The Feeding Ecology of Capelin (Mallotus villosus)
in the Estuary and Western Gulf of St. Lawrence

by .

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The feeding ecology of juvenile (< 140 mm TL) and adult (>140 mm TL) capelin (Mallotus villosus) in the St. Lawrence River estuary and western Gulf of St. Lawrence was studied between October 1974 and October 1975. Both juvenile and adult capelin fed almost exclusively on zooplankton. Three prey totally dominated the food of capelin. Copepods were the most numerous prey items in the diet (except in May -June when euphausiids were dominant) but euphausiids were the dominant prey in terms of biomass of food consumed. Appendicularians ranked third in their contribution to the diet both in terms of number and biomass. This pattern differs significantly from that reported for capelin from the Canadian Atlantic only to the extent that amphipods replace appendicularians in the diet. The relative importance of the three prey groups is, however, very similar. A clean shift in diet occurred during fish growth. Pre-metamorphic capelin consumed small prey exclusively; invertebrate eggs, cyclopoid copepods and diatoms forming the bulk of the diet. The diets of juvenile and adult capelin overlapped considerably but a pronounced shift in the diet Trom small copepods to adult euphausiids occurred at approximately 140 mm TL. Two distinct daily feeding peaks occurred between May and August, the first between sunrise and mid-morning and the second between 1 🐠 and 2200 h in the evening. A single midday feeding peak prevailed in October-November. Feeding of adult capelin was active in the spring prior to spawning but virtually ceased during spawning. Juvenile capelin fed actively throughout spring and summer. The ration of

zooplankton by capelin was estimated to be 5% of wet body weight in summer May - September and approximately 2.5% in October - November. The diets of capelin from the estuary and Gulf were similar, although large copepods were much less abundant in the diet of fish collected in the Gulf. The summer consumption of zooplankton by capelin in the Canadian Atlantic has declined from 334,000 to 83,000 metric tons per day between 1972 and 1978. Year-to-year changes in average daily consumption of greater than 100,000 metric tons have occurred during this interval. It is suggested that this significant year-to-year and long-term release of zooplankton from predation by capelin may be an important regulator of changes in year class strength, growth and species composition of the area.

RESUME

D'octobre 1974 à octobre 1975, nous avons étudié l'écologie alimentaire du Capelan (Mallotus villosus) de l'estuaire et du golfe du Saint-Laurent. Juvéniles (< 140 mm LT) et adultes (> 140 mm LT) se nourrissent presque exclusivement d'organismes zooplanctoniques. Trois groupes de proies parmi ceux-ci ont été trouvés essentiellement dominants dans le régime alimentaire des capelans. Les copépodes constituent les proies du régime les plus nombreuses (sauf en mai-juin où les euphausiacés sont les plus importantes), mais du point de vue des biomasses de nourriture ingérées, les euphausiaces en sont les proies dominantes. Les appendiculaires enfin se classent troisième en importance, tant à cause de leur nombre que de leur biomasse. Ces résultats sont comparables à ceux qui ont été trouvés chez le capelan de l'Atlantique canadien, et ils ne s'en distinguent de façon significative que par le fait que, chez ce dernier, les amphipodes remplacent les appendiculaires dans le régime. L'importance relative de ces trois groupes de proies demeure cependant très semblable dans les deux cas. Un changement progressif marqué se produit dans l'alimentation des capelans au fur et à mesure de leur croissance. Avant leur métamorphose les capelans se nourrissent exclusivement de petites proies, oeufs d'invertébrés, copépodes Cyclopoîdes et diatomées constituant l'essentiel de leur régime. Les régimes des capelans adultes et juvéniles sont à bien des égards semblables l'un à l'autre, mais nous notons un changement très net chez les poissons dont les tailles vont en s'accroissant à partir de 140 mm LT environ. Les copépodes de petite taille sont alors

remplacés progressivement par des euphausiacés adultes dans les contenus stomacaux. Entre les mois de mai et d'août, l'activité nycthémérale des capelans est marquée par deux périodes d'alimentation maximum, la . première entre le levée du soleil et le milieu de la matinée, la seconde entre 16h00 et 22h00 dans la soirée. En octobre et novembre, 🖅 nous n'avons observé qu'une seule période d'alimentation intensive, vers le milieu de la journée. Les capelans adultes se nourrissent de façon prononcée au cours du printemps, avant la période du frai, mais ils cessent de s'alimenter pendant le frai lui-même. Les juvéniles par contre se nourrissent tout au long du printemps et de l'été. La ration de zooplancton consommée quotidiennement par le capelan a été estimée à 5% du poids mouillé du corps du poisson, de mai à septembre, et à environ 2.5 % en octobre-novembre. Nous avons trouvé que les régimes des capelans de l'estuaire et du golfe étaient semblablés, bien que les gros copépodes soient beaucoup moins abondants dans la nourriture des poissons provenant du golfe. Nous considérons qu'entre 1972 et 1978 il s'est produit chez les capelans de l'Atlantique canadien une diminution de leur consommation estivale de zooplancton allant de 334,000 à 83,000 tonnes métriques par jour. Des différences annuelles de plus de 100,000 tonnes métriques dans la consommation fournalière moyenne de zooplancton sont apparues au cours de cette période. Cette baisse significative, observée d'une année à l'autre et à long terme, dans la consommation de zooplancton par Te capelan a entraîné dans le milieu une mise en liberté d'organismes zooplanctoniques qui, autrement, auraient été soumis à la prédation du poisson. Il est suggéré que cette libération puisse être un facteur important de régulation de l'abondance des classes d'âge, de la croissance et de la composition en espèces dans cette région.

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PREFACE

In keeping with the regulations for thesis style authorized by the Graduate Committee of the Biology Department at McGill, this thesis has been written in a form suitable for publication. Use was made of the style recommended by the Journal of the Fisheries Research Board of Canada and a manuscript embodying the results of the thesis has been forwarded to that Journal for publication.

