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Food and feeding of the short-finned squid (Illex illecebrosus) during its seasonal occurrence inshore at Newfoundland and a brief review of the trophic relationships of the species.

by

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Introduction

During the course of its migratory cycle the short-finned squid Illex illecebrosus spends up to 6 months or more in Newfoundland inshore waters. This inshore migration begins with the appearance of small squid on the Grand Banks in May. They grow rapidly and reach large sizes by October and November before migrating offshore (Squires, 1957). Their distribution in Newfoundland inshore waters varies but is usually quite widespread and along with such an extended period of occurrence in this area, one would expect that feeding conditions encountered and feeding requirements (related to increasing size) vary considerably.

Our purpose here is to examine the variation in feeding activity and diet of squid throughout the period of its occurrence in two widely separated inshore Newfoundland areas. In addition, since there has been no single paper dealing with the role of Illex illecebrosus in the food chain, we are including here a review of a number of papers containing short sections dealing with various aspects of this topic in order to bring together the information which illustrates the trophic relationships of this species.

Materials and Methods

In 1967 16 samples of squid were obtained from Holyrood on the east coast of Newfoundland throughout the period July-November and 11 from Rencontre West on the south coast during August-October. All samples were obtained from commercial catches and ranged from 77 to 492 (Av. 219) squid per sample. In addition samples were obtained from the Grand Banks south of Newfoundland in spring 1970 (May 20 - June 3) on A.T. Cameron cruise 173 and in fall 1967 (November 14 - December 5) on A.T. Cameron cruise 139. Part of the biological sampling routine was an examination of stomachs which included a rough estimate of stomach fullness and cursory identification of stomach contents. The stomach fullness scale included empty, 1/4 full, 1/2 full and full. Stomach contents were usually quite mutilated and no attempt was made at detailed identification, however, the following items made up nearly the entire bulk of stomach contents: euphausiids, amphipods, compound eyes, otoliths, scales, fish eggs, and squid suckers and beaks. These were grouped into crustacean, fish, and squid remains.

Results and Discussion

Percentage of empty stomachs

The percentage of empty stomachs was always quite high in the Holyrood samples. It ranged between 81% and 57% and although it fluctuated markedly from one sample to the next, it tended to decline over the course of the July-November period (Fig. 1). At Rencontre West this percentage ranged between 34% and 75% but the pattern of variation over the sampling period was entirely different (Fig. 2). In this area the percentage of empty stomachs increased dramatically between early August and mid-September and decreased again over the remainder of the season. Such a dramatic increase in the percentage of empty stomachs suggests a sudden decline in the availability of prey species.

The generally high percentage of empty stomachs observed does not fit with the observations that the occurrence of squid in the Newfoundland area is primarily a feeding migration (as opposed to a spawning migration) and that their growth rate over this period is high (Squires, 1957, 1967).

Stomach fullness

The percentage of full and 1/2 full stomachs among those that contained food tend to decrease over the period and the percentage of 1/4 full stomachs increased (Fig. 3, 4). This relationship was much more pronounced for Rencontre West samples. This appears to indicate that the level of feeding activity declines during this July-November period. However, squid grow rapidly over this period and the actual volume of food in a 1/4 full stomach of a large squid taken late in the year may be more or less equivalent to that in a full stomach of a small squid taken early. Larger squid, however, require a larger volume of food to achieve satiation and obviously in relation to increasing size feeding activity does decline. This may be related as well to a gradual shift from a predominately invertebrate diet in small squid to a predominately fish diet in large squid (Squires, 1957) and very likely to a generally lower availability of the latter.

Stomach contents

In view of Squires' (1957) observations on the gradual shift from an invertebrate to fish diet as size increases, one would have expected a declining incidence of crustacean remains and an increasing incidence of fish remains over the July-November period. This was not the case. At Holyrood there was a low incidence of crustacean remains throughout the period and the incidence of fish remains declined (Fig. 1). At Rencontre West the pattern was different (Fig. 2). There the incidence of fish remains dropped sharply from a very high level in early August to a very low level by mid-September after which it declined even further. The incidence of crustacean remains increased during August then decreased sharply to a very low level by mid-September and remained at a low level for the remainder of the season. The sharp drop in the incidence of both fish and crustacean remains corresponds with the sharp increase in the percentage of empty stomachs in this area.

