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Preliminary Estimates of Predation by the Short-finned Squid (*Illex illecebrosus*) on the Scotian Shelf

by

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INTRODUCTION

Biological information on Illex illecebrosus during their residency on the Shelf has been accumulating during recent years. Aspects such as maturation (Mercer, 1973a; Amaratunga and Durward, 1979; Durward et al., 1979) and food and feeding (Squires, 1957; Mercer and Paulmier, 1974; Amaratunga et al., 1979; Ennis and Collins, 1979; Vinogradov and Noskov, 1979; O'Dor et al., 1979) have been documented. It is recognized here that such biological studies, augmented with further studies during their residency on the Shelf, could provide a valuable basis to develop models for the fishery (Amaratunga, 1979). The primary objective of this study is to determine food and feeding patterns of I. illecebrosus and define realistic biological parameter values toward this purpose. Thus, preliminary estimates of predation by I. illecebrosus are made.

Before proceeding, however, it is necessary to recognize some major features of I. illecebrosus. I. illecebrosus is widely distributed in the northwest regions of the Atlantic Ocean. During a plankton survey in this study, I. illecebrosus larvae and juveniles were recorded for the first time in the Gulf Stream, seaward of the Scotian Shelf between March 7 and May 22, 1979. These records, compiled with data from various sources (Roper and Lu, 1979; Roper et al., 1979; Lu, 1973; Clarke, 1966), show distribution (Figure 1) from Labrador and Newfoundland to central Florida. This constitutes a variation of climatic conditions from arctic to virtually tropical. There are biological variations associated with distribution. For instance, these distributional differences have resulted in two main hypotheses for a life cycle. Squires (1967) proposed an annual cycle with a protracted breeding season while Mesnil (1977) described multimodal distributions and proposed more elaborate long and short cycles that cross one another.

On the other hand, it may be noted that during the fishing season I. illecebrosus distribution is along the landward skirt of the Gulf Stream. Their distribution in Nova Scotia (Amaratunga et al., 1978) and Newfoundland (Squires, 1957) waters is usually limited to the warmest period of the year, from spring (April to May) to late fall (as late as December). During their summer distribution, feeding patterns have also shown differences. For example, along the coastline of Newfoundland, squid prey heavily on capelin (Squires, 1957); and in Nova Scotia and New Brunswick they are known to prey on and disrupt the inshore herring and mackerel fishery, while offshore they prey predominantly on crustacea and other squid (as shown in this report).

MATERIALS AND METHODS

The biological data base for this study dates back to early 1977, when detailed studies on *I. illecebrosus* were undertaken. However, detailed studies on food and feeding were conducted with 1978 and 1979 data. The data sources comprised of i) International Observer Program in which observers placed on international fishing vessels routinely collected biological data and, when possible, obtained samples of frozen animals for detailed biological analyses in the laboratory; ii) Joint multinational research cruises which provided detailed biological data (Amaratunga, 1980). Squid examined in this study were collected randomly on a round-the-clock basis.

Stomach fullness of individual squid was determined on a scale of 0 to 3: 0 - empty, may contain clear fluid but may contain only very small quantities of particulate matter; 1 - half full of particulate matter; 2 - full of particulate matter; and 3 - distended with particulate matter. Since the caecum may constitute an independent digestive and absorptive system (Bidder, 1950), caecum fullness was neglected in this study. For convenience, the scale index 0 is referred to as "not recently fed" and scale indices 1, 2, and 3 combined are referred to as "recently fed".

The seasonal fluctuation of feeding activity was determined by taking frequency of recently fed animals on two-week time frames (Figure 2). Using only samples from research cruises, diurnal feeding activity was determined for June and October/November, 1978 (Figure 3) and compared with the overall data from 1979.

Qualitative descriptions of stomach and caecum contents were first undertaken in 1978. Detailed identifications were carried out on 538 animals from samples obtained in November and are listed in Table 1.

Usually, gut contents belonged to the prey groups, crustacea, fish, or squid. Frequency of occurrence of these prey groups (Figures 4a and 4b) were studied from animals obtained from May to November, 1978, and from February to December, 1979. The 1978 sample of about 3,000 animals (Figure 4a) were best representative of June, July, October, and November. The 1979 trends (Figure 4b) represent a sample size of 27,448 animals from 110 to 330 mm. A further sample of about 1,750 juveniles of less than 120 mm caught between February and May, 1979, in the Gulf Stream were also analyzed.

RESULTS

Seasonal fluctuations in the number of animals feeding are seen in Figure 2. In 1978, during the first week in May, 80% of the animals had recently fed. The frequency rapidly decreased to a low at about 40% early in July. There was another increase which peaked at 85% in the first week of September and once again dropped to about 45% by November. The 1979 patterns were similar, although percentages were considerably lower (Figure 2). The high values in May were in the 40-50% range and decreased to close to 20% in June and July. The next downward trend was seen after October.

In the juvenile studies, an attempt was made only to determine if particulate matter were present in the guts without using the fullness index. Thirteen percent had food material, which is a low percentage compared to early-season data in Figure 2.

