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THE FEEDING ECOLOGY AND BEHAVIOUR OF INSHORE FISHES

by

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ABSTRACT

The food and feeding relationships of 21 species of inshore fish from Loch Etive were examined over a 13 month period from October 1971 to October 1972. Some aspects of the feeding behaviour of two species *Spinachia spinachia* and *Pholis gunnellus* were investigated experimentally under laboratory conditions.

With the exception of three species which were zooplankton feeders, the majority of the fish examined were benthos feeders. Amphipods were the most heavily preyed upon benthic food group.

Most fishes depended on relatively few prey types as their major food, the number of principal food types were commonly between 2 to 5 and there was often an overlap between the main food types of both related and unrelated fish species. The majority of the fishes utilized similar sources of food, but the proportions of the most commonly occurring food types eaten by different fish species were significantly different.

The types of main food groups in the diet of individual species usually did not alter throughout the year, but their importance in relation to one another frequently changed. The quantity of food in most fishes diets, however, exhibited a marked

seasonal variation. In the diet of some fishes there was evidence for a clearly defined size-related feeding heterogeneity, in others prey size selection was less marked.

The effects of some visual cues utilised in prey selection by S. spinachia and P. gunnellus were tested. S. spinachia showed a marked prey size selection under experimental conditions when the catchability of prey was strictly controlled. Selectivity was found to be related to hunger level. There was an optimal prey size for which the fish showed greatest selection. This optimal prey size was much smaller than the maximum prey size the fishes could swallow, but it coincided with the critical prey size, defined as the size at which the prey handling time began to increase drastically. P. gunnellus exhibited a less clear prey size selection pattern and no optimal prey size was found. . The fish took prey of a wide size range, showing preference for the larger prey within the preferred size range. Both fishes showed a marked preference for moving prey, selection for movement overruling the selection for size. P. gunnellus had a narrower preferred speed range of prey than S. spinachia.

Further experiments with Spinachia in which the influence of shape and shade were tested, suggested that the order of importance of the visual stimuli presented by a prey organism was: movement > size > colour > shape.

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GENERAL INTRODUCTION

Fishes inhabiting shallow coastal waters are often present in considerable numbers and undoubtedly play a major role in the economy of intertidal areas, especially as predators. In general, however, the feeding habits of most inshore fish, particularly those which have no commercial value, have not been investigated as intensively as the commercially exploited species.

Most research on the food of fishes has been focused on single species, and other members of the same community are considered chiefly as predators or as potential food. Yet it is generally realised that interspecific competition for food may be as strong as intraspecific competition in its limiting effects on reproduction and growth etc. Nikolsky (1945) has commented that only by the comparative study of the feeding habits of different species can an understanding of the qualitative and quantitative connections between fishes and their food organisms be gained, thereby producing information on the dynamics of the food chain. The community approach in the study of the feeding habits of fishes is relatively rare. Frost (1946) studied the feeding relationships of six species of freshwater fish in Lake Windermere.

Hartley (1940, 1948) similarly adopted a community approach when examining the feeding habits of both estuarine and freshwater fishes. More recently Keast (1965) and Zaret & Rand (1971) have examined the resource subdivision among cohabiting fish species in freshwater systems. Studies on the feeding habits of marine fish species have been undertaken by Richards (1963), Nagabushanam (1965) and Tyler (1972). The results of all these studies support the view that a comparative study of the feeding habits of all members of a fish community do lead to a better understanding of the feeding ecology of that community.

Sampling carried out prior to the work described in this thesis had shown that a rich community of inshore fish exists in Loch Etive, comprising some 22 species. The aim of the first part of the present study was to obtain a comprehensive account of the food and feeding habits of the species concerned; to examine the seasonal variation in the quality and quantity of their food and to see how, and to what extent, the available food resources were exploited by the various components of the fish community.

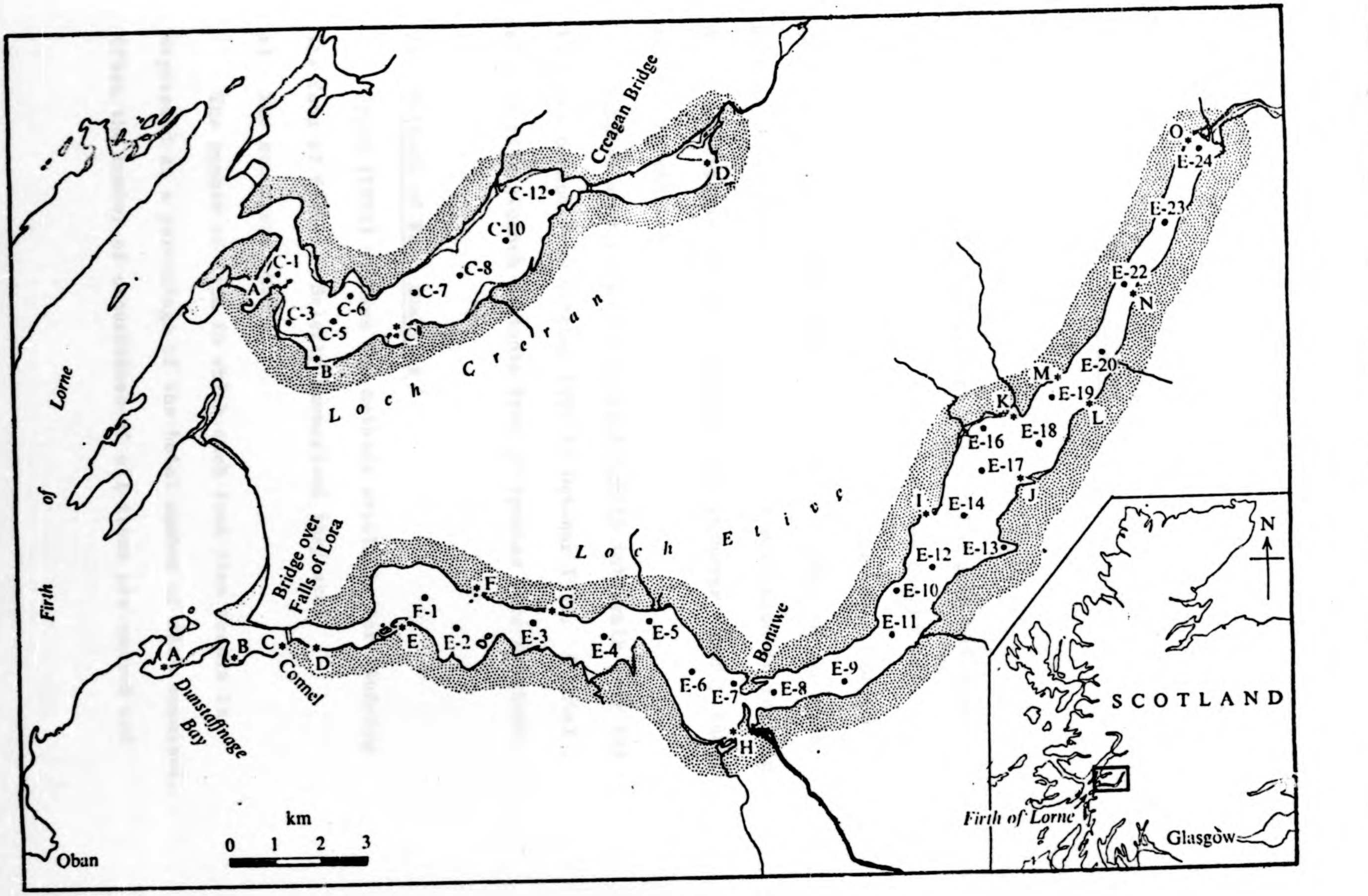
The second part of the thesis deals with some behavioural aspects of food selection using two species as examples, with a view to determine if possible, to what extent the feeding behaviour of the fish governs its diet. An extract from this work has already been published (Kislalioglu and Gibson, 1975).

Section I - FEEDING ECOLOGY

SAMPLING AREAS

Loch Etive is a sea-loch situated on the fjordic coastline of west Scotland. It is a double basin system, linked to the outside sea area by a shallow sill. An account of the hydrography and benthic communities of the loch has been given by Gage (1972). Three areas in this loch each with different bottom substrates and salinity were chosen for sampling. The sampling areas are shown in Fig. 1. Dunstaffnage Bay has both sandy and rocky bottom substrates; Airds Bay and Dail have shingle and rocky bottom types respectively. A decreasing salinity gradient exists from Dunstaffnage Bay to Dail. It was assumed that the sampling of these three stations would ensure a fair representation of all inshore fish species found in the loch.

Fig. 1. Map of Loch Etive showing positions of sampling areas. A. Dunstaffnage Bay, H. Airds Bay, K. Dail. (From Gage 1972).


Firth of Lorne
Oban
A
B
C
D
Dunstaffnage Bay
Connel
Bridge over Falls of Lora
Loch Creran
Creagan Bridge
C-1
C-3
C-5
C-6
C-7
C-8
C-10
C-12
Loch Etive
Bonawe
E
F
F-1
G
H
I
J
K
L
M
N
O
E-2
E-3
E-4
E-5
E-6
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km
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1
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N
SCOTLAND
Firth of Lorne
Glasgow

METHODS

1) Fishing Methods

A 45 m sand eel beach seine and a 1.7 m push net were used for collecting samples. All the fishes caught between 0 to 8 m depth were included in the food analyses. Samples were taken at low water and during the day only, to minimise any possible effects of tidal and diurnal variation in feeding. Shore collections were made at low tide whenever monthly sample sizes were small.

Samples were collected at fortnightly intervals over the 13 month period from October 1971 to October 1972. A total of 3638 fish stomach contents from 21 species were examined.

2) Methods of Food Analysis

Hynes (1950) reviews the methods available for studying the food of fishes. Briefly summarised they are:

a) The occurrence method:

The number of fish in which each food item occurs is expressed as a percentage of the total number of fish examined. Often the number of occurrences of all items are summed and scaled down to a percentage basis.

b) The number method:

The total number of individual food items in each food category is listed, often as percentages of the total numbers of animals found in all the fish examined.

c) The dominance method:

The number of fish in which each food item is the dominant food is expressed as the percentage of the total number of fish examined.

d) The volume and weight method:

The total volume or weight of each food item or of the total food of each fish is calculated, usually as a percentage of the total weight of the fish.

e) The fullness method:

Arbitrary estimations of the degree of fullness of the stomachs examined one used to express seasonal variations in food intake.

f) The points method:

The food items in each stomach are listed as common, frequent etc. on the basis of rough counts and visual estimation, making allowance for the differences in size of organisms as well as their abundance. This means a large animal would count as much as many smaller ones. Each category (common, frequent etc.) is alloted a number of points and all the points gained by each food item summed and expressed on a percentage scale to give the percentage composition of the diet of the fish examined. Consideration of the fullness of the stomach and the size of the fish affects the number of points allotted; a total number of points is allotted to a stomach on the basis of the size of the fish and the fullness of the stomach and this total is then divided proportionately among the food items present. This is essentially an approximate volumetric method.

Hynes (1950) shows that all the methods considered give substantially similar results, at least for the major components of the diet.

As the aim of the present study was to investigate and compare the food composition of a large number of species it was necessary to select a method that could be applied to all of them. It was also necessary to choose a method that was relatively rapid and easy so that as many fishes as possible could be examined.

A preliminary examination of the stomach contents of selected species showed that the fishes differed widely in the amount and state of food found in their stomachs. Theoretically, the most accurate method would be the weight and volume method; but this method would be practical only when large volumes of food were present and number of items to be segregated was small. This method could be applied with reasonable accuracy to crab-eating cottids for example. In most species, however, because of their small size, the total weight of food was very low and as well as being very laborious, the errors involved in weighing (or in estimating the volume of) very small amounts of food items would be quite large and would lead to a high degree of inaccuracy. This method was therefore considered to be unsuitable for the present investigation.

Examples of the dry weights of the total amount of food found in seven species are given below to demonstrate this point.

Table 1. Dry weights of the stomach contents of seven species in November 1971.

Fish species	Number of fish investigated	Total dry weight of food (g)	Dry weight of food/fish (g)
Spinachia spinachia	32	0.281	0.0087
Atherina presbyter	26	0.163	0.0063
Chaparrudo flavescens	60	0.133	0.0022
Myoxocephalus scorpius			
a) TL 62-63 mm	2	0.041	0.0210
b) TL 139-159 mm	2	3.767	1.8835
Taurulus bubalis TL (107-113 mm)	3	0.277	0.0923
Gasterosteus aculeatus	18	0.021	0.0012
Zoarces viviparus	6	0.204	0.0340

The numbers method was also found to be unsuitable because the food items in the stomachs of several species were not intact and often only parts were found instead of whole animals. In such instances the numbers could not be estimated accurately. It was also obvious that consideration of the number of various food items found could not give a realistic picture of importance of different foods because of the large differences in the size of individual food items.

It was possible to apply the occurrence and points methods to all species considered. The occurrence method is not affected by the state of the animals found as long as they were identifiable. It also demonstrates effectively which organisms are being eaten but gives no information on quantities or numbers. The points method does, however, determine the relative amounts of the food items in the diet. It is a rapid and easy method, is not influenced by the frequent occurrence of a small organism in large numbers, nor of heavy bodies and does not involve counting large numbers of small and broken organisms. The subjective allotment of points made by the investigator is the only obvious limitation. Hynes (1950) argues that although the method is subjective, such subjectivity also applies

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The method finally chosen was a combination of the occurrence and points methods. It involved estimating the degree of fullness of each stomach. Each stomach was treated as a unit and only the contents of stomachs were included in the analyses as the food in the intestines were often much digested. The fishes were placed in 70% alcohol immediately after they were caught to prevent further digestion.

