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Predatory Role of the Flying Squid (*Todarodes sagittatus*) in North Norwegian Waters

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Abstract

Analysis of the gut contents of *Todarodes sagittatus* were carried out from samples which were obtained by jigging in coastal waters of northern Norway. The food was comprised predominantly of pelagic species, with polychaetes, crustaceans and fish being the major prey groups. Feeding indices provided evidence of a size-related shift in dietary composition, with increased reliance on fish prey as the squid increase in size. Use of otolith size-fish size relationships to estimate prey size indicated that the range of prey size increased with squid growth. The presence of relatively undigested pieces of squid in the gut contents was interpreted as being an artefact of the fishing technique, and it is suggested that the importance of cannibalism may have been overevaluated in other studies on the feeding habits of squids. The ways in which choice of sampling and analytical techniques may influence the results of dietary studies are discussed.

Introduction

Although the European flying squid (*Todarodes sagittatus*) is thought to occupy a key position in the food web of Arctic regions in the Northeast Atlantic, comparatively little is known about its feeding biology, with the majority of available information being widely-scattered, unsystematic lists of the types of food organisms (Wiborg, 1972, 1978, 1979, 1980, 1981; Jonsson, 1980). The feeding habits of squids from other regions have been examined in more detail and the results of several studies have shown that they feed on pelagic or semi-pelagic prey (Squires, 1957; Vinogradov and Noskov, 1979; Macy, 1982; Mangold 1983; O'Sullivan and Cullen, 1983). Although some authors have reported that there is a change in dietary composition with increasing size of squid (see review by Mangold, 1983), most of these studies have been descriptive in nature and few attempts at detailed analysis have been made.

In the present study, the feeding habits of *T. sagittatus* have been investigated and possible mechanisms which lead to dietary changes are examined. Attempts were made to compare the findings with results of published studies, but comparison proved to be difficult due to differences in methodology. Unlike researchers who have studied fish diets (e.g. Berg, 1979; Hyslop, 1980), most of those who have studied the feeding habits of squids seem to be unaware of the importance of choice of methodology and of how the analytical methods may affect the results and conclusions. Consequently, a part of the discussion is devoted to methodology of feeding habit studies and the pitfalls to be avoided.

Materials and Methods

Samples of *T. sagittatus* were collected at various times from October 1982 to October 1983. Although it would have been desirable to have collected the samples at one specific location, movements and availability of squid made this impossible. Consequently, the samples were taken at several locations along the north coast of Norway between Andenes and Kamøyfjord (Fig. 1). Squid were captured by jigging in depths from the surface to 50 m. Jigging was not limited to particular periods of the day, and most of the samples include squid which were obtained at different times within a given 24-hr period. Ten samples, varying in size from 10 to 170 individuals, were collected during the course of nine research cruises. Relatively few (97) male squid were captured, and the numbers in the samples varied between 0 and 53 individuals. Consequently, this study refers predominantly to examination of the feeding habits of female squid.

Immediately after capture, the dorsal mantle length (ML) of each squid was measured to the nearest 0.5 cm, and the alimentary tract was usually removed, frozen in liquid nitrogen and stored at -20° C for later analysis of gut contents in the laboratory. On some occasions, whole squid were frozen and the alimentary tracts were removed in the laboratory.

After defrosting of the squid in the laboratory, gut fullness (stomach and caecum) was estimated by using a 5-point scale which ranged from 0 (empty) to 4 (completely full). The gut contents were then transferred to a petri-dish and examined under a binocular microscope at magnifications of 6.4-40 x with direct

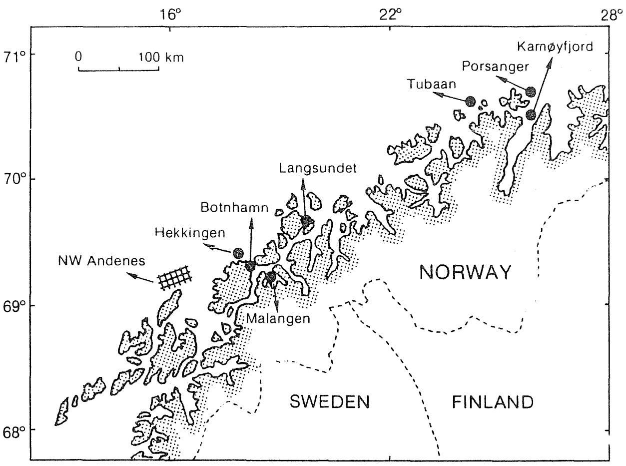

Fig. 1 Locations where samples of *T. sagittatus* were obtained along the north coast of Norway.