Diurnal trends early in 1978 (June) showed only 10-20% of the animals were recently fed between 0200 and 0700 hours (Figure 3). Two hours after sunrise (0800 hours) the frequency peaked suddenly and gradually decreased to less than 50% after 1800 hours. The peak period in October/November began at 1200 hours, four hours after sunrise and gradually diminished to less than 50% after 2200 hours. Patterns of early and late season bore a similar relationship to sunrise, with peak period lasting ten hours. Overall pattern observed in 1979 was similar to the 1978 patterns (Figure 3).

Although contents were in a macerated condition and prey identification was difficult, the presence of tissues such as otoliths, squid beaks and suckers, vertebrae, lenses, and scales permitted identifications at least to the family level. Table 1 shows the various prey components seen in the stomach and caecum.

Close to half of the juvenile samples were fixed in alcohol and hence difficulties in identification of prey items were further compounded. In many of these cases a reasonable indication of prey type was obtained from the texture and colouration of the food mass. An accurate study, however, was conducted on close to 1,000 frozen animals. Only 17 of these squid contained particulate matter. These guts revealed that they preyed on I. illecebrosus, amphipods, mysids, and copepods and mysid or copepod eggs. No phytoplankton were observed in the contents. Among the 17 juveniles that ranged from 45-94 mm, 8 had preyed on only squid, 7 on crustacea, and 2 on mainly squid and small quantities of crustacea.

As noted before, 13% of all the juveniles studied had gut contents. Of these, 5% were thought to have preyed on crustacea while 2% showed cannibalism.

Preliminary volumetric analysis indicated that guts usually carried one or two (e.g., when crustacea and squid occurred simultaneously) major components while the balance represented very small percentage or traces of other items. On this basis, the food components were broadly categorized into crustacea, fish, and squid. The occurrence of these prey components change with size of squid (Figures 4a and 4b).

In 1978, all squid less than 145 mm in length that had recently fed contained crustaceans as the principal component (Figure 4a). At sizes 145 to 165 mm, fish also constituted a prey component but at less than 5%. Squid as a prey component was first apparent in 160 mm squid, when more than 90% of the recently fed squid had taken crustacea. The frequency of occurrence of crustacea consistently dropped thereafter to 50% at 225 mm and less than 10% at 270 mm.

The occurrence of mixed squid and crustacea diets increased from 10% at 170 mm to a maximum of 24% at 210 mm and decreased rapidly to non-existence at 235 mm. Frequency of pure squid diets remained less than 10% at sizes 160-205 mm and then increased consistently from 17% at 210 mm to 50% at 270 mm and greater than 80% after 290 mm. Thirteen of the 14 animals (all females) encountered at sizes greater than 300 mm had recently fed on squid.

Fish as a prey component remained less than 10% (average 3.5%) at sizes between 145 and 210 mm, and increased to average 12.6% between 215 and 235 mm. Among the larger squid, the average was 10-15% with the largest (32%) noted at 270 mm.

The patterns were similar in 1979 (Figure 4b). The prey component in squid sizes 125-145 mm was not exclusively crustacean. The crustacean component ranged from 78-85%, while squid as a prey component ranged from 11-14%. The crustacean component gradually decreased to 59% as the animals grew in size to 185 mm. During this period, cannibalism increased to 24% and preying on fish increased from 1% to 6-7%. Between squid sizes 200-250 mm, the crustacean component continued to decrease to 31%, while the fish component increased close to 20% and the squid component averaged close to 35%. The crustacean component continued to decrease to 10%, the fish component remained close to 22%, and the squid component increased to greater than 50% in the larger size ranges of squid.

DISCUSSION

Preliminary experiments were conducted in the laboratory (I. Wallace and T. Amaratunga, 1980) to qualitatively describe food breakdown through digestion and quantify digestion rates. The digestive state of stomach contents were found to range from recently ingested chunky or macerated particulate matter to fluid in advanced-state digestion. Hence, in the fullness index the delineating criterion of presence of particulate matter for "recently fed" animals was satisfactory. In order to limit potential biases from incidental ingestion of food; for example, from hyperactivity in trawl nets and catch bins, the criterion for recently fed condition required that guts carried a reasonable amount of food (half full).

The experiments also showed that total breakdown of particulate matter into a clear fluid took about 14 to 16 hours at temperatures of 12 to 13 C. Comparatively, 4 to 6 hours have been observed in some European Loligo spp. and 18 hours for Octopus (Bidder, 1950). Although digestion is dependent on many factors such as activity, temperature, and type of food, these rates provide a general estimation of how long the recently fed criterion would apply after a feeding.

Diurnal feeding patterns (Figure 3) showed sudden influx of recently fed squid shortly after sunrise both in June and October/November. This would be expected if squid feeding in the upper region of the water column in the night descended (and became available to the bottom trawls) as surface light intensity increased. Bradbury and Aldrich (1969) reported that squid in captivity fed before daybreak. Figure 3 also showed a gradual decrease of recently fed animals as the daylight hours progressed. This may be interpreted as the period through which digestion progressed with particulate matter becoming fluid. Thus, the patterns suggest that squid have a single period of feeding each day. Diurnal feeding periodicities have been reported before (Vinogradov and Noskov, 1979; Fields, 1965).

