THE ECOLOGY AND FEEDING HABITS OF THE AMERICAN LOBSTER (HOMARUS AMERICANUS (MILNE-EDWARDS, 1837)) IN NEWFOUNDLAND

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AND FEEDING HABITS OF
THE AMERICAN LOBSTER (HOMARUS AMERICANUS (MILNE-EDWARDS, 1837))
IN NEWFOUNDLAND

by

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ABSTRACT

The feeding habits, energy intake, and prey preferences of Homarus americanus were examined in the laboratory. Preference was determined by placing various animals in tanks with lobsters. This confirmed that sea urchins, crabs, mussels and periwinkles are readily eaten by lobsters. Feeding was observed at night using an infrared light and the feeding actions were described. The caloric intake of four lobsters maintained for one year, two at 15°C. were measured. It varied directly with fluctuations in the water temperature. It was learned that a sea urchins ability to grip it's substrate depends directly on the sea water temperature. Thus as lobster food they are more easily acquired during the colder winter months.

A distribution study considered both food and bottom type. It indicated a direct correlation between landings and distribution of lobsters; and between lobsters, bottom type and food.

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INTRODUCTION

Homarus americanus (Milne-Edwards, 1837), occurs on the eastern coast of North America from North Carolina to Henley Harbour, Labrador (Templeman, 1940). It is most abundant in the centre of its range; the most productive areas (from the 1950 commercial landings cited by Wilder, 1954) being southern Nova Scotia, southern Gulf of St. Lawrence and the coast of Maine. In Newfoundland, the largest landings (also probably the greatest abundance) are on the West Coast and in Notre Dame Bay (Canada Fisheries Statistics Annual, 1956-1969).

In spite of the fact that the lobster is commercially quite valuable (cash value in Newfoundland is 9% of the landed value of fisheries products, Templeman, 1966), there is very little information on it's food habits and how these influence it's local distribution and abundance (Lewis, 1970). The objectives of this investigation were to determine the composition of the diet of lobsters in Newfoundland; their prey preferences; mechanisms of feeding; yearly nutritional requirements as related to the sea water temperature; their relationship with sea urchins; and the influence of bottom type and prey abundance on their populations.

In addition to the economic benefits of the fishery, lobsters also can have a great effect on their environment. For instance, in areas with a high density of lobsters the sea urchin population is reduced and kelp and other algae that the sea urchin feeds on increases (Himmelmann, 1969 and Mann and Breen, 1972). Conversely where lobster populations are low, sea urchins are abundant and the rocks are bare of kelps and most other algae. Consequently, it would be expected that lobsters might reduce populations of their other prey species eg. crabs, mollusks, etc.

Not only do lobsters control sea urchin populations hence affecting the amount of algae present (Mann and Breen, 1972), but they compete with Cancer borealis and irroratus in Nova Scotia, C. irroratus being found commonly on sand here (Scarratt and Lowe, 1972), rather than on rock.

To cognize the importance of the lobster on the ecology of the subtidal areas in Newfoundland, it is imperative to determine both the composition of lobster diet and any preferences in this diet. Also their feeding behaviour could indicate why one prey species is more popular than another. For instance, because C. irroratus has weaker claws than C. borealis and so is easier to capture, it is more often utilized than C. borealis as lobster food (Weiss, 1970).

In light of the close association between lobsters and sea urchins, studies were done to ascertain the force with which a sea urchin grips it's substrate and how this varies with temperature. This will indicate if sea urchins are more readily available at any one time of the year as prey species for lobsters.

The yearly nutritional requirements of lobsters are important for two reasons: first, how much of one species does a lobster consume at various temperatures and secondly, does the temperature control how much it consumes. From this something of the energy flow can be deduced and also the pressure on the invertebrate prey species.

Last is the correlation between the laboratory experiments and what occurs in the environment. While laboratory studies are worthwhile, they can not be applied in some cases to the environment. Ennis found that the growth increment with lobsters kept and fed in cages in the sea was higher than in the environment (Squires, Tucker and Ennis, 1971). In addition to this, the question of whether lobsters are located in certain habitats because of the bottom type or presence of food was investigated. Templeman and Tibbo (1945) state that lobster distribution is governed by larval drift but the presence of food and habitat could also influence this.

Since lobsters are widely distributed, they can be expected to have variable behavioural patterns over this wide range. Thus, a study of the above mentioned facts in Newfoundland is imperative both for the lobster fishery and for the ecology of the marine environment; both of which could be affected by the removal of large numbers of lobster.

MATERIALS AND METHODS

Prey Preference

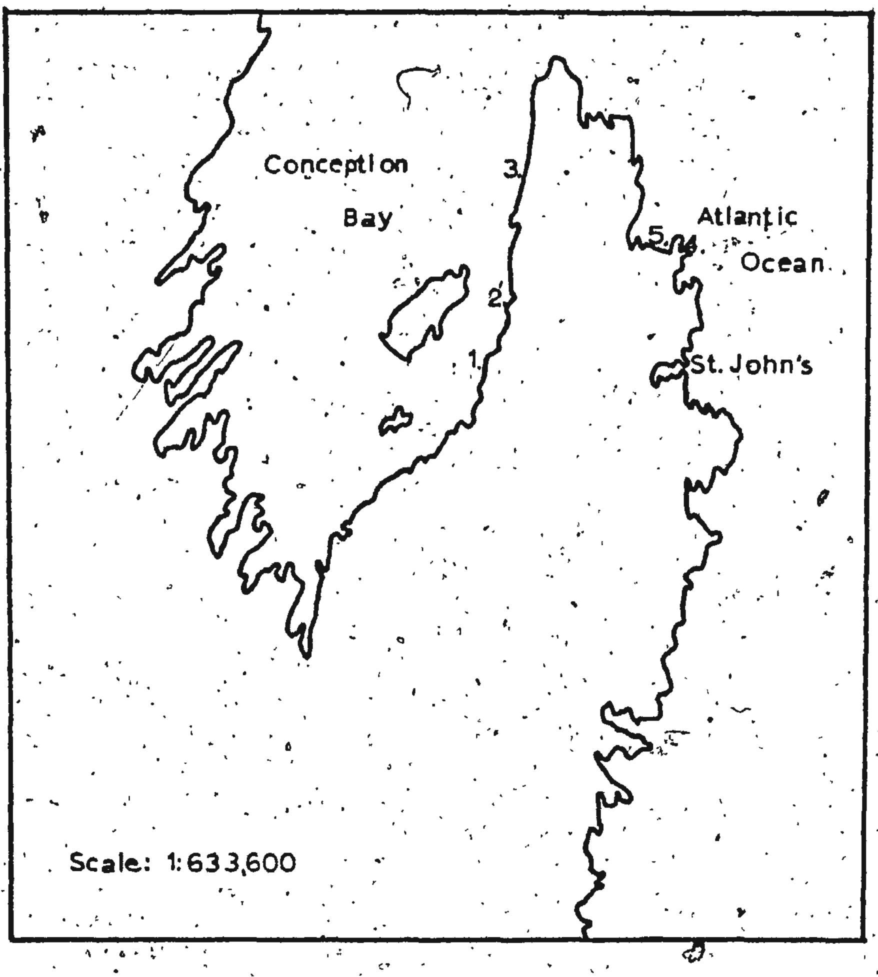
Lobsters were obtained for the preference experiments by self contained underwater breathing apparatus (SCUBA) and by purchasing them from local fishermen (see Appendix A); all of the sampling sites being located on the Avalon Peninsula (see Figure 1). A permit allowing lobsters to be sampled using SCUBA techniques was obtained from the Department of Fisheries (now Department of the Environment) covering the periods from April to September, 1971 and from June to September, 1972. Food for the lobsters was collected from both Logy Bay and Outer Cove (see Figure 1) at two week intervals throughout the study period and these were kept alive in continuously flowing sea water at the Marine Sciences Research Laboratory (MSRL).

The lobsters were placed in tanks (86x274x17cm) at the MSRL. The sea water in these tanks was never more than ±2.0°C. different from ambient sea water at a depth of 10 meters in Logy Bay. The tanks were covered over with black plastic garbage bags to reduce visual disturbances from the laboratory. Each of these tanks was divided in half using a meshed-in frame (built by MSRL technical staff). Artificial burrows made of field tile were added to the tanks.

A known weight (to nearest 1/10 of a gram) of live food was added to the tanks with the lobsters and left there either for two weeks or until it was consumed. Food was added quantitatively to approximate numbers in the environment (eg. five sea urchins at a time). The tanks were usually inspected daily for leftover material, and at no time did more than two days pass between inspections.

Figure 1. Locations from which lobsters and prey were obtained for preference studies.

Sites: 1. St. Thomas
2. Portugal Cove
3. Bauline
4. Logy Bay
5. Outer Cove


Conception
Bay
Atlantic
Ocean
St. John's
1.
2.
3.
4.
5.
Scale: 1:633,600

Consumption of prey was rarely observed, and therefore had to be deduced from what was left in the tanks compared to what had been originally placed there. An animal was considered consumed when it's shell had been broken open and the insides removed or in the case of soft-shell invertebrates (e.g. Bryozoans) when the animal was missing from the tank. The preference graphs (see Results) consider that an animal was consumed after it had all been eaten. For example, Figure 5 shows both a percentage of <u>Mytilus edulis</u> tested against <u>Strongylocentrotus droebachiensis</u> and the number of tests (67.8% and 31 tests). This means that <u>M. edulis</u> would be consumed over <u>S. droebachiensis</u> 67.8% of the time or that out of 31, <u>M. edulis</u> was consumed 21 times.

The diet and availability of prey to lobsters were determined from the laboratory preference experiments. For instance, lobsters selected <u>M. edulis</u> over many other organisms and so <u>Mytilus</u> is considered to be a major item of their diet. Some of the other organisms tested i.e. <u>Lunatia</u> are not found commonly with lobsters but prefer sandy bottoms and so while lobsters will consume them they weren't considered to be a major food source and so are listed as minor prey. Other animals because the lobsters were unable to break through their hard shells (e.g. <u>Placopecten</u>) were not eaten except in the case of very small individuals or if only fed viscera.

<u>Lobster Consumption</u>

For this portion of the study, lobsters and food were obtained as above (see Appendix A). As before, two lobsters were kept in partitioned tanks. One tank had sea water at ambient temperatures (see Figure 9(b)) flowing through it while the other had heated (15°C.)

sea water flowing through it for most of the year (see Figure 9(a)). The sea water was heated by a device designed and built by Technical Services, Memorial University.

For one year, one lobster in each tank was fed only Strongylocentrotus droebachiensis while the other was fed only C. irroratus. These species were chosen because they appeared to be the most common food of H. americanus. Material was wet weighed as before and the tanks were checked every two days at which time more material if required was added. In this manner the numbers of crabs and sea urchins consumed was determined.

Bomb Calorimetry. After observing what portions of the common prey species lobsters consume, these fractions were burned in an oxygen bomb calorimeter. The invertebrate specimens were obtained at the regular two week collection periods and were used in the bomb calorimeter as soon as possible after collection. All animals were dried to a constant weight in a Fisher Isotemp Oven at 45°C. and ground to pass through a number 60 mesh sieve. Approximately one gram samples were combusted in a Parr adiabatic oxygen bomb calorimeter. The samples were weighed on a Mettler Type H15 balance (Parr Instrument Co., 1964). After each combustion the acid and fuse wire determinations were made. In addition, sulphur content corrections were determined if necessary (above 0.1%). The sulphur method used is that involving precipitation of barium sulphate by the addition of barium chloride to a solution containing elemental sulphur.

All material was found to be easily combustible except Bryozoa probably due to it's high carbonate content.

The ash from the calorimetry studies was tested for complete burning by comparing weights before and after being placed in a Dubuque IV Type 10500 Furnace for a 24 hour period at 600^{0}C. The ash free weights were determined by comparing weights of the samples before being combusted and after being ashed as above. The cycle of caloric intake was determined from the calories in that portion of the prey consumed by the lobsters.

Sea Urchin Holding Force

To determine the force with which a sea urchin grips it's substrate, one hundred sea urchins (Strongylocentrotus droebachiensis) were held in a flat wet table through which sea water was continuously flowing. Not more than twice per day (more than this affected the holding force) they were pulled off of the substrate using a Chatillon 0-5kg spring scale hooked onto a harness which was attached around a sea urchin. By pulling on the handle attached to the spring balance, force was exerted at right angles to the substrate. Immediately after being removed from the substrate the sea urchins were weighed. All sea urchins that left their podia attached to the substrate were disposed of. The sea urchins were collected from Logy Bay just prior to testing. They were tested at the same temperature as the sea water flowing into the MSRL. A 48 hour stabilization period was given the sea urchins and the experiment ran approximately one and one half weeks at each of the temperatures used. The 15^{O}C. temperature was reached using the above mentioned heating apparatus. The temperatures and the times the experiments were run are: 0^{O}C. - February 8-20; 5.0^{O}C. - April 7-14; 9-11^{O}C. - July 16-23; 15.0^{O}C. - August 15-23, 1972.

Feeding Habits

This section of the study was done using Infrared light at night enabling observations on undisturbed lobsters. Kennedy and Bruno (1961) have described (see Figure 2) the sensitivity of lobster vision. It ranges from 450mu to 600mu peaking at about 510mu. The filter used on the safelight for illumination of the tank was a 1A medium red Kodak Wratten Filter which transmits light at greater than 1% above 615mu. This is above what the lobster can detect visually and ordinary movement of the observer seemed to have no effect on it. However, it was noticed during the experiments that excessive movements of the observer could disturb the lobster.

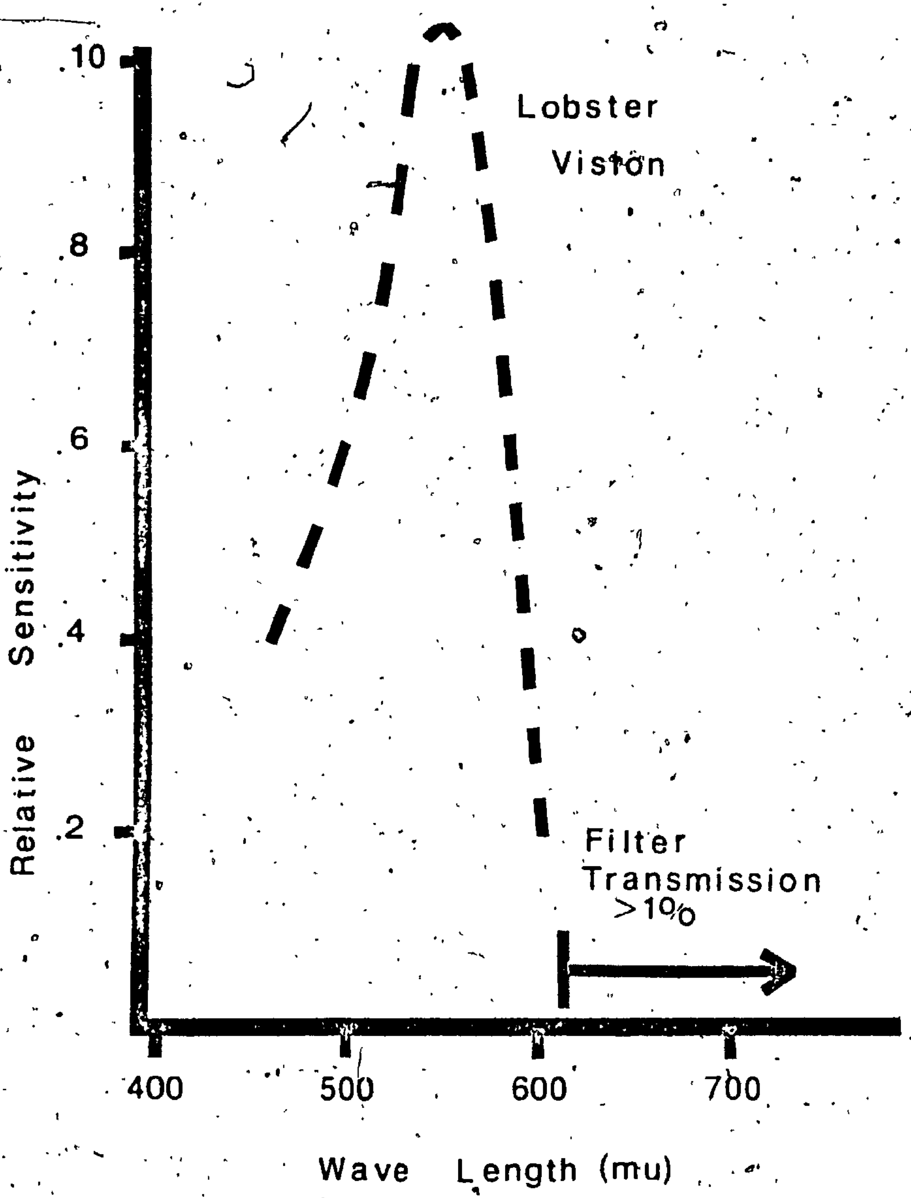
A lobster was placed in a tank (divided in half using a wooden divider) with a glass front through which it could be observed. The foods of the lobster used were S. droebachiensis, Pagurus spp., Buccinum undatum and C. irroratus. In between observation periods the lobster was starved. The typical feeding actions were recorded from these observations.

Field Experiment

A lobster habitat was set up in Logy Bay Gulch at a depth of 10 meters (using SCUBA). By using the walls of a natural crevice for support, three 4cm pipes were telescoped out against the wall. Over this frame a herring net was stretched enclosing the area on all sides. Into this enclosure were placed large rocks and field tile to act as lobster burrows.

Lobsters were introduced into this area (marked with paint and holes punched in the telson and uropods) on July 6, 1972. After this certain numbers of prey species were to be introduced and their numbers recorded. The habitat was visited every other day to count prey present

Figure 2. The range of sensitivity of lobster vision at different wave lengths and the filter transmission properties. (Kennedy and Bruno, 1961).