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INTRODUCTION

The capelin, Mallotus villosus (O.F. Miller), is a key element in the marine food web of the North Atlantic Ocean. Bailey et al. (1977b) reported the annual consumption of capelin by minke whales, fin whales, harp seals and cod in the Northwest Atlantic to be in excess of 30×10^5 metric tons, and listed an additional 23 species of fish, birds and mammals, known to be major predators of capelin, for which no estimates of consumption rates are available. Minet and Perodou (1978) have similarly demonstrated the importance of capelin in the diet of cod in the Gulf of St. Lawrence. Winters and Carscadden (1978) consider capelin to be "the most important fish fodder resource in Canadian waters of the Northwest Atlantic". The dramatic increase in commercial exploitation of capelin which began in 1971 (Winters 1975; Winters and Carscadden 1978), has led to concern for the continued viability of. capelin stocks and, equally importantly, for the possible impact of a reduction in capelin abundance on their predators (Winters 1975; Carscadden 1976; McCracken and MacDonald 1976).

Central to a complete understanding of the productive capacity of capelin is a knowledge of its feeding ecology. While the diet of capelin has been studied previously, a clear understanding of their feeding has been hampered by the fact that samples of fish used in these studies have been collected over relatively short time intervals, and have differed greatly both in terms of geographical area and size of capelin examined. For example, Jeffers (1931) examined the food types of a non-specified number of adult capelin sampled from the Strait of

Belle Isle during the spawning period; Templeman (1948) has briefly documented the feeding of a few offshore, immature and maturing capelin found in salmon stomachs, and of a small number of coastal adult capelin sampled immediately prior to, during, and after spawning; and Winters (1970) reported on the intensity of feeding and fat content of juvenile and adult capelin sampled in Trinity Bay from the over-wintering to the spawning period. Kovalyov and Kudrin (1973) described the feeding intensity and the main components of the diet of Grand Banks capelin in spring and early summer. Recently, Chan and Carscadden (1976) gave a brief account of the feeding of Labrador capelin in the fall.

This paper reports the results of the first comprehensive study of the food and feeding habits of juvenile and adult capelin over a full year. The study was conducted in the St. Lawrence estuary and the western Gulf of St. Lawrence.

MATERIALS AND METHODS

Juvenile and adult capelin used for stomach content analyses in this study were sampled in October and November 1974 and April through October 1975 during research cruises conducted between Ile aux Coudres in the St. Lawrence estuary and Natashquan on the north shore of the Gulf of St. Lawrence, and southward to the entrance of Baie des Chaleurs in the southern Gulf (Fig. 1). Juvenile capelin caught in July 1974 at the entrance of the Saguenay River were also included in the feeding analysis. This study forms part of a larger investigation of the ecology of larval, juvenile and adult capelin from this region (Bailey et al. 1977a,b; Jacquaz et al. 1977). The location of sampling sites for food analyses are given in Fig. 2. All sampling was conducted with a modified Boris midwater trawl (Bergeron 1973) equipped with a headline transducer (Boudreau 1973). The length of tows was generally restricted to less than 30 min to ensure the sampling of discrete groups of fish.

A random sample of 50 fish from each catch was preserved in 10% formaldehyde immediately after capture. This number was found to be sufficient to provide adequate representation of different size classes and/or fish of different stages of maturity. When the sample was composed of fish of uniform sizes and maturity, 15 adult or 10 juvenile fish were analyzed for stomach contents. The number of new prey categories identified in any sample when more than 10 juveniles or 15 adult capelin were examined was small, and never influenced estimates of the composition of the diet either by number or by weight (Fig. 3). In mixed schools of different size classes or maturity stages a sample of each category was analyzed.

Fig. 1. St. Lawrence estuary and western Gulf with important localities mentioned in the text.

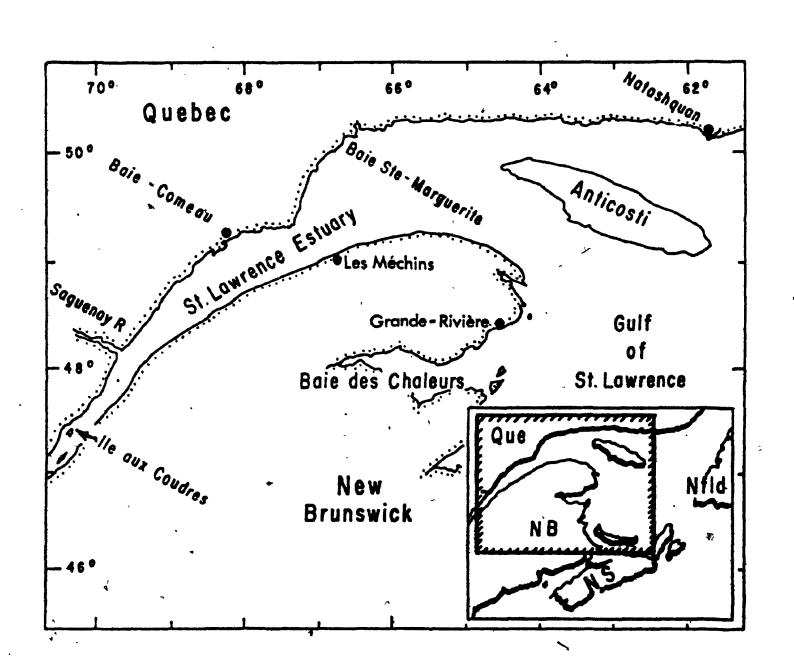
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Fig. 2. Locations of sampling sites for analyses of feeding intensity and composition of the diet of juvenile (Δ) and adult (·) capelin in the estuary and western Gulf of St. Lawrence,

1974-75. ■ juvenile and adult capelin sampled from the same school were analyzed. Δ capelin in these samples were analyzed only for feeding intensity and not the composition of the diet.