The incidence of cannibalism increased in both areas throughout the inshore season. At Holyrood, for example, squid remains were present in less than 4% of the stomachs in mid-July but were present in 35% of the stomachs in late November.

Offshore samples

In the offshore sample taken in spring the percentage of empty stomachs was high (66%) and the incidence of crustacean remains in the stomachs was higher (19%) than the incidence of fish remains (11%). Feeding conditions appear to improve as squid enter the inshore area in early summer as they switch to a fish diet. In the fall sample from offshore the percentage of empty stomachs was much lower (32%) than that for the inshore sample taken during the same period (58%) and the incidence of crustacean remains was higher (43%) than the incidence of fish remains (27%). This, along with the low incidence of cannibalism (3% compared with 35% in the inshore sample for this period), indicates much better feeding conditions offshore during the fall. The incidence of cannibalism was also very low (3%) in the spring sample from offshore. This suggests that in the offshore area, where squid presumably are either migrating to or from the inshore

area, behavior related to schooling and feeding is different from that in the inshore area.

Squid prey - a review

Mercer and Paulmier (1974) list ten taxa which form the principal components of the diet of Illex illecebrosus towards the northern part of its range. These are: Chaetognatha, Pteropoda, Cephalopoda, Ostracoda, Copepoda, Isopoda, Amphipoda, Euphausiidae, Decapoda (Natantia) and Teleostei. These authors have also identified many of the food items to the species level. In offshore samples large differences in stomach contents were found in different areas. In the Nova Scotian Shelf area amphipods (mainly Phronima atlantica and Parathemisto sp.) and copepods (mainly Euchirella rostrata and Candacia armata) were the most important food items whereas on the Grand Banks euphausiids (mainly Meganyctiphanes norvegica) occurred most frequently in the stomachs. The copepods which predominate in the plankton of this area (i.e. Calanus finmarchicus and Pseudocalanus minutus elongatus) were rarely found in stomach contents. This suggests that squid may feed selectively (Mercer and Paulmier, 1974).

Samples collected inshore at Newfoundland also show variation from area to area. During August, 1964 squid in Placentia Bay were feeding primarily on crustacea (unidentified) and to a much lesser extent on fish and other squid whereas in Conception Bay at Holyrood they were feeding on fish and other squid but not on crustacea (Mercer, 1965). Mercer (1965) also found green alga in a few stomachs from Holyrood. A high incidence of cannibalism is evident in samples from most areas (Squires, 1957; Mercer, 1965; Mercer and Paulmier, 1964). Cannibalism may not be as prevalent as these samples indicate, however, since captured squid attack anything with which they come in contact and this may account for much of the squid remains found among their stomach contents (Mercer, 1965). However, the wide variation in the incidence of squid remains in their stomachs suggests that cannibalism does exist in this species and at times is an important part of their feeding behavior.

As noted earlier Squires (1957) found a striking change in the food of squid as size increased. He found small squid to be feeding primarily on invertebrates (mainly euphausiids) and to a small extent on fish. As size increased the situation gradually reversed itself until at the larger sizes fish predominate in their diet. However, Squires combined samples collected over a 6 year period from the Grand Banks and inshore areas. In such a combination of samples a size-diet relationship would be marked. It seems more likely that squid feed opportunistically.

Fish remains found in squid stomachs by Squires (1957) were identified as capelin, redfish, cod, haddock, mailed sculpin and small flounders. He also includes three invertebrate taxa, namely Gastropoda, Polychaeta, and Mysidacea, not listed by Mercer and Paulmier (1974).