illumination. The degree of digestive breakdown of the gut contents was assessed by using a 6-point scale with empty guts being classified as 0 and the numbers 1 to 5 representing degrees of breakdown of the food. The gut contents were generally of a pulp-like or soup-like consistency, and the degree of digestive breakdown was most often assessed within the range of 3 to 5. This precluded the complete and accurate division of the food remains into specific prey for volumetric or gravimetric analysis. Consequently, dietary composition was investigated by using indices which were based on the presence or absence of particular prey groups (Berg, 1979; Hyslop, 1980). The feeding indices are defined as follows:

a) "Percentage occurrence" of a given dietary component was calculated as $(100 \times a)/N$, where a is the number of guts containing component a and N is the total number of guts with food. This index is, therefore, a measure of the proportion of squid that has consumed a particular prey.

b) "Relative frequency of occurrence" of a given prey was calculated by the formula $(100 \times a)\Sigma a...z$, where a is the number of guts containing component a and $\Sigma a...z$ is the sum of observations of all prey. This index gives an estimate of how often a particular prey appeared in the diet relative to other prey types.

c) For each gut examined, a subjective assessment was made of which prey contributed the greatest biomass to the gut content, and this was termed the dominant prey. The "dominance" index for a particular prey was calculated as the proportion of all dominance values, i.e. $(100 \times A)/N$, where A is the number of guts in which prey a dominated and N is the number of guts that were assessed for dominant prey.

As the gut contents of the squid were often well digested. prey species were usually identified from hard fragments such as skeletal and jaw elements, parapodia, shell remains and otoliths. Skeletal elements of invertebrates are often used for identification purposes and are well described in the literature. On the other hand, descriptions of the form and structure of fish otoliths are relatively scarce. In order to identify fish prey from the otoliths that were recovered from the gut contents of squid, it was necessary to collect otoliths from different fish species. Fish were collected with small-meshed bottom and midwater trawls, and the samples were selected to provide as wide a size range as possible for each species. Samples were frozen immediately after capture, and, after defrosting in the laboratory, the standard length (SL) was measured. Sagittal otoliths were removed from the fish and observed under a binocular microscope. Their lengths were measured and photographs were made to serve as a ready means of identification. The otoliths were stored in 70% ethanol for use when needed to check the identification of otoliths from the gut contents of squid. Furthermore, the linear relationships between otolith length and fish length (Table 1) allowed the size of the fish that were consumed by the squid to be estimated.

Results

The guts of the squid usually contained very small amounts of well-digested food items, with more than 75% of the guts having a fullness index of 0 to 2. More than 50% of the guts containing food were assessed as digestive stages 4 and 5. This made identification of individual prey items difficult and necessitated the use of small fragments of hard structures for identification purposes. The consequence of this is that the contribution of soft-bodied prey to the squid diet is likely to be underestimated.

Prey items in the gut contents of squid were classified into 28 different categories, many of which were identified as being representatives of species or genera of five major animal groups — Chaetognatha, Polychaeta, Mollusca, Crustacea and Pisces (Fig. 2). Some prey items, such as the chaetognath *Sagitta* and the polychaete *Eunice*, were identified on only one occasion, whereas others, such as the polychaete *Nereis pelagica* were found in the guts of some squid from almost every sample. Two molluscs (*Todarodes sagittatus* and *Limacina retroversa*) were found in the gut contents but the molluscan remains were most frequently squid suckers and pieces of arms. Among the crustacean prey, the euphausiid *Meganyctiphanes norvegica* and the shrimp *Pasiphaea* sp. were recorded most often, with other crustaceans, such as copepods, being observed sporadically. Fish remains and otoliths were found in the gut contents of some squid from each sampling period, and 11 fish species were identified. In the samples where pelagic schooling species were identified (*Clupea harengus*, *Mallotus villosus*

TABLE 1. Linear relationships between otolith length (OL) and standard length (SL) and the corresponding coefficients of determination (r^2) for various fish species. (SL and OL in mm.)