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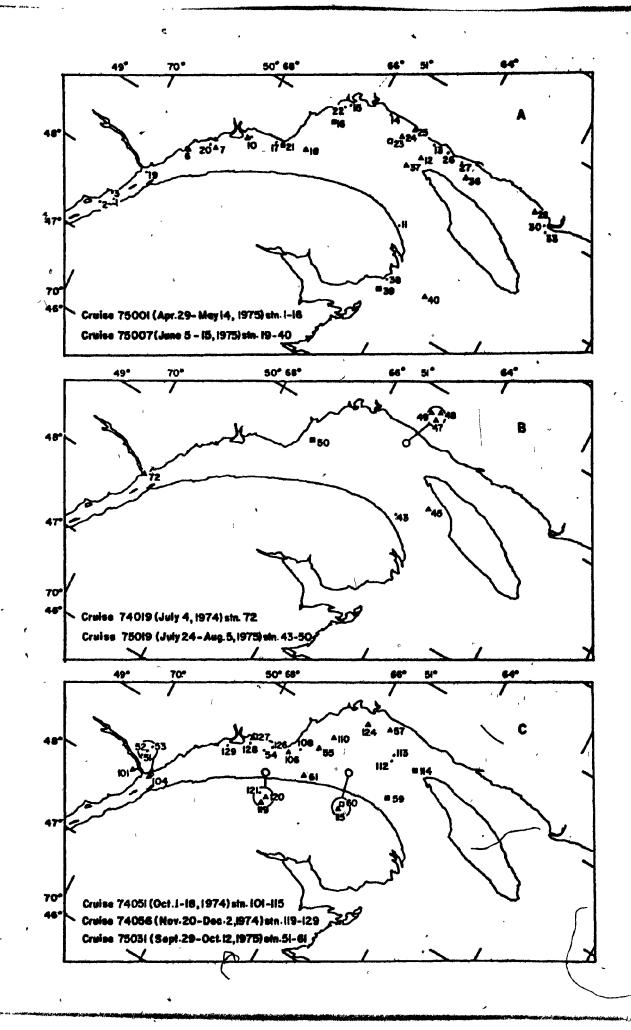
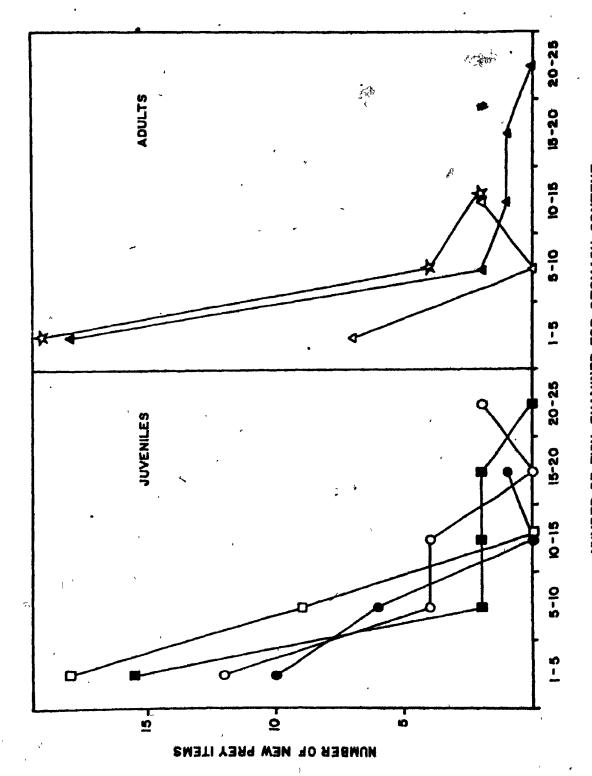


Fig. 3. Relationship between the number of stomachs

examined and the number of new prey items found

for each fish added to the sample.



NUMBER OF FISH EXAMINED FOR STOWACH CONTENT

Total length (TL mm), wet weight (g), sex, and maturity were recorded for each fish. No correction was made for shrinkage due to preservation, which we estimated to be 3-4%.

Food was removed from the stomach, placed on filter paper to remove excess moisture, and weighed to an accuracy of 0.1 mg. We then computed an index of fullness (IF) for each fish as follows: IF = (wet weight of food/wet weight of fish) x 1000. A mean value was calculated for each station, or if the sample contained capelin differing in maturity or in size, for each group.

To document the daily feeding chronology of capelin we performed an angular transformation on the ratio of wet weight of food to wet weight of fish to stabilize the variance of the samples (Sokal and Rohlf 1969; Foltz and Norden 1977). Means and 95% confidence limits of the ratios were then calculated for each station and back transformed to the original scale. Data from all stations at which capelin were spawning at the time of capture or had recently spawned were excluded from this analysis because the feeding behaviour of capelin is strongly depressed during spawning (Winters 1970).

The most abundant food items in the diet were identified to species. The larval stages of the most abundant copepod species were recorded separately. Counts were made of all prey items in each stomach except for appendicularians (Larvacea) which were impossible to separate when they occurred in tangled masses. An index of importance (IN = $\sqrt{(\text{% composition by number})} \times (\text{% occurrence})$) was calculated for each prey category (Windell 1971; Grabe#1977).

Dry weights of the more abundant prey (euphausiids, copepods and appendicularians) were summed for each station. An index of importance by weight (IW = $\sqrt{(% \text{composition by weight})} \times (% \text{occurrence})$; Windell 1971) was calculated for each prey category and a mean value of the index was derived.

We defined juveniles as post-metamorphic fish in the length category 75-139 mm (TL) and adults as fish > 140 mm. This separation was based on length ranges for the two categories reported in Bailey et al. (1977 a,b).

For the purposes of this study we defined the boundary between the estuary and the western Gulf as a line running from Baie-Comeau to Les Méchins (Fig. 1). This line delimited the presence or absence of Temora longicornis, a copepod common in the Gulf (Steven 1974) but absent from the estuary (Côté 1972), in the stomachs of capelin.

Diet Composition

Both juvenile and adult capelin fed almost exclusively on zooplankton (Table 1, Fig. 4). Copepods were the dominant prey category. Calanus finmarchicus, Temora longicornis, and Pseudocalanus minutus were the principal species consumed. Euphausiids occurred at moderate frequency in the diet but their numerical abundance was low relative to that of the copepods. Thysanoëssa raschii dominated the euphausiid group (Table 1).