Squid predators - a review

The major predator of Illex illecebrosus is the pilot whale, Globicephala melaena, at least during the 5-6 month period of its occurrence in Newfoundland waters each year (Squires, 1957; Sergeant, 1962) when pilot whales feed almost exclusively on squid. Mercer (1975) estimated the consumption of squid by an initial (pre-exploited) population of 50,000 pilot whales to be 166,000-249,000 metric tons for the approximately 100 day inshore season and annual consumption (assuming that pilot whales feed on these squid year-round) to be 605,900-908,850 tons.

Squid and pilot whales are seasonal migrants to Newfoundland inshore waters, the two arriving and departing almost simultaneously (Mercer, 1975). This inshore-offshore migration of pilot whales appears to be in pursuit of squid and it seems possible that this predator-prey relationship is maintained year-round, however, nothing is known of the feeding of pilot whales in offshore areas (Sergeant and Fisher, 1957). At least two, and probably more of the other smaller cetacea of eastern Canadian waters include squid in their diet (Sergeant and Fisher, 1957).

Squid is also a large part of the diet of bluefin tuna Thunnus thynnus when they occur inshore at Newfoundland during the summer months (Butler, 1971). Illex illecebrosus, however, has not been found among the stomach contents of seven tuna species, including Thunnus thynnus, from elsewhere in the Atlantic (Dragovich, 1969). Other species reported to prey on Illex illecebrosus are silver hake Merluccius bilinearis and red hake Urophysis chuss (Vinogradov, 1972) and spiny dogfish Squalus acanthius (Templeman, 1944).

Squid commonly school at the surface and undoubtedly provide an important source of food for a variety of seabirds. Vovk (1974) reports different species of seabirds having been observed feeding on Loligo pealei. References to similar observations on Illex illecebrosus were not found during this review. However, in a personal communication to M.C. Mercer, R.G. Brown mentions several seabirds common in the Northwest Atlantic which are squid eaters. Among those that probably prey quite heavily on Illex illecebrosus are the greater shearwater Puffinus gravis, the sooty shearwater Puffinus griseus, fulmars Fulmarus glacialis, the northern gannet Morus bassanus and larger gulls.

General trophic interrelations

In a general way the trophic interrelations of Illex illecebrosus are similar to those described for the long-finned squid Loligo pealei (Vovk, 1974). The food of Illex illecebrosus includes organisms from three trophic levels: primary consumers - copepods, chaetognaths, euphausiids, etc., secondary consumers - larger euphausiids, shrimp, amphipods, capelin, other squid, etc., and tertiary consumers - redfish, cod, haddock, other squid, etc. The incidence of green alga in squid stomachs was very low (Mercer, 1965) and such occurrences are most likely by chance rather than the result of active feeding.

This squid species in turn is preyed upon by a number of tertiary consumers. It is the most important food item of pilot whales and it is very important in the diet of bluefin tuna at least when the latter occur in the inshore Newfoundland area. This species is often eaten by silver and red hake and occasionally by dogfish. Cannibalism also appears to be a fairly common occurrence in Illex illecebrosus. Undoubtedly, in addition to those reported here, many other species of fish and marine mammals include this squid in their diets. It also seems quite certain that a variety of seabirds preys on this species.

The role of Illex illecebrosus within the second and third trophic levels is quite clearly that of a predator. Within the fourth trophic level its primary role is that of a prey species, however, even within this trophic level it functions as a predator and as a competitor. The short-finned squid is a migratory species and covers a very extensive depth range over the course of its migrations. It is to be expected that the structure of its trophic relationships is quite variable throughout this migratory cycle.

Estimates indicate that the annual production of Illex illecebrosus in the Northwest Atlantic is in the order of several hundred thousand tons (Mercer, 1975). It is obvious that this species plays a major role in the transmission of energy through the food chain to the higher levels of tertiary consumers.

Acknowledgements

The data presented here were collected while M.C. Mercer was scientist-in-charge of squid investigations at this establishment. His consent for us to make use of this information is appreciated.