Species	Size range (mm)	No. of fish	SL = a + b OL		r^2
			a	b	
Ammodytes tobianus	65–137	42	14.929	50.809	0.93
Clupea harengus	51–255	51	0.240	58.214	0.96
Gadus morhua	26–317	26	5.787	21.993	0.95
Mallotus villosus	62–145	63	25.333	41.780	0.82
Maurolicus mulleri	34–54	32	-7.229	32.091	0.73
Melanogrammus aeglefinus	20–180	20	8.890	17.764	0.98
Micromesisteus poutassou	56–318	27	-25.544	23.170	0.98
Sebastes sp.	37–238	37	-0.107	19.985	0.98
Trisopterus esmarkii	90–188	90	-15.884	23.670	0.98

and *Ammodytes tobianus*), these fish had been eaten by a large proportion of the squid. Usually several otoliths from one of these fish prey were recovered from the gut contents of a single squid. On the other hand, the remains of gadid species were found more sporadically, and it was rare to recover more than two otoliths of a gadid prey from the gut contents of a single squid.

The use of otoliths for the identification of fish prey presupposes that the squid consumes the entire fish, including the head and other hard parts. Obviously, if some fish were not consumed in their entirety, the otoliths from the gut contents of the squid would not give a complete qualitative picture of the types of fish species consumed, and it is equally obvious that the relationships between otolith size and fish size would not give an assessment of the size ranges of fish species that may be captured by the squid. By using the relationships between otolith size and fish size to estimate the sizes of fish prey, it is assumed that otolith form and size are not unduly affected by digestive fluids within the gut of the squid. Results of preliminary experiments indicated that the latter assumption is valid.

The squid might be expected to eat small fish in their entirety, but they may attack larger fish and consume only pieces of the flesh, leaving the head and skeletal structures uneaten. In such cases, scales should be frequently found in the gut contents of the squid. However, scales of a large fish were found on only one occasion, this being an age 4+ herring about 32 cm in length, as indicated from growth data of Ingolf Rottingen (Institute of Marine Research, Bergen, Norway, pers. comm., 1985). It appears, therefore, that the estimation of fish prey sizes from the otolith size-fish size relationships (Table 1) will give a reasonably realistic evaluation of the sizes of fish prey that are eaten by squid. The results of this study indicate that, although squid are capable of consuming large fish, they appeared to do so only rarely because most of the fish in the guts were relatively small (1.5–16.0 cm SL) (Fig. 2).

The sizes of the various prey types that were consumed by the squid varied considerably, ranging from calanoid copepods of a few millimeters in length to fish exceeding 15 cm in length, and it was therefore of interest to investigate whether there were any seasonal and/or size-related changes the dietary composition of the squid. However, problems arose in the selection of methods to be used for expression of the results, because the samples that were collected in different seasons differed both in numbers of squid caught (10–170 specimens) and in the proportion of males present (0–50% of sample size). Further difficulties involved the geographical spread of sampling locations and the tendency for the number of prey categories to be highest for those samples containing the greatest number of squid (Fig. 3). In an attempt to overcome these problems, the data were treated as follows:

a) Data for male squid, which constituted varying proportions of the different samples and were poorly represented overall (<20%), were excluded from the analysis of size-related changes in dietary composition.

b) The female squid were divided into size-groups such that each group had a reasonable number of individuals (see Fig. 4) and that specimens from as many sampling periods as possible were represented within each size-group.

c) Because the number of prey categories tended to increase with increasing sample size of guts, the feeding indices (percentage occurrence, relative frequency of occurrence, and dominance index) were not calculated for each individual prey category but were calculated for each of the major animal groups (Polychaeta, Mollusca, Crustacea and Pisces) which constituted the major portion of the gut contents of the squid.