Dry weight analysis of stomach contents revealed that, in spite of their smaller numerical abundance in the diet, the biomass of euphausiid crustaceans consumed was greater than that of the copepod crustaceans (IW 47:1 and 37.36 respectively). Appendicularians (Larvacea) ranked third in terms of their contribution to the biomass of food consumed (IW = 7.7). Other prey categories made a minor contribution to the diet both in terms of numbers and biomass (Fig. 4).

Size Related Differences in Diet

Considerable overlap occurred in the diets of juvenile and adult capelin (Figs. 4, 5). There was, however, a definite shift from a predominance of smaller prey to larger prey with increasing fish size (Fig. 5).

Copepods were the dominant prey of juvenile capelin both in numbers and biomass. Euphausiids and appendicularians, while common in the diet, were less important (Fig. 4 A,B). Among the residual food

Table 1. Diet composition of capelin from the estuary and the western Gulf of St. Lawrence, 1974-1975. (Juvenile and adult capelin combined: N = 683).

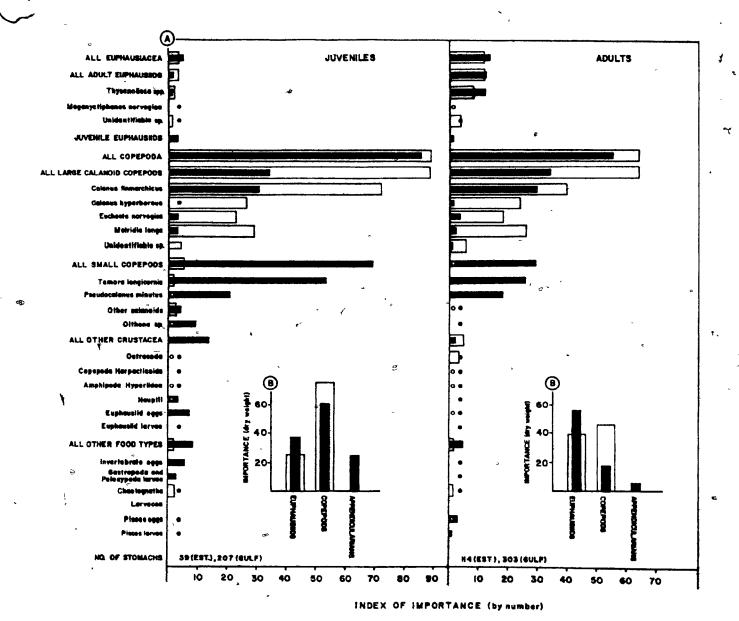
Food item	Prequency of occurrence (percent)	Percent composition (by number)	Index of importance
		ð	
EUPHAUSIACEA	33.4	2.3	8.8
Thysancessa ranchii (M. Sars)	17.0	1.2	4.5
Thysanoëssa inermis (Krøyer)	6.0	0.1	0.8
Thysanoëssa sp.	5.3	0.3	. 1.3
Meganyctiphanes norvegica (M. Sars)	0.9	< 0.1	0.1
Unidentifiable sp.	5.0	0.1	0.8
Euphausiacea juvenille	6.9	0.5	1.9
Subject of a contract of the c	00,	0.5	2
OPEPODA	53.2	92.1	70.0
		<i>T</i>	
Calanus finmarchicus (Gunnerus)	40.3	27.6	33.3
Calanus hyperboreus Krøyer	13.6	3.0	6.47
Euchaeta norvegica Boeck	23.1	2.0	6.8
Metridia longa (Lubbock) ²	22.1	3.0	8.1
Unidentified large Calanoida	5.9	1.7	3.2
Temora longicornis (0.F. Müller)	22.3	46.1	32.0
Pseudocalanus minutus (Krøyer)	16.4	6.8	10.6
Other small Calanoida3	13.9	0.4	2.3
Oithona sp. "	10,0	1.5	3.8
OTHER CRUSTACEANS	17.7	3.9	8.3
, g ₂			
OSTRACODA	3.4	0.1	0.5
COPEPODA Harpacticoida	2.2	< 0.1	0.3
AMPRIPODA Hyperiidea	5.1	0.1	0.7
Nauplii (Copepoda, Cirripedia, Euphausiacea)	7.2	0.4	1.6
Euphausiacea larvae (calyptopis, furcilia)	1.5	< 0.1	0.2
Euphausiacea eggs	3.2	3.2	3.2
OTHER FOOD TYPES	19.0	1.7	5.7
1 Invertebrate eggs	7.2	0.9	2.6
GASTROPODA and PELECYPODA larvae	6.4	0.2	1.2
CHAETOGNATHA (Sagitta sp.)	4.0	< 0.1	0.5
LARVACEA (Oikopleura sp., Fritillaria sp.)	25.0ª	- 001	
PISCES eggs4	2.9	0.4	1.1
PISCES larvae ⁵	1.8	0.1	0.4
LIDORD TELASE.	1.0	0.1	U. 4

Continued..../2

Table 1 (Cont'd)

- 1 No attempt was made to separate the closely related species <u>C. glacialis</u> Yaschnow from <u>C. finmarchicus</u> . <u>C. glacialis</u> did, however, occur.
- 2 M. lucens Boeck was found in 2 stomachs.
- 3 Includes Microcalanus sp., Eurytemora spp., Acartia spp., Centropages hamatus (Lilljeborg) and unidentifiable spp.
- 4 Almost exclusively capelin.
- 5 Almost exclusively capelin. Four redfish larvae (Sebastes sp.) were found in one stomach.
- Since they were not counted, appendicularians (Larvacea) were not included in the summarizing values of the "Other Food Types" category.