The total length, standard length and the mouth gape of each fish was measured, after which the stomachs were removed. It was fairly easy to delimit the stomach from the rest of the gut in most fishes and even in those fishes where the gut was tubular and no noticeable size differences existed between stomach and rest of the gut, it was still possible to distinguish the stomach by its relatively thicker walls. The pylorus was taken as the distal limit of the stomach. In some species a large food item was occasionally found lying in the oesophagus.

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In such cases the food was included in the stomach contents.

The most difficult part of the method and which was most subject to a high degree of error was to estimate the degree of fullness of a stomach. 0 to 20 points were used for different fullness categories except where the stomachs were distended which then received up to 30 points. A cut was made along the length of the stomach under a binocular microscope and all the food from the stomach was removed by carefully washing the inside of stomach.

Completely full stomachs offered no difficulty in estimation as the food filled the stomach completely; the wall was stretched thin and encased food closely. Such stomachs received 20 points or if particularly distended >20 points, with a maximum of 30. In completely empty stomachs the walls were thick. Between empty and full stomachs intermediate categories were recognised and a number of points were allotted to the total contents of stomachs accordingly.

As it was obvious that the degree of accuracy depended on experience, a large number of fullness estimation was carried out on most species to gain experience. The results are not included in the following food analyses.

After the number of points had been allotted to the total stomach contents according to fullness, the contents were then sorted into broad food groups such as amphipods, isopods etc. The total number of points was then divided proportionately among these groups making use of a scaled graph paper attached to the table of the microscope when appropriate. If any species or families could be identified among the food groups, the points received by the group were further subdivided to estimate the relative proportion of different species. The total length of any intact individuals was also measured and the numbers recorded whenever possible.

A set of comparisons was carried out between the percentage composition estimated by points as described above and by measuring the wet weights for 51 juvenile cod to obtain a measure of the accuracy of the points method. The proportion of different food groups in each stomach was first estimated by the points method then each group was weighed on a microbalance. The weight was expressed as the percentage of the total weight of food. The differences between the two percentages gave an indication of the errors inherent in the points method and also showed whether the points method tended to over-or under-estimate the amounts of various food groups.

Table 2 gives the proportion of different food groups in each fish in terms of percentage weight and percentage points.

The results showed that proportions of the five food categories in the fish stomachs as estimated by the points method did not differ very widely from those found by the weight method. The signs of the differences showed that in all food groups the points method tended to overestimate the amount of food in each category except in the largest food item, shrimps. The mean differences in the percentages were largest (8%) in the smallest food item (copepods) but in all others they were between 0.4–5.5%.

The results suggested that the points method could be satisfactorily used in the estimation of percentage food composition.

For each month the application of the above methods gave the following data:

1) The percentage composition of diet by points. The points received by each food category was expressed as a percentage of the total number of points gained by all stomachs for all food categories.

Table 2. Comparison of the points and weights method of food analysis for 51 juvenile cod

Food Category	No stomachs containing food category	No of times points estimate > weight estimate (+vedifference)	No of times weight estimate >points estimate (-ve difference)	Maximum -ve difference	Maximum positive difference	Algebraic mean of difference
Amphipods	33	23	10	-19.03	+31.56	+3.94
Shrimps	26	14	12	-26.19	+14.34	-0.88
Copepods	7	6	1	-10.23	+24.77	+8.12
Cumaceans	11	11	0	-	+ 9.51	+5.50
Isopods	8	7	1	-21.72	+ 7.44	+0.47

2) The percentage composition of diet by occurrence. The number of stomachs in which each food category occurred was expressed as a percentage of the total number of occurrences of all food categories in all stomachs.

3) The percentage number of stomachs that were full, ¾ full, ½ full, ¼ full, trace full and empty and the mean points/stomach/month giving a monthly fullness index.

RESULTS

The number of fishes caught at the three sampling stations and the number of hauls throughout the sampling period are given in Table 3. It can be seen that the catches from Dunstaffnage Bay, Airds Bay and Dail differed slightly in species composition. More P. microps and G. aculeatus and Anguilla anguilla were caught at Dail compared to Dunstaffnage Bay and Airds Bay which may be attributable to the low salinity preferences of these species.

The number of hauls shows that Dunstaffnage Bay has been most extensively sampled and Dail least. When the stations were compared haul by haul slightly larger number of fishes with a greater diversity were found at Dunstaffnage Bay.

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The number of hauls shows that Dunstaffnage Bay has been most extensively sampled and Dail least. When the stations were compared haul by haul slightly larger number of fishes with a greater diversity were found at Dunstaffnage Bay.

Table 3. The numbers and species of fish caught at the three sampling locations from October 1971 to October 1972

Location	**Dunstaffnage Bay**	**Airds Bay**	**Dail**	**Total**
Number of Hauls	141	85	81	307
Species				
Spinachia spinachia	188	282	161	631
Gasterosteus aculeatus	108	8	244	360
Myoxocephalus scorpius	184	26	24	234
Taurulus bubalis	39	41	36	116
Pholis gunnellus	245	32	29	306
Pomatoschistus minutus	399	5	55	459
Pomatoschistus microps	14	7	74	95
Chaparrudo flavescens	251	213	21	485
Atherina presbyter	334	0	0	334
Pleuronectes platessa	109	19	20	148
Platichthys flesus	43	28	55	126

Table 3 cont.

Location	Dunstaffnage Bay	Airds Bay	Dail	Total
Pollachius virens	106	38	5	149
Gadus morhua	23	8	5	35
Zoarces viviparus	126	47	8	181
Crenilabrus melops	19	4	-	23
Agonus cataphractus	19	3	4	26
Hyperoplus lanceolatus	61	6	2	69
Nerophis lumbriciformis	27	0	0	27
Syngnathus sp	10	4	10	24
Anguilla anguilla	2	1	14	17
Chirolophis ascanii	15	0	0	15
TOTAL ALL SPECIES	2322	772	767	3861

N.B. Salmo trutta is excluded from this list because its biology was being studied by another worker at the time (See Pemberton 1975, in press).

DIETARY COMPOSITION OF INDIVIDUAL SPECIES

1. Spinachia spinachia

There is very little known about the food or the feeding habits of S. spinachia. Wheeler (1968) states that the food of this fish is small crustaceans but no detailed information is available concerning the composition or the seasonal variation in diet. Judging from the occurrences in the catches, this fish forms a substantial part of the inshore fish populations in Loch Etive and therefore probably plays an important role in the community structure.

A total of 608 fish stomachs were examined from three different localities during the sampling period. As mentioned, earlier most of the sampling was carried out at low tide and substantial amounts of food were often present in fish stomachs. The state of the food varied; sometimes it was highly digested but it was generally possible to differentiate between the major food groups. The specific identification of food items was more difficult as the parts of the body with taxonomic characteristics were frequently missing. The food items were identified down to species whenever possible.

The list of food organisms encountered during the whole sampling period is given below. The relative importance of each food group in the diet is demonstrated by percentage occurrence (PO) and percentage points (PP). PO values show the proportional occurrence of each group as a percentage of total number of occurrences found in all months. PP values correspond to the percentage points received by each group out of total number of points given to all food groups estimating the proportional amounts of each category. The relative importance of different species of amphipods are shown by calculating PO, PP values for each species separately.

Local variation in the composition of the diet.

The main food types remained, on the whole, unchanged in the three localities, although Dunstaffnage Bay, Airds Bay and Dail Bay had very different bottom substrata. There were, however, differences in the relative importance of food groups between the three stations. Amphipods were the most important food group in the samples from Dunstaffnage Bay in all months.

The values of percentage occurrence (PO) and percentage

Table 4. The food composition and the relative importance of different food items in the diet of *S. spinachia*.

	PO	PP
CRUSTACEA		
AMPHIPODA	33	41
Amphithoe sp	0.8	0.5
Aora sp	0.3	0.4
Phistica sp & other caprellids	5	3
Corophium sp	8	7
Gammarids	39	58
Hyale sp	12	9
Microprotopus sp	2	1
Nototropis sp	3	3
Orchestia sp	1	0.3
Cressa sp	0.2	0.7
Periculodes sp	0.2	0.1
Melita sp	2	1
Indet. amphipods	26	16
ISOPODA	28	28
Jaera marina, *Jaera nordmandi*		
Idotea granulosa, *Sphaeroma* sp		
DECAPODA	2	3
Hippolyte sp		
EUPHAUSIACEA	<1	<1
MYSIDACEA	10	12
Hemimysis sp, *leptomysis* sp, *Praunus* sp, *Siriella* sp, Indet. Mysids		
COPEPODA	7	6
Calanoid copepods, Harpacticoid copepods		
OSTRACODA	1	1
ANNELIDA	1	1
Polychaeta, Oligochaeta		
MOLLUSCA	3	1
Gastropoda, *Hydrobia* sp, Bivalves, *Modiolus* sp		
INSECTA	8	6
Insect larvae, Caddis fly larvae, Adult insects		
NEMERTINA	<1	<1
PISCES (Fish eggs)	<1	<1
COELENTERATA (Hydrozoa)	<1	<1
PLANT MATTER	<1	<1
DIGESTED MATTER	<4	<1

points (PP) were consistently higher for this group than all the remaining groups. In stomachs of fish caught in Airds Bay, although amphipods were present throughout the year in substantial amounts and were the most important food group in most months, their dominance over all other types of food was not as consistent as in the diets of fishes caught in Dunstaffnage Bay. Isopods occasionally attained primary importance. The same was true for the Dail samples, where amphipods were often the most important group but in some months isopods occurred more frequently and in higher quantities. PO, PP values for isopods were generally higher in fishes caught in Airds Bay and Dail than those caught in Dunstaffnage Bay. In order to test whether samples from the three localities differed significantly with respect to isopods and amphipods, the total number of times each food type was present and absent in the samples from three stations were compared with a χ^2 test. The χ^2 values for these comparisons are given below.

Table 5 shows that the number of occurrences of amphipods in the diet of fishes caught at Dunstaffnage Bay were significantly different from those caught in Airds Bay. No difference was found in the occurrences of amphipods between

Table 5. χ^2 values for the comparison of occurrence of amphipods in fish stomachs between the three stations.

Station	Dunstaffnage Bay	Airds Bay	Dail
Dunstaffnage Bay		6.81*	0.87
Airds Bay			2.51
Dail			

* p 0.02

Table 6. χ^2 values for the comparison of occurrence of isopods in fish stomachs between the three stations.

Station	Dunstaffnage Bay	Airds Bay	Dail
Dunstaffnage Bay		54.23**	39.03**
Airds Bay			0.15
Dail			

**p 0.001

Dunstaffnage Bay and Dail and the difference between Dail and Airds Bay was also not significant. The comparisons support the indication given by PO and PP values that the fishes caught in Dunstaffnage Bay had the greatest frequency of occurrence of amphipods, those from Airds Bay lowest, and the Dail samples have intermediate values.

The differences in the occurrences of isopods in samples from the three localities were much more pronounced (Table 6). The number of times isopods were found in the stomachs of fish caught in Airds Bay and Dail was very significantly higher than in those caught in Dunstaffnage Bay. The differences between the samples from Airds Bay and Dail were negligible.

The examination of PO and PP values from three localities also suggested that although their occurrences in the samples were not continous, mysids might be a more important food group in the diets of fishes caught in Dunstaffnage Bay than in those caught in the other two localities. χ^2 values for the comparison of occurrences for the whole sampling period between localities are given below.

Table 7. χ^2 values for the comparison of occurrence of mysids in fish stomachs between three localities.

Station	Dunstaffnage Bay	Airds Bay	Dail
Dunstaffnage Bay		29.67	21.14**
Airds Bay			0.05
Dail			

** $p < 0.001$

The number of occurrences of mysids in fish stomachs caught in Dunstaffnage Bay were significantly higher from those caught in Airds Bay and Dail. Once again no differences were found between the samples from Airds Bay and Dail.

The differences between the stations with regards to mysids are likely to be the result of distribution patterns of mysids in the loch. Mysid populations are well established in Dunstaffnage Bay and Dail; Airds Bay may be poorer in this respect, but the distribution of mysids is extremely patchy and the presence of mysids in the diet of a fish in a particular month probably depends on whether fishes are feeding in the areas where mysids are numerous.

Insect larvae and molluscs also seemed to exhibit a certain degree of local variation. The occurrences of insect larvae in the Airds Bay and Dail samples were significantly higher than in the Dunstaffnage Bay samples. Rivers flow into both Airds Bay and Dail (Fig. 1) and it is likely that they carry to these localities a considerable amount of insect larvae in summer months when their numbers are high.

Table 8. χ^2 values for the comparison of occurrence of insect larvae in fish stomachs between three localities.

Station	Dunstaffnage Bay	Airds Bay	Dail
Dunstaffnage Bay		15.31**	8.08*
Airds Bay			0.78
Dail			

** $p < 0.001$

* $p < 0.005$

The number of occurrences of molluscs were higher in Airds Bay than Dail and Dunstaffnage Bay but the differences were not as pronounced as insect larvae occurrences.

Table 9. χ^2 values for the comparison of occurrence of molluscs in fish stomachs between three localities.

Station	Dunstaffnage Bay	Airds Bay	Dail
Dunstaffnage Bay		5.20*	0.14
Airds Bay			3.00
Dail			

*$p < 0.025$

It is well known that in brackish water or in areas with fluctuating salinity the specific diversity of the benthos is much more restricted than in fully saline waters. Gage (1972) has shown that in Loch Etive the number of benthic species is far greater in Dunstaffnage Bay, whose salinity is close to that of the open sea, than in the remaining part of Loch Etive where salinity decreases consistently towards the head of the loch.

Among all the amphipods identified in fish stomachs, 12 species were found in Dunstaffnage samples, 9 species in Airds Bay and 7 species in Dail. The percentage of unidentified amphipods in Dunstaffnage Bay was also greater than the other two localities. This may be a reflection of the differences in specific diversity of the three localities imposed by the salinity gradient that exists between Dunstaffnage Bay and Dail.

