other target.

Actual selection of intact prey by immature lobsters showed a higher attack rate for Cancer irroratus, compared to Mytilus and Strongylocentrotus, although factors other than olfactory preference, such as accessibility and size of prey, may be important determinants of food selection. For the natural environment, where a multitude of factors determine the selection of prey by immature lobsters, Ivlev's electivity indices showed a very high selection for Cancer, moderate selection for Mytilus, and negative selection for Strongylocentrotus. Gut content analysis showed that a high percentage of the immature lobster population feeds on sea urchins, mussels, and crabs. The gut content data in addition suggested that, at single feedings, greater amounts of crab are consumed compared to mussels and sea urchins. Controlled selection experiments and gut content analysis also revealed the potential importance of small prey such as brittlestars and polychaetes in the diet of immature lobsters.

The consistent attraction of immature lobsters to prey with high calorific and protein levels indicates that they probably forage in an optimal way, maximising energy and various nutrients per unit foraging time.

Future research is required on the selection of prey by immature lobsters in the natural environment to determine the decisions made by lobsters during foraging sequences, in the same manner as the study by Elner and Hughes (1978), and to test the scenario outlined in the discussion. Such variables as hunger and prey density would have to be carefully monitored. Experiments should be devised to determine which factors, such as short-term memory and a flexible olfactory threshold, are operative in the foraging behaviour of lobsters. Immature lobsters, by virtue of their probable numerical dominance over adult lobsters, may comprise a much more important component of the subtidal community than previously thought and deserve a greater attention in hypotheses of subtidal faunal relationships.

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APPENDIX A

Individual lobster data at time of collection.

Collection date	Location	Wet weight g	Carapace length mm	Sex	Lab. experiments	Gut content analysis
7/11/75	Grassy Pt.	68.8	44	f	✓	
"	"	55.9	41	f	✓	
"	"	98.4	49	f	✓	
"	"	48.6	39	m	✓	
"	"	21.0	31	m	✓	
"	"	44.0	37	f	✓	
"	"	74.3	46	m	✓	
"	"	12.1	27	m	✓	
"	"	55.8	42	m	✓	
"	"	59.2	42	f	✓	
"	"	55.1	42	f	✓	
"	"	49.1	39	f	✓	
"	"	163.8	58	m	✓	
"	"	21.0	30	f	✓	
"	"	71.7	44	f	✓	
"	"	38.4	37	f	✓	
"	"	124.0	53	m	✓	
"	"	74.5	45	f	✓	
"	"	23.5	32	f	✓	
"	"	69.2	46	m	✓	
"	"	41.2	40	m	✓	
"	"	11.0	23	f	✓	
30/01/76	"	59.7	43	m	✓	
"	"	45.7	38	m	✓	
"	"	12.3	27	f	✓	
"	"	64.8	46	m	✓	
"	"	30.9	34	m	✓	
"	"	38.3	37	m	✓	
"	"	34.5	35	f	✓	
"	"	46.3	38	f	✓	
"	"	20.8	29	m	✓	
"	"	39.5	37	m	✓	
27/02/76	"	32.8	36	m	✓	
"	"	1.5	13	?	✓	
"	"	24.9	32	f	✓	
"	"	162.1	59	f	✓	
"	"	113.2	51	f	✓	
4/06/76	Arnold's Cove	97.2	49	f		✓
"	"	72.3	45	f		✓
"	"	151.4	62	f		✓
"	"	48.2	41	f		✓
"	"	57.3	43	f		✓
"	"	108.7	52	f		✓

.... cont'd.

APPENDIX A cont'd.