Food of I. illlecebrosus is well documented. Squires (1957) listed food components of the squid in Newfoundland and Grand Banks while Mercer and Paulmier (1974) included the Scotian Shelf as well. More recently, Ennis and Collins (1979) and Vinogradov and Noskov (1979) examined feeding activities, diets, and predator-prey relationships. Essentially, authors arrive at the same three components of food: crustacea, fish, and squid, with seasonal, geographic, and short-term temporal variations. Similar components with similar variations have been recorded for Loligo pealei (Vovk, 1974) and Loligo opalescens (Fields, 1965).

While the three food components are very broad by definition, they in fact constitute limited numbers of prey items. Crustacea essentially constituted euphausiids similar to other reports (Squires, 1957; Vinogradov and Noskov, 1979) and the predominant euphasiids in the north Atlantic area are Meganyctiphanes norvegica, Thysanoessa inermis, and Th. rashii (Kulka and Corey, 1978; Mauchline and Fisher, 1969). Other crustacea such as copepods and amphipods were less important, although Mercer and Paulmier (1974) frequently observed copepods Euchirella rostrata and Candacia armata, amphipods Phronima atlantica and Parathemisto sp. and Decapod Nathantians in early-season samples from May 12 to June 13, 1973. The fish component was less easily identifiable because of food maceration; however, similarities to other studies are noted. Silver hake and myctophids (Table 1) were both reported by Vinogradov and Noskov (1979) while Squires (1957) reported gadids in a less important capacity. Squid as a food component was at times difficult to speciate based on observation of muscle tissue, and hence were recorded as "unidentified" cephalopods (Table 1). In nearly all instances where suckers, beaks, pens, and other tissue were present for positive identification, the prey species was I. illecebrosus. Since cannibalism is common (Squires, 1957; Mercer, 1965; Ennis and Collins, 1979) and very few other cephalopods were ever encountered in the nets, it is evident that much of the unidentified cephalopods were in fact I. illecebrosus.

Since growth is critically dependent on food supply, it is valuable to consider seasonal variations of feeding patterns (Figure 2) in relation to growth and maturation (Amaratunga, 1980) and food availability.

Juvenile squid obtained for this study were caught in the Gulf Stream, seaward of the Scotian Shelf. Although they are in a rapidly growing phase (Amaratunga, 1980), it is interesting to note that few had gut contents. The prey types were representative of a pelagic distribution and it is very probable that food availability was limited. This probably also relates to the high rate of cannibalism at this stage.

The squid first observed on the Scotian Shelf in May exhibited active feeding (80% recently fed in 1978). The high percentage also probably demonstrates a relationship to prey availability. Their diet, which consisted exclusively of euphausiids in 1978, coincides with the seasonal availability of Meganyctiphanes norvegica, Thysanoessa inermis, and Th. rashii on the Shelf (D.W. Kulka, pers. comm.)

Feeding frequency decreased (by about 40% in 1978) between May and late July. Seasonal variations in euphausiids corroborate this. The second year class of Meganyctiphanes norvegica spawn and die in June-July (Berkes, 1973; Hollingshead and Corey, 1974) while in Thysanoessa a similar spawning-stock mortality is known from April to the latter part of May (Kulka and Corey, 1978; Kulka, 1977). In Thysanoessa inermis, post-spawning mortality in fact represents a depletion of 30 to 40% of the adult population (Kulka, 1977). The seasonality of these mortalities provides a striking correlation between food resource limitation and decrease in squid feeding. The period of decreased feeding also represents an overlap in prey types (crustacea, squid, and fish), probably implying a switch from the lesser available euphausiids to more accessible types, a phenomenon observed in fishes (Murdock et al., 1975).

There was a subsequent increase in proportion of recently fed animals which reached a high of 85% early in September, 1978. Fish and squid increased in importance as prey components, while crustacea still constituted a major proportion of the diet. There was probably an accompanying replenishment of euphausiid size classes suitable for squid consumption, due to the rapid growth of the new year class (Kulka and Corey, 1978).

The increased cannibalism and fish predation probably relates to the fact that squid are very much larger by September, reaching climactic growth ranges (Amaratunga, 1980), and are preying on alternative size-related food types. Similar progression of prey types and size-related food preferences have been observed for I. illecebrosus (Squires, 1957; Vinogradov and Noskov, 1979) and Loligo species (Vovk, 1974; Fields, 1965) in the field. Size dependance has been demonstrated in the laboratory for I. illecebrosus with a possible upper limit to the prey size roughly equal to mantle length of the squid (O'Dor et al., 1979). Incidentally, 50% of males reaching the mature stage (3) at about 225 mm (Amaratunga, 1980) coincided with the size at which the total population registered the drop in frequency of crustacea component to less than 50%, and cannibalism accounted for about 30% (Figure 4). Subsequent to 50% of females reaching Stage 3 (when maturity is induced by gonadotrophic hormones) at 250-258 mm, cannibalism rapidly replaced predation on crustacea, especially in 1978. At this stage there is an increasing size differential between sexes, which could account for the increasing cannibalism. This is further supported by the fact that 13 of the 14 females in 1978 greater than 300 mm in size had cannibalized.