Table 9 gives the relative importance of different species in three stations.

The greatest percentage of amphipods both in occurrence (PO) and bulk (PP) were Gammarids in all three localities. The only amphipods which showed a clear local variation were the family Corophidae. These amphipods were the second most important amphipods at Dail both in terms of their percentage of occurrence and volume. The differences between Dail and both Dunstaffnage and Airds Bay samples were significant at $p < 0.01$.

Hyale sp. were found to occur more frequently in the Dunstaffnage Bay and Airds Bay samples, where they were the second most important types of amphipods, than at Dail.

The seasonal variation in the composition of the diet of Spinachia spinachia.

Table 11* and Fig. 2 show the percentage composition of the

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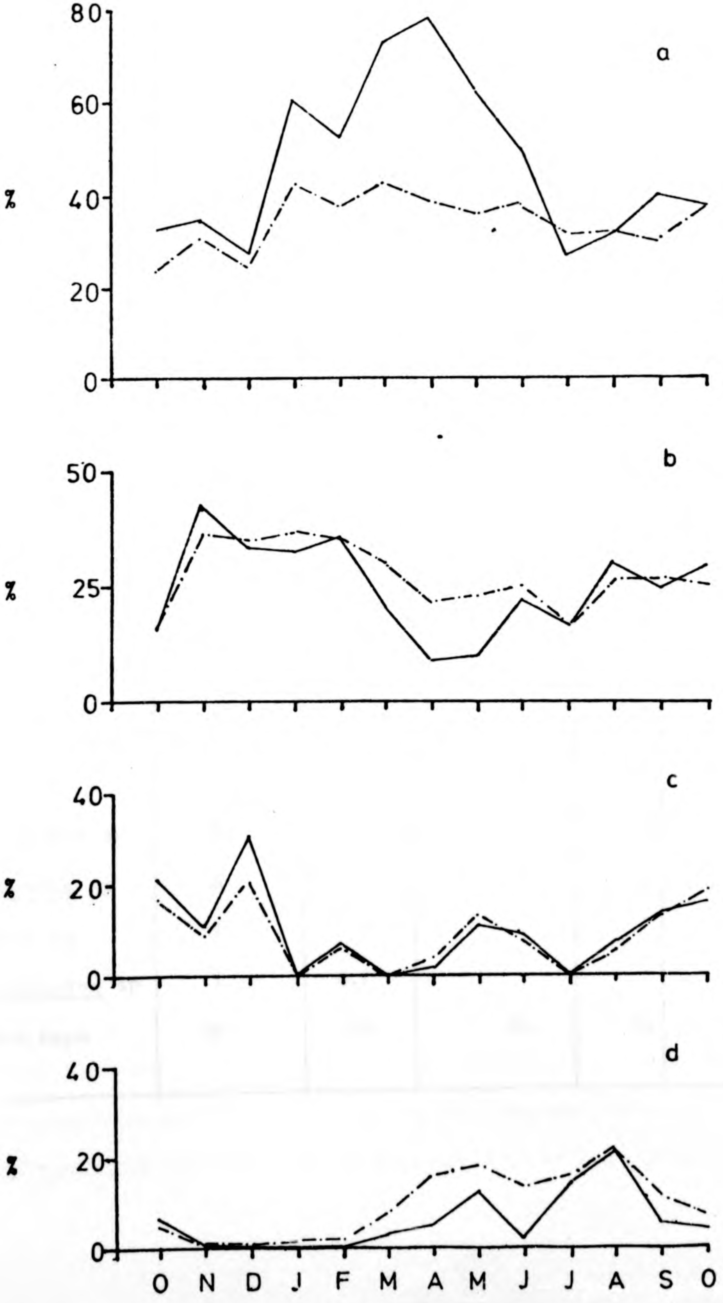
* See Appendix.

Fig. 2. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of *Spinachia spinachia*. Solid lines: PP values, dot:dash lines PO values.

a) Amphipods, b) Isopods, c) Mysids d) Insects.


a
80
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40
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0
%
b
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25
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Table 10. **Comparison of relative importance of different species of amphipods in three localities.**

Location	Dunstaffnage Bay		Airds Bay		Dail	
Amphipod species	% occurrence	% points	% occurrence	% points	% occurrence	% points
Amphithoe sp	2	1	0.4	0.1	1	0.2
Aora sp	1	1	0.4	0.1		
Caprellidae	17	9	0.4	0.1		
Corophium sp	5	5	6	2	19	15
Gammaridae	38	46	49	69	46	70
Hyale sp	16	12	18	10	5	2
Microprotopus sp	1	1	3	1	1	0.2
Metopa sp	1	0.3	4	2	2	0.5
Nototropis sp	3	2	4	4	3	0.4
Orchestia sp	6	1	-	-	-	-
Cressa sp	1	2				
Pariculodes sp	1	0.1				
Indet. Amph.	38	22	30	12	21	12

diet in each month throughout the sampling period.

The number of main food groups in the diet of *S. spinachia* were found to be relatively few, and they showed very little variation throughout the year. Amphipods on the whole were the most important food item. They had the highest PO and PP values among all food groups in most months except in November and December when isopods became the primary food group, and in July when harpacticoid copepods became most important. In some months amphipods formed up to 75% of the total amount of food. The greatest portion of amphipods consisted of gammarids throughout the year, with the exception of July when they were absent. In this month *Amphithae* and *Hyale* spp became important. The lack of gammarids in the July sample is thought to be a result of size-related food selection. The total length of the fishes caught in July varied between 35 and 57 mm. On the whole, as fish size increased the proportion of gammarids in fish diets also increased.

No other amphipod group has the same importance in the fishes diet as gammarids, although the amount of *Hyale* sp. reached high levels in January, June, July and August. The importance of *Corophium* sp. in the diet increased in the spring months, March, April and May. Whether the increase was a reflection of a change in the abundance of this species is not known.

Isopods formed the second most important food group all the year round (Fig 2). The greatest proportion of isopods consisted of Jaera sp. Mysids on the whole were third in importance in the diets of S. spinachia; their occurrence seemed to exhibit some seasonal variation. The sampling period could roughly be divided into two parts with respect to the importance of mysids. They were the third important food category from October to December; their significance decreased during the late winter and early spring and increased again in May, June, September and October. This agrees well with the seasonal abundance of mysid populations in the loch. The biology of Praunus flexuosus and the brackish water species Neomysis integer have been well studied in Loch Etive (Mauchline 1971). In December the large population of Praunus flexuosus in Dunstaffnage Bay consists predominantly of juveniles and immature males and females; breeding continues throughout the winter but at a greatly reduced intensity. The proportion of juveniles in the population decreases in January and February. In March and April juveniles mature sexually reaching larger sizes. From June to October the number of very young juveniles increases again. During these months, except July, mysids also become an important component of the fishes diet.

In July 1972, mysids were not found in fish stomachs. This could be explained by the fact that all fishes caught were juveniles with a mean total length of 42 mm. When the occurrence and the quantity of mysids in different fish size groups were examined, it was found that mysid feeding begins to be important in fish above 70 mm total length. In July, the lack of mysids in the fishes diet is though to be related to the fish sizes being smaller than the size at which mysid feeding begins.

The monthly composition of the population of *Neomysis integer* found at the head of Loch Etive and at Dail gives essentially the same picture as *Praunus flexuosus*. As in *Praunus* the number of small sized very young juveniles is high in December, decreases in January and they are rare until late May, becoming abundant again from July onwards. Hence the summer and autumn generations contain many small sized juveniles with total size range between 4–14 mm, a size suitable for predation by the fish. The 90–100 mm size group of *Spinachia* which was the commonest size group in the catches feeds mostly on mysids of the size range 5-15 mm.

The variations in the seasonal importance of mysids in the fishes diet seem to be affected therefore by three factors. First, by the seasonal abundance of mysid populations, secondly, seasonal differences in the total length of the fish in the samples and thirdly by local variations between samples due to the patchy distribution of mysids. This may serve as an example of a case where misleading conclusions may be drawn if all possible factors causing dietary variation are not taken into account.

Another example of the food group whose occurrence in the fish diets is a combined result of the factors mentioned above are insect larvae. Table 11 and Fig 2 show that this group has a clear seasonal variation. Insect larvae were important in fish diets from early summer to autumn. Percentage occurrence and percentage points were very low in the winter months. Insect larvae gained importance once again in the spring and retained this position until October. Their increasing abundance as well as small size rendered them a suitable food item for the juveniles which were mostly present in the summer months. As mentioned earlier, this food group also showed considerable local variation.

Molluscs, especially gastropods occurred frequently in fish stomachs in most months, but they never became an important part of the diet. Their occurrence increased slightly in winter months when the overall feeding intensity was low and their importance in the diets is likely to be accentuated in the winter due to the low levels of food found in the stomachs.

Harpacticoid copepods occurred fairly regularly in all months although their PO and PP values were very small. Their importance in the diet of Spinachia increased considerably in the summer months, especially in July, where they formed the greatest portion of the juvenile fishes diet. The mean total length of fishes in the July sample was the lowest among the summer months. The variation in the amounts of harpacticoids thus seems to depend primarily on fish size and not season or locality.

The frequency of occurrence and the volume of calanoid and ostracods in the diet of Spinachia throughout the year is similar to that of harpacticoids. Although these groups never became an important part of the diet, their numbers increased from May onwards. September values for the planktonic copepods were the highest and this month was unusual in the sense that some adult fishes turned to planktonic feeding habits and had taken large quantities of planktonic copepods. In this case their consumption was not clearly related to fish size. No explanation is available for such a change except that they may have come across a shallow water plankton patch. It demonstrates that although the fishes are primarily benthic feeders, under certain circumstances they can feed on zooplankton. They thus show a certain degree of flexibility in their feeding habits and are not compulsory benthic feeders.

Polychaetes were not an important group in Spinachia's diet; they occurred irregularly in some months but never in large quantities. Oligochaetes were recorded only once.

2. Gasterosteus aculeatus

G. aculeatus is essentially a freshwater species although its distribution extends to estuaries and sometimes well into the sea. In Loch Etive, out of 360 fishes examined throughout the sampling period, 108 were caught in Dunstaffnage Bay where marine conditions were prevailing, only 8 were caught in Airds Bay and 244 were caught in Dail which had the lowest salinity.

Several early authors give lists of food of the three-spined stickleback, Day (1880–4), Smith (1892) Tate Regan (1911) also Bertin (1925), Leiner (1930) Heilborn (1931) and Fisher (1948). Their results agree that the diet of G. aculeatus consists of worms of various kinds, small crustacea, aquatic insects, larvae, occasional aerial insects and fish eggs.

Saunders (1914), Blegvad (1917), Hartley (1940) and Hynes (1950) have made more detailed studies of the food of this species. Saunders examined a large number of sticklebacks from a pond near Cambridge and found at all times of the year larger fish consumed large quantities of diatoms, whereas smaller fish were carnivorous, feeding on insect larvae and crustacea; in nearby ponds all fish were carnivorous.

Blegvad (1917) investigated the stomach contents of 736 fishes from the brackish waters of the Zostera region of various Danish waters. He states that young fish feed on copepods, cladocerans, mollusc larvae and ostracods and as they grow they begin to eat young gammarid amphipods, isopods and mysids, also the eggs of fish.

Hartley (1940) examined the stomach of 129 fishes from two Cambridge rivers. His results, assessed by the occurrence method, show that insects formed 60% of the food and crustacea 29%, small molluscs and some plant material were also present. Crustacea were the most important food in the winter; in the other nine months of the year insects predominated.

Hynes (1950) analysed the food of fishes from a small stream in Westmorland and from Easdale Quarry in Argyllshire. He found that the main food groups were Cladocera, Copepoda, Ostracoda, insect larvae, Annelida and Mollusca.

The list of the food items found in the stomachs of G. aculeatus and relative importance of food groups shown by percentage occurrence, percentage point values are given below (Table 12).

Table 13* gives the PO, PP values for different food groups throughout the year for the combined localities.

Amphipods occurred consistently in fish stomachs in considerable amounts. The percentage occurrence values for this group varied between 1-32 and percentage point values 1-52 (Fig 3). The lowest PO and PP values for amphipods were found in August and September. Percentage point values, which are the estimates of the amount of food in fish stomachs, were often higher than the percentage occurrence values in terms of the

* See Appendix

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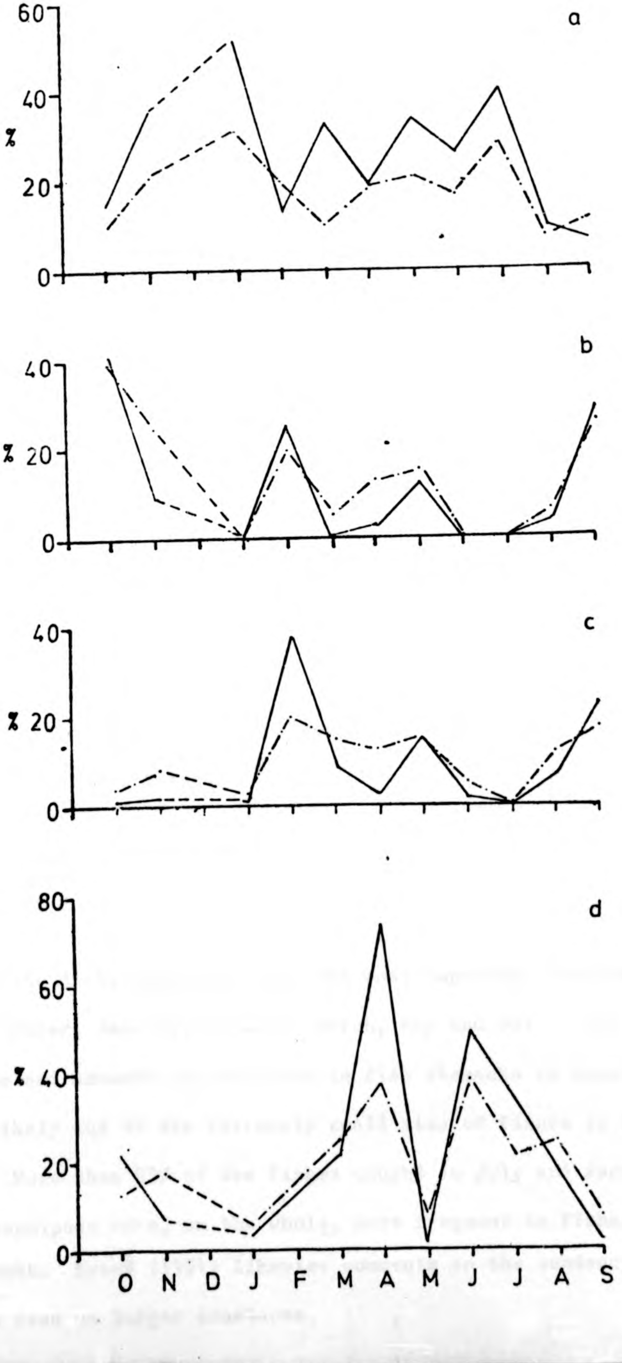
* See Appendix

Fig. 3. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of Gasterosteus aculeatus.