Lobster
Vision
Filter
Transmission
>1%
.10
.8
.6
.4
.2
Relative Sensitivity
400
500
600
700
Wave Length (mu)

and introduce more if necessary.

Unfortunately, the net was damaged by a summer storm and the lobsters escaped. The habitat was rebuilt only to be broken up again by another storm before more lobsters could be introduced. Due to inclement weather conditions the experiment was abandoned August 15, 1972.

Lobster Distribution

SCUBA is a good technique for studying lobster distribution and habitats (Scarratt, 1968). This method also minimizes "bias in the overall lobster population measures due to gear selectivity or catchability," (Stewart, 1970). In addition, lobsters have been found to migrate only very short distances (Stewart, 1970; and Thomas, 1968); and during the colder months lobsters are basically inactive (M^{c}Leese and Wilder, 1958). Any SCUBA study of distributions of crustaceans should be conducted over a short period (ensuring a stable temperature) such as during the summer or winter so the results will be comparable.

For this portion of the study 71 diving sites (see Figure 3) around the coast of Newfoundland were chosen for diversity of bottom types (sand-bedrock or boulder etc.), ease of accessibility to divers and varying lobster populations. The number of lobsters present in any one location were censused by counting the number of lobsters sighted per diver hour. This method was chosen because of its ease of use and fairly valid results, (Scarratt, 1968). Also subsequent dives to the same areas resulted in similar numbers of lobsters being sighted. Numbers of prey species present and bottom type were classified on a scale of 0-4.

Bottom Scale: 0 - sand bottom, 1 - sand or mud substrate with scattered rocks or bedrock, 2 - bedrock bottom interspersed with areas of sand, 3 - loose rubble on sand or bedrock substrate, 4 - much loose rubble associated with a steep slope.

Prey Scale: Prey species are those from the preference experiments in the laboratory. 0 - no prey species present, 1 - few prey species were present either in species or numbers, 2 - moderate numbers of prey species present either in species or numbers, 3 - good numbers of species were present either in species or numbers, 4 - high numbers of species were present either in species or numbers.

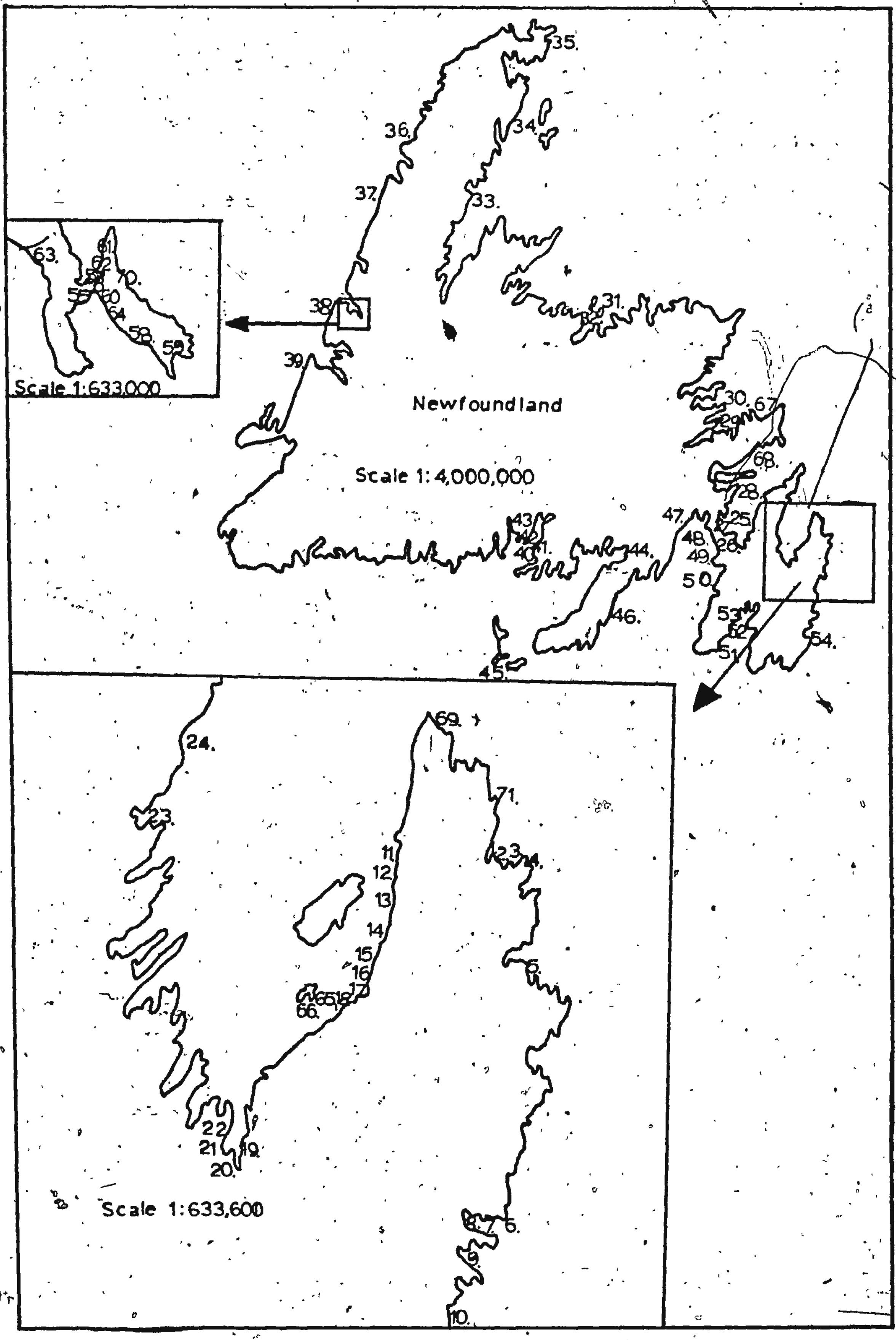
Also nine dive sites were chosen on the Labrador Coast to study the distribution there (see Figure 4). The diving was conducted from M.V. Christmas Seal chartered by Mr. R.A. Prince of the Newfoundland Fisheries Authority on loan to Memorial University of Newfoundland.

Figure 3. Diving sites for the distribution study around Newfoundland.

1. Torbay
2. Middle Cove
3. Outer Cove
4. Logy Bay
5. Freshwater Bay
6. Boone Point
7. Bread & Cheese Cove
8. Bay Bulls
9. Tors Cove
10. Le Manche
11. Portugal Cove
12. Portugal Cove
13. Beachy Cove
14. St.Phillips
15. St.Thomas
16. St.Thomas
17. St.Thomas
18. Topsail
19. Holyrood(refinery)
20. Holyrood(fishplant)
21. Holyrood(South Arm)
22. Chapel Cove
23. Salmon Cove
24. Northern Bay Sands
25. Islington
26. Spreadeagle Cove
27. Bellevue Beach
28. South-West Arm
29. Bonavista Bay(Clode Sound)
30. Bonavista Bay(Eastport)
31. Notre Dame Bay(Camel Is.)
32. Cottrell's Cove
33. Crouse
34. Groais Is.
35. St. Anthony Bight
36. White Lace Cove
37. Portland Creek
38. Trout River
39. Bottle Hr.
40. Bois Is.
41. Riche Is.
42. Roti Bay
43. St. Alban's
44. Fortune Bay (Grand le Pierre)
45. St.Pierre
46. Baine Hr.
47. North Hr.
48. Arnolds Cove

continued.

49. Fairhaven
50. Ship Harbour
51. St.Mary's Harbour (Branch)
52. Salmonier Arm
53. Salmonier Arm
54. Fermeuse
55. Burnt Point #1
56. Burnt Point #2
57. Burnt Point #3
58. Payne's Cove Point
59. South Head
60. Gadd's Head
61. Deer Arm
62. Shoal Point
63. Pinnacle Point
64. Shagg Cliff
65. Little Bell Island (Barachois Pond)
66. Little Bell Island
67. Hodderville
68. Old Bonaventure
69. Biscayne Bay
70. Bonne Bay
71. Flatrock


Newfoundland
Scale 1: 4,000,000
Scale 1:633,000
Scale 1:633,600
35.
34.
36.
37.
33.
31.
38.
39.
30.
67.
29.
68.
28.
47.
25.
48.
26.
49.
50.
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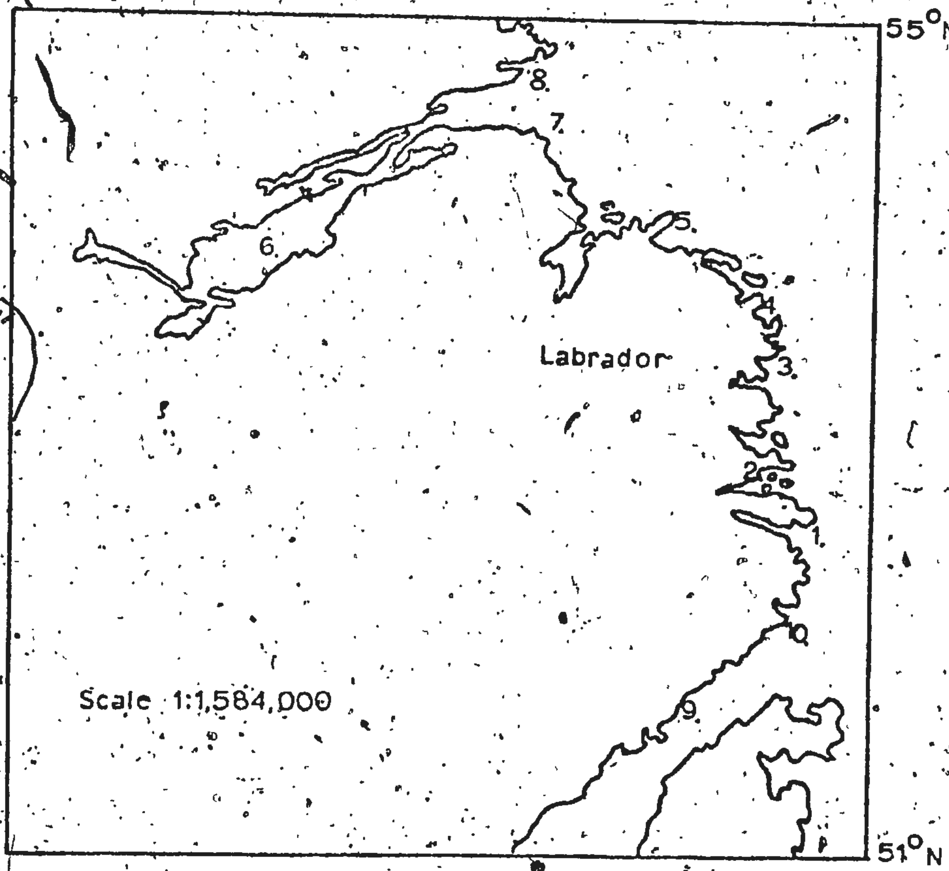
64.
58.
59.
69.
24.
23.
71.
2.
3.
4.
11.
12.
13.
14.
15.
16.
17.
18.
65.
66.
5.
22.
21.
19.
20.
8.
7.
6.
9.
10.

Figure 4. Dive sites in Labrador except the last two sites which are referred to in the text.

1. 53°47'N 56°29'W
2. Fox Harbour
3. 54°13'N 58°33'W
4. Domino Run
5. Run by Guess
6. Cartier Shoal (L. Melville)
7. East and West Sister Is.
8. Ice Tickle
9. Red Bay
10. Henley Harbour


55°N
8
7
6
5
4
Labrador
3
2
1
0
9
Scale 1:1,584,000
51°N

RESULTS

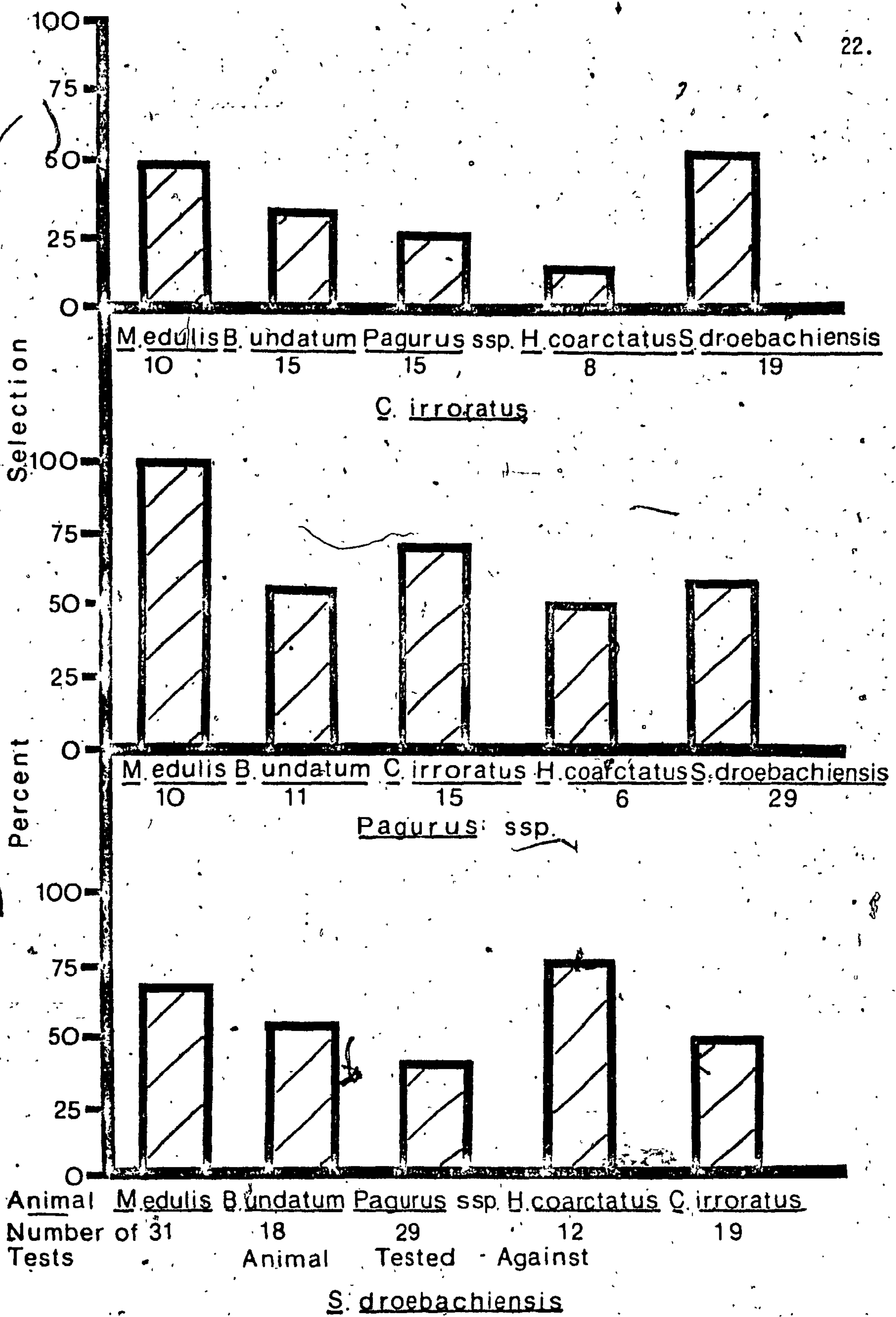
Lobster Prey and Preferences

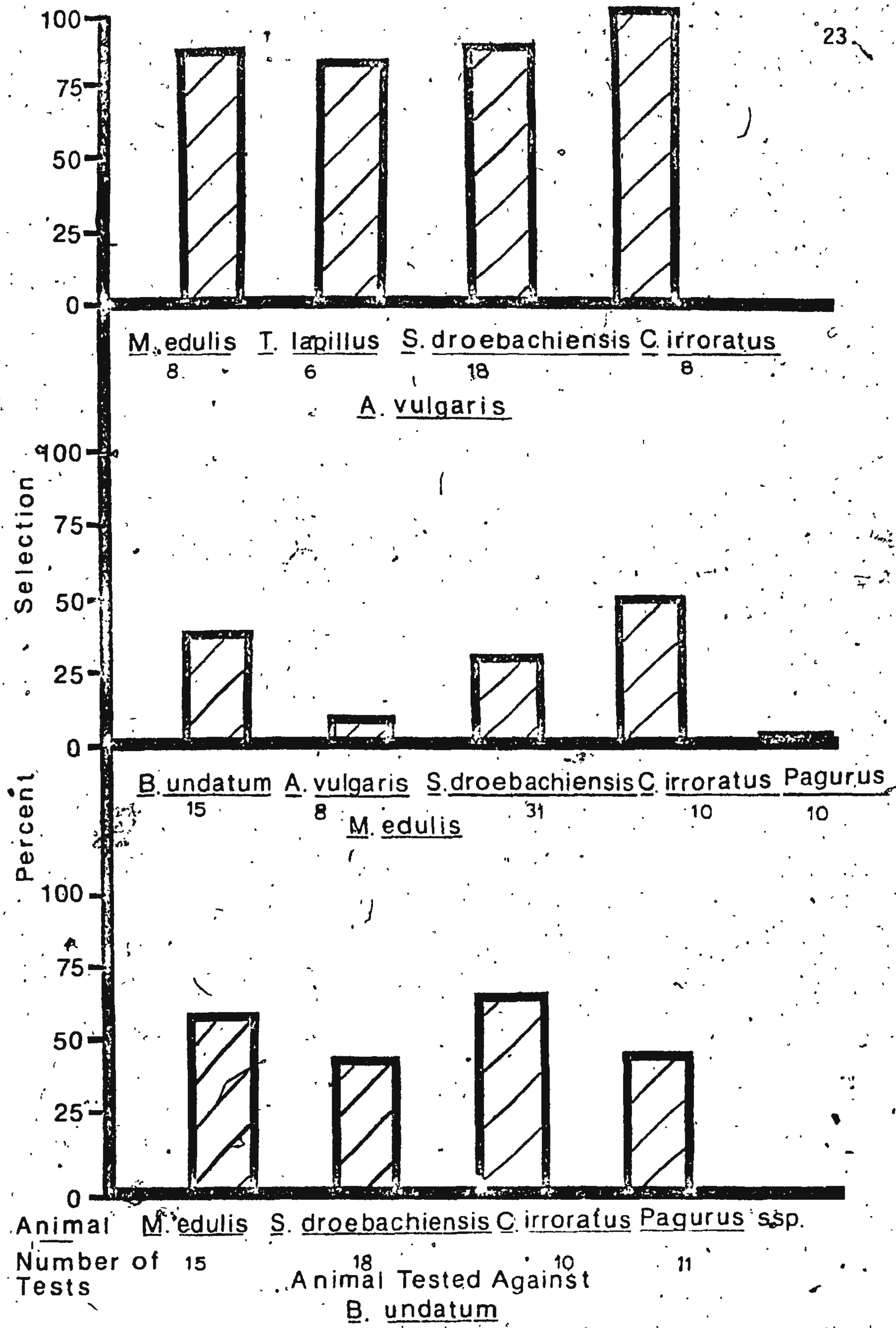
In the experiments Cancer irroratus was generally preferred over other organisms (see Figure 5). Only Strongylocentrotus droebachiensis (52.6%) and Mytilus edulis (50.0%) were comparatively selected when tested with Cancer irroratus.