Collection date	Location	Wet weight g	Carapace length mm	Sex	Lab. experiments	Gut content analysis
4/06/76	Arnold's Cove	97.8	49	f		✓
"	"	42.4	38	f		✓
"	"	97.0	49	f		✓
"	"	115.8	54	m		✓
"	"	89.2	47	m		✓
"	"	111.9	52	m		✓
"	"	50.5	40	m		✓
"	"	129.0	54	f		✓
"	"	35.6	35	f		✓
"	"	40.0	37	f		✓
"	"	2.4	15	?		✓
"	"	38.7	37	f		✓
"	"	14.3	27	m		✓
"	"	46.8	39	f		✓
"	"	44.6	39	f		✓
"	"	47.6	40	f		✓
"	"	50.7	40	f		✓
"	"	21.8	31	m		✓
"	"	19.6	30	f		✓
"	"	16.0	27	m		✓
"	"	10.8	23	f		✓
"	"	1.3	12	?		✓
23/06/76	Grassy Pt.	90.3	48	f		✓
"	"	12.4	25	f		✓
"	"	142.0	54	m		✓
"	"	129.8	52	f		✓
"	"	65.8	43	m		✓
"	"	84.4	47	m		✓
"	"	72.8	45	f		✓
"	"	64.1	43	f		✓
"	"	66.0	44	m		✓
"	"	30.5	33	f		✓
"	"	24.8	32	f		✓
"	"	19.3	28	f		✓
13/08/76	Spencer's Cove	251.9	72	f		✓
"		254.3	70	m		✓
"	"	271.4	69	f		✓
"	"	197.9	65	m		✓
"	"	60.0	42	f		✓
"	"	275.4	73	m		✓
"	Grassy Pt.	143.7	55	f	✓	
"	"	151.4	56	m	✓	
"	"	133.3	54	f	✓	
"	"	144.4	58	m	✓	
"	"	40.0	36	f	✓	
"	"	94.7	48	f	✓	

.... cont'd.

APPENDIX A cont'd.

Collection date	Location	Wet weight g	Carapace length mm	Sex	Lab. experiments	Gut content analysis
13/08/76	Grassy Pt.	59.9	42	m	✓	
20/08/76	Arnold's Cove	83.0	50	m	✓	
"	"	61.7	50	m	✓	
"	"	14.6	27	f	✓	
"	"	37.0	35	f	✓	
"	"	67.7	50	f	✓	
"	"	55.3	42	f	✓	
"	"	16.4	27	f	✓	
"	"	25.3	32	f	✓	
"	"	97.9	51	m	✓	
"	"	84.8	47	f	✓	
"	"	58.0	43	m	✓	
"	"	82.2	47	m	✓	
27/08/76	Grassy Pt.	74.7	49	f		✓
"	"	150.1	57	f		✓
"	"	117.7	53	f		✓
"	"	138.3	57	m		✓
"	"	176.3	58	f		✓
"	"	196.6	62	f		✓
"	"	171.3	61	m		✓
"	"	109.1	53	m		✓
"	"	129.6	54	m		✓
"	"	122.0	54	m		✓
"	"	97.5	50	m		✓
"	"	44.5	40	m		✓
"	"	24.4	31	m		✓
3/09/76	"	90.7	49	f	✓	
"	"	57.2	41	m	✓	
"	"	65.7	48	m	✓	
"	"	91.9	49	f	✓	
"	"	92.2	51	f	✓	
"	"	144.8	58	f	✓	
"	"	133.6	61	m	✓	
"	"	51.5	41	f	✓	
"	"	52.2	41	f	✓	
"	"	104.7	52	f	✓	
"	"	134.4	55	m	✓	
"	"	138.6	55	m	✓	
"	"	107.9	53	m	✓	
10/09/76	Spencer's Cove	49.0	40	f	✓	
16/09/76	"	59.9	42	m		✓
"	"	92.8	49	m		✓
"	"	178.6	60	f		✓
"	"	119.0	54	f		✓
"	"	92.9	51	m		✓
"	"	106.2	51	f		✓
"	"	103.9	52	m		✓

.... cont'd.

APPENDIX A cont'd.

Collection date	Location	Wet weight g	Carapace length mm	Sex	Lab. experiments	Gut content analysis
16/09/76	Spencer's Cove	89.4	49	f		✓
"	"	4.4	18	f		✓
"	"	9.3	23	f		✓
"	"	19.1	30	m		✓
26/10/76	"	10.2	23	f		✓
"	"	30.9	35	m		✓
"	"	32.9	36	m		✓
"	"	87.6	47	f		✓
"	"	149.2	57	f		✓
"	"	244.3	71	f		✓
"	"	248.2	67	m		✓
18/11/76	Grassy Pt.	89.9	49	m		✓
"	"	201.7	64	m		✓
"	"	140.0	55	m		✓
"	"	31.3	34	f		✓
"	"	79.1	45	f		✓
"	"	55.2	43	m	✓	
"	"	24.7	31	m	✓	
"	"	43.2	37	f	✓	
24/11/76	Arnold's Cove	95.2	49	f		✓
"	"	106.5	51	m		✓
"	"	107.7	52	f		✓
"	"	68.7	46	f		✓
"	"	60.7	44	f		✓
"	"	74.9	45	f		✓
"	"	51.2	41	m		✓
"	"	41.1	39	m		✓
"	"	33.6	35	f		✓
"	"	28.5	34	f		✓
"	"	16.4	28	m		✓
"	"	2.9	16	m		✓
"	"	1.9	15	?		✓
25/11/76	Spencer's Cove	70.5	44	f		✓
"	"	151.8	58	f		✓
"	"	101.1	50	m		✓
"	"	84.3	46	f		✓
"	"	67.7	45	m		✓
"	"	48.4	40	m		✓
"	"	6.2	20	m		✓
"	"	5.6	20	f		✓