Solid lines: PP values, dot:dash lines PO values; broken lines indicate a break in the sampling series.

a) Amphipods b) Calanoid copepods c) Harpacticoid copepods d) insects.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60
40
%
20
0
b
40
% 20
0
c
40
% 20
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Table 12. The food composition and relative importance of different food items in the diet of *G. aculeatus*

	PO	PP
CRUSTACEA		
AMPHIPODA	17	19
Ampelisca sp	1	1
Caprellidae	4	1
Corophium sp	32	44
Gammaridae	21	24
Hyale sp	5	4
Microprotopus sp	1	1
Nototropis sp	3	1
Orchestia sp	< 1	< 1
ISOPODA	8	4
Jaera sp		
DECAPODA	2	2
Indet. Decapod larvae		
MYSIDACEA	1	1
Hemimysis sp, *Neomysis* sp, Indet. mysids		
CIRRIPEDIA	1	1
CLADOCERA	9	16
COPEPODA		
Calanoid copepods, *Pseudocalanus* sp., *Temora* sp, *Calanus* sp.		
Harpacticoid copepods	9	10
CUMACEA	2	1
OSTRACODA	2	1
MOLLUSCA	2	2
Gastropods, Bivalves		
ANNELIDA	9	6
Polychaeta, (Sabellids), Oligochaeta		
INSECTA	18	21
Insect larvae, Insects		
NEMERTINI	< 1	< 1
PISCES	< 1	< 1
Fish eggs, Juv. flat fish		
PLANT MATTER	< 1	< 1
Indet. Digested Matter	3	1

volume of the diet, amphipods were the most important food item during the months November, January, January, March, May and July. The relatively low occurrence and amounts of amphipods in fish stomachs in August and September is most likely due to the extremely small size of fishes in these months samples. More than 85% of the fishes caught in July and August were below 30 mm. Amphipods were, on the whole, more frequent in fishes above 40 mm total length. Hynes (1951) likewise comments on the tendency of larger fishes to feed on larger crustacea.

Among amphipods *Corophium* sp was the most frequently occurring amphipod, followed by gammarids. Other amphipod types were much less common.

The occurrence of zooplankton (calanoid copepods, cladocerans, cirripede nauplii, planktonic prosobranchs, etc) was not continuous in all months but whenever found they were taken in large quantities. In terms of PO and PP values they were highly significant in October, November, February, August and September. In general, copepods produce a succession of broods throughout the summer Marshall (1949). It is, on the whole, true that small copepods such as *Temora* sp. and *Pseudocalanus* sp. are more numerous in spring and summer than in winter but it was not possible to follow this trend from the PO, PP values for calanoid copepods; for example they are poorly represented in the April, June, July samples. The occurrence of zooplankton in fish stomachs seem to depend on fish size as well as the seasonal abundance of plankton. Generally, the amount of zooplankton was found to be greater in smaller fishes. The largest proportion of plankton consisted of calanoid copepods, but the amount of cladocerans were exceptionally high in August and September.

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Insects were well represented in the fishes diet, often occurring in large quantities in most months (Fig 3). In *S. spinachia* it was shown that the occurrence of insect larvae was significantly higher at Dail than in Dunstaffnage Bay. Local differences in the abundance of this group may be the reason for their abundance in *G. aculeatus* as most of the fishes were caught at Dail. In October 1971, for example, insect larvae were present in very large quantities in the Dail sample, but they were almost absent in Dunstaffnage sample. Terrestrial and aerial insects also frequently occurred in most months, but on the whole they were not as important as insect larvae, except in July and November.

Harpacticoids were an important food group, present in all months except July (Fig 3). Their significance in fish stomachs, like that of planktonic copepods, seemed to depend primarily on fish size. They were better represented in the months where the proportion of smaller fishes in the sample was large.

Isopods and polychaetes occurred in most months samples in varying quantities; neither of them showed a seasonal pattern. The most common isopod was *Jaera* sp. Oligochaetes were found in fish stomachs in May, June and July with relatively high PO and PP values.

The other food groups such as mysids, Decapoda, Nemertini and molluscs were very poorly represented in fish stomachs. They occurred very occasionally and in small quantities.

Plant matter formed a small proportion of the food and appeared to be taken accidentally in most seasons. No individual stomachs contained a large amount of plant matter, unlike Saunders (1914) and Blegvad's (1917) results.

One juvenile flatfish of 11 mm was found in May in the stomach of a 56 mm specimen.

3. Myoxocephalus scorpius

This fish is not restricted in its habitat and can be found equally on sandy, muddy and rocky bottom substrata. The largest numbers in the present investigation were caught in Dunstaffnage Bay, probably as a result of more intensive sampling carried out at this location.

The food and feeding habits of M. scorpius have not been thoroughly investigated and the only references to its food are found among the early literature. More recent work covers the age, growth and bionomics of this fish (Ennis 1963, Lamp 1966). Wheeler (1968) mentions that M. scorpius feeds on a wide range of food items, intertidal specimens mostly eating amphipods, especially gammarids, decapods (shore crabs), polychaete worms and fishes. Sublittoral populations feed on the same types plus mysids and shrimps.

Blegvad (1917) determined the food composition of 233 Danish M. scorpius varying in length from 80-270 mm, and expressed the importance of the various food types by the weights method. He found that more than half of the weight of total food contents consisted of various small fish such as sticklebacks, gobies, pipe fish, sand eels, herring, small cod, eel, Zoarces and whiting. The second most important group by weight was crustacea. In the Zostera region the main crustaceans were Idotea Gammaridae, prawns and crabs. Outside the Zostera belt the food consisted mostly of shrimps. Polychaete worms formed a small proportion of the diet and molluscs were negligible.

Larsen (1935) also gives a short description of the food of M. scorpius from Danish waters. He lists the numbers of occurrence of various food items found in stomachs of 33 specimens, varying in size netween 120-260 mm. The percentage occurrences of the different food types were calculated from his figures in order to compare the food composition with the results of present investigation. Larsen found that shrimps had the highest frequency in fish stomachs, Leander sp being found to occur more frequently than Crangon vulgaris. Juvenile fish was the second most important food group in terms of occurrence, followed by amphipods and isopods. The frequency of occurrence of insect larvae, molluscs and mysids was very small.

In the present investigation a total of 232 fish stomachs were examined, most of them caught in Dunstaffnage Bay.

The list of food items found in the diet of M. scorpius and relative importance of food groups in the pooled samples are given below (Table 14).

The PO and PP values for the different types of food found in fish stomachs throughout the year are given in Table 15*. Pebbles occurred in most fish stomachs in all the months, especially in large specimens, reflecting the fishes habits of living and feeding among rocky substrata. The occurrence of sand and stones was noted but they were not expressed in terms of percentage occurrence and percentage points as they cannot be considered as food items.

* See Appendix

Table 14. The food composition and relative importance of various food items in the diet of *Myoxocephalus scorpius*.

	PO	PP
CRUSTACEA	41	49
AMPHIPODA	2	1
Amphithoe sp	13	23
Ampelisca sp	<1	<1
Bathyporeia sp	14	10
Corophium sp	8	5
Caprellidae	22	33
Gammaridae	11	3
Microprotopus sp	1	1
Nototropis sp	3	2
Monoculopsis sp	26	23
Indet Amphipods	2	1
ISOPODA		
Jaera sp, *Idotea* sp.	30	33
DECAPODA		
Carcinus maenas, *Maia* sp, *Pilumnus hirtellus*, *Portunus* sp, Hermit crabs, Indet. crabs, *Crangon* sp, Hippolutidae, Indet. shrimps.	5	2
MYSIDACEA		
Hemimysis sp, *Praunus* sp, Indet. Mysids	2	2
COPEPODA		
Harpacticoids	<1	<1
OSTRACODA	2	1
MOLLUSCA		
Gastropoda, Bivalves, *Hydrobia* sp	3	2
ANNELIDA		
Polychaeta, *Arenicola* sp, Nereidae, Indet. polych.	1	<1
INSECTA		
Insect larvae	6	7
PISCES		
Crenilabrus melops, *Myoxocephalus scorpius*, *Pomatoschistus minutus*, *Zoarces viviparus*, *Gasterosteus aculeatus*, *Anguilla anguilla*, Indet. fish, Fish eggs.	7	4
DIGESTED MATTER		

The main food items of M. scorpius are relatively few, namely crabs, shrimps, amphipodes, fish and mysids. The types of food remained relatively constant throughout the year. The proportions of different food items varied, chiefly with the size of fish present in the samples.

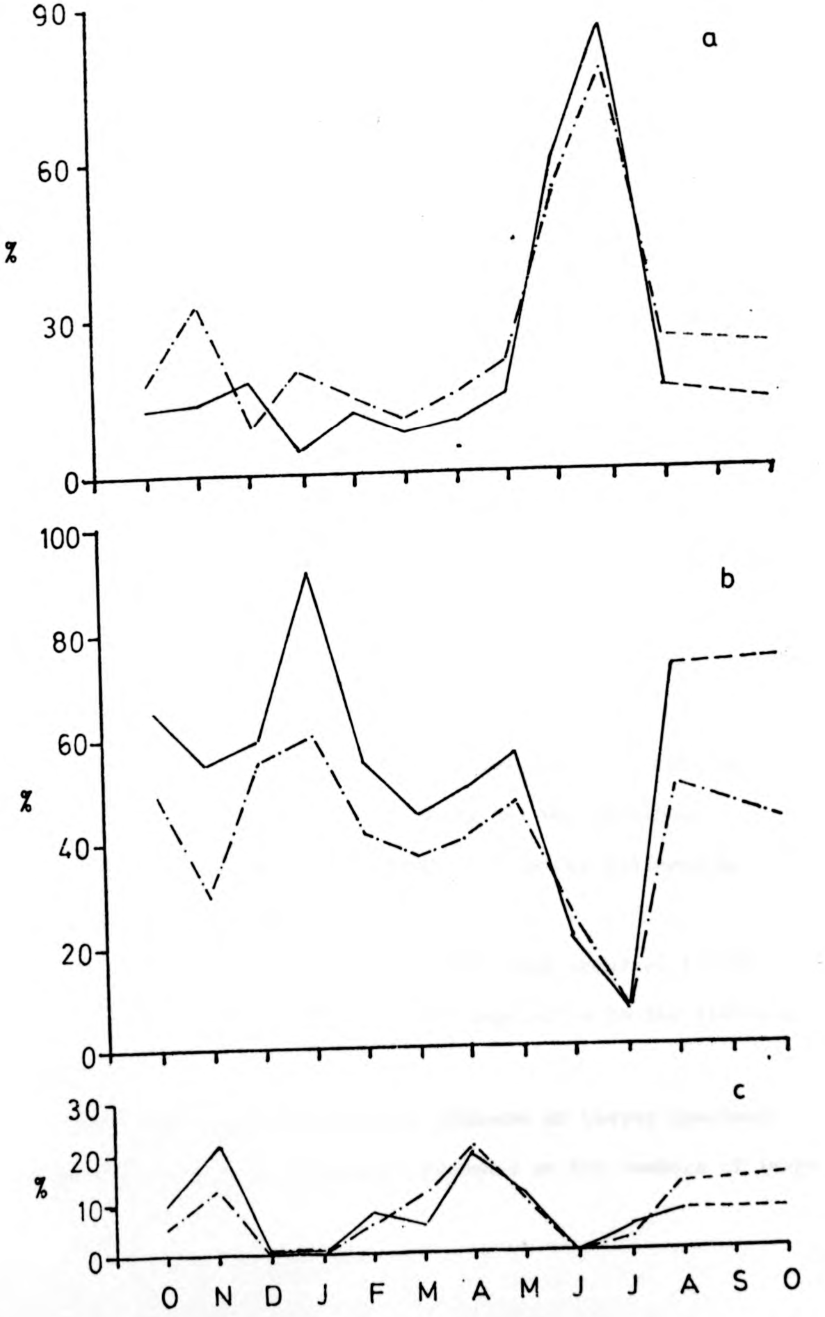
Decapods, namely crabs and shrimps,were present in very large quantities in all months, making up about half or more of total amount of food except in June and July (Fig 4). Shore crabs were a very important constituent of the diet, occurring in all months except July, often making up one third of the total food. When large fishes were present in the samples the PO and PP values for this group were very high. Among the crabs identified, Carcinus maenas occurred most frequently, followed by other species. Hermit crabs were least frequent.