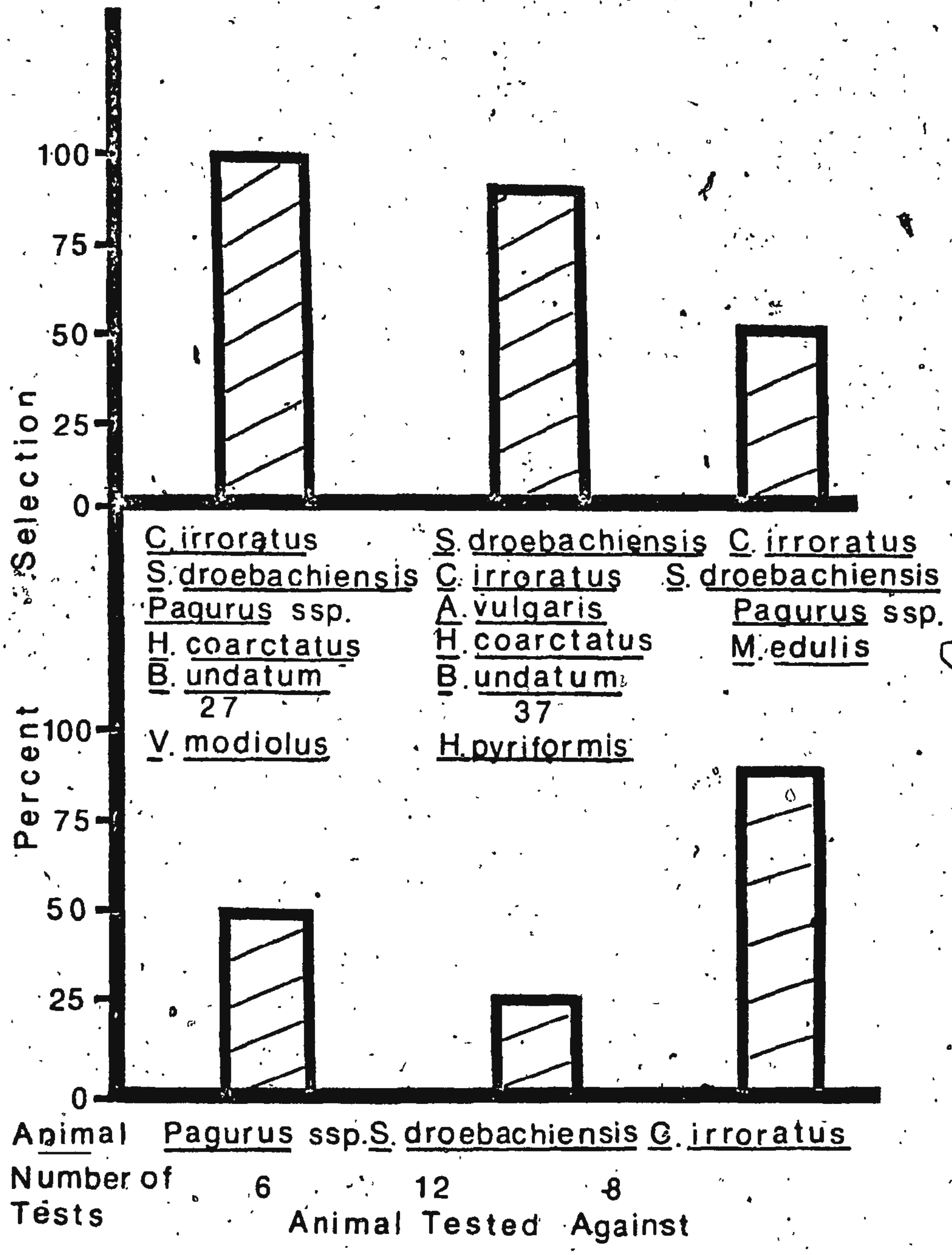
The other crabs (see Hyas coarctatus Figure 7 and Pagurus spp. see Figure 5) were selected quite regularly although not as frequently as C. irroratus (C. irroratus over H. coarctatus 87.5% and 93.3% over Pagurus spp.). H. coarctatus was selected equally to Pagurus spp. in 50.0% of cases, S. droebachiensis over H. coarctatus in only 25.0% but over Pagurus spp. in 58.6% of cases. Asterias vulgaris was selected infrequently in only 11.1% over Pagurus spp. Note that Mytilus edulis was selected over Pagurus spp. 100.0% which is rather anomolous in that Pagurus spp. was selected 26.7% over C. irroratus. If C. irroratus and Mytilus edulis are equal then C. irroratus should be selected over Pagurus spp. 100.0% of the time. It is not however, being selected only 73.3% over Pagurus spp.

The more intermediate prey in selection preference are Strongylocentrotus droebachiensis, M. edulis, Thais lapillus, and Buccinum undatum. M. edulis was selected over S. droebachiensis in 67.8% of cases, Asterias vulgaris only 11.1%, B. undatum in 55.6%, Pagurus spp. in 41.4%, H. coarctatus in 75.0% and C. irroratus in 47.4%. C. irroratus, S. droebachiensis, Pagurus spp., and M. edulis were

Figures 5,6, and 7. Percentages of selection of prey species eaten by H. americanus. This shows that the species below the histogram was chosen over the species tested against it, which is found listed below this. The number of tests are also recorded in each case.


Percent Selection
100
75
50
25
0
M. edulis B. undatum Pagurus ssp. H. coarctatus S. droebachiensis
10 15 15 8 19
C. irroratus
100
75
50
25
0
M. edulis B. undatum C. irroratus H. coarctatus S. droebachiensis
10 11 15 6 29
Pagurus ssp.
100
75
50
25
0
Animal M. edulis B. undatum Pagurus ssp. H. coarctatus C. irroratus
Number of Tests 31 18 29 12 19
Animal Tested Against
S. droebachiensis


Percent Selection
100
75
50
25
0
M. edulis
8
T. lapillus
6
S. droebachiensis
18
C. irroratus
8
A. vulgaris
B. undatum
15
A. vulgaris
8
S. droebachiensis
31
C. irroratus
10
Pagurus
10
M. edulis
Animal
Number of Tests
M. edulis
15
S. droebachiensis
18
C. irroratus
10
Pagurus ssp.
11
Animal Tested Against
B. undatum



H. coarctatus

selected over Thais lapillus in 51.7% of cases, Buccinum undatum was not selected as regularly as the above two species since Mytilus edulis was selected over it in 60.0% of cases, sea urchins in 44.4%, C. irroratus 66.6% and Pagurus spp. 44.4%. M. edulis was the most popular of this intermediate group since B. undatum was selected over it in only 40.0% of cases, Asterias vulgaris 12.5%, sea urchin 32.2%, C. irroratus 50.0% and Pagurus spp. not at all.

A. vulgaris, Volsella modiolus, and Halocynthia pyriformis are overall rather unpopular. M. edulis was selected instead of A. vulgaris 87.5% of the time, T. lapillus 83.3%, sea urchin 88.9% and C. irroratus 100.0%. C. irroratus, sea urchin, Pagurus spp., Hyas coarctatus and B. undatum were selected instead of V. modiolus 100.0% of the time. C. irroratus, sea urchin, Pagurus spp. and M. edulis were selected instead of H. pyriformis 92.0% of the time. With V. modiolus and H. pyriformis it may be the great difficulty that lobsters have penetrating the shell of V. modiolus and the tough skin of H. pyriformis that gives them their low preference.

Another aspect of lobster diet is cannibalism. Dead lobsters will be consumed by other lobsters; and if they are in close quarters i.e. lobster cars they will kill each other and eventually the dead will be eaten, (Templeman, 1940). In the laboratory, lobsters wouldn't attack each other if food was readily available, but would under conditions when food was scarce. Five lobsters lived together in the laboratory on two separate occasions for two weeks without attacking each other. At this time food was made readily available. But a lobster that had been starved for two weeks attacked and killed another.

There is also a noticeable selection by lobster for certain

Table 1. List of the major and incidental food of H. americanus plus those species that the lobster will not eat at all.

Major Food

Cancer irroratus
Hyas coarctatus
Pagurus acadianus
P. longicarpus
P. pubescens
P. arcuatus
Strongylocentrotus droebachiensis
Mytilus edulis
Buccinum undatum
Thais lapillus
Littorina littorea
Volsella modiolus
Hiatella arctica
Fish: *Pseudopleuronectes americanus*
Leptasterias polaris
Asterias vulgaris
Mya truncata

Incidental

Corallina officinalis
Hydroids: *Thuiaria cupressina*
Bryozoa: *Eucratea* spp.
Tunicates: *Halocynthia pyriformis*
Ophiopholis aculeata
Amphipoda: *Gammarus lawrencianus*
Polychaetes: *Nereis pelagica*
Echinarachnius parma
Lunatia heros
Lacuna spp.
Ischnochiton ruber
Acmaea testudinalis
Balanus balanoides

Never Eaten

Placopecten magellanicus
Cucumaria frondosa
Psolus fabricii
Gersemia spp.
Coelenterata: *Mitridium senile* and *Actinauge rugosa*
Porifera
Algae: *Fucus* spp., *Alaria* spp., *Laminaria* spp.
Flustra foliacea

size prey. For instance, a 120 gram lobster was able to consume up to a 20 gram sea urchin but no larger than this. Another example is a 1623 gram lobster that wouldn't consume *C. irroratus* any larger than about 110 grams.

Also of noteworthy importance (see Table 1) is algae. Although it is common in many areas inhabited by lobsters they do not appear to selectively consume it but do ingest some accidentally while eating other prey. For instance, they remove algae from *Mytilus* shells enabling their claws to grip and break open the shells easier. Also lobsters would not eat *Fucus* spp., *Laminaria* spp., or *Alaria* spp. even when they were starved for two to three week periods in the presence of this alga.

The food of the lobster is listed in Table 1. This table is arranged as closely as possible in an order of preference although there are no definite preferences. The table shows both those animals that lobsters will consume and those they will not. In the laboratory, lobsters would not eat food that was older than three days; even if they had been previously starved. Polychaetes proved impractical to test in this manner and so are not included in the preference tests but are found listed in Table 1.

Food (see Table 1) listed as incidental includes that which is low in abundance around lobster beds i.e. *Lunatia heros* (which mostly inhabits sand bottoms); that difficult for lobsters to scrape from the rocks i.e. *Ischnochiton ruber*; or that eaten only if starved i.e. Tunicates.

The lobster food over a yearly period changes only at ecdysis. Lobsters discontinue feeding about one day before moulting and for a week to two weeks after they have moulted their diet is quite different. At this time, they demonstrate a marked preference for material containing Ca^{++} ions such as it's own shell (always the first food consumed on completing the moult), Corallina officinalis, Mytilus shells, Cancer shells and sea urchin tests. By eating these they would be increasing the Ca^{++} ion content of their new shell. They do not feed on live animals at all due to the fact that their chelae are too soft for breaking into hard invertebrate shells and because hard shelled animals such as Cancer would definitely have the advantage.

In the sea, lobsters were observed (from diving) eating C. irroratus, S. droebachiensis, M. edulis and calcareous material from these species is found in great abundance around lobster burrows.

Force Required to Remova a Sea Urchin from Substrate

In most cases lobsters removed sea urchins from the substrate before consuming them. Thus, a lobster's ability to eat a certain size sea urchin may depend on it's ability to remove it from the substrate.

Irrespective of the sea water temperature the heavier the sea urchin the more difficult it is to remove from the substrate (i.e. the slope is from left to right). Also by comparing the curves at different temperatures (see Figure 8), it is evident that it becomes more difficult to remove a sea urchin as the water temperature increases. Also in a number of cases the tube feet (podia) were left on the substrate before being eaten by lobsters.

Caloric Intake

Comparing Figures 10 and 11 (graphs of the yearly cycle of caloric intake at ambient and the sea water temperature graph) we see

Figure 8. Depicts the effect of weight (grams) of a sea urchin on the force required to pull it off of it's substrate. The four lines represent this force at different temperatures. See Appendix B for more information.

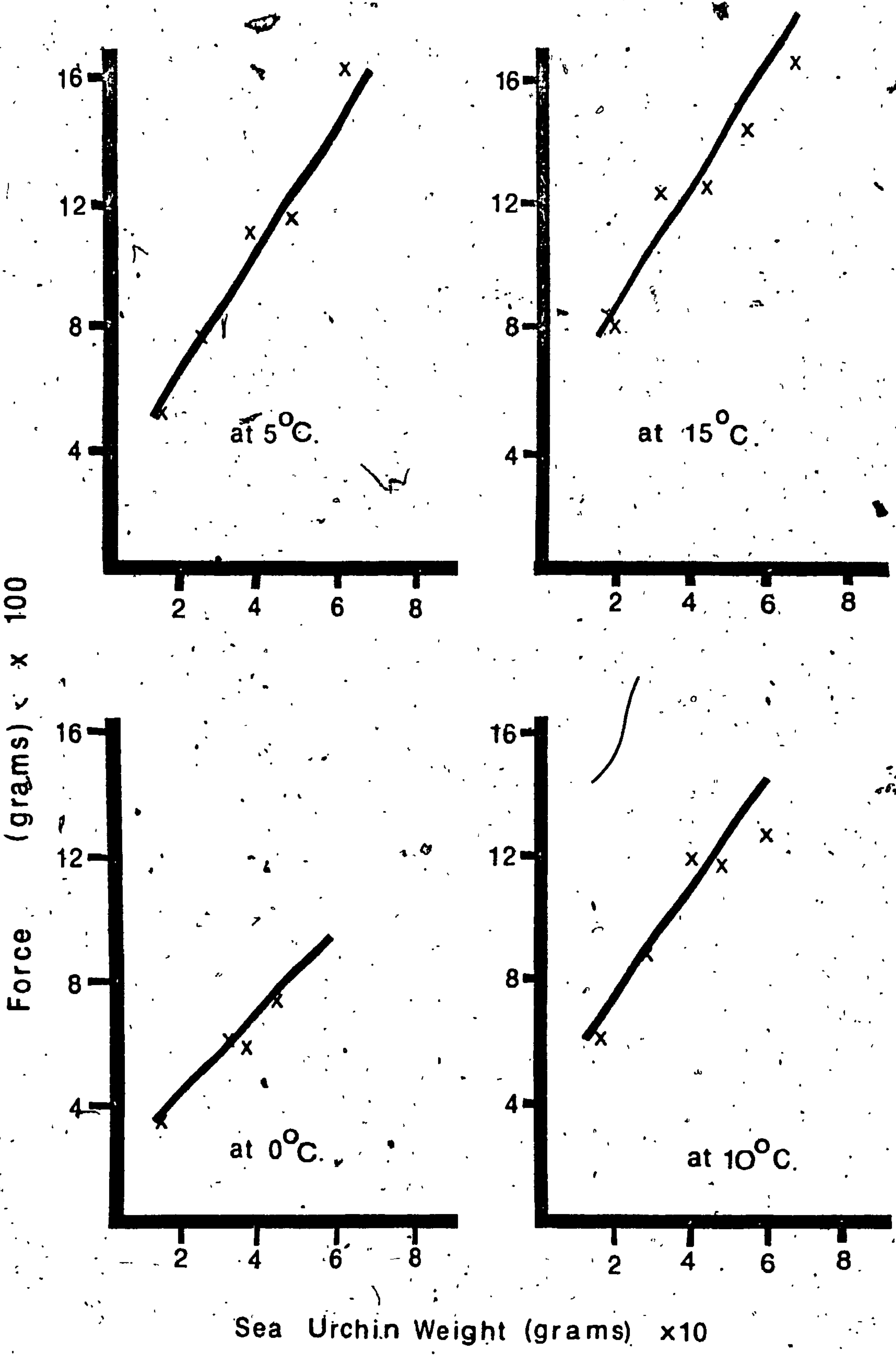

16
12
8
4
at 5°C.
2
4
6
8
16
12
8
4
at 15°C.
2
4
6
8
Force (grams) x 100
16
12
8
4
at 0°C.
2
4
6
8
16
12
8
4
at 10°C.
2
4
6
8
Sea Urchin Weight (grams) x10

Table 2. The results of the bomb calorimetry tests giving the average calories per gram ash free dry weight of each species listed. For a sample calculation see Appendices C, D, E, and F.