In conclusion, the progression of predation from crustacea to fish and squid may be attributed to availability and size-related prey preference. It is unclear as to why the fish component was relatively unimportant. Fish have been reported to constitute an important proportion (Squires, 1957; Ennis and Collins, 1979), and indeed squid are known to prey on inshore herring and mackerel stocks in Nova Scotia. It is probable that fish were less available; i.e., density dependent, since cannibalism was not observed in captive squid that were adequately fed (O'Dor, 1979). However, cannibalism is a widespread phenomenon among cephalopods (Vovk, 1974; Fields, 1965); and physiologically, the conversion efficiency of fish diets is less than that of crustacea which have a composition more similar to that of cephalopods (O'Dor et al., 1979). Hence, it is conceivable that both availability and suitability (in terms of energy conversion) promote cannibalism among squid. O'Dor et al. (1979) suggested that the presence of both large and small squid in the late season is a predictable consequence to the hierarchal feeding observed in captive schools. It is proposed here that size disparities within schools in turn promotes cannibalism, while the existence of size disparities between schools (Amaratunga, 1980) would promote inter-school predation.

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REFERENCES

Amaratunga, T. 1979. The importance and preliminary estimates of predation by short-finned squid Illex illecebrosus on the Scotian Shelf. Jour. Fish. Res. Bd. Canada in press.

Amaratunga, T. 1980. Growth and maturation patterns of short-finned squid Illex illecebrosus on the Scotian Shelf. NAFO SCR Doc. 80/II/30, Serial No. N062.

Amaratunga, T. and R.D. Durward. 1979. Standardization of data collection for the short-finned squid, Illex illecebrosus. ICNAF Sel. Papers No. 5: 37-41.

Amartaunga, T., J.D. Neilson, D.J. Gillis, and L.G. Valdron. 1979. Food and feeding of the short-finned squid Illex illecebrosus on the Scotian Shelf in 1979. ICNAF Res. Doc. 79/II/35, Serial No. 5361.

Amaratunga, T., M. Roberge, and L. Wood. 1978. An outline of the fishery and biology of the short-finned squid Illex illecebrosus in eastern Canada. In Fish. Mar. Serv. Tech. Rep. 833: 2.1-2.17.

Berkes, F. 1973. Production and comparative ecology of Euphausiids in the Gulf of St. Lawrence. Ph.D. Thesis, McGill University, Montreal, P.Q.

Bidder, A.M. 1950. The digestive mechanism of the European squids Loligo vulgaris, L. forbesii, Allotetuhis media, and A. subulata. Quart. Jour. Micr. Sci., 91(1): 1-43.

Bradbury, H. and F. Aldrich. 1969. Observations on feeding of the squid Illex illecebrosus (LeSueur, 1821) in captivity. Canad. J. Zool. 47(5): 913-915.

Clarke, M.R. 1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol., 5: 91-300.

Durward, R.D., E. Vessey, R.K. O'Dor, and T. Amaratunga. 1979. Aspects of maturation, mating, spawning, and larval development of Illex illecebrosus relevant to field studies. ICNAF Res. Doc. 79/II/3, Serial No. 5338.

Ennis, G.P. and P.W. Collins. 1979. Food and feeding of the short-finned squid, Illex illecebrosus, during its seasonal occurrence in the Newfoundland area. ICNAF Sel. Papers, No. 5: 25-29.

Fields, W.G. 1965. The structure, development, food relations, reproduction, and life history of the squid Loligo opalescens Berry. Calif. Fish Game Bull. 131: 1-108.

Hollingshead, K.W. and S. Corey. 1974. Aspects in the life history of Meganyctiphanes norvegica (M. Sars), crustacea (Euphausiacea), in Passamaquoddy Bay. Can. J. Zool. 56(3): 492-506.

Kulka, D.W. 1977. The life history of Thysanoessa inermis (Kroyer) and the community structure of Euphausiids in the Bay of Fundy. M.Sc. Thesis, University of Guelph, Guleph, Ontario: 167 pp.

Kulka, D.W. and S. Corey. 1978. The life history of Thysanoessa inermis (Kroyer) in the Bay of Fundy. Can. J. Zool. 56(3): 492-506.

Lu, C.C. 1973. Systematics and zoogeography of the squid genus Illex (cephalopoda:oegopsida). Ph.D. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland, Canada: 389 pp.

Mauchline, J. and L.R. Fisher. 1969. The biology of Euphausiids. In Advances in Marine Biology, Vol. 7. Ed. F.S. Russel and M. Yonge. Academic Press Inc., New York.

Mercer, M.C. 1965. Contribution to the biology of the short-finned squid, Illex illecebrosus illecebrosus (LeSueur), in the Newfoundland area. Fish. Res. Bd. Canada, MS Rept. (Biol.) 834: 36 pp.

------------ 1973. Sexual maturity and sex ratios of the ommastrephid squid, Illex illecebrosus (LeSueur, 1821), at Newfoundland (Subarea 3). ICNAF Res. Doc. 75/71, Serial No. 3023.