Shrimps, too, were very common in the stomach contents throughout the year, the mean PO and PP values for the whole sampling period were lower than crabs, Crangon sp was the most commonly occurring shrimp.

Amphipods were found in fish stomachs in every month; their percentage occurrence values were generally high though not as high as those for crabs, except in June and July. The overall

Fig. 4. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of *Myoxocephalus scorpius*. Symbols as Fig 3.

a) Amphipods b) Decapods c) Fish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60
30
0
%
a
100
80
60
40
20
0
%
b
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20
10
0
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PO and PP values for this group are higher than Decapods due to the exceptionally large quantities found in June and, especially, July samples. Table 15 shows that in all other months amphipods had much lower PO and PP values than Decapods. Their importance in the diet varied directly with the fish size throughout the year, otherwise they did not show a seasonal trend. For example, their importance increased three and four fold in June and July where the fish in the samples were small. 67% of the June samples consisted of juvenile M. scorpius under 50 mm; in July 87% of the fishes were between 21 and 52 mm; 46% of total sample alone were in 30 mm size group. In 30 mm to 50 mm size group practically all the food consisted of amphipods. The proportion of different types of amphipods varied in different size groups. Among all the amphipods identified gammarids were of primary importance, followed by Ampelisca sp and Corophium sp.

Ostracods and harpacticoid copepods only occurred in the June and July samples. Their overall importance in the diet was negligible.

Fish commonly occurred in the stomachs of larger specimens and their frequency of occurrence depended on the numbers of large fish in the samples. PO and PP values for this group, on the whole, were not as high as those for crabs. No seasonal trend was apparent as the samples in most months showed a large size variation. The PO and PP values indicate that if the fish was large enough it preyed upon other fish regardless of the time of the year and fish species; juvenile members of the same species were also taken. In October 1971 a 20 mm P. minutus was found in the stomach of a 57 mm fish and in July, a cottid of 11 mm was found to have been taken by a fish of 45 mm. Apart from these two occurrences, specimens with fishes in their stomachs were found to be greater than 120 mm in total length.

The occurrence and the amount of mysids in M. scorpius diets did not show any regular seasonal pattern. Percentage occurrence values for mysids were often higher than PP values, sometimes as high as those for shrimps.Mysids were relatively common between October and March.

Polychaetes became a relatively important food group only in February and March. They also occurred in November, April, May and October 1972 samples in small quantities. Members of the families Nereidae and Arenicolaidae were mostly taken.

Molluscs occurred infrequently in fish stomachs in small quantities between October and February and also in May and July. PO values for this group were always higher than PP values. Isopods, insect larvae and fish eggs were similarly found in a few fish stomachs throughout the year and never became a substantial part of this fishes diet. Insect larvae occurred only in the spring and summer months. Larsen's (1935) and Blegvad's(1917) results were converted to percentage occurrence and percentage weight values and compared with the PO and PP values found in the present investigation. Spearman's Rank correlation was used for the comparisons (Fritz 1974). A closer correlation was found between Blegvad's percentage weight values and PP values of the diet of fishes of Loch Etive ($r_s = 0.72$, $n = 13$, $p < 0.01$) than between Larsen's PO values and those of the present study ($r_s = 0.51$, $n = 12$, $p < 0.05$).

Larsen's (1935) results differed mainly in the absence of crabs, smaller bodied food groups such as harpacticoids, fish eggs and the much higher significance of isopods.

The main differences between Blegvad's (1917) results and the results of present study were the much higher importance of fishes as a food group in Nyborg Fjord. Isopods were also a more significant group, whereas in the Loch Etive samples amphipods occurred in greater quantities and smaller bodied food groups were also present.

4. Taurulus bubalis

This fish is closely related to M. scorpius. It is confined mainly to rocky bottoms with a reasonable amount of seaweed cover. The food of T. bubalis is relatively well known compared to the other species previously examined. Early workers (Yarnell, 1859; Couch, 1863; Gosse, 1865; Murie, 1903) all mention that T. bubalis feeds mainly on small crustacea and fish. Blegvad (1917) and Hartley (1940) gave some details of the diet based on the stomach contents of two and three fish respectively.

Rice (1962) gives the first detailed account of the food of T. bubalis in Manx waters. He examined a large number of specimens collected intertidally and sublittorally. The relative importance of various food items in the diet was assessed by the points method. He found that the main food groups were Decapoda, Amphipoda, Teleostei and Isopoda in that order. He came to the conclusion that decapods, isopods and tanaids were more important food items in the intertidal than in the sublittoral fish, whereas mysids and teleosts were of greater importance in sublittoral specimens. Also, larger fish fed more on decapods and teleosts and smaller fish took more tanaids, copepods, insect larvae and isopods.

Western (1969) gives a brief account of the diet of T. bubalis and compares it with Cottus gobio, concentrating mainly on the morphology of alimentary canal. He mentions that fish of 4-8 cm in length feed mainly on amphipods and other small crustaceans. Gibson (1972) found that T. bubalis on the Atlantic coast of France fed primarily on amphipods and secondarily on brachyuran decapods. Isopods, copepods, molluscs and polychaete also had relatively high frequency of occurrence values in the diet.

A total of 116 specimens from Loch Etive were examined. The food composition list and the percentage occurrence and percentage point values for the food groups are given below. (Table 16).

It will be seen from the overall PO and PP values and their monthly variation (Table 17* & Fig 5) that amphipods were the most important food item in the diet of T. bubalis in Loch Etive. The presence of amphipods in the fishes diet

*See Appendix

Fig. 5. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of Taurulus bubalis. Symbols as Fig. 3.

a) Polychaetes b) Amphipods c) Crabs

d) Isopods e) Molluscs f) Fish.

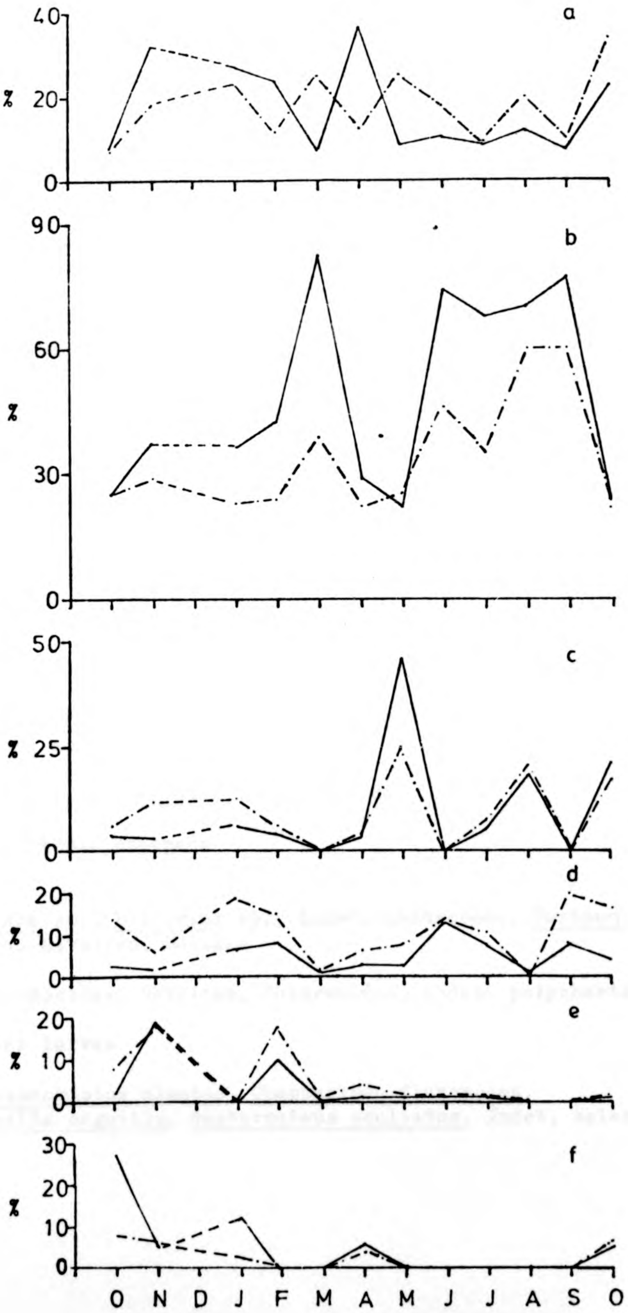
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Table 16. The food composition and the relative importance of various food items in the diet of T. bubalis.

	PO	PP
CRUSTACEA		
AMPHIPODA	29	42
Ampelisca sp	2	1
Aora sp	0.8	1
Amphithoe sp	3	2
Bathyporeia sp	0.8	0.2
Bathymedon sp	0.8	0.5
Corophium sp	27	24
Caprella sp) Phistica sp)	4	3
Gammaridae	32	45
Hyale sp	0.8	0.4
Nototropis sp	3	2
Microprotopus sp	4	2
Urothoe sp	4	2
Indet. Amphipoda	18	17
ISOPODA	13	5
Jaera sp. Idotea sp., Sphaeroma sp., Indet. Isopods		
DECAPODA	11	15
Carcinus maenas, Pilumnus hirtellus, Hermit crabs, Crangon sp., Indet. natantia		
MYSIDACEA	2	2
Praunus sp., Neomysis., Indet mysids		
COPEPODA	0.4	0.1
Harpacticoid copepods		
CUMACEA	0.4	0.1
MOLLUSCA	6	3
Spisula sp., Littorina sp., Indet. gastropods, Cardium sp., Indet. bivalves, Doridae		
ANNELIDA	17	19
Phyllodocidae, Nereidae, Chloramidae, Indet. polychaetes.		
INSECTA	4	1
Insect larvae		
TELEOSTEI	3	6
Pomatoschistus minutus, Chapparrudo flavescens, Anguilla anguilla, Gasterosteus aculeatus, Indet. teleosts.		

Table 16 cont.

	PO	PP
ALGAE	2	1
INDET. MATERIAL	13	5

was consistent through the year and their PO, PP values were above 22% in all months sampled. Percentage point values, which measured the amount of food in fish stomachs, were often higher than percentage occurrence values. In the summer months, especially, amphipods formed up to 79% of the diet. The most important amphipods were gammarids, followed by Corophium sp. The other types listed were much less frequent. The greater importance of amphipods in the summer months may be a result of the greater proportion of juveniles in the samples. Rice (1962) states that in the smaller intertidal Manx fish, amphipods become the most important food in April–June. In the period from July to September, unlike Loch Etive fishes, isopods became the main constituent of the smaller fishes diet.

Insect larvae were absent in the winter months but appeared sporadically in the stomachs of smaller fish between March-October. They always had higher frequency of occurrence values than percentage point values and were never of great significance in the diet.

Polychaetes were the second most important food group in the diet of T. bubalis in Loch Etive. They were present in all samples. The monthly variations in the PP values show that the volume of polychaetes in the fishes diets was higher in the winter months than in the summer months, (Fig 5). Their occurrence did not demonstrate a seasonal pattern. Members of the families Phyllodocidae and Nereidae were most common.

The occurrence of isopods was continuous throughout the year except in March and August. Their percentage occurrence values were sometimes as high as those for polychaetes but because of their relatively small volume they had much lower PP values. The greatest proportion of isopods consisted of Jaera sp, the larger isopods, Idotea sp and Sphaeroma sp were less frequent. Rice (1962) found that isopods were mainly eaten in the first and third quarters of the year by the larger fish and in the third quarter by the smaller fish. Fig 5 shows that PP values for isopods were highest between May and July and the peak in June may reflect the higher degree of isopod feeding by juvenile fishes in this month.

The main food of M. scorpius, decapods, were much less well represented in the diet of T. bubalis. Crabs were more important than shrimps (PO, PP values 8%, 10% and 3%, 5% respectively). This difference may indicate that the greatest proportion of the fish caught were intertidal and not sublittoral Wheeler (1968). If this was true, it might also explain the low number of teleosts found in fish stomachs since Rice (1962) demonstrated that teleosts are of greater importance in the diets of sublittoral specimens than of intertidal fish. The overall PO, PP values for teleosts were under 10%. They appeared irregularly in the samples between October and April and were absent in the summer. Like crabs and shrimps they were found in the stomachs of larger specimens.

Molluscs were more important in the diets of the fish in the winter than in summer months. In November and February they were the third most important food group in terms of PO, PP values. Their occurrences in fish stomachs were negligible during the summer months.

The results of the present study differ from those of Rice (1962) in several respects. In the diet of Manx fishes decapods and amphipods were of primary importance, followed by teleosts and isopods, the percentage point values for polychaetesbeing much lower. In Loch Etive, amphipods were of much greater significance than all remaining groups, the occurrence and amounts of polychaeta were also much higher, forming the second most important food group, decapods being third. Isopods and teleosts were more poorly represented in the diet of Loch Etive fish.

On the basis of these results it was concluded that although M. scorpius and T. bubalis have seemingly overlapping diets (see species composition list) they differed considerably in the proportion of their principal food. M. scorpius took more shore crabs and shrimps whereas T. bubalis fed more heavily on amphipods and polychaetes throughout the year.

5. Pholis gunnellus

P. gunnellus has a wide geographical distribution, being found on both sides of Atlantic. The first information on the food of this species in the western Atlantic was given by Stroud (1937). This species diet was later examined by Sawyer (1967). In the eastern Atlantic Qasim (1957) gave the first account of the food of P. gunnellus from North Wales.

Stroud (1939) found that the main food groups in the diet of rock gunnels were Polychaeta, Amphipoda and Isopoda. Qasim's (1957) results showed that in addition to these groups, barnacles and decapods were an important part of the diet of this species on the east side of Atlantic. Sawyer (1967) listed the main food groups as Amphipoda, Isopoda, Decapoda, insect larvae and Molluscs. On comparing his results with Stroud's and Qasim's he came to the conclusion that this species apparently feeds on similar organisms on both sides of Atlantic.