APPENDIX B

Free ninhydrin-positive compound (NPC) concentrations of prey organism tissue extracts. (µmoles/ml)[a]

NPC	Asterias (n=3)	Ophiopholis (n=1)[b]	Strongylocentrotus (n=4)	Littorina (n=1)[b]	Mytilus (n=4)	Nereis (n=1)[b]	Cancer (n=4)
alanine	0.667 ± 0.239	1.204	1.873 ± 0.721	7.284	2.693 ± 0.835	28.880	20.261 ± 7.734
ammonia	1.261 ± 0.363	10.694	1.665 ± 1.021	16.060	3.285 ± 1.495	65.254	22.536 ± 11.814
arginine	0.326 ± 0.090	0.068	1.050 ± 0.246	1.343	0.398 ± 0.255	0.120	11.816 ± 5.345
asparagine	0.040 ± 0.021	0.176	0.137 ± 0.054	-[c]	0.306 ± 0.129	unres.	2.152 ± 1.096
aspartic acid	0.191 ± 0.048	0.171	0.220 ± 0.084	0.718	1.837 ± 0.557	0.050	2.711 ± 1.239
glutamic acid	0.258 ± 0.085	0.975	0.679 ± 0.127	13.468	1.763 ± 0.626	11.240	11.239 ± 3.278a
glutamine	0.055 ± 0.019	0.136	0.311 ± 0.105	7.828	0.614 ± 0.124a[d]	5.560	6.473 ± 0.778a,s,m
glycine	15.001 ± 6.090	36.124	14.075 ± 4.922	3.573	11.510 ± 8.053	48.200	35.703 ± 8.210
leucine	0.262 ± 0.081	0.110	0.565 ± 0.139	1.785	0.359 ± 0.156	21.272	12.277 ± 3.770
lysine	0.153 ± 0.088	0.377	0.735 ± 0.219	0.362	0.907 ± 0.342	6.358	11.037 ± 3.380
proline	0.024 ± 0.024	trace	0.110 ± 0.066	13.036	0.612 ± 0.340	5.667	12.729 ± 3.803a,s
serine	0.487 ± 0.138	0.204	0.454 ± 0.180	3.703	1.134 ± 0.517	0.550	5.067 ± 2.736
taurine	0.742 ± 0.373	43.769	0.983 ± 0.129	6.984	10.337 ± 5.062	0.580	21.111 ± 2.977a,s
valine	0.312 ± 0.094	0.160	0.693 ± 0.161	5.865	0.316 ± 0.152	20.126	10.328 ± 3.023
urea	13.530 ± 9.273	120.000	76.956 ± 68.188	trace	719.973 ± 206.581a	-	66.485 ± 39.275
other NPCs[e]	1.615	2.618	2.859	24.765	3.424	72.794	40.186
polyamines	0.035	-	0.275	0.348	0.029	-	0.175
total concentration[f]	21.394	96.786	26.409	106.774	39.495	286.651	225.626

a mean ± standard error
b one sample from eight individuals
c not detected; for polyamines not determined

.... cont'd.

APPENDIX B cont'd.

<u>d</u> significantly greater than: a - <u>Asterias</u>; s - <u>Strongylocentrotus</u>; m - <u>Mytilus</u>, $p < 0.05$

<u>e</u> β-alanine, α-amino adipic acid, α-amino n butyric acid, β-amino isobutyric acid, γ-amino butyric acid, anserine, citrulline, cystathionine, cysteic acid/phosphoserine, half cystine, ethanolamine, reduced glutathione, glycerophosphoethanolamine, histidine, hydroxylysine, hydroxyproline, isoleucine, methionine, methionine sulphoxide, 3-methylhistidine, ornithine, phenylalanine, phosphoethanolamine, sarcosine, threonine, tryptophan, tyrosine

<u>f</u> excluding urea, unknowns, trace amounts, and polyamines

APPENDIX C

Gut items of immature lobsters (<u>Homarus americanus</u>) - characteristic hard parts.