Species	Average Calories per gram dry weight	Average Calories per gram ash free dry weight
S. droebachiensis	3448	*
C. irroratus	4211	*
M. edulis	4448	*
P. acadianus	3313	4522
L. polaris	2073	3238
H. coarctatus	5278	5820
B. undatum	5185	9900
Alaria esculenta	3121	3847
Thuiaria spp.	would not ignite	
Halocynthia pyriformis	4026	5226
Halichondria panicea	2372	4732

* no values due to error in the sulphur test

that 10(a) and (b) are very similar to each other. They both have low points during February, March and April with highs occurring in September to November. The caloric intake corresponds closely to the sea temperature (Figure 9(b) with 10), in it's fluctuations over the year. The peak in temperatures (September to October) corresponds to the high point in caloric intake in both Figures 10(a) and (b). As well, the low points also conform closely. In both Figures 10(a) and (b), there is a drop in caloric intake of 39 and 80 in August, which is about the time of moult. The preference portion of the study showed that lobsters eat very little before moulting and for about two weeks after. After ecdysis, the caloric intake rises again and then drops off during the winter. Figure 10(a) shows a second smaller peak and a low occurring in October and November. Since Figure 11(a) also shows this peak at about the same time, it is likely due to difficulties encountered in finding enough crabs to feed the lobsters during this period. Lobsters feeding on S. droebachiensis do not show this low in November.

The 15°C. tank was maintained at a constant temperature for eight and half months only. Since the control equipment was being installed and adjusted from September to mid-November the water temperature was not stable. The effect of this is shown in Figures 11(a) and (b) which have lows during this period of temperature fluctuations when the MSRL water system was not working well. This also causes a drop in the caloric intake at each of the temperature fluctuation points. Figure 11(a) and (b) shows another drop in caloric intake - Figure 11(a) - September and Figure 11(b) from July on. Again this is the reproductive and moult period. The lobster Figure 11(a) was a berried female whose eggs hatched in May. It didn't moult however,

Figure 9(a). Graph of the monthly sea water temperature in the laboratory over the study period at 15°C.

Figure 9(b). Graph of the monthly sea water temperature in the laboratory over the study period at ambient temperature.

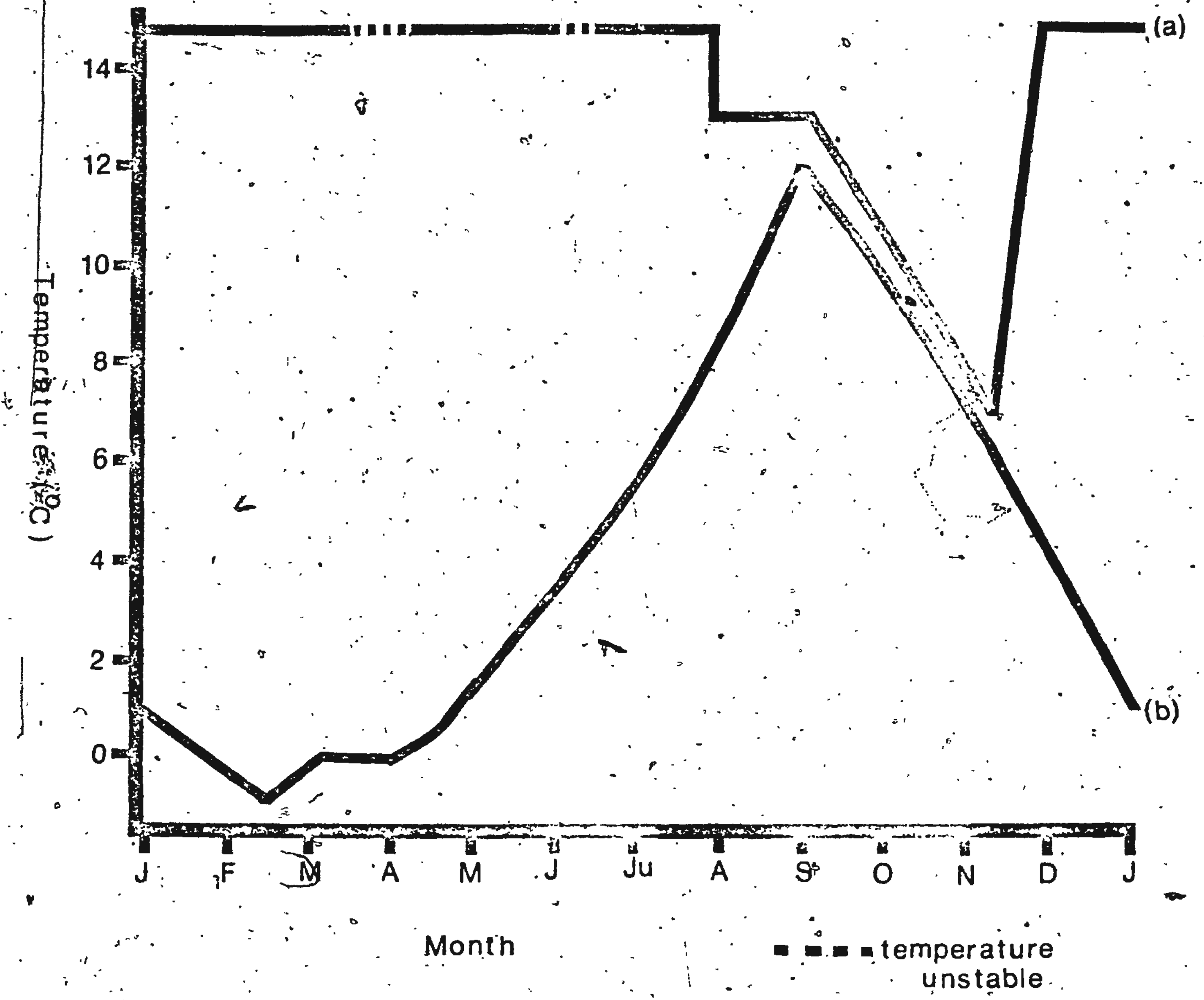

Temperature (°C)
14
12
10
8
6
4
2
0
(a)
(b)
J
F
M
A
M
J
Ju
A
S
O
N
D
J
Month
■ ■ ■ ■ temperature unstable

Figure 10. Graph of the cycle of monthly caloric intake per gram of H. americanus on (a) C. irroratus and (b) S. droebachiensis at ambient sea water temperature. For the actual values see Appendices G and H.

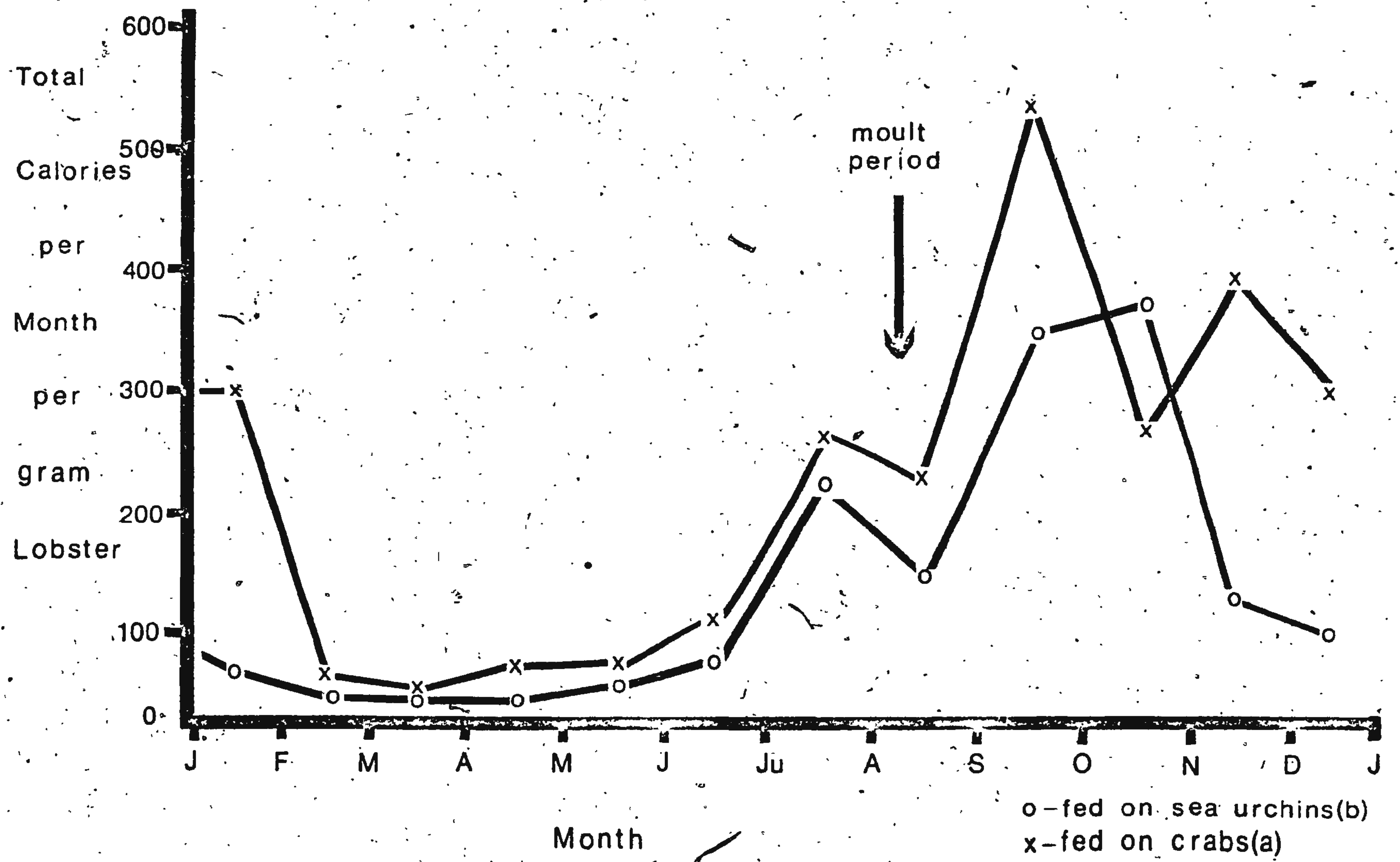
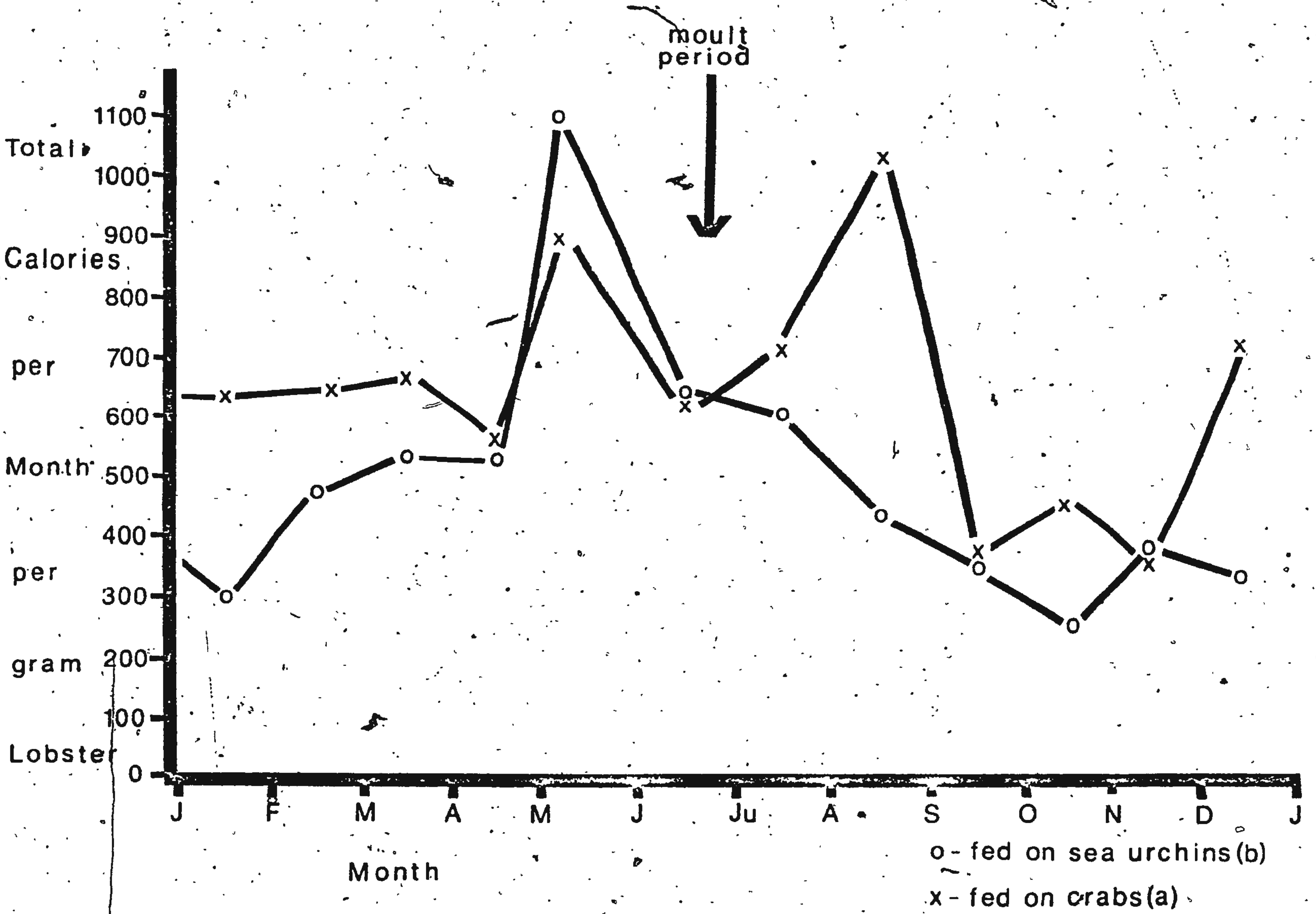

Total Calories per Month per gram Lobster
600
500
400
300
200
100
0
moult period
J
F
M
A
M
J
Ju
A
S
O
N
D
J
Month
o-fed on sea urchins(b)
x-fed on crabs(a)

Figure 11. Graph of the cycle of monthly caloric intake per gram of H. americanus fed only (a) C. irroratus and (b) S. droebachiensis at a sea water temperature of 15°C. For full details see Appendices I and S.


moult period
Total Calories per Month per gram Lobster
1100
1000
900
800
700
600
500
400
300
200
100
0
J
F
M
A
M
J
Ju
A
S
O
N
D
J
Month
o - fed on sea urchins (b)
x - fed on crabs (a)

until September when the caloric intake also dropped. In Figure 11(b), the animal appeared to be starting to moult in September but didn't (died when the water system was shut off by Technical Services).

In Figures 10(a) and 11(a) versus 10(b) and 11(b) the average value of caloric intake differs. In both cases of C. irroratus the values are higher (Figure 10(a) - 222 and Figure 11(a) - 630) than in the case of S. droebachiensis (Figure 10(b) - 127; Figure 11(b)-461).

Distribution

Northern Limits of Range. Templeman (1940) reports that lobsters are found in Labrador as far north as Henley Harbour and in Newfoundland up to Cape Norman. Mr. R. Hooper (personal communication) reports that lobsters also occur at Red Bay, Labrador and south. Observations conducted while aboard M.V. Christmas Seal tend to confirm that Henley's Harbour is their northern limit. No indications of any lobsters were seen on eight dives from Fox Harbour (52°21'N) to Ice Tickle (54°24'N).

Distribution of Lobsters with Respect to Presence of Food and Bottom Type. Where lobsters are not present there is also poor bottom type and a marked reduction in prey species (Figures 12, 13 and 14). There is no sequence over the province but a mixture of good and poor areas (except perhaps in Bonne Bay which was consistently good, see Figures 13 and 14). The West Coast areas however, did seem to have more lobsters than most other areas (see Figure 12).

Figure 15 shows that as the bottom type improves so does the number of lobsters but coincidentally or otherwise, so does the amount of food present (Figure 17). Also as the amount of food increases so does the number of lobsters (see Figure 16). However, note the great increase in numbers of lobsters at food scale of 3 compared to other values.

Figure 12. This map shows the abundance of lobsters from the dive sites listed in Figure 3 in the Materials and Methods. Also see Appendix M for more information.