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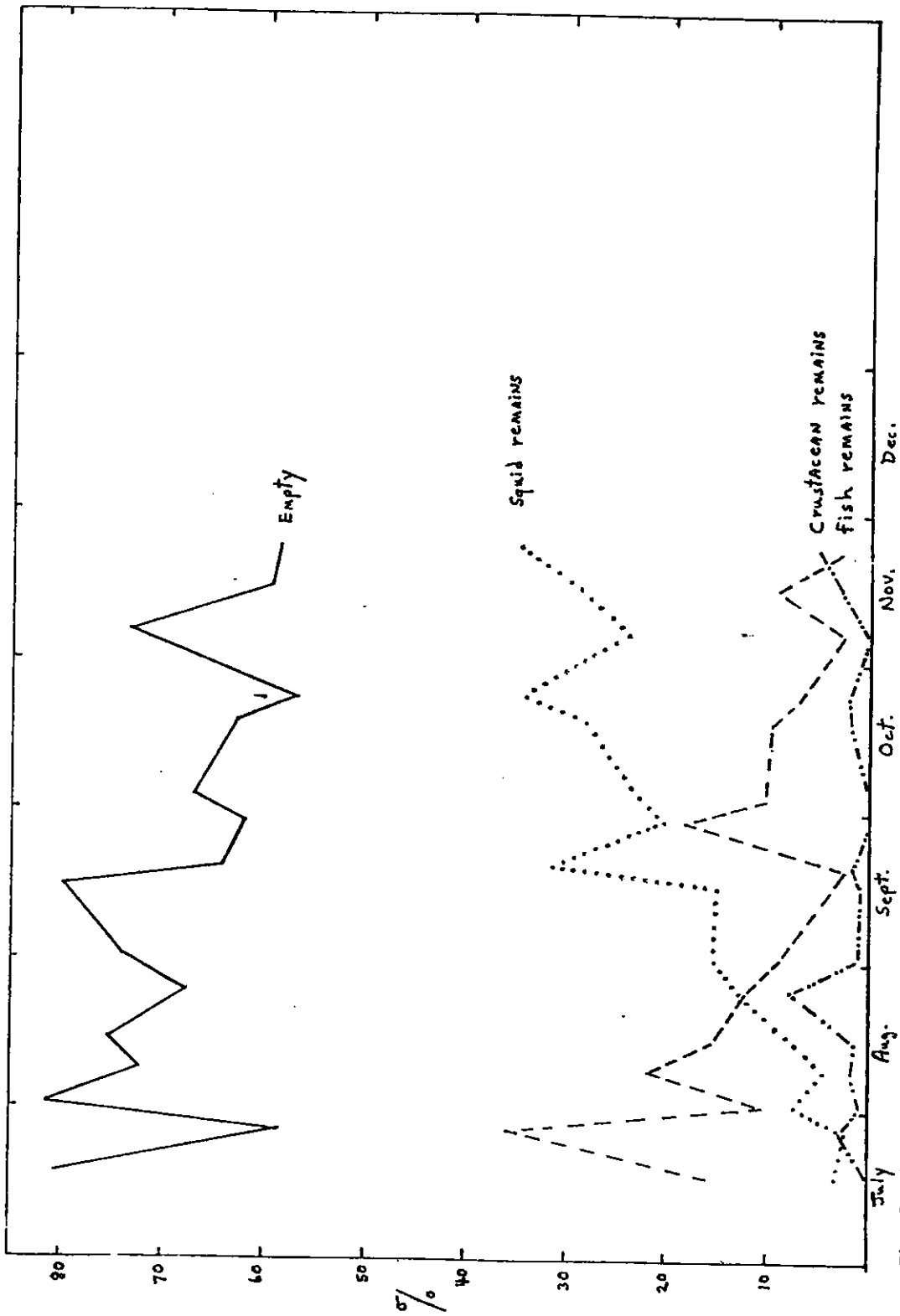

Fig. 1. Percentage of empty stomachs and incidence of various food remains (i.e. percentage of stomachs in which they occurred) in squid collected at Holyrood July-November, 1967.