Prey organism	Characteristics
<u>Cancer irroratus</u>	fragments of carapace with characteristic pigmentation; portions of pereiopods; pereiopod tips very common; claw knuckles common; apodemes occasional; parts of maxillipeds and maxillae; eyes; gills; parts of antennae occasional
<u>Hyas araneus</u>	portion of pereiopod
<u>Pagurus arcuatus</u>	characteristic claw and portions of pereiopods
unidentified crustacean	usually heavily worn or digested portions of carapace and pereiopods
<u>Nereis</u> sp.	jaws extremely common, frequently numerous in a single gut; denticles common; setae extremely common; acicula common; occasional complete parapodium; peristomial cirri occasional
polynoid polychaete	jaws extremely common, frequently numerous in a single gut; elytra very common; denticles occasional; peristomial cirri occasional; frequently portions of body intact
unidentified polychaete	only setae evident
amphipod	portion of body with large coxal plates
chiton	shell valves intact
sponge	some tissue with spicules
<u>Lacuna vincta</u>	portions of characteristic shell occasional; opercula common
<u>Littorina littorea</u>	portions of shell common; thick characteristic opercula common
<u>Lora bicominata</u>	complete shell
<u>Margarites costalis</u>	complete shell
unidentified gastropods	small portions of abraded shell

....cont'd.

APPENDIX C cont'd.

Prey organism	Characteristics
Anomia aculeata	portions of characteristic shell
Hiatella arctica	one complete valve
Mytilus edulis	portions of shell; periostracum extremely common; byssus threads occasional
Tellina agilis	complete set of valves
unidentified bivalve	portions of abraded shell common
Asterias vulgaris	calcareous portions of arms occasional
Ophiopholis aculeata	calcareous vertebrae of arms common; small arm spines common
Strongylocentrotus droebachiensis	spines common; portions of test extremely common; pedicellaria occasional; portions of jaws occasional
bryozoan	zoecia with spines occasional

APPENDIX D

Percentage of immature lobsters (*Homarus americanus*) from Placentia Bay in various moult stages.

Collection date	n	Moult stage[a]								
		C_4	D_0	D_1'	D_1''	D_1'''	D_2'	D_2''	D_3'	recent moult
June 4, 1976	28	82.1	17.9	-[b]	-	-	-	-	-	-
June 23, 1976	12	66.7	25.0	8.3	-	-	-	-	-	-
August 13, 1976	6	-	-	-	-	16.7	16.7	16.7	16.7	33.3
August 27, 1976	13	15.4	-	-	-	-	-	23.1	7.7	53.8
Sept. 16, 1976	11	54.5	-	-	-	-	-	-	9.1	36.4
Oct. 26, 1976	7	100.0	-	-	-	-	-	-	-	-
Nov. 18, 1976	5	100.0	-	-	-	-	-	-	-	-
Nov. 24, 1976	13	100.0	-	-	-	-	-	-	-	-
Nov. 25, 1976	8	100.0	-	-	-	-	-	-	-	-

[a] moult stage classification according to Aiken, 1973

[b] no lobsters in this stage observed

APPENDIX E

Considerations of gut content analysis

Gut analysis based on indicator particles has been criticised by Reddin (1973). He suggested that this method is invalid for determining diet since lobsters do not seem to actively consume shells except at moult. This latter statement is inaccurate. In all cases of immature lobsters feeding on ad libitum diets of Cancer irroratus, Mytilus edulis, and Strongylocentrotus droebachiensis, enough shell or test was consumed by lobsters to be readily detected in the guts. While Reddin's criticisms of the 'indicator' technique of gut analysis are not strictly applicable, some important points or assumptions inherent in the method are raised.

In the first instance, the sources of indicator fragments are either active predation of live prey or incidental/deliberate ingestion of shell fragments from the bottom. Laboratory experiments show that ingestion of shell is common during feeding on crabs, mussels, and sea urchins, and ingestion of small hard parts is very probable in the case of feeding on polychaetes and brittlestars, considering their size and morphology. An indeterminable proportion of prey hard parts may originate from the guts of lobster prey such as crabs and polychaetes, but this must be small. Deliberate ingestion of shell fragments appears to be common in post-moult lobsters. The high number of mollusc species in immature lobster guts and the low individual species occurrence support this hypothesis.

Several other factors may influence the percentage frequency of occurrence of prey species in immature lobster guts and the percentage of guts in which a single species is dominant. These are summarised below.