281 specimens were examined in Loch Etive. The food composition list and the percentage occurrence and percentage points values for each food group are given below. (Table 18).

It is evident both from Table 19*and Fig 6 that the most important food item in the diet of this species caught in Loch Etive was amphipods. The percentage occurrence and percentage points values for this group were above 20% in all months.

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* See Appendix

Table 18. The food composition and the relative importance of various food items in the diet of *Pholis gunnellus*.

	PO	PP
CRUSTACEA		
AMPHIPODA	38	57
Ampelisca sp	0.5	0.5
Amphithoe sp	6	7
Aora sp	0.5	1
Caprellidae	6	9
Corophium sp	4	3
Gammaridae	26	43
Hyale sp	2	4
Microprotopus sp	13	6
Nototropis sp	5	3
Dexamine sp	3	2
Melita sp	0.5	0.5
Cressa ap	3	2
Probolium sp	1	0.3
Indet. amphipoda	29	19
ISOPODA	14	9
Jaera sp., *Idothea* sp.		
DECAPODA	4	4
Decapod larvae, Indet. Natantia, *Dilumnus hirtellus*, Hermit crab, Indet. crabs		
MYSIDACEA	1	3
Praunus sp., Indet. mysids.		
CIRRIPEDIA	<1	<1
COPEPODA	10	6
Calanoid copepods, Harpacticoid copepods		
CUMACEA	<1	<1
OSTRACODA	7	3
MOLLUSCA	4	2
Bivalves, Gastropoda		
ANNELIDA	5	6
Polychaeta, *Pomatoceros* sp., indet. polychaetes		
INSECTA	8	7
Insect larvae, adult insets		
PISCES	<1	<1
Fish larvae		
ALGAE	2	1
INDET. MATERIAL	3	1

PP values were higher than PO values throughout the year. Both indices showed that amphipods were the most frequently occurring animals in fish stomachs as well as constituting the bulk of the diet. No seasonal variation in their occurrence was found.

Among the amphipods which could be identified, gammarids occurred most frequently and were present in most months samples.

Microprotopus sp has also a high frequency of occurrence. Other species found frequently were Amphithoe sp, Corophium sp, Nototropis sp, and members of the family Caprellidae.

Isopods were the second major group. They were present in all months except March which was also the smallest sample, the number of fish stomachs containing food being only three. They were not always the second most important group in terms of numbers and amounts. They appeared more important if their frequency of occurrence only was considered, but they usually formed a smaller fraction of the total amount of food in a months sample. This is clearly seen when PO and PP values are compared. Most of the specimens were caught in Dunstaffnage Bay, therefore most monthly values demonstrate the dietary composition at this location. It was shown in the food analyses of S. spinachia that there was a clear difference in the occurrence of isopods between Dunstaffnage and Airds Bay and the overall low values for the frequency of occurrence of isopods in P. gunnellus may reflect this local variation and may not be a true estimation of the selection shown by the fish. Qasims (1957) values for the occurrence of isopods in fish stomachs were much higher than those found in the present study.

Polychaeta were present in most months except in March, August and September. In October, November and February they formed a large portion of the total amount of food found in the stomachs and became the second most important food group. Their actual amount is likely to be greater than those indicated by PP values because polychaete remains were often found in form of bristles and fragments of the body. Fig 6 suggests that they may be more significant in the diet in colder months than in the summer.

The greatest proportion of Copepoda consisted of harpacticoids. Harpacticoids were found to be an important part of the diet of P. gunnellus in Loch Etive. Their occurrence in fish stomachs showed a clear seasonal pattern. Fig 6 shows that they gained importance as a food group between April and August and were not significant in other months. They were the second most important food group in terms of occurrences and quantities in April and July. Calanoid copepods were poorly represented. They were present in most months samples in small numbers but never became an important constituent of the diet.

Ostracods occurred fairly regularly in most months with

Fig. 6. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of Pholis gunnellus. Symbols as Fig. 3.

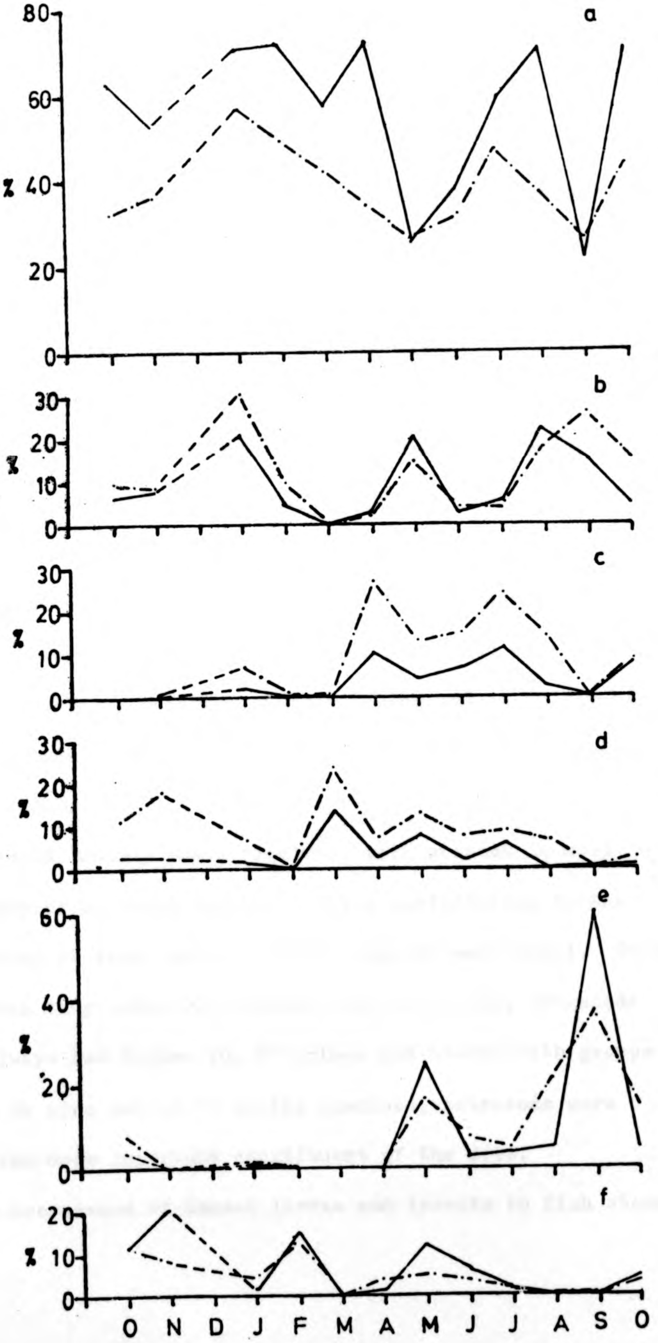
a) Amphipods b) Isopods c) Harpacticoid copepods

d) Ostracods e) Insects f) Polychaetes.

Fig. 6. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of *Pholis gunnellus*. Symbols as Fig. 3.

a) Amphipods b) Isopods c) Harpacticoid copepods

d) Ostracods e) Insects f) Polychaetes.

a
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relatively high frequency of occurrence values and sometimes in considerable numbers. The monthly variation in PO and PP values suggest the presence of some seasonal trend. Like harpacticoids, they appear to be more important in spring and summer than at other times. Percentage occurrence values for ostracods, like harpacticoids, were always higher than percentage point values. This difference between PO and PP values demonstrates the overestimation of the importance of a small sized food group by the occurrence method and underestimation by the points method as mentioned earlier. As ostracods regularly occurred in most months and in fairly high numbers however, their significance in the diet of P. gunnellus is quite clear.

Molluscs, mainly small bivalves, were present in most months samples in small numbers. Their contribution to the total amount of food in each month's samples were small. In the months when they occurred together with ostracods, ostracods almost always had higher PO, PP values and though both groups appeared in nine out of 12 months examined, ostracods were clearly the more important constituent of the diet.

The occurrence of insect larvae and insects in fish stomachs showed the most marked seasonal trend among all the food groups. They were present, but not in significant amounts in October 1971, then diminished throughout the winter, reappearing in May, occurring frequently and in large quantities. They were particularly important in September when the whole sample consisted of fishes caught at Dail and Airds Bay. In S. spinachia it was shown that more insect larvae were present in these two localities than at Dunstaffnage Bay. As in the case of isopods, the importance of insect larvae in the diet of P. gunnellus could be underestimated because of the fact that most specimens were caught in Dunstaffnage Bay.

Shrimps and crabs occurred occasionally and in low numbers. Decapoda other than crabs were often present in fish stomachs in the form of portions of the head and eye stalks. As they were not found as whole animals the estimated PP values are likely to be lower than the actual amounts consumed. But as their occurrence was also low and they did not appear regularly in the samples, it can be concluded that they were not an essential part of the diet.

The occurrence of mysids in the monthly samples was irregular, they were often broken or in a digested state. Other food groups which occurred occasionally and in low numbers were barnacles and cumaceans.

When the food composition of P. gunnellus from Loch Etive is compared with that of specimens from North Wales, Qasim (1957), the food categories on the whole are found to be similar in both places; there are however differences in the relative importance of various groups in the diet. Amphipods were the most important food group for Loch Etive and polychaetes, isopods and decapods were less well represented in the diet when compared to the fish from North Wales. Harpacticoids and ostracods were also of higher significance whereas barnacles, which were an important part of the diet of this fish in North Wales, were not significant.

6. Pomatoschistus minutus

This is the common sand goby found on sandy and muddy substrates. Although it is a marine species it also enters estuaries. In Loch Etive, the highest catches were made in Dunstaffnage Bay. The stomach contents of 391 specimens were examined.

The earliest account of the food of P. minutus is given by

Blegvad (1917). He found that in Danish waters the diet of this species consisted of pelagic and benthic copepods, amphipods, mysids, shrimps and molluscs. Miller (1963) also examined the food of P. minutus. He found its diet mainly consisted of Crustacea, Polychaeta and also Mollusca. Macer (1967) found that P. minutus from the Red Wharf Bay (North Wales) also fed mainly on amphipods and secondarily on polychaetes and copepoda. Hesthagen (1971) found that the main food groups in the diet of P. minutus from the Belt sea were Polychaeta, Copepoda, Mysidacea and Amphipoda. Healey (1971) who studied the distribution and abundance of P. minutus in the Ythan estuary found that amphipods had the highest frequency of occurrence in the diet, followed by mysids, isopods and shrimps.

The food composition list and PO, PP values for each food group in specimens from Loch Etive are given below (Table 20).

The major constituent of the diet of P. minutus in Loch Etive was amphipods. Fig 7 and Table 21* show that they occurred in very high quantities all the year round, sometimes forming 90% of the diet.

The most commonly occurring amphipods in the diet, according to the order of importance were 1). Ampelisca sp,

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* See Appendix

Fig. 7. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of Pomatoschistus minutus. Symbols as Fig. 3.

a) Amphipods b) Polychaetes c) Decapods

d) Mysids e) Insects.

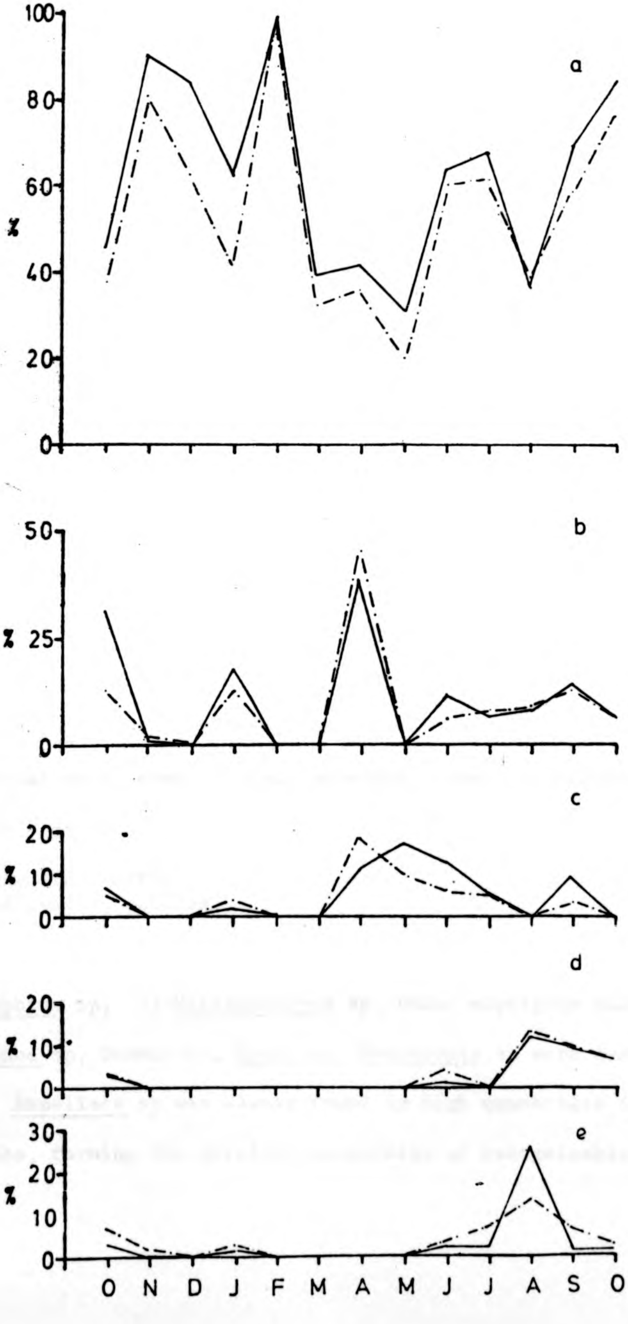
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Table 20. The food composition and the relative importance of various food items in the diet of *P. minutus*.