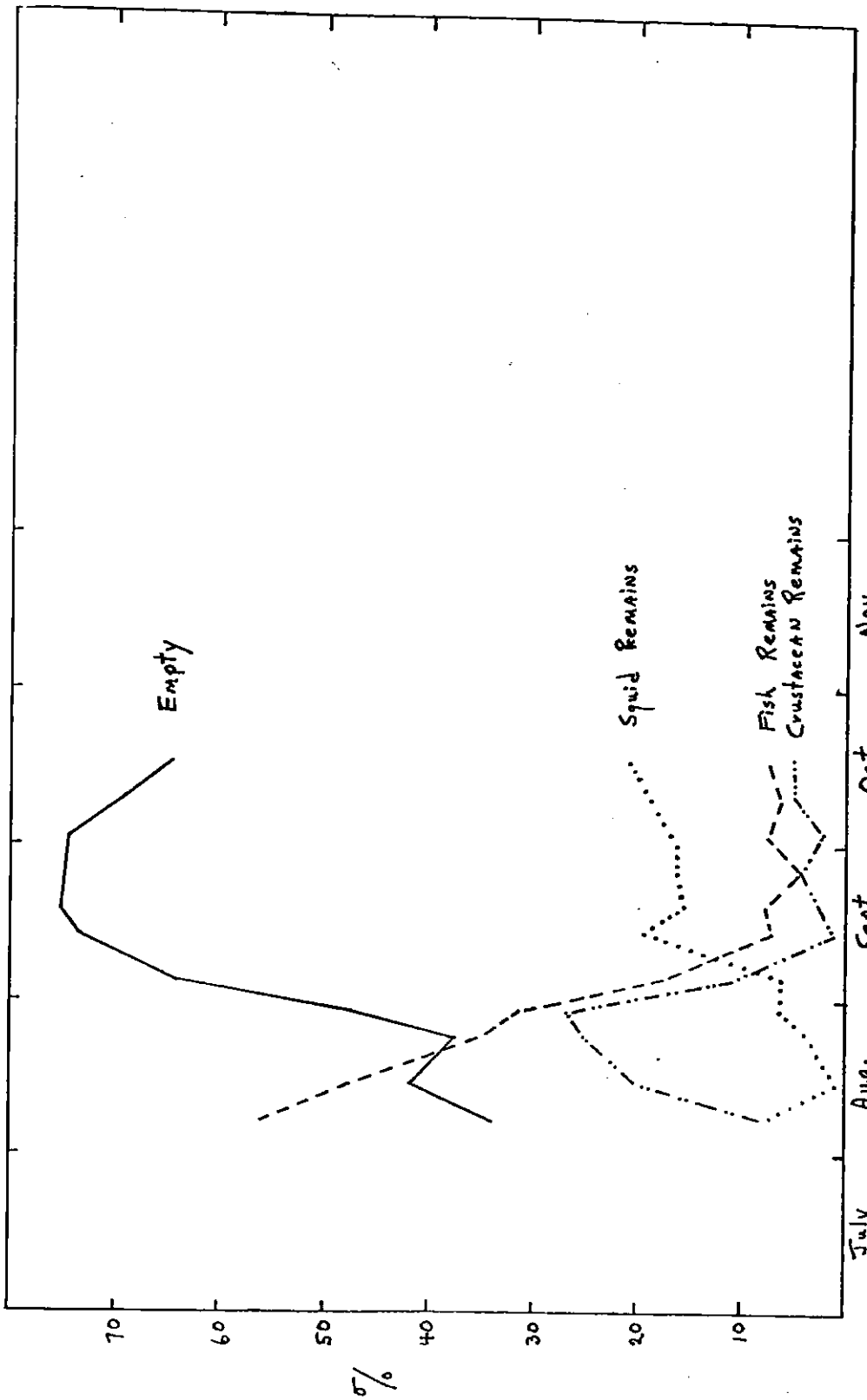

Fig. 2. Percentage of empty stomachs and incidence of various food remains (i.e. percentage of stomachs in which they occurred) in squid collected at Rencontre West August-October, 1967.