Factors which may bias values for incidence of prey items in immature lobster guts

Percentage frequency of occurrence of items in lobster guts:

1. The probability of ingestion of indicator parts of a particular prey species.
2. The length of residency of indicator parts in a lobster gut.
3. Real differences in the percentages of the lobster population feeding on various prey species.

Percentage frequency of occurrence as dominant gut item:

1. The differential rate of ingestion of indicator parts; i.e., for a species A, there may be a greater probability of consuming more indicator parts than for a species B.
2. The length of residency of indicator parts in the lobster gut; i.e., there may be a net accumulation of hard parts of a particular species to the point of dominancy in the gut.
3. Sequence of feeding on various species; i.e., a species A was consumed more recently than a species B and therefore is dominant in the gut. This is related to gut clearance times.
4. Assuming an equal chance of consuming indicator parts, more of one species was consumed than any other individual species.

In terms of the percentage frequency of occurrence of species in immature lobster guts, factor 1 will probably cause little bias of results. Results of the present study show a definite ingestion by immature lobsters of prey hard parts, regardless of the species. Presence of a species was noted regardless of the relative quantities of hard parts.

Factor 2 has been suggested by Burokovskiy and Froyerman (1974) and Peterson and Bradley (1978) as a source of error in determination of diets of predators. They defined residence time as the period of time during which the prey item remains recognisable in the gut. Those prey species with characteristically long average residence times will tend to be overrepresented among the gut contents. Christensen (1970) noted that in the gut contents of an asteroid, Astropecten irregularis, the residence times of gut items differed by a factor of more than 50, substantially biasing the determination of feeding proportions. Two indications in the present study reduce the possibility of factor 2 influencing the value of incidence of prey items. Observations of guts of immature lobsters deprived of food or fed diets of cod and liver showed that prey hard parts, regardless of the species, were capable of remaining in the gut for long periods. For example, parts of all the major prey species could remain in lobster guts for at least 10 days, albeit in progressively smaller quantities as the period of food deprivation increased. There were no obvious trends indicating that parts of some prey were more likely to have longer gut residence times than other prey, with the possible exception of Asterias and Strongylocentrotus with apparently shorter residence times. Secondly, the gut evacuation rates of hard parts from sea urchin, crab, and mussel are apparently quite similar, substantial clearance of the guts occurring by the third or fourth day after feeding. In the case of lobsters feeding on Ophiopholis, parts of the brittlestar arms were observed in the faeces within one day after feeding. Brockerhoff et al. (1970) found that lobsters fed chopped mackerel and held at temperatures of 9° C. to 12° C. had guts free of food particles on the third day after feeding and that gastric juice was clear by the fifth day.

Assuming that factors 1 and 2 do not significantly bias percentage frequencies of occurrence of prey in immature lobster guts, then the third factor, real differences in the proportion of the lobster population feeding on prey, must be the factor with the greatest influence on percentage frequency of occurrence of gut items.

Several factors may influence the recorded percentage frequency of occurrence of dominant gut items. Factor 1 in the previous summary may influence dominancy values. Two prey species of equal mass may have different quantities of hard parts. For example, an ingested nereid would probably contribute fewer hard parts in the gut of an immature lobster than an ingested crab. Although the same quantity of tissue may be ingested, the gut would show a greater contribution of crab parts to the total volume of gut contents. However, the influence of factor 1 is minimised if capture of the lobster to be examined occurs soon after ingestion of its last meal, before significant digestion of the soft tissues has occurred. For example, in the case of polychaetes being dominant in the gut, considerable quantities of soft tissues with associated hard parts were observed. Table 19 (p. 58) indicates that Factor 1 has a negligible effect on dominancy values when comparing diets of Cancer, Mytilus, and Strongylocentrotus.

Factor 2 probably has little influence on percentage frequencies of occurrence for reasons stated above (lengths of residency of items in immature lobster guts are similar). Assuming that gut clearance rates are approximately the same regardless of prey species, and that factor 1 does not have a profound effect on recorded occurrence values, the last species consumed before capture of the lobster will probably be the dominant item in the gut. Experiments in the laboratory indicated that last meals always contributed the greatest proportion to the total volume of gut items, at least within eight days of the last feeding. If factor 3 is generally operative, then the values for dominancy of gut items can be considered equivalent to the percentages of the population feeding on certain species just before capture. Factor 4 probably has a real effect on dominancy values as well. If more of one species is consumed than other individual species during a single feeding period such as one night, then that species will be dominant in the gut. This is intuitively obvious.