Scale:

x - no lobsters present

● - low numbers (1-8 per diver hour)

d - fairly abundant (9-16 per diver hour)

■ - abundant (17-24 per diver hour)

0 - numerous (greater than 25 per diver hour)

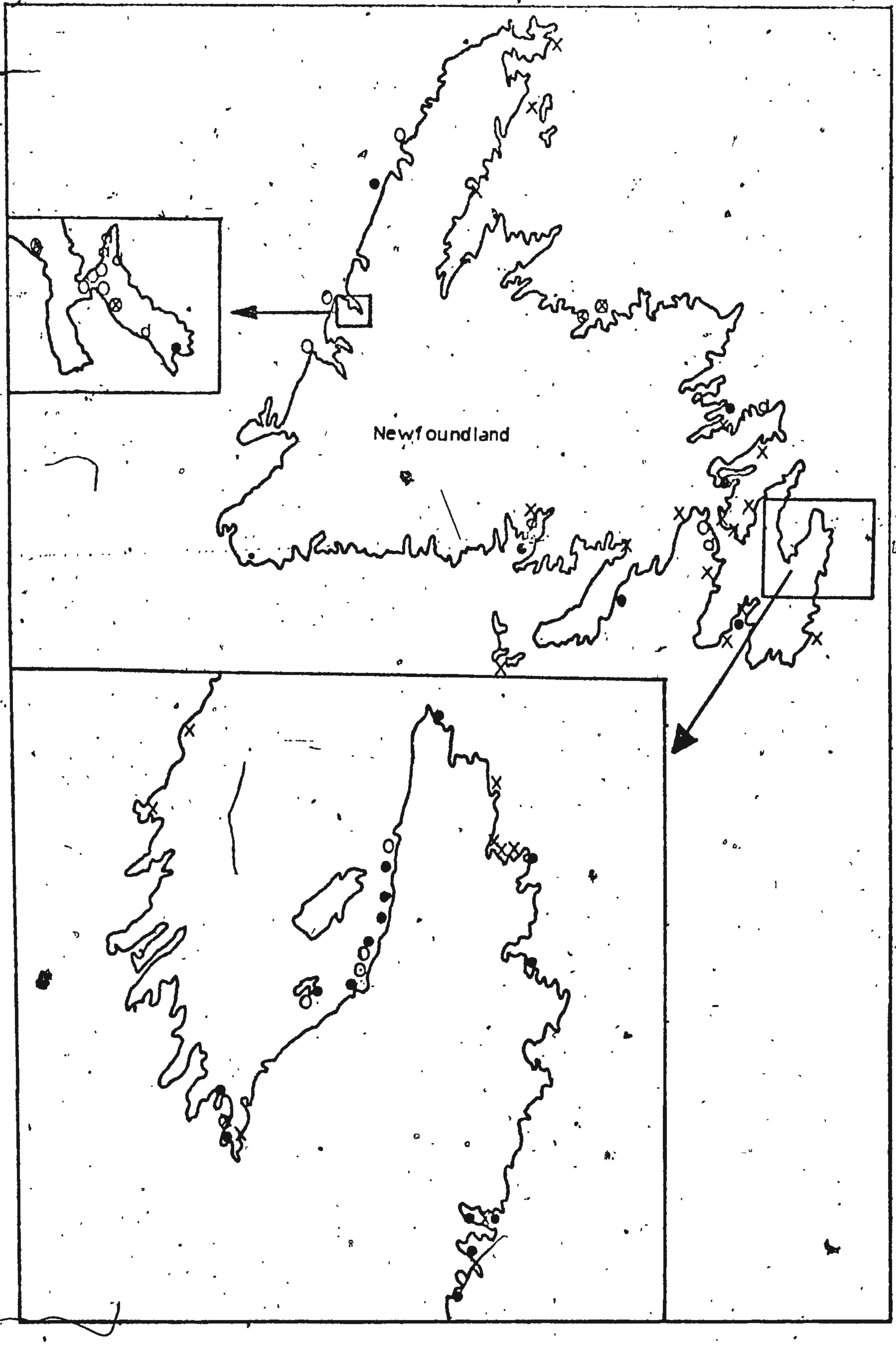

Newfoundland

Figure 13. This map shows the abundance of suitable bottom type for lobsters from the sites listed in Figure 3 in the Methods and Materials. Also see Appendix M for more information.

Scale:

x - sand bottom

● - sand or mud substrate with scattered rock

d - bedrock bottom with sand

⊠ - loose rubble on sand or bedrock substrate

0 - much loose rubble associated with a steep cliff

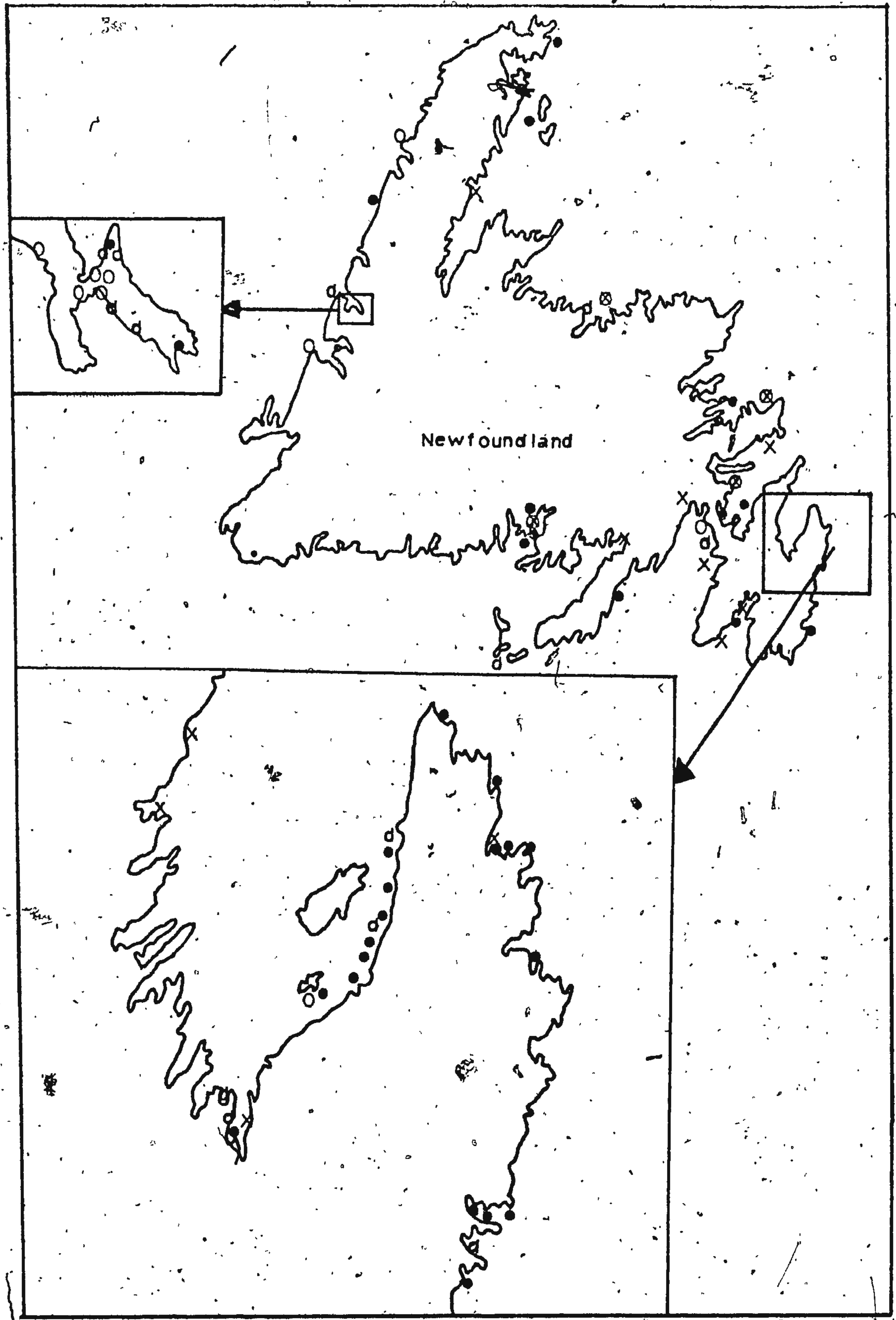

Newfoundland

Figure 14. This map shows the simultaneous abundance of lobster prey at the lobster diving sites. Also see Appendix M for more information.

Scale:

x - none present

● - few present

d - moderate numbers present

⊠ - fairly abundant

0 - abundant

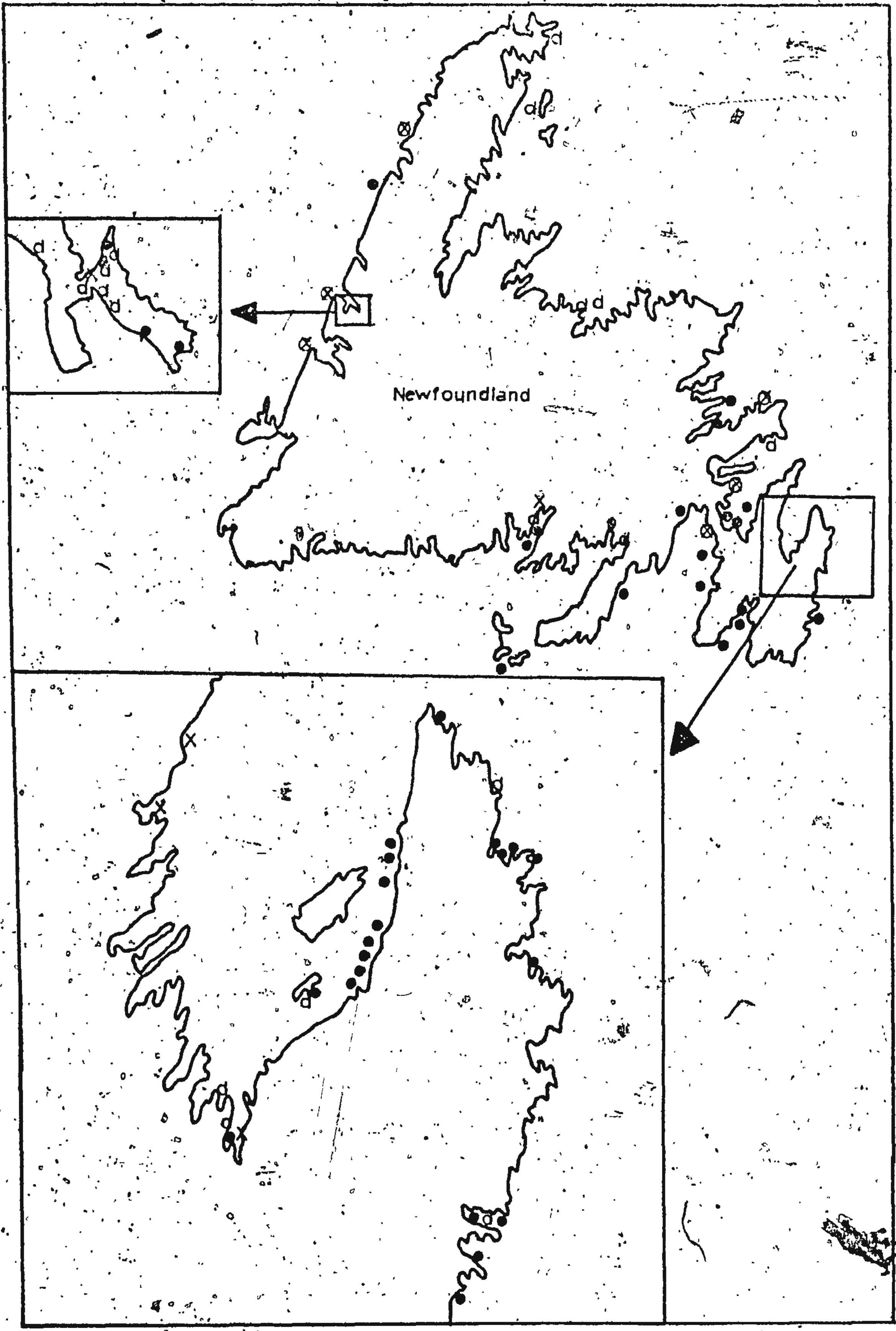

Newfoundland
d
x

Figure 15. This graph compares the number of lobsters with the bottom type that they were located on.

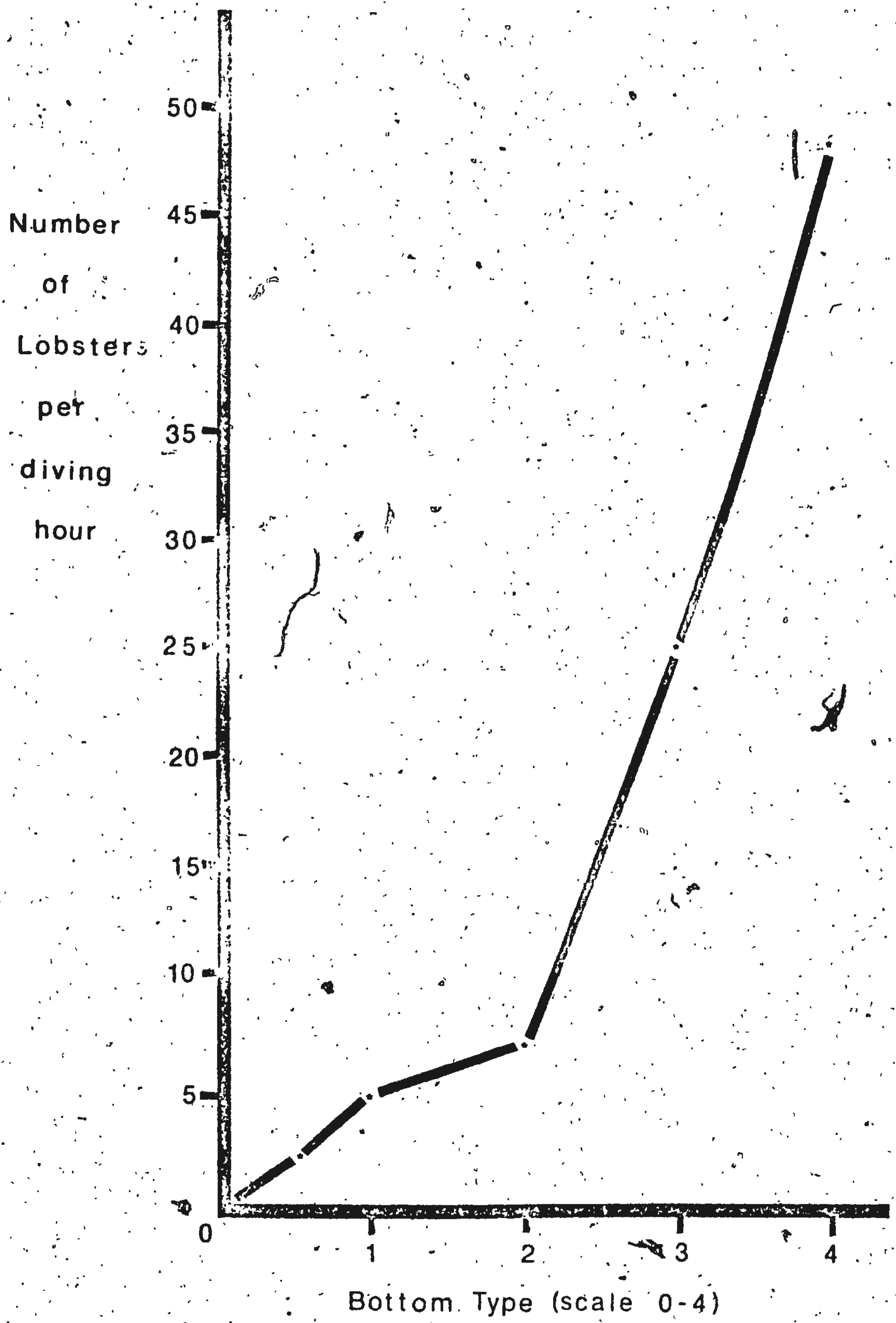

Number of Lobsters per diving hour
50
45
40
35
30
25
20
15
10
5
0
1
2
3
4
Bottom Type (scale 0-4)

Figure 16. This graph compares the number of lobsters to the abundance of their prey species.

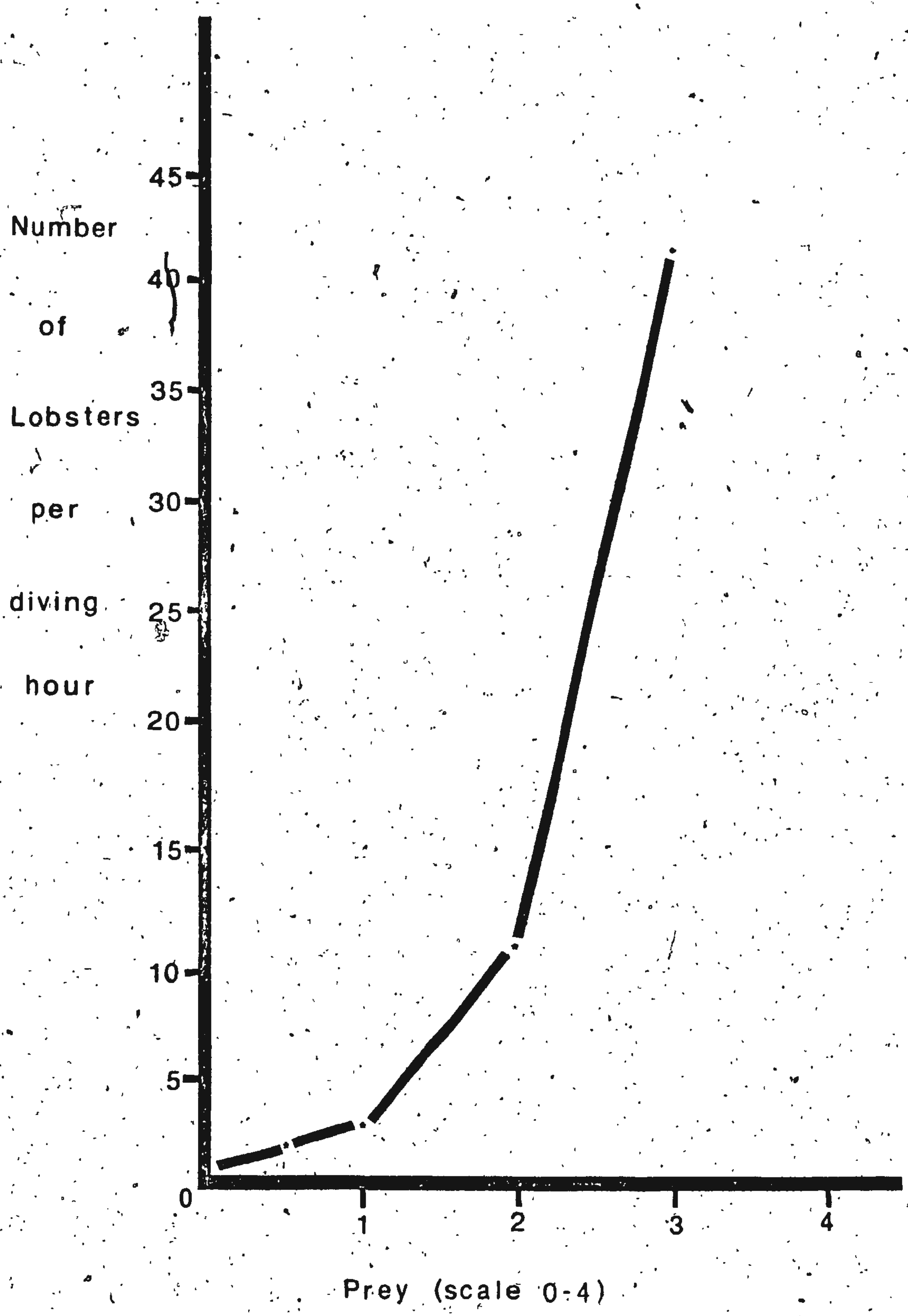

Number of Lobsters per diving hour
45
40
35
30
25
20
15
10
5
0
1
2
3
4
Prey (scale 0-4)

Figure 17. This graph compares the type of bottom to the abundance of food.