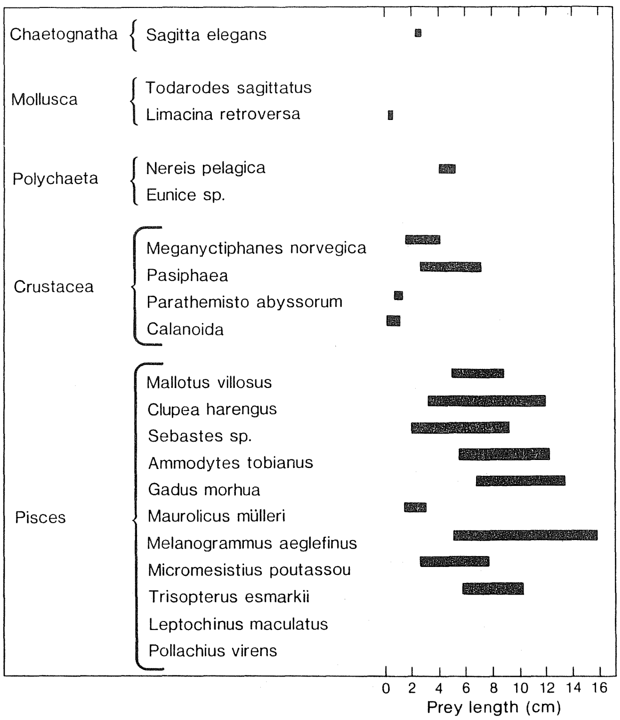

Fig. 2. Types and approximate size ranges of prey organisms found in the guts of *T sagittatus*.

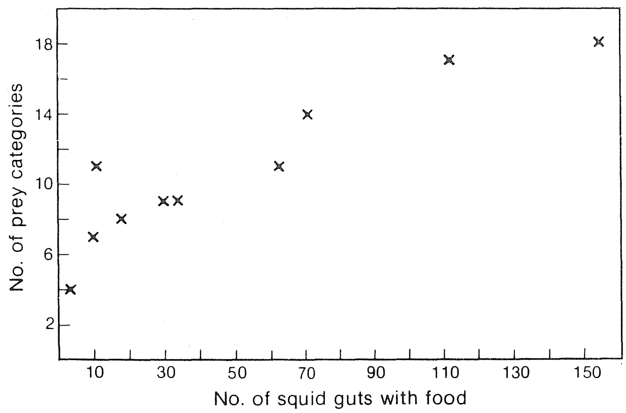

Fig. 3. Variation in number of identifiable prey categories with sample size of *T. sagittatus*.

The results of the analyses (Fig. 4) show that representatives of the four major prey groups were present in the diet. irrespective of squid size, but some general trends are apparent. The percentage occurrence of fish in the gut contents increased with increasing size of the squid. The other feeding indices for fish prey (relative frequency of occurrence and dominance index) also tended to increase with increasing squid size. In contrast, the feeding indices for the polychaete and crustacean prey groups tended to decline with increasing size of predator.

Despite attempts to ensure that the size groups of squid contained representatives from each sampling period, some of the groups were comprised largely of individuals from only one or two samples. Because the samples were taken in differ^nt seasons and at various localities, the observed changes in dietary composition with predator size could have been an artefact of squid growth coupled with seasonal and geographic variation in the availability of different prey types. Although most of the samples were composed of rather small numbers of squid within limited size ranges, it was possible to test, for some samples, whether there was evidence of within-sample variation in prey composition relative to squid size. Squid from the six largest samples were arranged by 2-cm groups, and the results relating to prey composition were examined by applying the Spearman Rank Correlation test. In five of the six cases, there was a positive correlation between percentage occurrence of fish prey and squid size. Negative correlations between percentage occurrence of crustaceans and squid size were found for four of the samples tested. Thus, there appeared to be size-related differences in dietary composition, independent of any seasonal or geographic variation in the abundance of prey organisms, with squid being increasingly dependent upon fish prey as they grew in size.

The feeding indices for molluscan prey did not show any consistent trends. During the course of the investigation, it was noticed that remains of molluscs in the squid guts were usually less well digested than other food. An analysis of the data confirmed this (Table 2), the results showing that, of 60 guts which were assessed to be digestive stages 1 and 2, 48 contained molluscs (squid remains) as the dominant prey. This implies that molluscan prey had been eaten only a short time before the squid were captured, in sharp contrast to the data for other prey types. In the majority of cases, the squid remains in the guts were pieces of arms. During the jigging process, it was noticed that some squid arms were torn loose by the hooks of the jigging lures and either became enmeshed in the lures or fell back into the water. It is possible, therefore, that squid attacked and consumed these loose pieces of arms and that the finding of squid remains in the gut contents did not reflect the normal food composition but was more the result of behavior induced by the fishing technique.