Mercer, M.C. and G. Paulmier. 1974. Distribution and biological characteristics of the short-finned squid (Illex illecebrosus) on the Continental Shelf of Subareas 3 and 4 in May-June 1973. ICNAF Res. Doc. 74/87, Serial No. 3323.

Mesnil, B. 1977. Growth and life cycle of squid, Loligo pealei and Illex illecebrosus, from the northwest Atlantic. ICNAF Sel. Papers, No. 2: 55-70.

Murdoch, W.W., S. Avery, and M.E.B. Smith. 1975. Switching in predatory fish. Ecology 56: 1094-1105.

O'Dor, R.K. R.D. Durward, E. Vessey, and T. Amaratunga. 1979. Feeding and growth rates in captive squid (Illex illecebrosus) and the influence of food availability on growth. ICNAF Res. Doc. 79/II/16, Serial No. 5342.

Roper, C.F.E. and C.C. Lu. 1979. Rhynchoteuthon larvae of ommastrephid squids of the western north Atlantic, with the first description of larvae and juveniles of Illex illecebrosus. Proc. Biol. Soc. Wash. 91(4): 1039-1059.

Roper, C.F.E., C.C. Lu, and K. Mangold. 1969. A new species of Illex from the western Atlantic and distributional aspects of other Illex species (cephalopoda:oegopsida). In Proc. Biol. Soc. Wash., Vol. 82: 295-322.

Squires, H.J. 1957. Squid, Illex illecebrosus (LeSueur), in the Newfoundland fishing area. J. Fish. Res. Bd. Canada 14(5): 693-728.

------------- 1967. Growth and hypothetical age of the Newfoundland bait squid, Illex illecebrosus illecebrosus. Ibid. 24(6): 1209-1217.

Vinogradov, V.I. and S. Noskov. 1979. Feeding of short-finned squid, Illex illecebrosus, and long-finned squid, Loligo pealei, off Nova Scotia and New England, 1974-75. ICNAF Sel. Papers, No. 5: 31-36.

Vovk, A.M. 1974. The position of the long-finned squid, Loligo pealei LeS. in the ecosystem. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rvbn. Khoz. Okeanogr., 58: 1668-176 (Transl. Ser. Fish. Mar. Serv. Canada, No. 3977).

Wallace, I., R. K. O'Dor and T. Amaratunga. Sequential observations on gross digestive processes of Illex illecebrosus. NAFO SCR Doc. 80/II/29, Serial No. N061

Table 1. A list of prey components found in the digestive tracts of *Illex illecebrosus*.

Prey species of adult *I. illecebrosus*	Prey found in juvenile *I. illecebrosus*
Fish:	**Crustacea:**
Myctophum punctatum	Amphipods
Ceratoscopelus maderensis	Mysids
Notolepis rissoi	Copepods
Urophycis chesteri	Also egg of Mysid or Copepods
Merluccius bilinearis	
Gadidae	**Cephalopods:**
Macrouridae	*Illex illecebrosus*
Unidentified fish	
Crustacea:	
Euphausiids (*Meganyctiphanes* sp. and/or *Thysanoessa* sp.)	
Unidentified euphausiids	
Candacia armata	
Euchaeta norvegica	
Unidentified copepods	
Parathemisto sp.	
Unidentified crustacea	
Cephalopods:	
Illex illecebrosus	
Gonatus fabricii	
Histioteuthidae	
Unidentified cephalopods	
Miscellaneous:	
Pteropods	
Chaetognaths	
Unidentified prey items	