	PO	PP
CRUSTACEA		
AMPHIPODA	52	65
Ampelisca sp	23	38
Amphithoe sp	4	3
Caprellidae	4	1
Corophium sp	12	18
Gammaridae	4	4
Hyale sp	2	3
Other Talitridae	<1	0.4
Nototropis sp	3	1
Microprotopus sp	14	6
Bathymedon sp	3	0.5
Indet. Amphipoda	29	26
ISOPODA	4	2
Jaera sp., *Idotea* sp., indet. isopods.		
DECAPODA	4	5
Crangon sp., indet. Natantia, *Pilumnus hirtellus*		
MYSIDACEA	3	4
Neomysis sp., *Leptomysis* sp., Indet. mysids		
CIRRIPEDIA	1	1
COPEPODA	5	1
Harpacticoid copepods, *Temora* sp., *Pseudocalanus* sp., *Acartia* sp., Indet. calanoid copepods		
CUMACEA	3	1
OSTRACODA	1	1
MOLLUSCA	1	1
Littorina sp., Indet. bivalves		
ANNELIDA	9	13
Terebellidae, Arenicola sp, Nereidae, Indet. polychaetes		
PISCES	<1	<1
Fish eggs		
ALGAE		
INDET. DIGESTED MATTER	11	5
Sand grains, pebbles		

2) *Corophium* sp, 3) *Microprotopus* sp. Other amphipods such as *Ampithoe* sp, Gammarids, *Hyale* sp, *Nototropis* sp were less common. *Ampelisca* sp was always found in high quantities in all the months, forming the greatest proportion of recognisable

amphipods, except in July, August, September when Corophium sp gained primary importance. Microprotopus sp also occurred fairly regularly but in much smaller quantities, becoming especially important only in July. Healey (1971) found that in P. minutus from the Ythan estuary, Corophium sp was by far the most important amphipod all the year round and does not mention Ampelisca sp. Loch Etive fishes appear to differ from those of Ythan estuary in this respect.

Polychaeta were the second important food group in the diet of P. minutus. They were taken frequently, but in relatively small amounts. PO and PP values exceeding the 10% level only in October 1971, January, April, September 1972. (Fig. 7). Their monthly occurrences, like those of amphipods did not show a seasonal pattern.

The greatest part of the decapods in P. minutus stomachs consisted of Natantia; crabs formed a very small fraction of the total food. Common shrimp, (Crangon sp) were the most frequently occurring form. Fig 7 suggests that the importance of decapods in P. minutus was highest between April and July.

The occurrence of mysids was not consistent throughout the year. (Fig. 7). They were absent in the winter and early spring, having high percentage frequency and percentage point values between August and September. The occurrence of insect larvae in fish diets followed a similar pattern. They were insignificant during late autumn, winter and early spring, were found in fairly high numbers between July and September and then decreased once again in October.

Other less important food groups which occurred from time to time without any apparent seasonal pattern included isopods, molluscs, ostracods, cumaceans and harpacticoids. Harpacticoids, cumaceans and ostracods occurred very infrequently and in negligible quantities.

Planktonic food, mainly in the form of calanoid copepods were taken in three months, October, December and May. In all these instances only planktonic food was found in some stomachs. Although this plankton feeding did not persist, it was important in demonstrating the versatility of feeding in this species.

7. Pomatoschistus microps

P. microps is found in intertidal areas on sandy or muddy shores. It prefers low salinities and is common in estuaries. In Loch Etive most specimens were caught at Dail where the salinity is lowest of three stations sampled. The stomach contents of 95 specimens were examined.

The biology of P. microps was studied by Miller (1963) and later its diet was examined by Muus (1967). Muus found that young fish fed exclusively on young copepods and other juvenile stages of crustacea in the meiofauna. As the fish became larger, adult harpacticoids and polychaetes increase in importance.

Because the monthly samples for this fish were often small, the results have been pooled and only a brief analysis of seasonal variation attempted.

Amphipods were the primary food group all the year round, Corophium sp being the most commonly occurring species (Table 22). Polychaetes were of secondary importance. Among other food groups harpacticoids occurred quite frequently but other copepods were poorly represented. Table 23* shows the relative importance of various food groups in the four quarters of the year.

8. Chaparrudo flavescens

This goby differs from all the other inshore species in

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* See Appendix

Table 22. The food composition and the relative importance of various food items in the diet of *P. microps*.

	PO	PP
CRUSTACEA		
AMPHIPODA	34	49
Ampelisca sp	3	5
Bathymedon sp	5	2
Corophium sp	37	49
Cressa sp	2	1
Caprellidae	2	1
Gammaridae	9	7
Microprotopus sp	7	6
Indet. amphipoda	35	27
ISOPODA	4	2
Jaera sp		
DECAPODA	1	1
Decapod larvae		
MYSIDACEA	3	5
CIRRIPEDIA	3	1
COPEPODA	12	6
Calanoid copepods, Harpacticoid copepods, Cyclopoid copepods.		
CLADOCERA	2	2
OSTRACODA	1	1
CUMACEA	1	2
INSECTA	9	5
Adult insects, Insect larvae		
ANNELIDA	16	21
Polychaeta, Oligochaeta	1	1
MOLLUSCA	1	<1
Gastropoda		
PISCES	1	<1
Fish eggs		
NEMERTINI	<1	<1
ALGAE	2	2
INDET. DIGESTED MATTER	6	3

being much less dependent on the sea bed. They are found in small shoals near the surface and around seaweeds. The literature on the food of *C. flavescens* is limited. Wheeler (1968) gives the food of this species as copepods, mysids, gammarids and isopods. Hesthagen (1971) examined the stomach contents of only 3 specimens. He found Copepoda, Amphipoda and bivalves were the predominant food items. In Loch Etive a total of 389 specimens were examined. They were mostly caught in Dunstaffnage Bay and Airds Bay.

C. flavescens from Loch Etive was predominantly a plankton feeder. (Table 24) With the exceptions of December, February and July, plankton occurred in most stomachs and provided the bulk of the food in each months sample. The February samples was exceptionally small (n = 7) and only two stomachs contained food which consisted of mysids. In December and July the fish were found to be feeding solely on benthic food.

The majority of the planktonic food in the fish stomachs consisted of calanoid copepods. Fig 8 shows that their occurrences and amounts were high in all months except the three months mentioned above and April. In April the primary importance of calanoid copepods in fish stomachs was replaced

Fig. 8. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of Chaparrudo flavescens. Symbols as Fig. 3.

a) Calanoid copepods b) Amphipods c) Cirripedes

d) Insects.

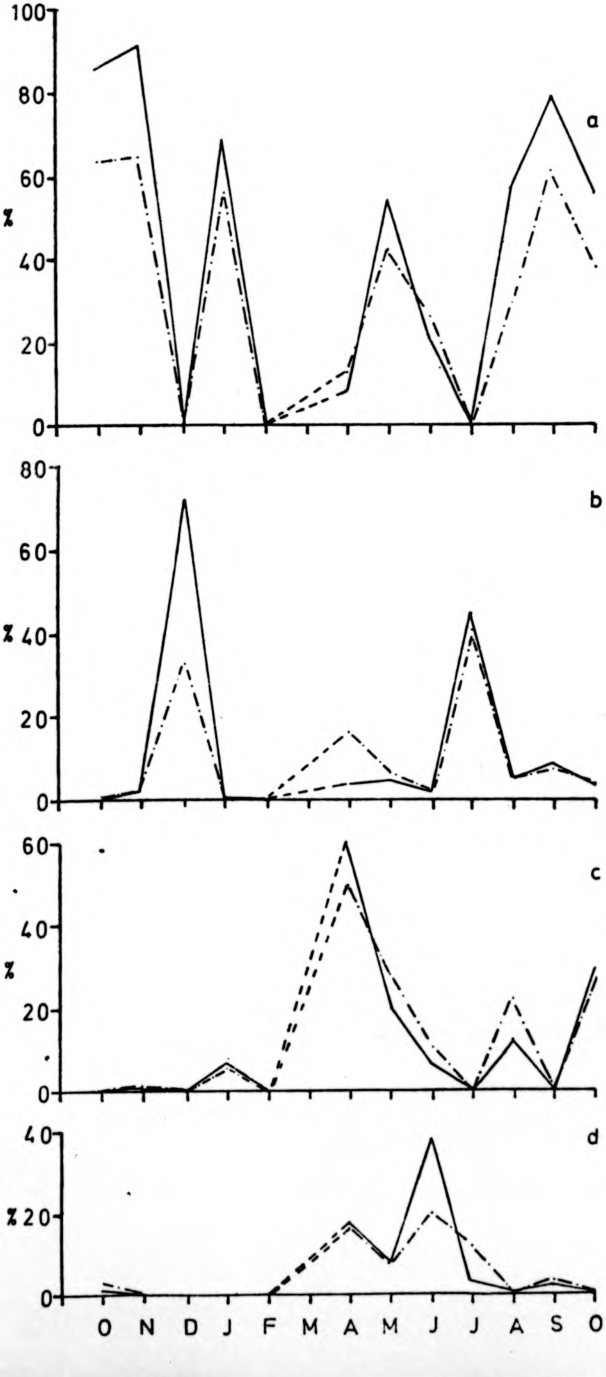

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Table 24. The food composition and the relative importance of various food items in the diet of *Chaparrudo flavescens*.

	PO	PP
CRUSTACEA		
AMPHIPODA	5	4
Corophium sp., Caprellidae, Gammaridae, *Microprotopus* sp., *Nototropis* sp., *Hyale* sp., *Stenopleustes* sp., Indet. *Amphipoda*.		
ISOPODA	2	2
Jaera sp., *Eurydice* sp.		
DECAPODA	2	2
Decapod larvae		
CIRRIPEDIA	10	8
Cirripede nauplii, Cirripede cypris		
COPEPODA	43	66
Calanoid copepods, *Paracalanus* sp., *Eurytemora* sp., *Temora* sp., *Calanus* sp., *Pseudocalanus* sp.,*Centropages* sp., *Acartia* sp., *Candacia* sp., Cyclopoid copepods, *Oithona* sp., Harpacticoid copepods, *Microsetella* sp.		
OSTRACODA	1	1
CLADOCERA	7	4
MOLLUSCA	8	3
Gastropods, *Hydrobia* sp., indet. prosobranchs, *Acmea* sp., Bivalves		
ANNELIDA	3	2
Polychaeta, polychaete larvae		
INSECTA	7	8
Adult insects, Insect larvae		
PISCES	1	1
Fish eggs, Fish larvae,		
INDET. DIGESTED MATTER	1	1

by cirripede nauplii.

Among the calanoid copepods eaten, Temora sp, Pseudocalanus sp, Paracalanus sp and Acartia sp had especially high frequency of occurrences, Centropages sp and Calanus sp being less common. Among the cyclopoids Oithona sp was frequent. Harpacticoid copepods were present in most months in small quantities. The percentage occurrence and percentage points were 4% and 2% respectively.

Among the plankton food in C. flavescens diets, cirripede and cladocerans were also common, they occurred in much smaller quantities than calanoid copepods. Their occurrence and abundance in fish stomachs showed a more seasonal pattern than that of calanoid and cyclopoid copepods. Cladocerans were most abundant between June and August. The highest occurrences of cirripede nauplii were recorded in April, May and August. Cirripedes were present in considerable numbers in the October 1972 sample in the form of cyprids.

Polychaete larvae, decapod larvae and ostracods were also found among the zooplankton in the fishes stomachs, but their occurrences and numbers never reached significant levels. Molluscs were also poorly represented. They mostly consisted of small planktonic gastropods.

Amphipods were found in fish stomachs in small quantities in most months (Table 25*) often mixed with zooplankton organisms except in December and July when they became the most important food group. In these two months commoner benthic amphipods such as gammarids, *Corophium* sp, *Nototropis* sp were found in relatively high quantities. The amphipods found together with the zooplankton in fish stomachs could not be identified. They did not however belong to the fully planktonic family Hyperiidae which were easily recognised by their head being distinctly marked off from the mesosome and by their large eyes. It is thought that these amphipods were benthic forms. The low occurrences of amphipods in the months when the food was predominantly planktonic may suggest that they may be accidentally taken and not specifically chosen. Isopods were rare in *C. flavescens* stomachs, planktonic forms being common. A benthic form, *Jaera* sp was found in very large quantities in July, together with benthic amphipods. Other non-planktonic food were insects and insect larvae present between April and July with a peak in June. Large quantities of insects were found in the stomachs at this time.

* See Appendix

From the food analysis it was concluded that C. flavescens feeds primarily on plankton. It is however not an obligate plankton feeder as the December and July samples demonstrate. In these months the fish changed to benthic food.

9. Atherina presbyter

Atherina presbyter is a shoaling fish; the occurrence of this species in the catches in Loch Etive was discontinuous. Relatively large numbers were caught between October-December also in February. None was caught until April but they occurred in large numbers between May and July, disappearing from the catches once again in late summer and autumn. Only one fish was caught in October 1972.

Wheeler (1968) mentions that this species feeds on small crustaceans in general. No previous information was found about its food in the literature.

A total of 334 fishes were examined between October 1971 and July 1972. The results of the stomach analyses are given in Table 26.

The monthly food analysis showed that this species largely feeds on zooplankton, but like Chaparrudo flavescens, it is not entirely a plankton feeder. Planktonic organisms were the primary

Table 26. The food composition and the relative importance of various food groups in the diet of *Atherina presbyter*.