If the presence of molluscan remains in the squid guts is assumed to be an artefact of the fishing technique, in order to make realistic comparisons between the food composition of the different size groups of squid, it was necessary to recalculate the feeding indices in the absence of the data for molluscan prey. The exclusion of molluscan prey data did not alter the percentage occurrence values of other prey groups, but the relative frequency of occurrence indices did change. Because only the dominant prey were

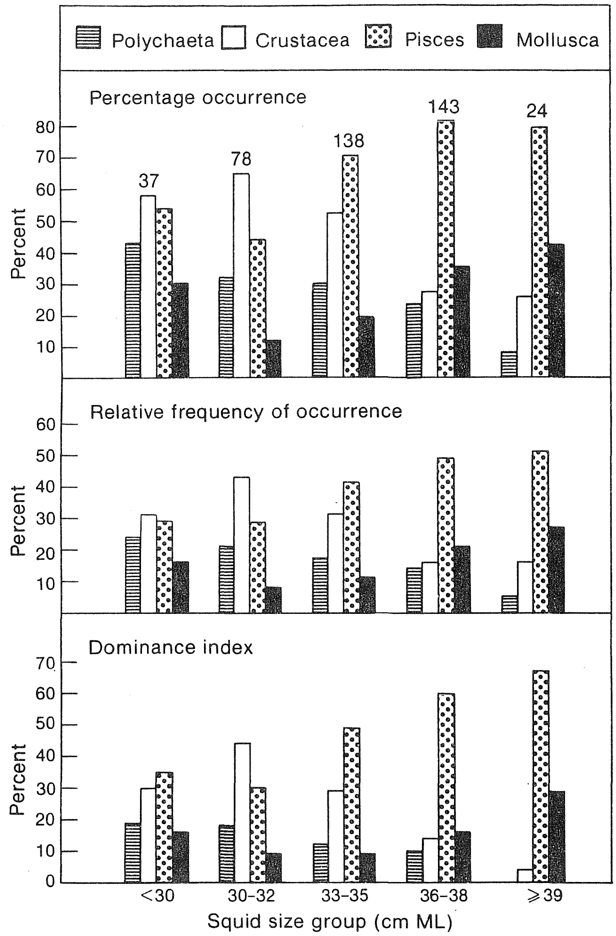

Fig. 4. Variation in food composition of *T. sagittatus* with size, based on percentage occurrence, relative frequency of occurrence and indices of dominance of four major components of the diet. (Numbers of squid by size-group are given in upper panel.)

recorded (rather than making an attempt to rank the dominance of prey in each gut), squid in which molluscan prey was dominant had to be removed before any recalculation of dominance indices could be contemplated. This led to a reduction in numbers of squid within the various size groups, with a consequent reduction in reliability of the results. The results with molluscan prey excluded (Fig. 5) display the same trends as in the analysis of total material (Fig. 4), but the increasing reliance on fish prey with increasing squid size is more clearly demonstrated.

Discussion

The prey species that were consumed by the squid, with the exception of *Nereis pelagica*, were of pelagic orgin. Although *Nereis* is usually considered to be a bottom-living species, it does have a pelagic swarming phase, and the parapodia in the squid guts were characteristic of this free-swimming heteronereid, indicating that the nereids were taken pelagically.

TABLE 2. Influence of dominant prey group on assessment of degree of digestive breakdown of gut contents in *Todarodes sagittatus*.

Dominant prey group	No. of squid guts	Degree of digestive breakdown of gut contents				
		1	2	3	4	5
Molluscs	62	20	28	6	5	3
Other prey	445	0	12	55	111	267
Total	507	20	40	61	116	270

This reliance of *T. sagittatus* on pelagic food organisms is in general agreement with previous findings for this squid (Wiborg, 1972, 1978, 1979, 1980, 1981) and other squid species (Okiyama, 1965; Macy, 1982; Mangold, 1983; O'Sullivan and Cullen, 1983), although Jonsson (1980) reported that *T. sagittatus* may also eat benthic organisms. In the present study, the prey ranged from calanoid copepods and other small crustaceans of a few millimeters in length to fish larger than 150 mm in length (Fig. 2), and an analysis of the diet revealed that the squid became more dependent upon fish prey as they increased in size. The hypothesis that these changes in dietary composition were size-related rather than due to seasonal or geographic variation was confirmed by trends in dietary patterns within the samples.