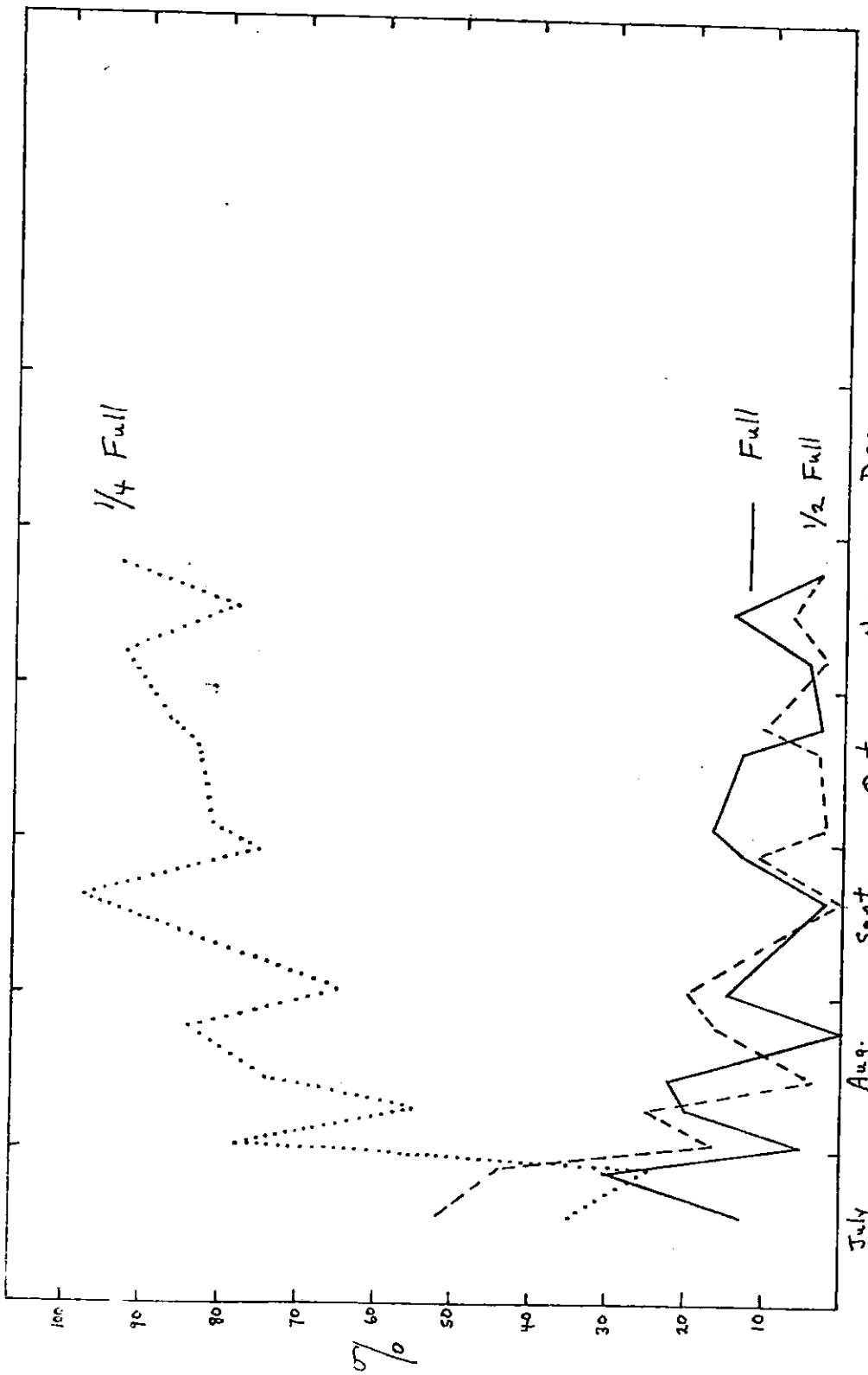

Fig. 3. Percentage of full, 1/2 full and 1/4 full stomachs among those that contained food in squid collected at Holyrood July-November, 1967.