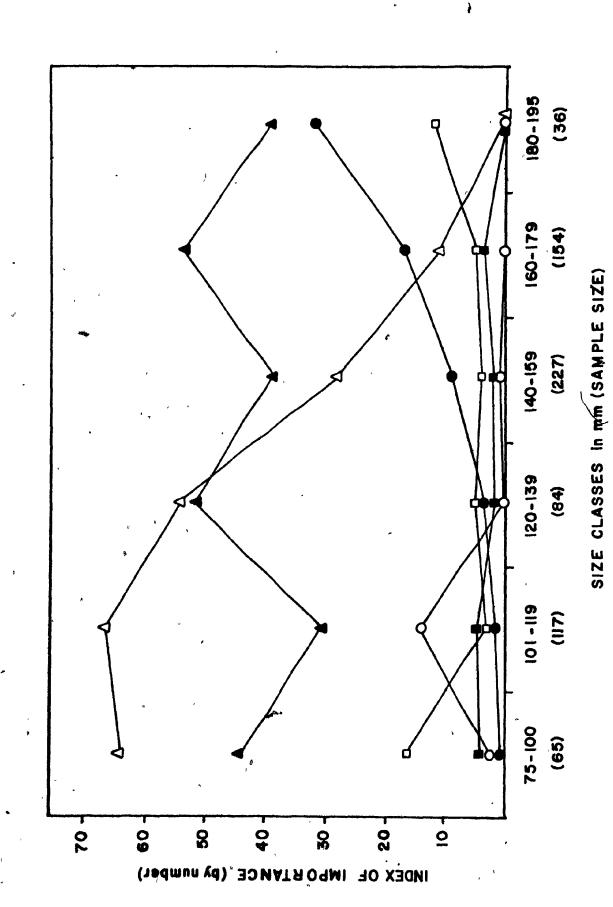
Index of importance by number (A) and weight (B) Fig. 4. of components of the diet of juvenile and adult capelin sampled in the estuary (open bars) and western Gulf (solid bars) of St. Lawrence. O and • indicate an index value of 1 for estuary and Gulf respectively.



- Fig. 5. Index of importance (by number) of prey of

 varying sizes in the diets of fish of varying
 sizes.
 - adult euphausiids
 - Alarge copepods (1)
 - △ small copepods (2)
 - ■other small crustaceans (nauplii, Amphipoda Hyperiides, Ostracoda, Copepods Harpacticoida)
 - O euphausiid eggs
 - D other food types (invertebrate eggs,
 Pelecypoda and Gastropoda larvae,
 Chaetognatha, fish eggs and larvae)
 - Large copepods include principally <u>Calanus</u>
 <u>finmarchicus</u>, <u>C. hyperboreus</u>, <u>Euchaeta</u>
 norvegica, <u>Metridia longa</u>.
 - 2) Small copepods include principally Temora

 longicornis, Pseudocalanus minutus, Oithona
 sp.



items eaten, smaller prey such as invertebrate eggs, nauplii, euphausiid eggs and larval, gastropod and pelecypod larvae were more abundant in the stomachs of juveniles than of adults (Fig. 4). Euphausiid eggs formed a major portion of the diet of juvenile capelin in May (Fig. 8). The copepod prey of juvenile capelin was dominated by small species, principally the calanoid species <u>T. longicornis</u> and <u>P. minutus</u>, and to a lesser extent by cyclopoids of the genus <u>Oithons</u>.

In contrast, adult euphausiids were significantly more abundant in the diet of adult capelin, both in terms of numbers and biomass, and the importance of small copepods was depressed (Fig. 4, 5).

The diet of pre-metamorphic capelin (Bailey et al. 1977a) differed greatly from that of juveniles and adults, being dominated by smaller prey items than that fed on by the larger fish. Invertebrate eggs, cyclopoid copepods, and diatoms were major components of the diet and generally increased in importance as the fish increased in length.

Nauplii, copepodites and adults of small copepod species formed the balance of the diet (Fig. 6).

Spatial and Temporal Variation in Diet

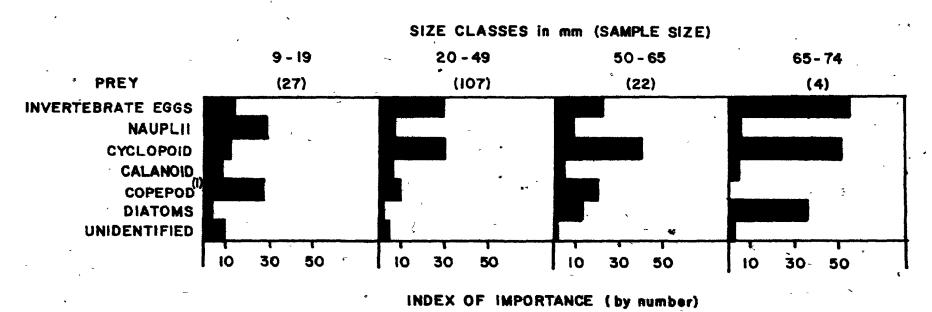
a) Diel Periodicity

Two distinct diel patterns of feeding were evident. These patterns were similar for both juveniles and adults. From May to August two feeding periods occurred (Fig. 7). The quantity of food in the stomachs was high from sunrise to mid-morning; the proportion of empty stomachs between 0600 and 1000 h averaged 34% and the mean index of fullness (IF) was 10.3. In contrast, capelin sampled between 1000 and 1600 h did not appear to be feeding heavily. The mean proportion of

Fig. 6. Index of importance (by number) of components of . the diet of pre-metamorphic capelin.