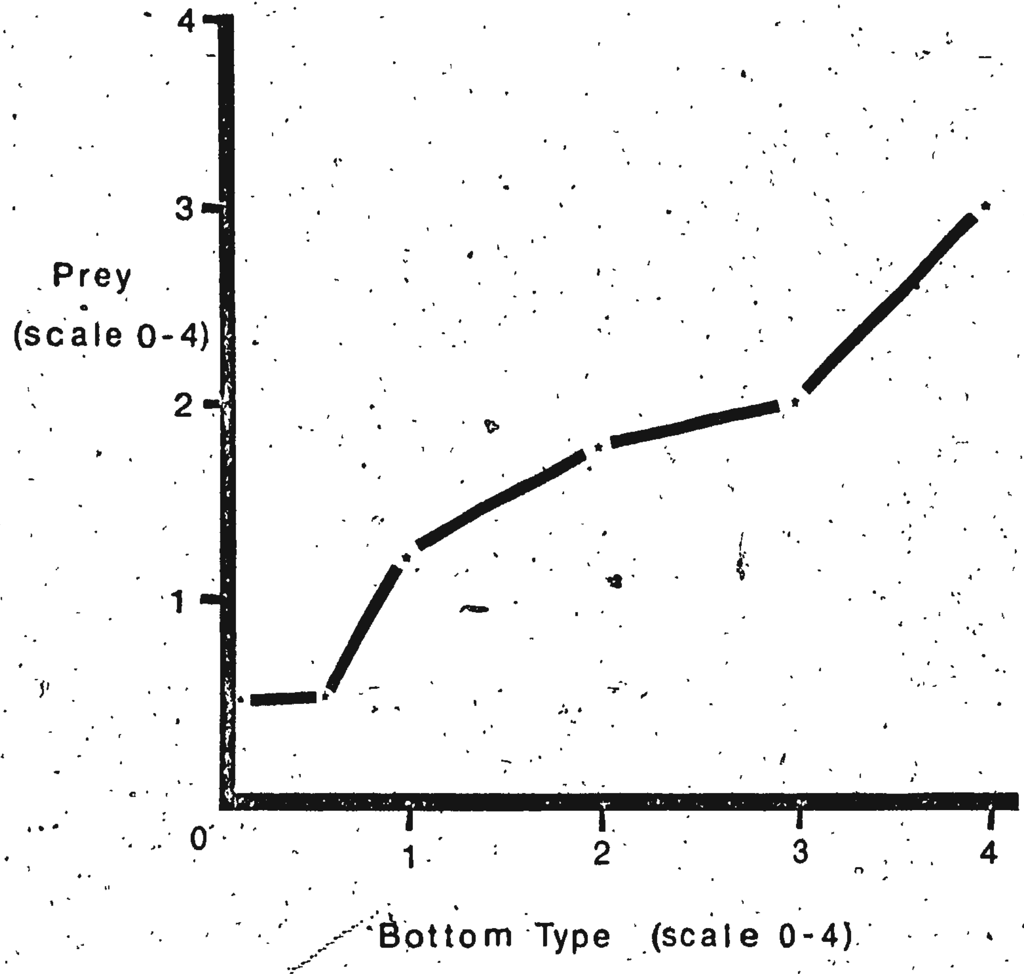

4
3
2
1
0
Prey
(scale 0-4)
1
2
3
4
Bottom Type (scale 0-4)

Figure 18. This graph compares numbers of lobsters and their food supply for a specific bottom type.

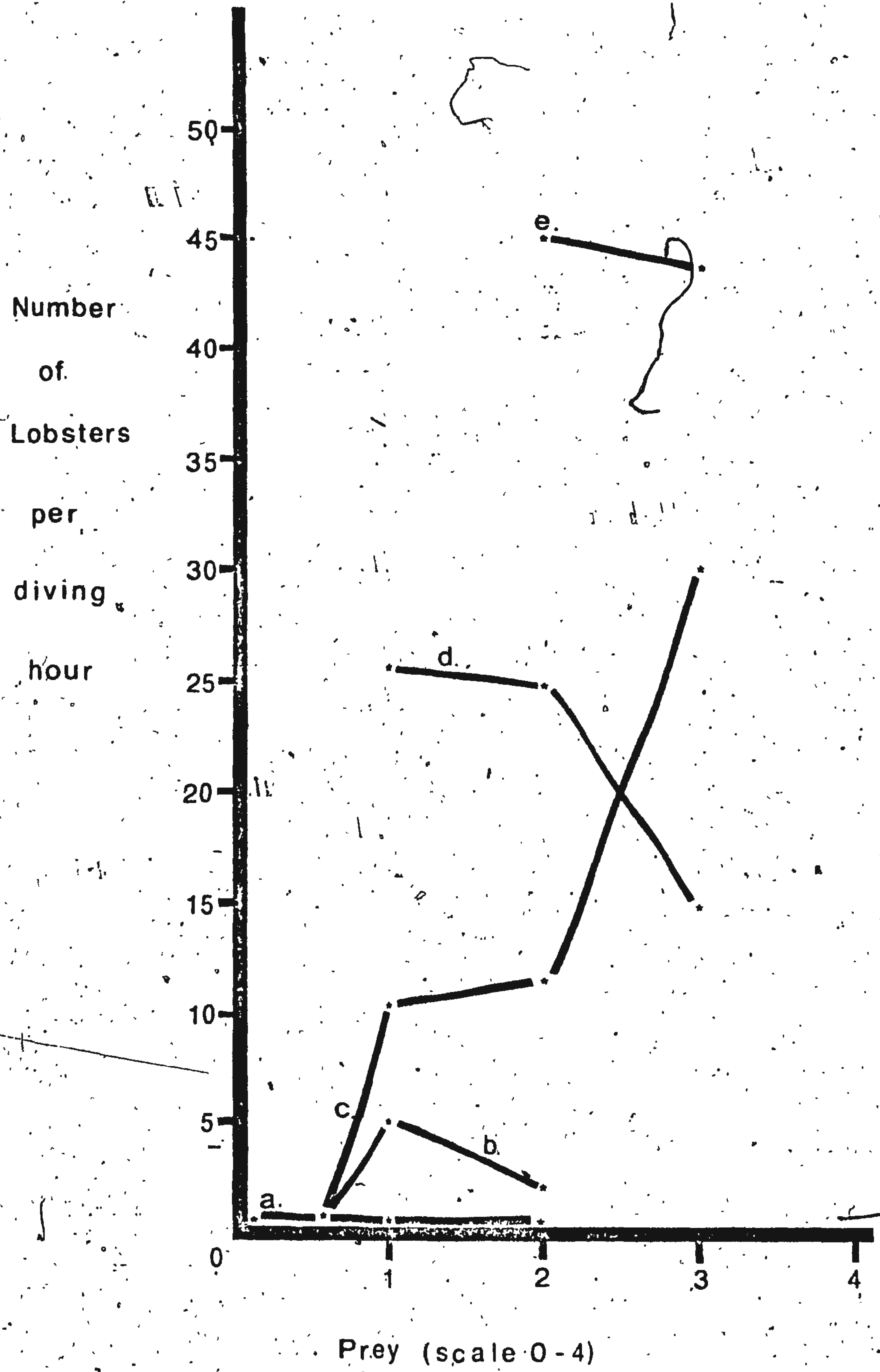
a. Bottom Scale 0

b. Bottom Scale 1

c. Bottom Scale 2

d. Bottom Scale 3

e. Bottom Scale 4


Number of Lobsters per diving hour
50
45
40
35
30
25
20
15
10
5
0
1
2
3
4
Prey (scale 0 - 4)
a.
b.
c.
d.
e.

In Figure 15, there is also a similar increase in lobsters at bottom scale values of 3 and 4. Bottom type and prey species are also related, since prey increases as the bottom improves.

From Figure 18 it can be seen with bottom types of 1 and 0 that an increase in food does very little to increase the number of lobsters, present in the area. With bottom type 2 however, note the substantial increase (Figure 18) in the number of lobsters as prey improves. Bottom type and prey species are also related, since prey increases as the bottom improves.

Feeding Habits

With the infrared light source the feeding behaviour of lobsters was easily observed. The amount of time spent in the three stages of capture, immobilization and opening, and consumption is depicted in Table 3.

Table 3

The amount of time spent by the three animals in each stage of feeding. All of the times are in minutes.

Stage	Animal		
	C. irroratus	S. droebachiensis	M. edulis
I - Capture	9	25	10
II - Immobilization & opening the shell	33	38	30
III - Consumption	58	38	60
Total Time	100	101	100
Number of Trials	15	20	10

The only species that can actually defend itself by claws or by moving rapidly is *C. irroratus* and so the lobster must move in and capture it fast. Their capture took a very small percent of the total feeding time.

There is a long capture period for *S. droebachiensis* above the other species. This is caused by the fact that the lobster has to remove it from the substrate which at times can be difficult. For instance, a 56.0 gram sea urchin can hold onto the substrate with an average force of 1740 grams. *M. edulis* in the wild would be harder to capture since the individuals I used didn't have much of a chance to anchor themselves and they weren't in a large compact bed.

Immobilization (Stage II) took about the same time with *S. droebachiensis* and *M. edulis* but with them more of the time was spent opening rather then immobilization of them. With *C. irroratus* however, most of this time was spent in immobilization. Once immobilized *Cancer* shells are much easier to open than the others.

Consumption of *S. droebachiensis* was much quicker than that of the others probably because once opened they are easy to eat. The meat isn't stuck to the shell as it is in *C. irroratus* and *M. edulis*.

DISCUSSION

Lobster Sources of Food and Preferences

The omnivorous diet of Homarus americanus has been known for a long time but some workers in the field also unjustly accused lobsters of being scavengers of decaying fish and debris (Buchsbaum, 1951). However, as early as 1875, Wheildon wrote, "the statement that the food of the lobster is seaweed, filth, and garbage is untrue". In fact, lobstermen have stated that lobsters cannot be caught with anything but fresh bait (Wheildon, 1875; Templeman, 1940; and personal communication from Mr. Art Spurrell, Trinity Bay). While lobsters readily consumed fresh fish in the laboratory, they would have nothing to do with material dead longer than about three days. Also live animals that were placed in the tanks with lobsters and subsequently killed by them would not be consumed once they had begun to rot.

Lobsters eat all of the material listed in the Results (Table 1); the common food items of the lobster in the laboratory environment are C. irroratus, H. coarctatus, Pagurus spp., S. droebachiensis, M. edulis, and B. undatum but there is little preference within this group. The other material (see Table 1) was either low as a preferred food or it does not commonly occur in the same areas as lobsters. Some of the material listed as incidental is readily consumed by lobsters but does not occur in the same areas and so cannot be considered as a major food of the lobster. For example, moon snails (Lunatia heros) and sand dollars (Echinarachnius parma) are most commonly found on sand far from any lobster habitat. While lobsters would readily consume them in the laboratory, they wouldn't have the opportunity to eat many in the environment.

Waterman (1960) discusses feeding Brachyurans in relation to moult stages. He has divided the moult cycle into five stages: Stage A - newly moulted (7-8 days); Stage B - hardening of shell (29 days); Stage C - hard shelled (224 days); Stage D - premoult (91 days); and Stage E - moult (1 day). The animal stops feeding at stage D_3 and begins again at B_2. There is no feeding at stages A or E with full feeding during Stage C. The period of no feeding lasts about 9.5% of the year or about 4½ weeks.

The lobsters kept at the MSRL, stopped feeding 12-24 hours before moulting (Stage D_4) and started again just after they moulted (2-3 days or Stage B_1). It was about two weeks before they resumed feeding on live animals (Stage B_2). The shell became hard in about three to four weeks.

Regarding the moult cycle, it was observed while diving in Bonne Bay and Bottle Cove, Bay of Islands during the last week in August (26-31) that out of 150 lobsters examined about 140 (94%) had recently moulted. Squires, Tucker and Ennis (1971) from their excellent study in Bay of Islands report that 89% of males moulted (this was also during August). Templeman (1940), reports that St.George's Bay in 1938 - 96% of the lobsters caught were new shelled. This study also was during the later part of August.

There is also a size preference by lobsters in that they will only attack and eat a certain size of prey. For instance, a 120 gram lobster could not consume a sea urchin larger than about 20 grams. Generally, the large lobsters can consume the larger size of prey. This size selection occurs with all of the lobster's hard shelled prey and is because of the difficulty of opening the animal.

The feeding habits of the lobster have been divided into three actions: capture, opening and immobilization of prey, and consumption. With S. droebachiensis feeding occurs as follows: the sea urchin is pried from the substate using the chela and walking legs (see Figure 21, Plates 1 and 2). There was only one instance of consumption where a lobster failed to remove a sea urchin from the substrate first. In that case the sea urchin was successfully consumed by opening it while it was still attached. Prior to opening it the sea urchin is carried around by the lobster using the first pair of walking legs and the maxillipeds (see Figure 21, Plate 2). The sea urchin is manipulated using the maxilliped, the first pair of walking legs, and the chela into a position where the crusher claw can grab it while it is supported by the pincer claw (see Figure 21, Plate 3). The shell is crushed in half (see Figure 20, Plate 5) if the sea urchin is small and if large compared to the lobster a hole or holes are worked into the test (see Figure 20, Plate 4) and the shell split until the holes are joined. The shell is then fully opened by pulling pieces off with either claw (see Figure 21, Plate 3 and 4). Another method although seldom used by lobsters was to break the animal open by entering through Aristotle's lantern. The broken pieces of the shell are held against the mandibles while being manuevered by the first pair of walking legs, maxillipeds and claws - the flesh is systematically scrapped off and fed into the mouth by the mandibles. The flesh is split into small pieces by the mandibles and the maxillipeds (see Figure 21, Plates 5 and 6).

Capture of C. irroratus is made difficult by the defense mechanisms of the crabs. They either run away and they can easily outdistance a lobster or if the lobster succeeds in backing it into a corner, it will defend itself with it's claws. The crab backs into a corner raising it's claws and body towards the direction of attack. The lobster attempts to grab the crab on the body with the crusher claw or grabs the legs with the pincer. The crab if small compared to the lobster is then immediately killed by crushing the body (see Figure 19, Plates 2 and 3) and then the legs are pulled off. If the crab is large, the legs are pulled off first by the large chela or the maxillipeds while the walking legs cradle the crab (see Figure 19, Plate 1). Once the legs have been removed the crab is broken open and killed using the crusher claw. The crab is sometimes left alive once immobilized to be eaten at a later date. The actual consumption is similar to that described in the sea urchin.

M. edulis is pulled off of it's substrate similarly to sea urchins by using the chela and the advantageous use of gravity. The mussel is manipulated by the first walking legs and maxillipeds prior to opening. It is passed back and forth over the mandibles which appear to remove the algae from the surface. The mussel is then placed in the crusher chela and broken in half (see Figure 20, Plate 3). When the shell can not be crushed the lobster scrapes at the algae some more and then tries again. The mussel is broken into small pieces and the meat scrapped off by the mandibles and maxillipeds (see Figure 20, Plate 3).

With B. undatum the only defense is moving to higher ground. The lobster however, moves much faster and knocks it off the substrate with it's claws. The whelk is then toyed with for some minutes before

Figure 19. This is the material leftover from lobster feeding.

Plate 1. *Cancer irroratus*

Plate 2. *C. irroratus*

Plate 3. *C. irroratus*

1.

2.

3.

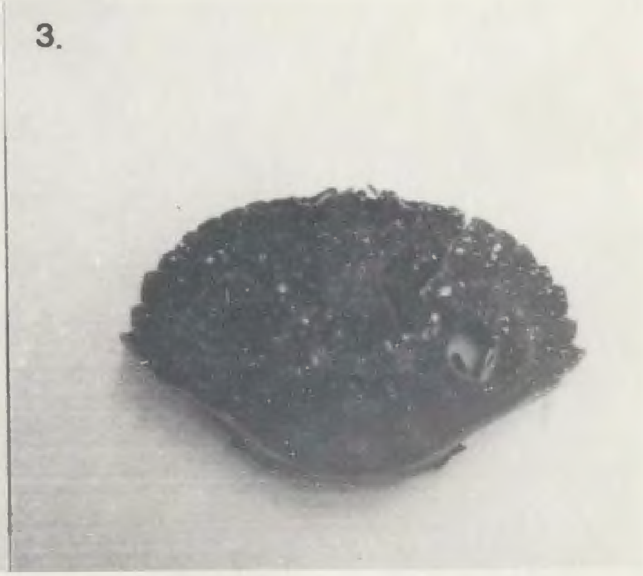


Figure 20. This is the material leftover from lobster feeding.