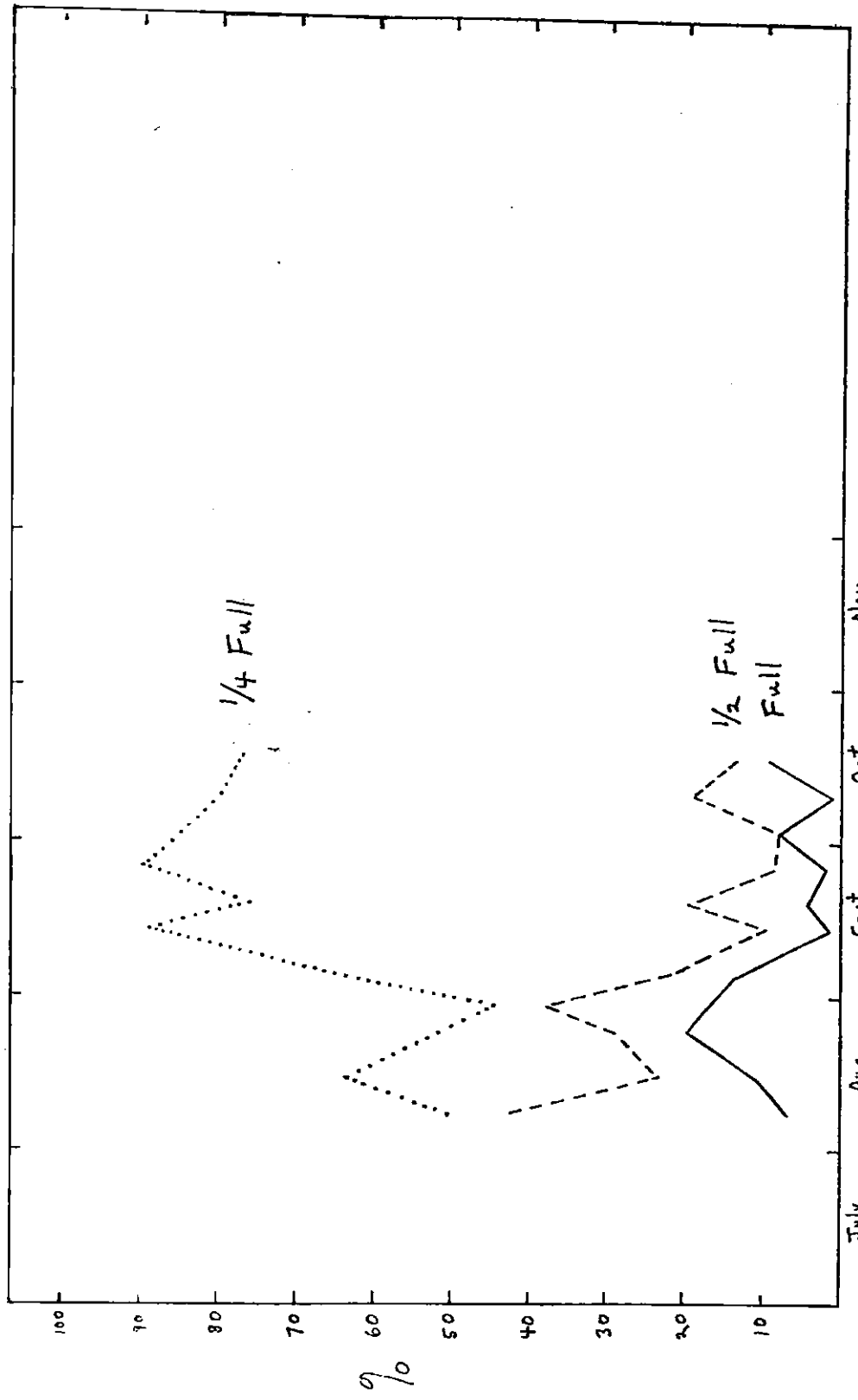

Fig. 4. Percentage of full, 1/2 full and 1/4 full stomachs among those that contained food in squid collected at Rencontre West August-October, 1967.