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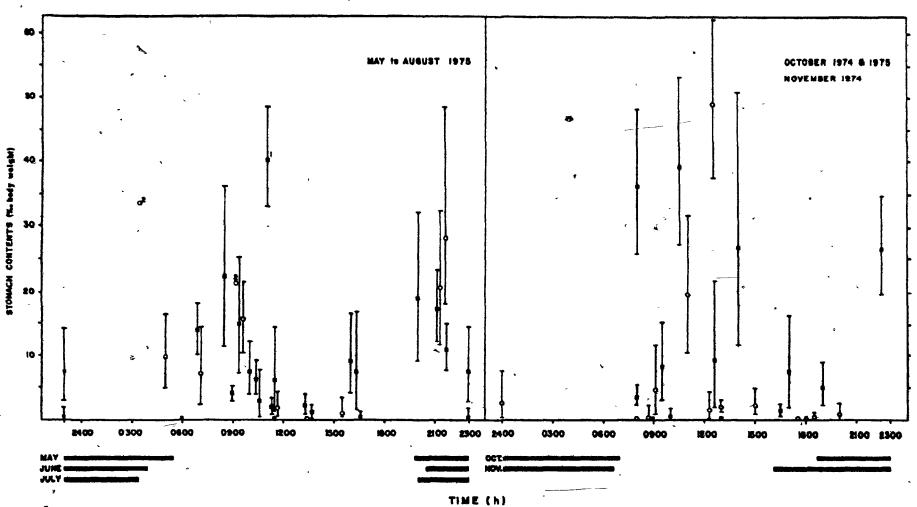


(1) Copepodite stages and adults of small species.

Fig. 7. Diel feeding activity of juvenile O and adult means capelin from the estuary and western Gulf of St.

Lawrence. Mean weights (g) of stomach contents per kg of fish per station. Vertical lines above and below means, 95% confidence intervals. Solid bars, hours of darkness.

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1Station 72 (July 1974)

²Each of these samples represent only 4 stomachs.

empty stomachs during this interval was 54% and the mean index of fullness (IF) declined to 6.2. A second feeding peak occurred in the early evening (1600-2200 h). During this interval the proportion of empty stomachs corresponded closely to the early morning level (32%) and the mean index of fullness increased sharply to 13.1. Additional evidence of diel periodicity in feeding during these months is given by our observation that prey items in the stomachs of fish sampled in the 1000-1600 period were in a much more advanced state of digestion than were prey items in stomachs of fish sampled during the morning and evening peaks.

A distinctly different feeding chronology appears to prevail in October and November. The intensity of feeding at this time was much more variable, with some samples containing fish having an index of fullness equal to or greater the maximum observed in the May-August period. Numerous other samples, collected during the same time interval, contained fish whose index of fullness was very low (Fig. 7). A precise interpretation of the daily periodicity of feeding during these months is made difficult by the smaller number of samples available from the dark period. Nonetheless the average index of fullness for 9 night samples was significantly (p = 0.001) lower (IF = 5.05; SD 8.42) than the average index for the 18 samples from the light period (IF 11.3; SD 15.79). Similarly, the proportion of empty stomachs in the nighttime samples was higher (night 77.3%; day 59.2%).

This data suggests the presence of a single feeding peak in late fall - early winter. The apparent longer period of feeding at this time may be the result of slower evacuation rates due to the lower average temperatures at this time of the year (Bailey et al. 1977b, Table 1).

b) Seasonal Variation

Capelin exhibited a seasonal variation in feeding intensity which differed between juveniles and adults and was strongly related to spawning activity. Adult capelin captured prior to spawning in the spring were feeding heavily. For example, in the western Gulf where spawning had not yet commenced at the time of the May cruise the frequency of empty stomachs in the samples was 36% and the index of fullness (IF) was 17.7. In contrast, in the estuary where spawning had already begun (Bailey et al. 1977b) 83% of the stomachs sampled were empty and the feeding intensity was low (IF = 2.7). Many of the stomachs of these spent capelin in these estuary samples contained sand in variable quantities together with small numbers of capelin eggs.

The intensity of feeding by adult capelin sampled in the western Gulf one month later, in June, had declined sharply (% empty stomachs 89%; IF = 2.8%). Spawning was occurring or had recently terminated throughout the western Gulf at this time. The only exception to this general cessation of feeding by adults during the period of spawning occurred at Baie Ste-Marguerite. There, recently spent females were feeding actively (IF = 14.4). A similar pattern was observed in the southern Gulf at Grande-Rivière.

Very few post-spawning capelin were sampled anywhere throughout the study area during the summer. This was largely attributed to the heavy mortality known to occur after spawning (Templeman 1948; Bailey et al. 1977b). Where adult capelin were collected (Stations 43-50, Fig. 2B) they were feeding actively (% empty stomachs 14.3%; IF = 21.1).

A

As previously noted (Fig. 7) the feeding intensity of both juvenile and adult capelin in October and November was highly variable. In general, however, feeding intensity was lower at this time. In 1975, 69% of the stomachs of capelin > 140 mm TL which would spawn the following spring were empty and the mean index of fullness was low (IF = 7.80). Similar sized capelin sampled in the western Gulf in 1974 had virtually ceased feeding (IF = 1.9%, empty stomachs 85%).

In contrast to adult capelin, which virtually ceased feeding during the spawning period (estuary April-May; Gulf May-June; Parent and Brunel 1976), juvenile capelin fed actively throughout the spring and summer. The only juvenile capelin sampled in May of 1975 were collected at midday when feeding intensity is at its daily low (Fig. 7).

Nonetheless, only 12% of these fish had completely empty stomachs indicating that feeding had been active earlier. Juveniles collected in early June, simultaneously with spent females, at several stations in the estuary and Gulf, were feeding actively (IF = 10.9 - 23.9). During the remainder of the summer and fall the feeding intensity of juvenile capelin was similar to that of the adults (Fig. 7).

In addition to these changes in feeding intensity, some seasonal changes were also observed in the composition of the diet of juvenile and adult capelin. The most significant change was a dramatic shift from euphausiids, which dominated the diet of juveniles and adults both in numbers (Fig. 8) and biomass (Fig. 9) in May and of adults in June. In the summer and fall the importance of euphausiids declined and they were replaced by copepods, principally, <u>Temora longicornis</u>, which had previously been absent from the diet (Figs. 7, 8). From August through

Fig. 8. Seasonal and geographical variation in the diet of juvenile and adult capelin from the estuary (open bars) and Gulf of St. Lawrence (solid bars). O and indicate an index value of l for estuary and Gulf respectively. For each area the number of stations are indicated outside the parentheses while the numbers inside the parentheses represent stomachs analyzed.

Food items: 1. Thysanoëssa spp., 2. M. norvegica,

3. unidentifiable Euphausiacea, 4. Euphausiacea juveniles, 5. Calanus finmarchicus, 6.