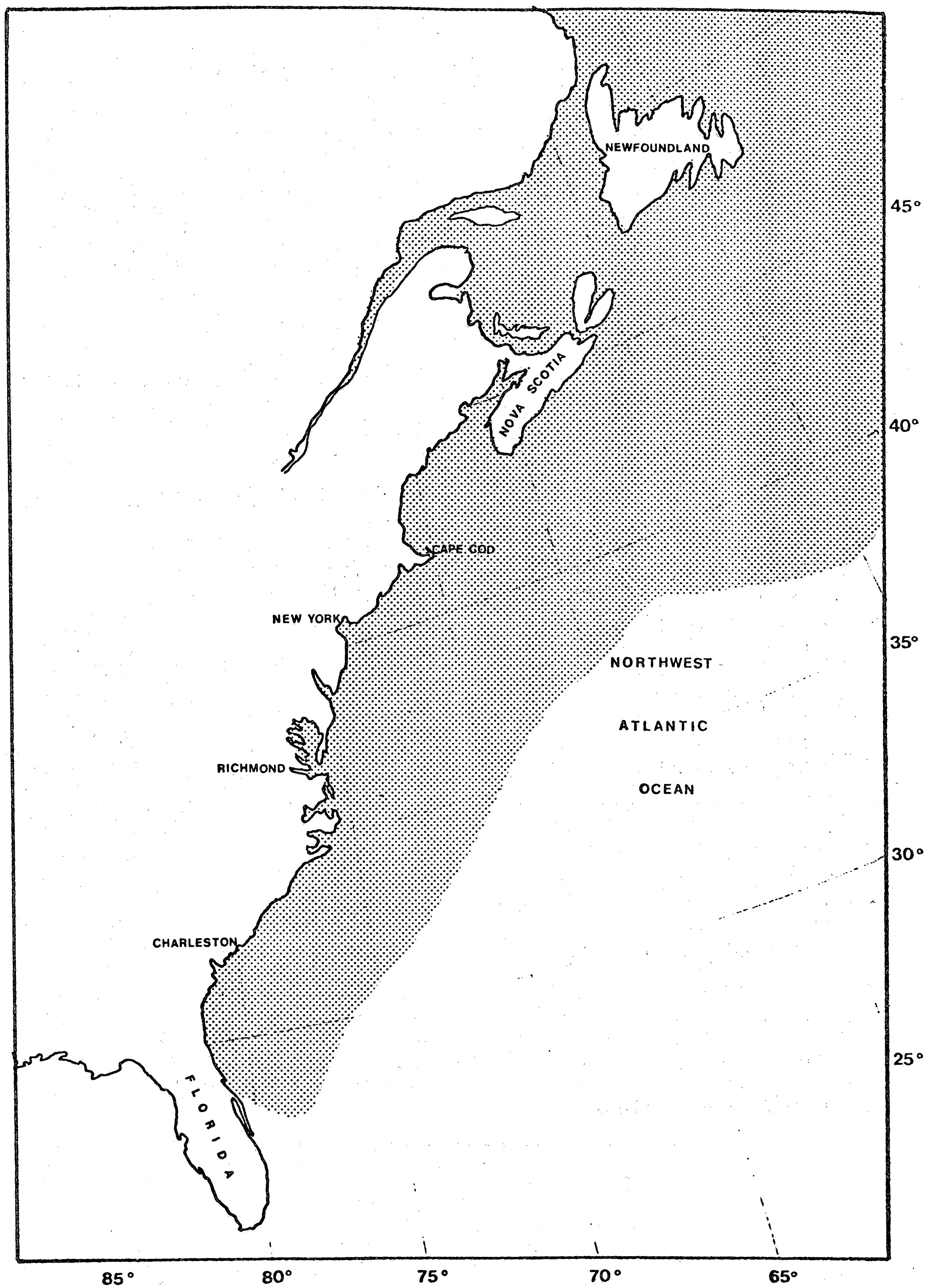


Figure 1. Known distribution (shaded area) of Illex illecebrosus in the northwest Atlantic region.