The changes in dietary composition may have resulted from the addition of new prey types to an already existing diet, replacement of one or more prey types by others, or a combination of both factors. The addition of fish to the existing diet would result in an increase in the relative frequency of occurrence of fish with increasing squid size. This additional consumption of fish would also result in increasing the percentage occurrence. If the increase in relative frequency of occurrence was brought about merely by increased consumption of fish, the percentage occurrence indices of other prey types should remain more or less the same irrespective of squid size. If, on the other hand, the increase in relative frequency of occurrence of fish in the diet was brought about by fish replacing other prey types, the occurrence indices of other prey types would decline with increasing squid size. In this study (Fig. 4 and 5), the percentage occurrence of fish in the diet of squid increased and, at the same time, the percentage occurrence of other prey types, particularly crustaceans, tended to decline with increasing predator size. Consequently, the change in dietary composition appears to be the result of both increased consumption of fish and reduced consumption of other prey items.

The fish prey of the squid consisted largely of 0-group and 1-group juveniles of several species (length range 1.5–16.0 cm). Most of these were considerably larger than the other prey types that were consumed (Fig. 2). Thus, the change in dietary

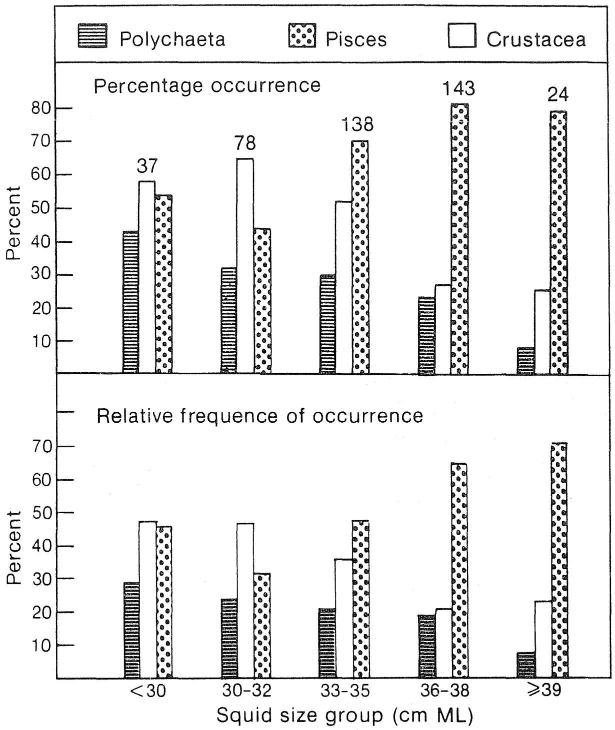

Fig. 5. Variation in food composition of *T. sagittatus* with size, based on percentage occurrence and relative frequency of occurrence of three major components of the diet excluding molluscan prey. (Numbers of squid by size-group are given in upper panel.)

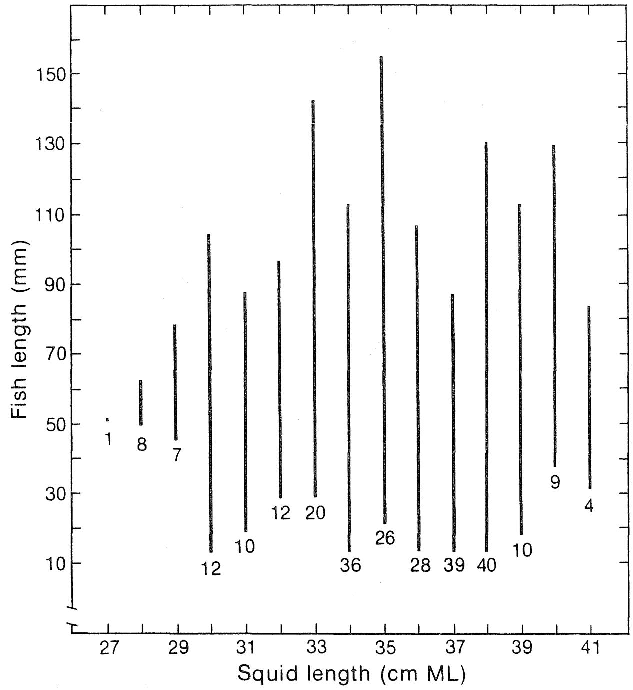

Fig. 6. Variation in estimated length of fish prey with increasing size of *T. sagittatus*. (Number of squid in each size-group is indicated.)