Calanus hyperboreus, 7. Euchaeta norvegica, 8.

Metridia longa, 9. unidentified large Calanoida, 10. Temora longicornis, 11. Pseudocalanus minutus, 12. other small Calanoida,

13. Oithona sp., 14. Copepoda Harpacticoida,

15. Ostracoda, 16. Amphipoda Hyperiidea, 17.

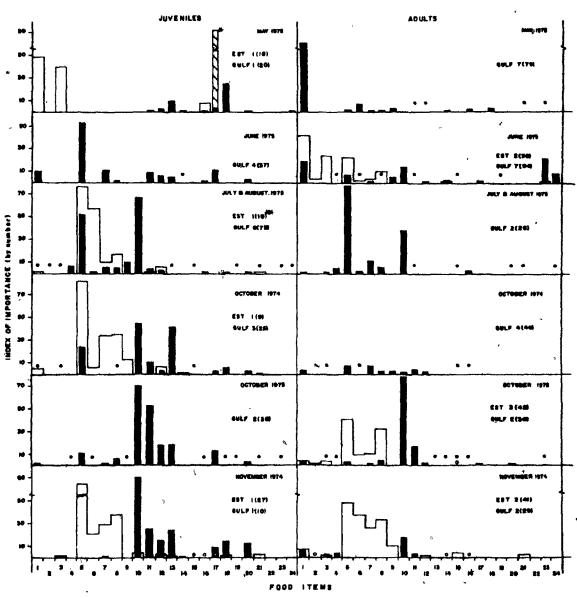
Invertebrate eggs, 18. Nauplii (Copepoda,

Cirripedia, Euphausiacea), 19. Euphausiacea

larvae, 20. Gastropoda and Pelecypoda larvae,

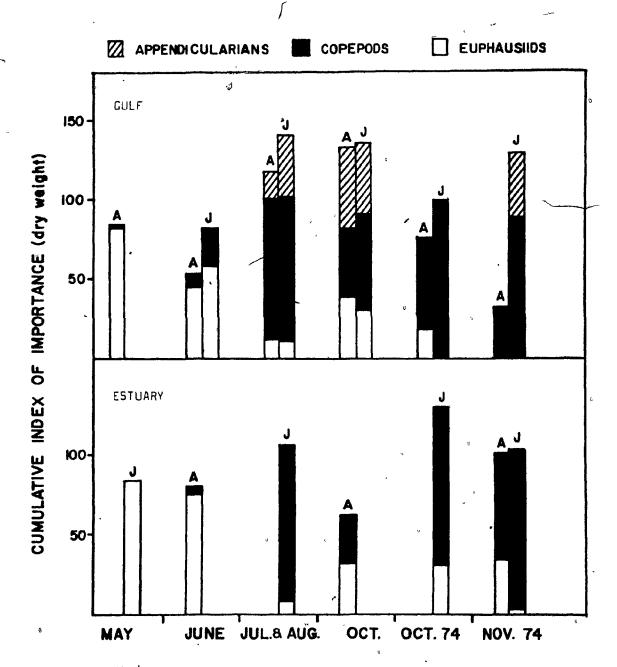
21. Chaetognatha, 22. Larvacea (no value indicated since they were not counted), 23. Pisces

eggs, 24. Pisces larvae.



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Seasonal changes in the occurrence of the Fig. 9. dominant prey of juvenile (J) and adult (A) capelin in the estuary and western Gulf of St. Lawrence during the fall of 1974 and the summer and fall of 1975.



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November appendicularians also contributed significantly to the diet of juvenile, and to a lesser extent adult, capelin from the Gulf (Fig. 9). Euphausiid eggs comprised an unusually large proportion of the diet of juvenile capelin sampled in the Gulf in May (Fig. 8).

c) Geographical Variation

Although, in general, the diet of juvenile and adult capelin was similar in the estuary and the Gulf, large copepods were much less abundant in the diets of capelin from the Gulf. In contrast to the general situation in the estuary where juvenile and adult capelin occurred in small numbers from July through October, large concentrations of juvenile capelin were present near the mouth of the Saguenay River throughout this period (Bailey et al. 1977b). When sampled for diet analysis in July and October these fish were found to be feeding at some of the highest intensities (IF = 33.3 - 40.9) observed during the study.

DISCUSSION

Diet Composition

The limited data available from previous studies indicated that copepods, amphipods, and euphausiids, were the principal components of the diet of juvenile and adult capelin in the Northwest Atlantic. For example, Chan and Carscadden (1976) reported copepods comprised 50.7%, amphipods 35.9%, and euphausiids 11.1% by weight of the diet of adult capelin sampled from August through January 1973-74. Kovalyov and Kudrin (1973) reported the percent frequency of occurrence (by number) of copepods, euphausiids, and amphipods sampled from March to June 1972 to be 55.4%, 44.1%, and 31.5%. Copepods and euphausiids were also dominant in the diet of capelin from the estuary and western Gulf of St. Lawrence where they occurred in 53.2% and 33,4% of the stomachs examined and comprised 47% and 38% of the diet (by weight) respectively. The major difference between the diets of capelin from the estuary-Gulf and from the Northwest Atlantic was the very low abundance of amphipods (which ranked 20th on the list of 27 prey items) in the diet of capelin from the former area.

In the Northwestern Gulf, appendicularians replaced amphipods as one of the three major prey items, occurring in 25% of the stomachs examined and constituting approximately 7.7% of the diet by weight.

The reasons for the poor representation of amphipods in the stomachs of capelin sampled in the estuary is unclear. In contrast to their infrequent occurrence in the diet of capelin, amphipods ranked 5th in abundance in 1970 and 4th in 1971 out of 11 holoplankton groups

reported for the estuary, occurring in 13.5% and 8.5% of the zooplankton samples taken (Côté 1972). Also conspicuous by their absence from the diet of capelin were fish larvae which ranked 3rd and 2nd in frequency of occurrence in 1970 and 1971 respectively. Copepods, which were the dominant food item of capelin in the estuary, were also the dominant form of zooplankton in 1971 and 1972, occurring in 97% and 95% of the samples respectively. Knowledge of the composition and relative abundance of zooplankton in the western Gulf is inadequate to allow meaningful comparisons of diet and prey availability.