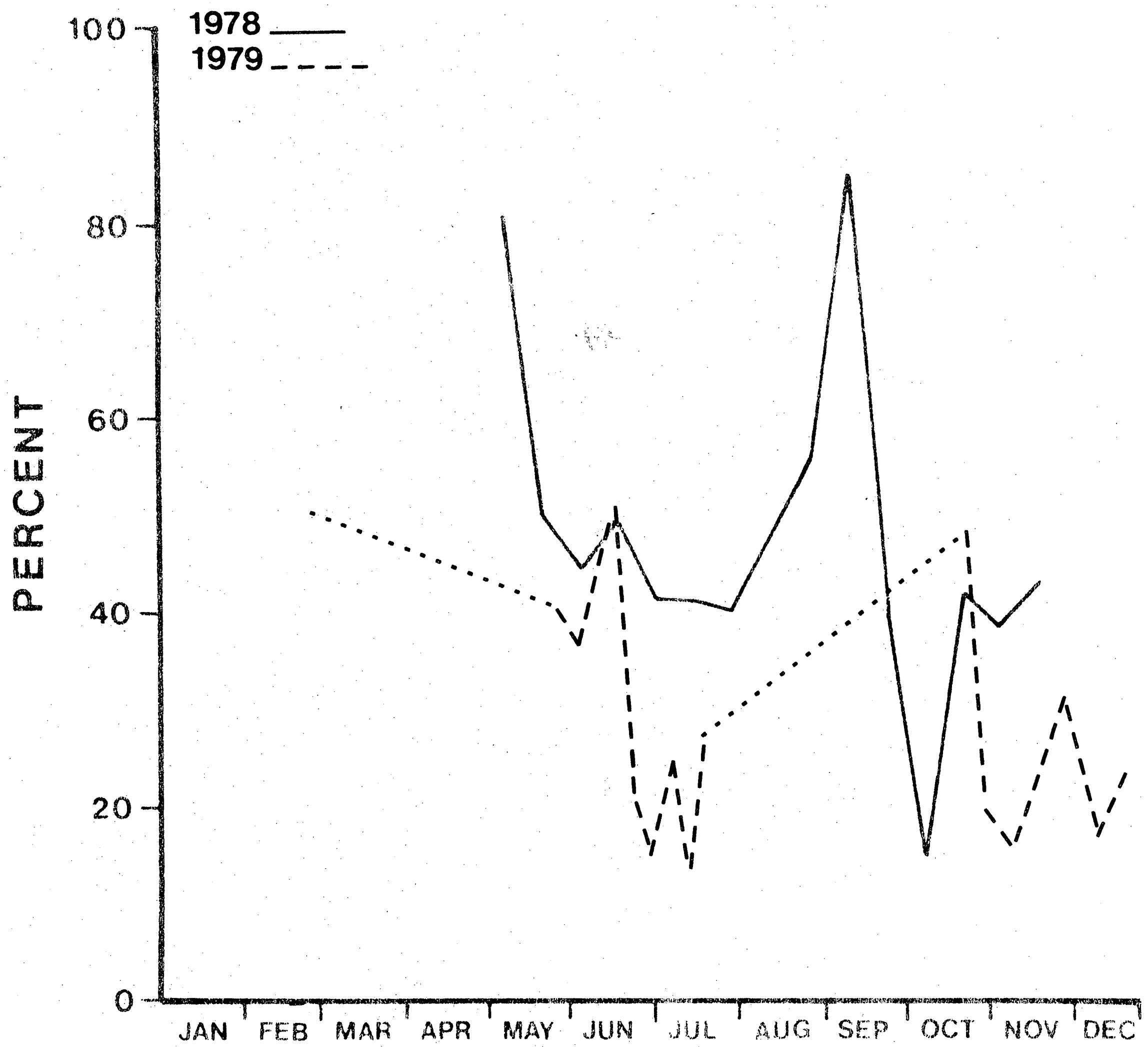
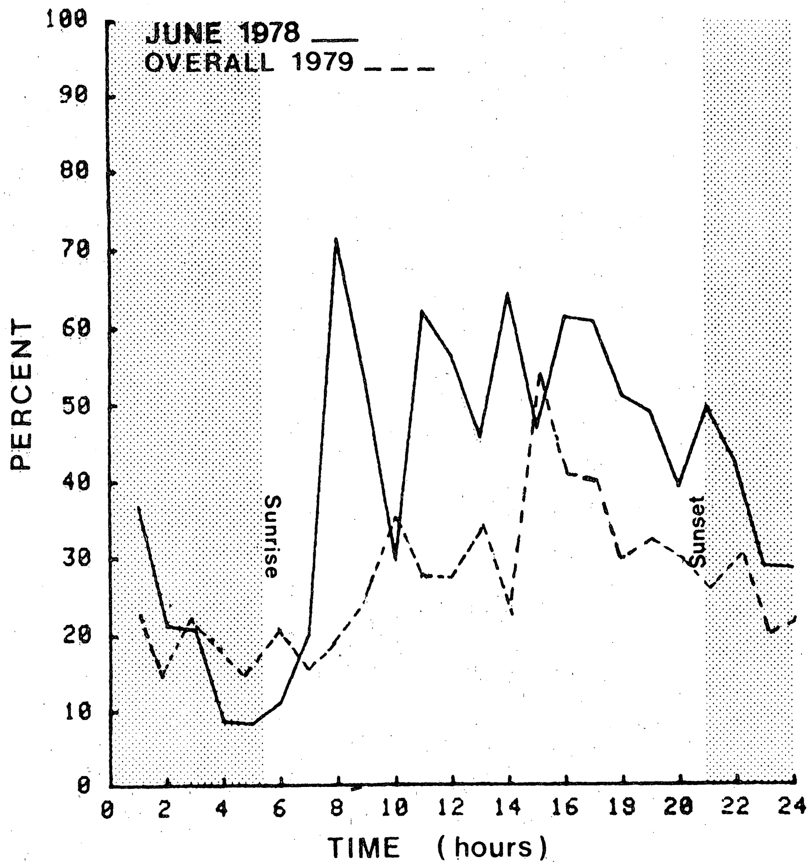


Fig. 2. Percentage of "recently fed" animals in samples plotted through season showing fluctuation of feeding activity. Dotted lines represent periods in which there were no data.