composition reflected not only an increase in consumption of fish but also a change to consumption of larger prey with increasing size of squid, indicating the existence of a predator size-prey size relationship. Examination of the data indicated a general increase in the size range of fish prey with increasing size of squid. Squid of all size-groups consumed small fish, but larger squid preyed upon larger fish. Consequently, as larger fish became potential prey for squid, the absolute amount of fish prey would increase, and an increasing proportion of the squid population would be expected to have fish remains among the gut contents. Hence, the percentage occurrence of fish prey would increase with increasing size of squid. In contrast, the availability of other prey types, such as crustaceans and polychaetes, would not be expected to be greater for the larger size-groups of squid because of their restricted size range (Fig. 2). Thus, the percentage occurrence of these organisms should not increase with increasing predator size. The observed decrease in percentage occurrence of the smaller prey types with increasing squid size would not be predicted, and it may be necessary to invoke the concept of prey preference in order to explain the shift away from crustacean and polychaete prey.

The results from the present study of *T. saggittatus* are in general agreement with those from investigations of several other squid species. The diets of juvenile *Illex illecebrosus* from the Northwest Atlantic (Froerman, 1984), *Todarodes pacificus* from the Northwest Pacific (Okiyama, 1965; Hamabe and Shimizu, 1966), and *Nototodarus gouldi* from southern Australian waters (O'Sullivan and Cullen, 1983) are largely comprised of crustaceans, but, as the squid increase in size, they take an increasing proportion of fish and other large prey organisms.

Although seasonal and size-related changes in the diet of squids have been demonstrated, few attempts have been made to examine the factors which are responsible for these changes. Consequently, it was difficult to make between-study comparisons, and further problems arose when a survey of the published literature indicated that validity of the methodology in some earlier investigations may be questionable. For example, volumetric or gravimetric methods have been used for analysis of the gut contents of squids and determination of feeding indices, but, in this study of *T. sagittatus*, the gut contents were usually found to be so macerated that such methods were inappropriate. This could imply fundamental differences between *T. sagittatus* and other squid species in feeding and digestive physiology, but such differences are unlikely when it is considered that digestion is known to occur rapidly in a variety of species (Bidder, 1966; Boucher-Rodoni, 1975; Karpov and Cailliet, 1978; Wallace *et al*., 1981). Thus, volumetric and gravimetric methods will tend to emphasize recently-consumed prey as being the most important components of the squid diet. This study of *T. sagittatus* pointed to squid remains as being the most recently-consumed "prey", and a dietary analysis by gravimetric methods would have indicated that cannibalism was widespread and an important part of the feeding behavior of this species. However, the occurrence of squid remains in the guts was interpreted as being a consequence of using a jigging technique for catching the squid, and cannibalism may, therefore, not be an important feature of the natural feeding behavior of the squid. The use of trawl-caught samples may not be completely without problems, because squid may attack and ingest "prey" while they are confined within the codend of the trawl. If this behavior occurred, it would be difficult or impossible to determine which components of the gut contents were representative of the normal spectrum of prey consumed by the squid. Although several authors have reported that squid are cannibalistic (Squires, 1957; Ennis and Collins, 1979; Vinogradov and Noskov, 1979; O'Sullivan and Cullen, 1983; Froerman, 1984), it is interesting to note that in none of these earlier studies has the possibility that cannibalism was induced by the sampling technique been investigated or discussed.

Froerman (1964) suggested that well-filled guts with easily recognizable food remains should be selected for the qualitative and quantitative study of the feeding habits of squid. This method cannot be recommended, because the results would be subjected to possible errors due to unnatural feeding which occurred during sampling. For example, when using trawl-caught squid, the squid that had consumed prey while confined in the trawl may be included in the sample taken for analysis of feeding habits. The result of such an analysis would be expected to reveal a high degree of correlation between the contents of the codend and the animal remains in the squid guts. It is questionable whether such an analysis would give an accurate reflection of the feeding habits of the squid population as a whole. A more reliable method for obtaining a qualitative assessment of the feeding spectrum of squid would be to select for examination only those guts which contained well-digested and macerated food remains, but the danger here is that small soft-bodied, easily-digested prey organisms may not be recorded as being part of the squid diet.

The foregoing discussion points out how the sampling and analysis techniques could influence the results of studies on dietary composition and thereby lead to questionable conclusions about the feeding habits of the species under investigation. It is of utmost importance, therefore, that comparative investigations be conducted in order to assess the influences of different methodologies on the results of feeding studies, before quantitative assessment of the food intake by squid can be contemplated.

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