Plate 1. Buccinum undatum

Plate 2. Hyas coarctatus

Plate 3. Mytilus edulis

Plate 4. Strongylocentrotus droebachiensis

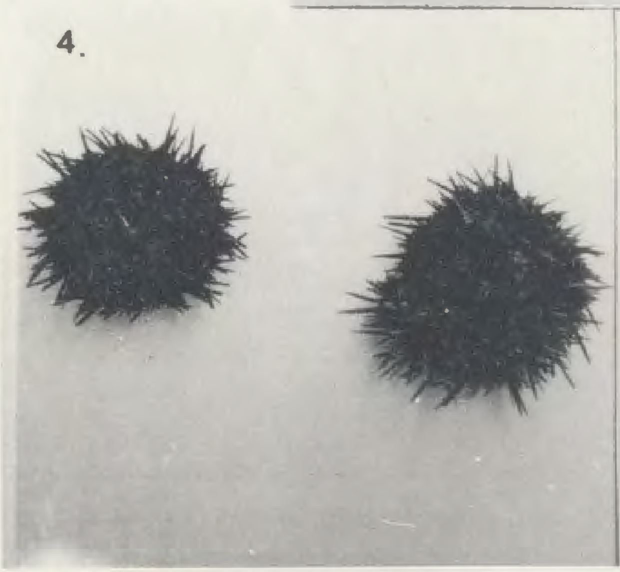
Plate 5. S. droebachiensis

1.

2.

3.

4.



5.

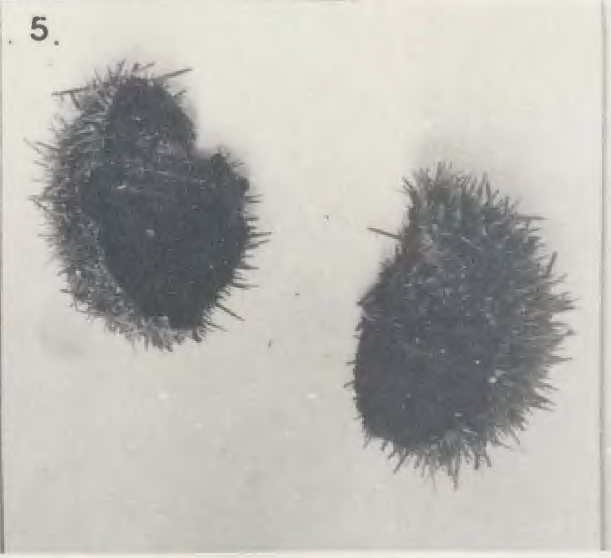


Figure 21. The three stages of lobster consuming *S. droebachiensis*.

Plates 1 and 2. Stage I - Capture. The lobster captures the sea urchin.

Plates 3 and 4. Stage II - Opening the shell. The sea urchin is manipulated until the crusher claw can grip it and split it in half.

Plates 5 and 6. Stage III - Consumption. The sea urchin is held against the mandibles and the flesh removed.

1.

2.

3.

4.

5.

6.

being crushed by the large chela. If it is extra large it is opened from the foot end one piece at a time until (usual method) the meat can be pulled out by the maxillipeds (see Figure 20, Plate 1). The meat is cut up using the first walking legs, chela and the maxillipeds and then eaten.

This portion of the study showed that lobsters did not eat all of an animal but only the soft material on the inside of the shell. With C. irroratus it was found that only 23% of the total weight of the crab (40 averaged) was actually consumed. With S. droebachiensis only 11% (106 averaged) of the animal was consumed.

The sea urchin force experiments showed that sea urchins are more difficult to remove when the sea water temperature is warm than cold. Also the larger the sea urchin the more difficult it is to remove from it's substrate. A certain size lobster can consume only a certain size range of sea urchin (see preference). This may be because a lobster could not remove from the substrate those sea urchins that are too large. In a population of lobsters that is overfished resulting in the removal of the large lobsters there would be selection favouring the consumption of smaller sized sea urchins. Also sea urchins could be a winter food since they would be easier to remove. Once a sea urchin has been pulled from the strata it would have little chance to escape since they take about two hours at a minimum to attach themselves.

Both Herrick (1911) and Templeman (1940) from analysis of stomach contents similarly stated that lobsters eat mussels, sea urchins, starfish, worms, crabs, small fish, crustaceans (ie. isopods) and some algae. Neither one, however, discusses his sampling procedures or sample sizes.

Weiss (1970) found that C. irroratus was the most predominate food in the stomachs of 553 lobsters that he examined. Also occurring with great frequency were the Gastropods – Lacuna vincta, and Mitrella lunata, Polychaeta – Nereidae, and plant material. Incidentally, he found other organisms such as other Crustaceans (Libinia, Carcinus meanas, and C. borealis), Gastropods (Polinices spp. and Littorina spp.), fish, Hydrozoa, Ascidiacea, Echinodermata, and Ectoprocta.

In Newfoundland, besides the early work of Templeman (1940), cited above, Squires (1970) has analyzed the stomachs of 182 lobsters from Port au Port Bay and the Bay of Islands, Newfoundland. He states that "Fish bones present in 50% of the stomachs were possibly from fish bait. . . . Periwinkles (Littorina spp.) occurred in significant numbers. Bivalves were fairly common . . . In about 1% of the stomachs examined hermit crabs (Pagurus spp.), brittle stars, sea cucumbers, sea stars, amphipods, hydroids, and brown seaweed were found attesting to the omniverous feeding of lobsters".

There are several problems inherent in this method of assessing lobster diet. First, the use of "indicator" particles (Weiss, 1970) could be very misleading for ascertaining the diet. Also this method would be invalid for determining the diet since lobsters do not seem to actively consume shells except at the time of moult. Any "indicator" particles found would be those pieces of shell accidentally ingested while feeding. For instance, with sea urchins, they eat only the inside of the ~~test~~ and nothing else (see Figure 20, Plate 5). With other organisms ie. crabs it is possible that more shell fragments are accidentally ingested with food so further biasing these results. According to Herrick (1911) and Templeman (1940), these fragments remain in the stomach to provide calcium carbonate for the shell after the lobster has moulted and as such would give an incorrect picture of the diet. Also some researchers refer to an unidentifiable mass found (Weiss, 1970) in the stomachs which is the viscera of prey animals.

The other problem involved with this is the sampling techniques. This includes both the time of year that the collection was made and the method itself. If the specimens were collected over a year then the results would be fairly valid. But if they were collected at the moult period; then the experimental results will be biased by the presence of calcium particles from the food eaten at this time (sea urchin tests, Cancer shells, etc.) and may not be an accurate representation of the diet. If commercial gear was used rather than SCUBA a bait must be used to attract the lobster (commonly fish). This would account for the presence of fish bones reported in the lobster's diet.

Herrick (1911) and Templeman (1940) do not discuss their sampling procedures, but it can be presumed they did not use SCUBA but commercial gear. This would explain their placing of fish in Lobster diet.

Squires (1970) reports a 50% value for ingested fish which I feel is quite an inflated value since he used fish for bait (samples not collected by SCUBA) and only the insides of invertebrates are eaten whereas bones, scales etc. of fish are consumed. Squires' (1970) stomach content values are assumed to be occurrences of indicator particles; but nowhere does he actually ~~describe his~~ methods. He also reports a cucumarian. Again Squires listed a low value for echinoderms of 4% which is probably a underestimation since lobsters only consumed the insides of these animals and there would be very few indicators of sea urchin presence in the diet (except at moult which is only a small percentage of the time sampling took place).

Weiss' study was carried out over a full year and so will not be biased towards those animals consumed after the moult. He also used SCUBA to collect his samples. However, he does use the "indicator particle" method thus biasing his results. He reports low values for Echinodermata and Gastropoda which this study indicated high values for. He used SCUBA and so lists fish as incidentally occurring.

Scarratt (unpublished data from Miller, Mann and Scarratt, 1971) circumvented these problems by analyzing the contents by percent of stomachs containing material. These values are: mussels 67%, rock crabs 50%, polychaetes 42%, periwinkles 36%, sea urchins 23% and starfish 5%. This compares well with my data in that mussels, rock crabs, periwinkles and sea urchins were all readily eaten in the laboratory. Polychaetes were not examined too closely in my study since preliminary investigations showed that while lobsters would eat them (see Table 1) they were difficult for them to obtain and low in caloric value (Brawn <u>et al</u>, 1968).

<u>Distribution</u>

Distribution of lobsters is influenced by a great many parameters; such as bottom type, food and larval drift.

The distribution map of lobsters (see Figure 16) indicates that the best areas are the West Coast and Notre Dame Bay. The Canada Fisheries Statistics Annual (1956-1969) shows that these areas have always been among the more productive areas in Newfoundland. For instance, in 1969 Area M (covers from Cape St. Gregory to Point Riche including Bonne Bay) had 15.2% of the total catch for Newfoundland; Area L (Port-au-Port Bay and Bay of Islands) had 15.9% and Area B 21.9% (Notre Dame Bay) which conforms quite closely to the above. Lesser areas being Conception Bay (Area E) 1.07%, Trinity Bay (Area D) 2.17% and the Avalon Peninsula - East Coast (Area F) 0.34%; all of which correspond to my more general data on abundance (see Figure 16). This can be related to the recruitment of small lobsters on the bottom, which is related to production of larvae and their drift. The latter is determined by water movements and the duration of larval life.

Reproduction in the warm water tank was also affected. One lobster in the ambient and one in the 15°C. tank became berried in early August of 1971. The eggs in the warm tank hatched on April 24 the others not hatching until July 26 - a difference of three months. Approximately 60 larvae were observed as they passed through the stages; 1st. stage - 9 days; 2nd. stage - 9 days; 3rd. stage - 12 days (lobster larvae died at this point). Herrick (1911) lists the time spent in the stages as: 1st. stage 2-3 days and no more than 5; 2nd. stage 2-5 days no greater than 5 days and 3rd. stage no greater than 5 days at 80°F. Templeman (1936b) compared the length of time the larvae spent moulting to the fifth stage. He states that at 13°C. with the hatching by mid-August "should reach the sixth stage before winter, thus ensuring a better chance of survival than if winter caught them in some earlier stage less fitted for bottom life". He also says that during "the first three stages the lobster is free swimming and does not retreat from danger and seemingly has no awareness nor fear of enemies". Any lobster caught in these stages once the water becomes colder than 6°C. would have very little chance of survival. Extrapolating to the Labrador condition - the water there will be colder than in Newfoundland because of the Labrador Current, the temperature not rising to much above 10°C. by the end of August. If the larvae hatched at this point, according to Templeman (1936b), they would take 105 days to reach the fourth stage. But water becomes cold fast - it was 5.0°C. close to the surface the first week of October in 1971. At this temperature larval moulting doesn't occur at all (Templeman, 1936b; Stewart and Squires, 1968) and so it is unlikely that the larvae would pass the third stage. Chances of their survival over the winter would be slim.

Templeman (1937) also states "Since the larvae spend much of their time at the surface they are driven by the wind and offshore winds may carry them many kilometers offshore with the surface water". Scarratt (1964) agrees with Templeman and also states that survival rate is quite low even under the best of conditions.

Lobsters are not found any farther north than about Henley Harbour, Labrador. The reasons for this are twofold; one being that the northern waters are just too cold (Templeman, 1937) for the development of the lobster larvae (Labrador Current sweeps in through here) or for the successful moulting of the adult lobsters (Stewart and Squires, 1968). In addition, the predominately westerly winds and downflowing Labrador Current would tend to drive the planktonic larvae away from the coast and southward. Food and suitable bottom type are quite abundant in Labrador and so wouldn't be limiting. Henley Harbour is the most northerly position on the Labrador Coast that could come under the influence of the warm current from the Gulf of St.Lawrence.

Lobster populations also vary around Newfoundland i.e. high on the West Coast and in Notre Dame Bay and low on the East Coast. Again the reasons for this are twofold; being temperature and larval drift. In Newfoundland, the wind direction is predominately South West, West and South during the months of July, August and September (Templeman and Tibbo, 1945). As larvae hatch they will be pushed inshore ; only a few will drift offshore. When the larvae settle at the fifth stage they remain (Templeman and Tibbo, 1945) in the areas where they were hatched. Another aspect of this is sea water temperature. The temperature here is 16°C. during the summer (Templeman and Tibbo, 1945) because of warm currents from the Gulf of St.Lawrence and the shallowness of the water. The larvae develop faster enabling them to settle earlier than elsewhere (Templeman, 1936a Templeman, 1937; Templeman and Tibbo, 1945; and also see previous discussion of larvae) and hence more survive (Scarratt, 1964). This is not the case however, on the East Coast. Not only is the water colder (Labrador Current water temperature - 13°C.) so that the larvae have to spend a longer period in planktonic stages plus the winds tend to push them offshore. This results in less larvae developing inshore and hence a lower population.

The other high return area mentioned was Notre Dame Bay. This area is anamolous compared to other areas because the many estuaries and islands prevent the larvae from being blown offshore holding them in the bay. Also due to it's shallow nature (Templeman and Tibbo, 1945) the water attains as high a temperature as recorded on the West Coast so enabling the fast development of larvae and higher survival.

Lobster prey Cancer, Strongylocentrotus, etc. are commonly found with lobsters and so would be expected to increase since as lobster habitat improves so does prey habitat. The number of lobsters also increases with improved bottom type and increased abundance of prey (see Figures 15 and 16). At bottom type 0 as prey increases lobsters remain the same, that is 0. With a bottom type of 2 an increase in prey causes an increase in lobsters of quite substantial numbers, so prey would be limiting in this environment. However, considering bottom types 3 and 4, as the amount of prey increases the number of lobsters decreases. With bottom type 3 it is quite significant with 4 not so much so. What would limit lobsters here then I don't know but lobsters are very limiting to their prey in that with less lobster present there are more prey (see Figure 16). This could be influenced by lobster fishing that would reduce the abundance substantially at different localities that were sampled.

In this connection Squires suggested (Squires, Tucker, and Ennis, 1971), that cheap fish offal if spread over the grounds would increase lobster net yield. From the above I feel this would work well in some areas with good bottom type (type 3 and 4) where food could be limiting. Such areas as these are commonly found on the West Coast (see Figure 18, Results). Elsewhere, it wouldn't be very useful, since food doesn't limit numbers of lobsters. It could however, still increase individual lobster weight.

Himmelman (1969) reported that from November 22, 1968 to

June 24, 1969 two large male lobsters were able to consume 7.0 grams of sea urchin per lobster per day. He also states that "it may be that lobsters are more destructive in the natural environment." For instance, in areas with a high density of lobsters the sea urchin population is vastly reduced so that kelp and other algae that the sea urchin feeds on increases. So important environmentally is the lobster that Mann and Breen, (1972) feel that "the lobster is a key species controlling sea urchin populations in eastern Canada." Lobsters can also affect their other co-inhabiters such as Cancer (see introduction), by competing for niche space or by changing it's habitat (Stewart, 1970; Scarratt and Lowe, 1972).

In Newfoundland, this could be very significant to the environment. For example, it was noticed while diving in Bonne Bay that in the presence of a large lobster population (living from 4-25 meters) there was a marked reduction in S. droebachiensis, B. undatum, M. edulis and almost a total absence of C. irroratus. This greatly affected the algae population which is extremely abundant similarly to that suggested by Himmelman (1969) and Mann and Breen (1972). In contrast to this consider the situation at Outer Cove near St. John's on the Avalon Peninsula. Here there are no lobster and there is a large population of C. irroratus. Also S. droebachiensis are far more abundant than in Bonne Bay.

Energetics

Lobsters being poikilothermic, both growth and metabolism are directly controlled by the temperature of the sea water environment (see Results, Figures 10 and 11). The average consumptions per month over a year for the lobsters in the ambient tanks are 222 calories per gram of lobster per month when fed (*C. irroratus*) and 127 (*S. droebachiensis*) and 630 (*C. irroratus*) and 470 (*S. droebachiensis*) for the 15°C. tanks (each value is for a single lobster). At both temperatures, the monthly average of *C. irroratus* was considerably higher than for *S. droebachiensis* (ambient - 95; warm - 170 higher). This could be because the lobster expends more energy in capturing and consuming a crab than a sea urchin (see Table 3, Discussion). In the cold water tank the caloric intake fluctuated directly as the water temperature varied except at the time of moult when the monthly calories consumed dropped although the temperature remained the same. The warm water (15°C.) tank drops at this time also. The other fluctuations in the warm water tank are due I feel to fluctuations in temperatures during the period of March and the first of June (see Figure 11(a)). The drop in November - December (Figure 11) occurred during the period the warm water was being set up.

It has been proven that the lobsters at higher temperatures do grow faster (Hughes, 1971; Hughes, Sullivan and Shleser, 1972). The caloric intake at 15°C. was greater than at ambient temperature but since the consumption of calories would be proportionately less (M^{c}Leese and Wilder, 1958) there should be more calories available for growth at the higher temperature. Also the growth of lobsters in the lab can't be applied to growth in the environment (Wilder, 1958) and neither can caloric intake. Feeding rate may be higher than in the lab but more calories are used here because of the added area to move around in. Ennis (Squires, Tucker and Ennis, 1971) suggested that "growth increments are dependent upon the rate of feeding and that a relatively high rate of feeding in cages will give a greater moult increment than on the lobster grounds". It may well be that the feeding rate is similar but higher use of calories of free living lobsters results in a decreased growth rate. Also Ennis' study was conducted using opened mussels and scallop mantles which are not natural lobster food so adding further to the differences.

What is needed is a growth study in the environment including feeding rates and caloric intake. This was attempted by the author but the experiment failed due to inclement weather conditions.

A paper by Miller, Mann and Scarratt (1971) gives an energy flow study for a seaweed - lobster community. In it, they compute an estimated consumption by lobsters (kcalories per m^2 per year) using stomach content data by Scarratt and caloric content of invertebrates from Brawn et al (1968). The caloric content is measured for the whole invertebrate and not just the portion consumed (see previous discussion - Sources of Food and Preference) and therefore their analysis underestimates the calories consumed by the lobsters. This study considered the caloric content of only that portion consumed and so should be more accurate.