Size Related Differences in Diet

The principal difference in the diet of juvenile and adult capelin was the shift from small copepods to adult euphausiids as fish length increased beyond approximately 140 mm (Fig. 5). The apparent preference by juvenile capelin for small copepods over euphausiids may explain the limited contribution by euphausiids to the diet of capelin during the summer and fall. During this time the preponderance of capelin are 1 and 2 year old fish which in general are < 140 mm TL, larger fish having been greatly reduced in numbers by high post-spawning mortality (Bailey et al. 1977a,b). It is considered unlikely that seasonal changes in the occurrence of euphausiids was a major factor contributing to their virtual disappearance from the diet of capelin during the summer and fall since they are known to be present in the estuary and western Gulf at that time (Berkes 1976; Sameoto 1976). The apparent absence of small copepods from the diet of juvenile capelin sampled in the estuary may be an artifact resulting from the limited number of juvenile samples from that area since Côté (1972) reported that 5 of the 9 abundant copepods in the estuary were small species.

Diel Periodicity

Two daily peaks of feeding activity were evident from May to August. The morning peak, which occurred between 0600 and 1000 h. coincided with the movement of capelin to deeper waters. During midday, when feeding was at a minimum, both juvenile and adult capelin were concentrated into compact schools and were found at their maximum depth (Bailey et al. 1977b). The evening peak, occurring between 1600 and 2200 h, corresponded with the evening vertical migration. This pattern of vertical migration in capelin is essentially the same as that known to occur in many planktonic crustacea (Cushing 1951) and has been documented for euphausiids which are one of the dominant prey groups of capelin in the estuary and Gulf (Berkes 1976). The correspondence between the periods of maximum vertical migration and maximum feeding intensity suggest that feeding is most active during the transition periods. Similar patterns of intensive feeding during periods of vertical migration were reported by Narver (1970) for juvenile sockeye salmon.

The reasons for the apparent shift to a single feeding peak corresponding with midday in October and November are unknown. One possibility is that the combination of colder $(1-2^{\circ}C)$ near isothermal waters, which would tend to retard evacuation rates, and the shortened day length act to merge the summer peaks and reduce the period of active feeding.

Seasonal Variation

The cessation of feeding by spawning capelin, with the exception of capelin eggs which may have been consumed incidental to respiratory movements during spawning, was consistent with the findings of previous

studies (Templeman 1948; Prokhorov 1965; Winters 1970). Similarly, the decline in intensity of feeding from August through November was similar in magnitude to that reported by Chan and Carscadden (1976).

Geographical Variation

Bailey et al. (1977b) reported the occurrence of large concentrations of juvenile capelin near the mouth of the Saguenay River in summer, fall, and early winter when few juveniles occurred in other areas of the estuary. They hypothesized that the year round occurrence of juveniles in this area was made possible by the stable concentrations of zooplankton that occur in and near the mouth of the Saguenay. This situation is contrasted with the situation in the estuary where the zooplankton densities decline rapidly to near zero in August and September (Rainville 1979; Jacquaz et al. 1977). Our observation that juvenile capelin sampled from stations near the mouth of the Saguenay were feeding at high levels throughout the summer and fall provide support for this hypothesis.

Estimates of Zooplankton Consumption By Capelin

We estimated daily ration of capelin during May-August by summing the values of food consumed at the two peaks of feeding activity.

Nakashima and Leggett (1978) have shown that this method provides realistic estimates of daily ration provided the feeding peaks are discrete and the range of temperatures over the sampling period are small. The former restriction appears to be adequately met. The range of maximum daily temperatures experienced by capelin during their vertical migration increased approximately 13°C between May and August

but these higher temperatures were experienced only during their stay near the surface at night. The range of daytime temperatures experienced was approximately 7°C. Errors introduced into estimates of daily ration by the effect of these temperature changes on assimilation rates would be smoothed to some degree by our use of a single representation of feeding peaks for the entire interval.

Daily ration was estimated to be 5% of the wet body weight per ' day. This represents a minimum estimate since the method used normally includes the weight of intestinal contents when determining the weight of food consumed. It nonetheless falls at the midpoint of the range of in situ estimates of daily ration for several species of marine (Clarke 1978) and freshwater (Nakashima and Leggett 1978) fishes. Estimates of the total daily consumption of zooplankton by capelin in the Canadian Atlantic (Table 2) were derived by applying this estimate of daily ration to estimates of total capelin biomass for the region reported in Carscadden and Miller (1979) and Miller and Carscadden (1979). We estimate the daily consumption has declined from 334,000 metric tons to 83,000 metric tons over the period 1972 - 1978. This has resulted in a surplus production of approximately 250,000 metric tons of zooplankton daily which is potentially available to other zooplanktivores. Year to year changes in the daily consumption of zooplankton by capelin in the two such areas for which estimates of capelin biomass are available have also been significant (Table 2). Annual changes in the quantity of zooplankton released from predation as a result of these changes could potentially influence year class strength and/or growth of capelin or other species. Winters and Carscadden (1978) used a similar rationale to assess the surplus production of capelin as a result of reductions in the abundance of major predators by commercial exploitation.

Table 2. Daily consumption of zooplankton by capelin in ICNAF areas 3LNO, 2J + 3K (metric tons \times 10⁻³)

,	1972	1973	1974	1975	1976	1977	1978	•
Grand Banks (ICNAF 3LNO) ^a)	160	11-5	56	47	41	25	10	•
NE Nfld Labrador (ICNAF 2J+3K)b)	174	132	, 116	, 209	217	116	73	
Total	334	247	172	256	258	141	83	

a) Capelin biomass (total minus age 2) estimates from Carscadden and Miller (1979) Table 9.

b) Capelin biomass (total) estimates from Miller and Carscadden (1979) Table 9.

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