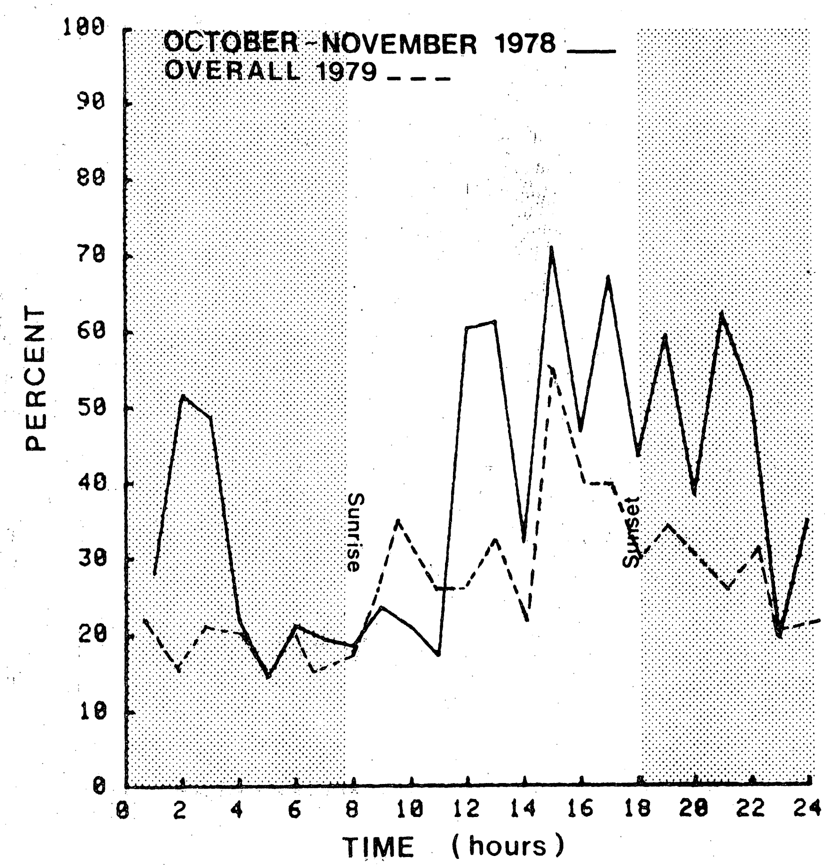


Figure 3. Percentage of "recently fed" animals in samples plotted through time of day, comparing diurnal fluctuations of feeding activity during June and October-November, 1978, with overall 1979 activity.

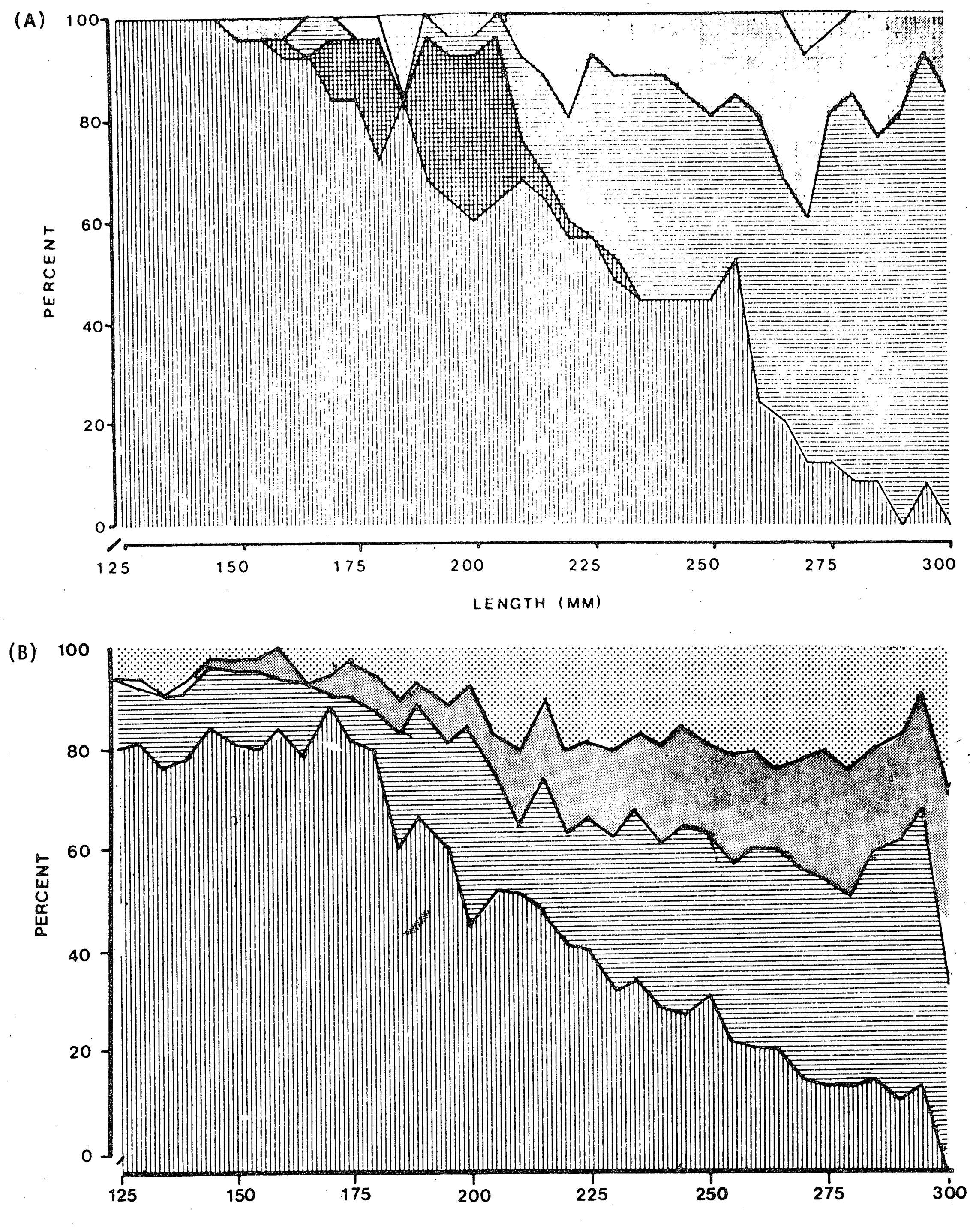


Fig. 4. Percent frequency of occurrence of three main prey groups plotted against mantle length of squid. Fig. 4A - 1978 data; Fig. 4B - 1979 data (mixed diets were recorded as unidentified in 1979).