Another aspect to consider here is the cycle of feeding from the warm and cold water tanks. Most obvious in this is the drop in calories per gram of lobster taken during the moult cycle. In all of the cases (at ambient or 15°C.) the number of calories drop quite drastically just before moult and then rise again but slowly at first for two weeks after.

For analytical purposes the caloric intake of the lobsters was applied to the following formula:

Input = Growth + Respiration + Egestion (Teal, 1957)

For this formula, the input is the values from my data, egestion is 50% of the total input (using the value of 50% assimilation for the lobsters) and respiration was calculated using O_2 consumption of M^c^Leese (1964). Oxygen consumption was converted to calories with the average oxycaloric coefficient of Ivlev (1934), which is 3.38 calories per milligram of O_2 consumed (see sample calculation, Appendix O). This average coefficient was used as the respiratory quotient was not known. The 50% assimilation value is the work of Phillipson (1960) who found with Mitopsis morio (Class Arachnida) that it varied from 25.0 - 89.2% in the male and 38.0 - 98.0% in the female. This averages close to 50%. M. morio is a carnivore and so is comparable to H. americanus except that one is a land invertebrate, the other marine. Miller, Mann and Scarratt (1971) used a value of 80% assimilation efficiency (from Winberg, 1956). This value is however for carnivorous fish and not invertebrate carnivores and so I felt it was better to use the value of Phillipson.

The most salient difference of course is between the warm and cold tanks (see Appendices, P, Q, R and S). The lobsters in the warm tanks consumed 1832 calories per year (C. irroratus) and 1095 (S. droebachiensis) left over for growth and reproduction after respiration and egestive loses were considered; the cold water tanks consumed 716 calories per year (C. irroratus) and 158 (S. droebachiensis) leftover. This is probably not very comparable to the natural situation since many more calories would be used due to the animal's increased mobility. Thus in the environment, they would have to consume more prey than in the laboratory. These values would be higher therefore than in nature. This increased feeding rate in the warm water also agrees with growth observations in that lobsters do grow faster in warmer water (Wilder, 1953). Miller, Mann and Scarratt (1971) report production of 1.8 kilocalories per m^2 in a lobster community of 5.4 grams per m^2 or a total of 333 calories per year. This seems to be lower than my data but is due to using caloric content based on whole invertebrates and not on the portion lobsters do consume.

Also this would indicate an increased growth in the warm tanks over those in the cold tanks. Lobster consumed sea urchins at 14% of that consumed in the warm tanks and 38.2% with crabs. This also demonstrates that crab is more suitable prey for the lobster since more calories resulted from consuming this species.

In the ambient tanks during the colder months (February - March - April - May) there is very little leftover for growth 6, 6, 7, and 3 calories with S. droebachiensis and 27, 14, 31 and 25 calories with C. irroratus. The best growing months for extra calories are September to January with 24, 93, 17 and 54 for S. droebachiensis and 124, 41, 148 and 138 calories for C. irroratus (see Appendices P and Q).

This means that animals in nature in Newfoundland waters will grow very slowly, since the only months they can really increase in weight are September to January. During the winter months, since very little is ingested there can be little growth. However, in warmer waters than Newfoundland (i.e. Northumberland Strait, southern Maine, etc.) growth would be much faster since compared to Newfoundland the water is warm most of the year.

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Appendix A.

Lobster collection dates, methods and locations.

Location	Number Collected	Method	Sex	Wet Weight (grams)	Date
Bauline	4	purchased	male	861	May 17, 1971
		"	female	1740	"
		"	male	682	"
		"	female	1781	"
St. Thomas	7	SCUBA	male	282	July 18, 1971
		"	male	395	"
		"	male	665	"
		"	female	364	"
		"	male	505	"
		"	male	746	"
		"	female	269	"
Portugal Cove	3	"	female	336	June 1, 1972
		"	male	511	"
		"	male	1155	"
Portugal Cove	2	"	female	188	June 2, 1972
		"	male	407	"
Logy Bay	1	"	male	1689	July 3, 1972
St. Thomas	4	"	female	546	July 5, 1972
		"	female	350	"
		"	female	239	"
		"	male	1225	"

Appendix B.

Mean force (grams) required to remove a sea urchin from it's substrate at different temperatures. Values are averaged from not less than 25 tests. Sea urchin weights were grouped: 0-19.9, 20.0-29.9, 30.0-39.9, 40.0-49.9, and greater than 50.0. The total weight for each group is then averaged.

Sea Water Temperature	Sea Urchin Weight (grams) / Force (grams)				
0°C.	16.3/344	26.5/548	33.0/545	46.3/753	
5°C.	13.7/546	24.3/791	34.3/1001	42.0/1085	63.0/1673
9-11°C.	16.2/559	26.5/917	34.3/1170	44.3/1159	55.5/1313
15°C.	16.5/816	25.2/1211	34.8/1259	42.9/1458	56.0/1694

Appendix C.

A sample calculation of caloric content.

Example species is Pagurus spp.

$$Hg = \frac{(tW)}{m} - e_1 - e_2 - e_3$$

m = 1.0003 grams
t_1 = 68.600°F.
t_2 = 71.055°F.
e_1 = 6.60 milliliters
e_2 = 0
e_3 = 13.00 centimeters
W = 1360.79 calories per gram per degree.

where:
Hg - gross heat of combustion
t - temperature change ($t_2 - t_1$).
W - energy equivalent of calorimeter
e_1 - milliliters of standard alkali solution used in titration
e_2 - percentage of sulphur in sample
e_3 - centimeters of fuse wire consumed in firing
m - mass of the sample in grams

$$\begin{aligned} Hg &= (2.453 \times 1360.79/1.0003) - 6.60 - 0 - 13.00 \\ &= 3317 \text{ calories per gram} \end{aligned}$$

Appendix D.

Sample calculation for sulphur content of test material.

$$\text{Sulphur,\%} = \frac{\text{weight } BaSO_4 \times 13.734}{\text{weight of sample}}$$

weight of $BaSO_4$ = 0.0831 grams

weight of sample = 1.0002 grams

$$\text{sulphur,\%} = \frac{0.0831 \times 13.734}{1.0002}$$

$$= 16$$

If less than 1% then the results of this test were ignored.

Appendix E.

Lists the value of the sulphur correction factor in percent unless it is lower than 1%.

Species	Value
S. droebachiensis	16
M. edulis	19
Pagurus spp.	--
Halocynthia pyriformis	15
Halichondria spp.	--
Alaria spp.	--
C. irroratus	--
Hyas coarctatus	--

Appendix E.

Lists the value of the sulphur correction factor in percent unless it is lower than 1%.

Species	Value
S. droebachiensis	16
M. edulis	19
Pagurus spp.	--
Halocynthia pyriformis	15
Halichondria spp.	--
Alaria spp.	--
C. irroratus	--
Hyas coarctatus	--

Appendix F.

Results of the complete combustion of the samples from the bomb calorimetry.

Sample	weight before (grams)	weight after (grams)	Difference	%	CO_3^{--}
S. droebachiensis	0.8348	0.8020	0.0328	3.93	+(slight)
A. vulgaris	2.5243	1.9000	0.6243	24.73	+(excessive)
T. cupressina	will not fire at all				+(excessive)
M. edulis	not enough ash left to do this test				–
C. irroratus	0.9417	.8814	0.0603	6.4	+
Pagurus spp.	1.4743	1.2829	0.1914	12.98	+(excessive)
B. undatum	0.0955	0.0926	0.0029	3.04	–
H. coarctatus	0.2396	0.2205	0.0191	7.97	–
Alaria spp.	0.1929	0.1802	0.0127	6.58	+
Halichondria spp.	1.0682	1.0569	0.0113	1.06	+

Since ash was the proper colour ie. white grey despite the above changes I feel the results are still accurate. In the above cases were the change is excessive it can be attributed to the formation of CO_2 and hydroscopic changes in weight.

Appendix G.

Tabulated values of the number of calories of *C. irroratus* consumed monthly per gram of lobster at ambient sea water temperature. The lobsters wet weight was 1623 grams.

Month	Calories per gram of lobster per month
September	532
October	271
November	394
December	302
January	300
February	62
March	39
April	70
May	77
June	127
July	264
August	225
Mean	222

Appendix H.

Tabulated values of the number of calories of S. droebachiensis consumed monthly per gram of lobster at ambient sea water temperature. The lobsters wet weight was 845 grams. These values are for one lobster.

Month	Calories per gram of lobster per month
September	341
October	375
November	132
December	101
January	54.2
February	19.9
March	22.1
April	21.4
May	33.2
June	58.2
July	223
August	143
Mean	127

Appendix I.

Tabulated values of the number of calories of *C. irroratus* consumed monthly per gram of lobster at 15°C. The lobster weight was 684 and 813 grams. These values are for one lobster.

Month	Calories per gram of lobster per month
September	387
October	442
November	337
December	667
January	634
February	648
March	666
April	548
May	898
June	607
July	699
August	1024
Mean	630

Appendix J.

Tabulated vlaues of the number of calories of S. droebachiensis consumed monthly per gram of lobster at 15°C. The lobster weight was 1666 grams. These values are for one lobster.

Month	Calories per gram of lobster per month
September	351
October	280
November	387
December	367
January	350
February	484
March	545
April	545
May	1103
June	656
July	598
August	409
Mean	461

Appendix K.

Table of the percentage of C. irroratus consumed by H. americanus.

Total Weight(grams)	Percentage
95.5	23.56%
144.4	17.86%
109.3	24.06%
133.5	25.39%
84.9	21.67%
212.0	25.14%
110.9	23.62%
96.2	21.93%
75.5	24.11%
95.6	23.95%
113.2	23.14%
28.2	25.53%
97.7	21.70%
89.8	24.94%
103.6	18.44%
193.7	24.94%
127.8	22.22%
115.6	21.89%
112.4	20.46%
76.1	20.76%

mean = 22.67%
≈ 23%

Appendix L.

Table of the percentage of *S. droebachiensis* consumed by *H. americanus*.

Total Weight(grams)	Percentage
18.64	4.77%
16.69	1.71%
26.33	11.01%
25.91	9.96%
26.71	7.04%
25.48	6.79%
25.79	7.40%
24.50	19.59%
22.70	7.05%
26.90	5.95%
21.10	14.69%
28.70	17.77%
29.50	16.27%
28.60	11.54%
29.50	16.27%
28.60	11.54%
24.80	17.74%
36.00	10.83%
39.50	12.66%
30.20	11.92%
30.80	11.36%
34.80	14.08%
31.50	20.00%
36.70	17.71%
38.57	7.31%
37.18	8.04%
31.27	7.99%
33.12	3.41%
111.20	11.60%
82.40	17.96%
63.80	10.34%
58.52	10.22%
51.32	19.47%
58.70	7.80%
52.50	7.05%
54.20	9.23%
59.60	17.62%
41.10	13.38%
43.50	9.80%
46.60	10.30%

CONTINUED from Appendix L.

44.30	12.42%
44.00	8.18%
46.00	14.57%
46.50	14.19%
41.30	10.41%
44.60	13.00%
40.40	15.10%
47.78	10.09%
40.38	7.06%
44.61	12.33%
47.30	6.13%
34.50	11.88%
39.30	10.94%

mean = 11.29%

≃ 11%

Appendix M.

Table of distribution of lobster, abundance of food and type of bottom at each of sampling sites.

Location	Lobsters (number per diving hour)	Lobsters (scale)	Food	Bottom Type
Salmon Cove	0	0	0	0
Beachy Cove	2.5	1	1	1
St. Thomas	2	1	2	1
Logy Bay	1	1	1	1
Bellevue Beach	0	0	1	0
Bay Bulls	2.4	[illegible]	1	1
Bay Bulls	4	1	2	1
Portugal Cove	2.4	1	1	1
Middle Cove	0	0	1	0
Salmonier	0	0	1	0
North Harbour	0	0	1	0
South West Arm	4	1	3	3
Holyrood South	2.4	1	1	1
" Refinery	0	0	0	0
" fish plant	17	3	2	2
Freshwater Bay	2	1	1	2
Eastport	3.6	1	1	1
Clode Sound	0	0	1	1
Chapel Cove	2	1	2	2
St. Thomas	5	2	1	1
Tors Cove	1.5	1	1	2
Outer Cove	0	0	1	1
Baine Harbour	2	1	1	1
Arnolds Cove	31	4	3	4
St. Thomas	13	2	1	1
Le Manche	2	1	1	1
Portugal Cove	26	4	1	3
Topsail Beach	6	1	1	2
Trout River	30	4	3	2
St. Anthony Bight	0	0	2	1
Crouse	0	0	1	0
Port Saunders	62	4	3	4
Portland Creek	5	1	1	1
Bonne Bay	31	4	2	2
St. Phillips	3	1	1	1
Northern Bay Sands	0	0	0	0
Notre Dame Bay	22	3	2	3
Fortune Bay	0	0	0	0
Grouais Island	0	0	2	1
Flatrock	0	0	2	2
Torbay	0	0	2	0

Appendix M. continued.

Spreadeagle Cove	0	0	1	1
Fairhaven	14	2	1	2
Fermeuse	0	0	1	1
Islington	0	0	1	1
St. Albans	0	0	0	0
Roti Bay	16	2	2	3
Riche Island	12	2	1	1
Cottrell's Cove	31	4	2	3
Ship Harbour	0	0	1	0
St. Pierre	0	0.	1	2
Salmonier Arm	2	1	1	1
Biscayne Bay	0	0	1	1
Old Bonaventure	0	0	2	0
Hodderville	14	2	3	3
St. Mary's Bay (Branch)	0	0	1	0
Bay Bulls (mouth)	2	1	1	1
Little Bell Island (Barachois Pond)	4	1	1	1
Little Bell Island	28	4	2	3
Burnt Point#1	51	4	3	4
Burnt Point#2	42	4	2	4
*Burnt Point#3	36	4	2	4
Payne's Cove Point	9	2	1	2
South Head	6	1	1	1
Gadd's Harbour	38	4	2	4
*Bottle Harbour	30	4	3	4
Deer Arm	12	2	1	1
Shoal Point	15	2	1	2
Pinnacle Point	60	4	2	4
Shagg Cliff	24	3	2	2

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* snorkel rather than SCUBA was here

Appendix N.

Table of oxygen consumption and calories used per month calculated as O_2 consumption/gram of lobster/month.

Month	Temperature	O_2 Consumption*	Calories burned
September	12°C.	36	146
October	8°C.	22.5	94
November	5°C.	12	49
December	2°C.	3	13
January	0	1	5
February	-1°C.	1	4
March	0	1	5
April	1	1	4
May	2	3	13
June	4	10	40
July	8	22.5	94
August	12	36	151

*M^c^Leese (1964); values are milligrams of O_2 consumed per 1000 grams per hour

Appendix O.

Sample calculation of the calories respired per gram of lobster month.

Ivlev,(1934): 3.38 calories per milligram of oxygen consumed.

M^cLeese (1964): the number of milligrams of oxygen consumed at various temperatures.

39.5 mg O_2 / 1000 grams of lobster.

lobster weight = 1666 grams

hours in 31 day month = 744 hours.

Calories burned = 39.5 x 3.38 x 1666/1000 x 744

= 165 k - calories/ 1000 grams

or 165 calories / gram of lobster.

Appendix P.

Table of the number of calories per gram of lobster of respiration, egestion, and growth and reproduction. Also shown are the total calories intake. The table assumes a value of 50% assimilation efficiency for egestion (Phillipson, 1960), respiration was calculated (see sample calculation, Appendix O) and the calories left for growth and reproduction are shown. In this table, the lobster weighed 1623 grams, consumed C. irroratus, and was at ambient sea water temperature.

The table is based on the equation:

Growth + Reproduction = Intake - Respiration - Egestion

Month	Calories per gram lobster intake	Respiration	Egestion	Growth+Reproduction
September	532	146	262	124
October	271	94	136	41
November	394	49	197	148
December	302	13	151	138
January	300	5	150	145
February	62	4	31	27
March	39	5	20	14
April	70	4	35	31
May	77	13	39	25
June	127	40	64	23
July	264	94	132	38
August	225	151	113	-38
				Total =716

Appendix Q.

Similar to Appendix P except S. droebachiensis was consumed and the sea water temperature was ambient. The lobster weighed 845 grams.

Month	Calories per gram lobster intake	Respiration	Egestion	Growth+Reproduction
September	341	146	171	24
October	375	94	188	93
November	132	49	66	17
December	101	13	51	54
January	54.2	5	27	22
February	19.9	4	10	6
March	22.1	5	11	6
April	21.4	4	10	7
May	33.2	13	17	3
June	58.2	40	29	-11
July	223	94	112	17
August	143	151	72	-80
				Total = 158

Appendix R.

Similar to Appendix P except C. irroratus was consumed and the sea water temperature was 15°C. The lobster weighed 684 and 813 grams.

Month	Calories per gram lobster intake	Respiration	Egestion	Growth+Reproduction
September	387	160	194	33
October	442	165	221	56
November	337	160	169	8
December	667	165	334	168
January	634	165	317	152
February	648	149	324	175
March	666	165	333	168
April	548	160	274	114
May	898	165	449	284
June	607	160	304	143
July	699	165	350	184
August	1024	165	512	347
				Total = 1832

Appendix S.

Similar to Appendix P except S. droebachiensis was consumed and the sea water temperature was 15°C. The lobster weighed 1666 grams.

Month	Calories per gram lobster intake	Respiration	Egestion	Growth+Reproduction
September	351	160	176	15
October	280	165	140	-25
November	387	160	194	33
December	367	165	184	18
January	350	165	175	15
February	484	149	242	93
March	545	165	273	107
April	545	160	273	112
May	1103	165	552	368
June	656	160	328	168
July	598	165	299	134
August	409	165	205	39
				Total = 1095