	PO	PP
CRUSTACEA		
AMPHIPODA	8	10
Ampithoe sp., *Corophium* sp., Gammaridae, Hyperiidae, *Hyale* sp., Centromedon sp., Urothoe sp., indet.Amphipoda		
ISOPODA	3	2
Idotea sp., *Eurydice* sp., indet.isopods.		
DECAPODA	13	6
Decapoda larvae, indet.Natantia		
MYSIDACEA	<1	<1
EUCARIDA	<1	<1
Nyctiphanes sp	1	1
CIRRIPEDIA		
Cirripede nauplii, cirripede cypris, barnacle cirri		
COPEPODA	34	42
Calanoid copepods, *Acartia* sp., *Calanus* sp (juvenile & adult), *Centropages* sp., *Pseudocalanus* sp., *Paracalanus* sp., *Temora* sp., unid. calanoids		
Cyclopoid copepods, *Oithona* sp.		
Harpacticoid copepods, *Microsetella* sp., *Sapphirina* sp., *Euterpina* sp.		
OSTRACODA	1	1
CLADOCERA	10	17
Podon sp., *Evadne* sp., indet. cladocerans.		
CUMACEA	<1	<1
MOLLUSCA	5	3
Prosobranchs (eggs, larvae), *Littorina* sp., indet. gastropods, indet. bivalves.		

Table 26 cont.

	PO	PP
ANNELIDA Polychaeta, polychaete larvae, indet. polychaete	12	9
INSECTA Insect larvae, adult insects	2	2
PISCES Fish larvae	1	2

food item in fish stomachs in all months samples with the exception of December and July when the fish became a predominantly benthic feeder. Only 1 specimen was caught in October 1972, its stomach contained decapod larvae, calanoid copepods and broken natantia parts indicating planktonic feeding.

Among the planktonic food taken, calanoid copepods had the highest PO and PP values. They were present in considerable quantities in all months examined, except in July; Pseudocalanus sp, Paracalanus sp and Temora sp were common. Adult Calanus sp seemed to occur more frequently in larger specimens suggesting the possibility of prey size selection in this species. Harpacticoid copepods were much less common than calanoid copepods. Both planktonic and benthic species were found. Other important components of the planktonic food were cladocerans, cirripedes, polychaete larvae and decapod larvae. Cladocerans occurred in significant quantities in October and also between the months April-June. Cirripede nauplii were especially important in April and May. In December, barnacle cirri were also found in fish stomachs. The greatest percentage of polychaetes were present as planktonic larval forms but In February some adult polychaetes were found. Most of the decapods were also larvae. Parts of natantia were recorded in a few instances.

Amphipods were not well represented in Atherina presbyter except in December and especially in July (Fig 9, Table 27*). 70% of the total amount of food consisted of amphipods in July most of which were benthic forms, Corophium sp being especially important. Similarly in December benthic amphipods has a high frequency of occurrence. A large proportion of amphipods found in fish stomachs could not be identified in most months, therefore it is not possible to estimate the relative amounts of benthic and planktonic amphipods in the diet

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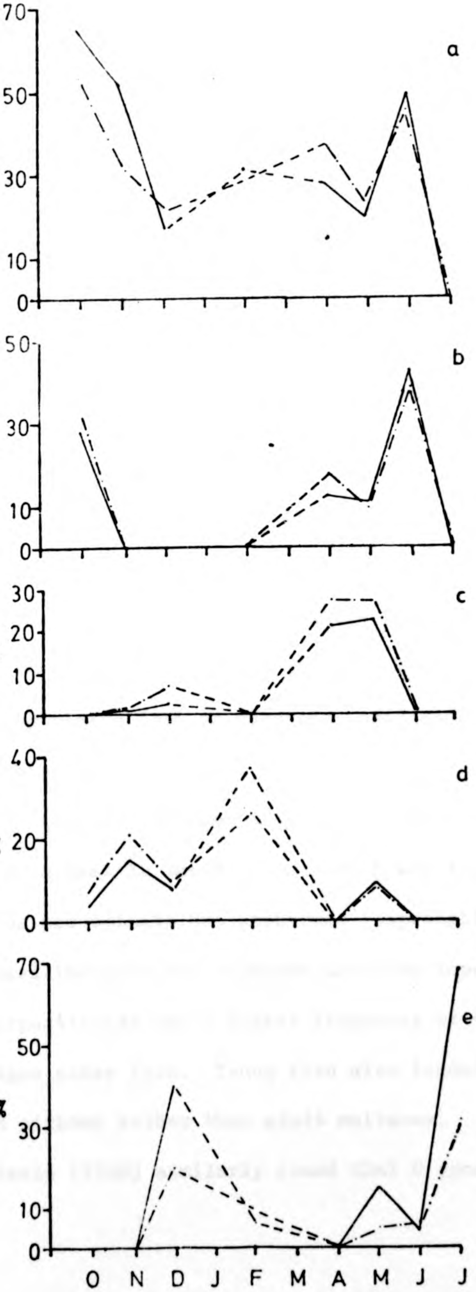
* See Appendix

Fig. 9. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of *Atherina presbyter*. Symbols as Fig. 3.

a) Calanoid copepods b) Cladocerans c) Cirripedes

d) Polychaetes e) Amphipods.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with any certainty.

The results of the food analysis suggest that Atherina presbyter is basically a zooplankton feeder but is also capable of benthic feeding. Among the benthic food, amphipods, polychaetes, isopods and mysids are taken.

10. Pleuronectes platessa.

The diet of plaice has been widely studied and only a few of the previous references will be mentioned here. Blegvad (1917) found that adult plaice in Danish waters feed mainly on small bivalves, gastropods, polychaetes and to a lesser extent on crustacea. Young plaice feed on copepods, ostracods, polychaete and amphipods.

Macer (1967) examined the food of young plaice from North Wales, he found that in the diet of born 0 and I group plaice, polychaetes predominate but amphipods (especially Ampelisca sp), lamellibranchs and copepods are also important. Cyclopoids and harpacticoids had a higher frequency of occurrence in younger fish than older fish. Young fish also tended to eat lamellibranch siphons rather than adult molluscs.

Edwards & Steele (1968) similarly found that 0 group plaice from Loch Ewe fed on bivalve siphons, amphipods, polychaete, harpacticoids and cumaceans. They noted that the diet of younger fish largely consists of bivalve siphons and polychaete tentacles; as the fish grow older they change to diets of whole polychaetes, amphipods and cumaceans.

De Groot (1973) showed that in the southern North Sea, polychaetes and molluscs were the most important components of the plaice's diet. Younger fish mainly fed on polychaete worms and _Macoma baltica_ siphons; as they grow older, crustaceans become an important part of the diet in addition to molluscs.

Thijssen, Lever & Lever (1974) also examined the food composition of 0 group plaice from a sandy beach. They found polychaetes were the most important food item, followed by crustaceans.

In Loch Etive a total of 148 specimens were caught and examined throughout the year. Table 29* shows the monthly sample sizes and food composition. The sample size range for the whole year was 29-175 mm.

* See Appendix

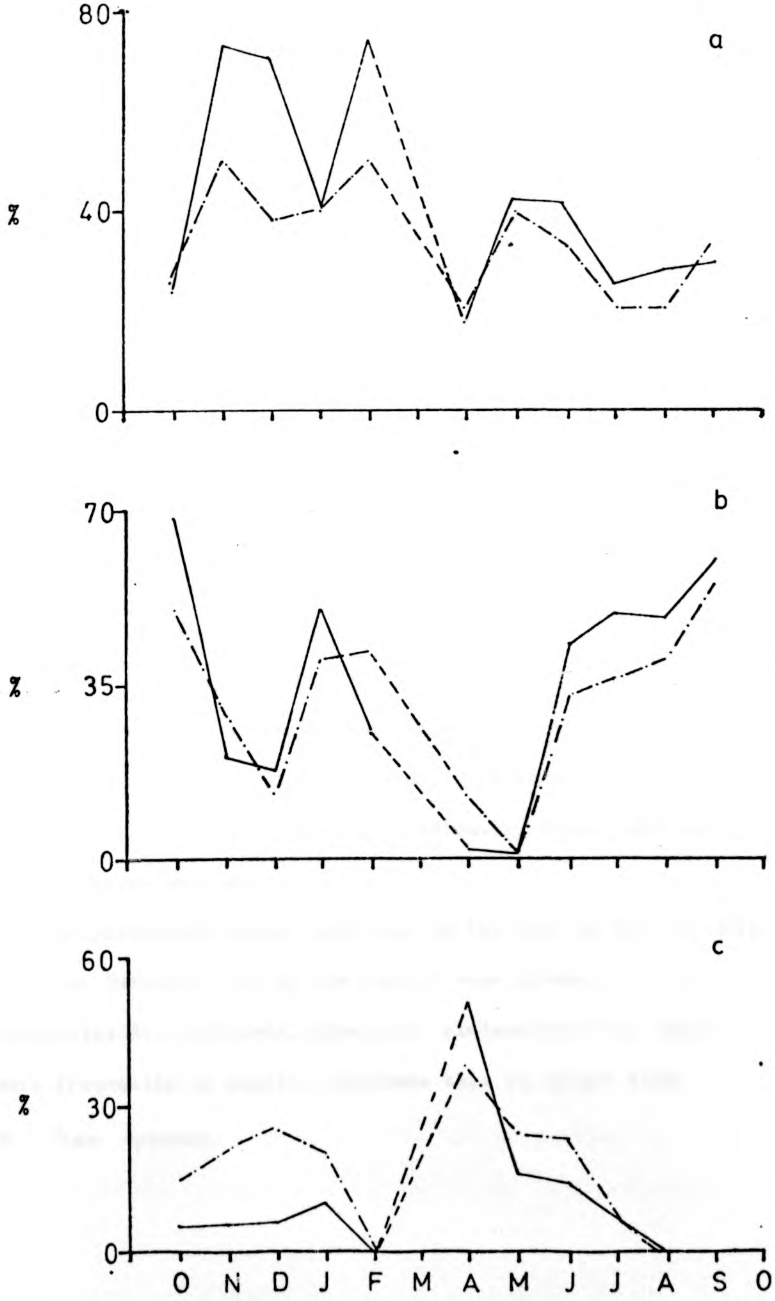
Table 28. The food composition and the relative importance of various food groups in the diet of *P. platessa*.

	PO	PP
CRUSTACEA		
AMPHIPODA	31	38
Microprotopus sp	15	13
Corophium sp	12	10
Caprellidae	2	0.7
Harpinia sp	1	0.2
Ampelisca sp	38	56
Nototropis sp	1	0.2
Bathyporeia sp	3	2
Gammaridae	3	4
Indet. Amphipoda	24	15
ISOPODA	3	1
Jaera sp, *Idotea* sp, *Eurydice* sp, indet Isopoda		
DECAPODA	<1	<1
Indet. crabs		
COPEPODA	7	8
Harpacticoid copepods		
CLADOCERA	1	1
OSTRACODA	2	1
MOLLUSCA	15	10
Cardium sp, Bivalves, Bivalve siphons, Gastropods, Placophora.		
ANNELIDA	27	34
Polychaeta, *Nephthys* sp, *Arenicola* sp, Phyllodocidae, Sabellidae, Aphroditidae, Nereidae, Spionidae, Orbiniidae, Polych. tentacles, indet. polychaete, Oligochaeta	3	2
INSECTA	5	2
Insect larvae		
NEMATODA	<1	<1
OPHIUROIDEA	<1	<1
ACTINARIA	<1	<1
ROTIFERA	<1	<1
ALGAE	<1	<1
INDET. DIGESTED MATTER	2	2

The most important food groups in the diet of young plaice from Loch Etive were polychaetes and amphipods (Table 28). Polychaetes were present in all monthly samples in considerable quantities often as the primary food item (Fig 10). Adult

Fig. 10. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of Pleuronectes platessa. Symbols as Fig. 3.

a) Polychaetes b) Amphipods c) Molluscs.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polychaetes occurred in fish stomachs in most months, in May, June and July small sabellids and polychaete tentacles had a higher frequency of occurrence than adult polychaetes.

Amphipods also had high PO and PP values in most months except in April and May (Table 29*, Fig 10). Ampelisca sp was the most common amphipod in the diet. Corophium sp and Microprotopus sp also had relatively high frequencies of occurrence. Edwards & Steele (1968) mention that in Loch Ewe, Microprotopus sp were eaten by dabs (Limanda limanda) but not by plaice. In plaice stomachs from Loch Etive, however, this species was also found to occur.

Molluscs were the third most important food group in the plaice's diet. They consisted mainly of bivalve siphons; gastropods, whole bivalves being occasionally found; chitons were recorded only once.

Harpacticoids became important in the diet in May and July, when the juvenile fish in the samples were abundant. Like harpacticoids, ostracods, cumaceans, cladocerans were found more frequently in smaller specimens than in larger fish .

* See appendix

11. *Platichthys flesus*.

Relatively comprehensive data on the food of flounder exists in the literature. Blegvad (1917) found that flounders om Danish waters fed on bivalves, gastropods, polychaetes and crustacea. Among the crustacea, Gammaridae, *Idotea* sp, *Crangon* sp were common. Larsen's (1935) stomach content analyses showed similar results; he found *Idothea* sp and *Gammarus* sp were of major importance in the stomachs of flounders. Muus (1967) investigated the food of flounder in Danish waters; his results agree with those of Larsen and Blegvad.

In Loch Etive 126 specimens were caught and examined, throughout the sampling period. They ranged in size from 37-227 mm.

Amphipods were the most important food item in the diets of flounders from Loch Etive (Table 30, Fig 11). *Corophium* sp occurred with greatest frequency and constituted the bulk of the amphipods. Gammarids were the second most frequent group.

Polychaetes were consistently present in all months in substantial quantities, forming the second most important food item in the diet (Fig 11). The other important food categories were molluscs and isopods. Among isopods *Jaera* sp

Fig. 11. The seasonal variation in the percentage occurrence and quantity of various food groups in the diet of Platichthys flesus. Symbols as Fig. 3.

a) Polychaetes b) Amphipods c) Molluscs.

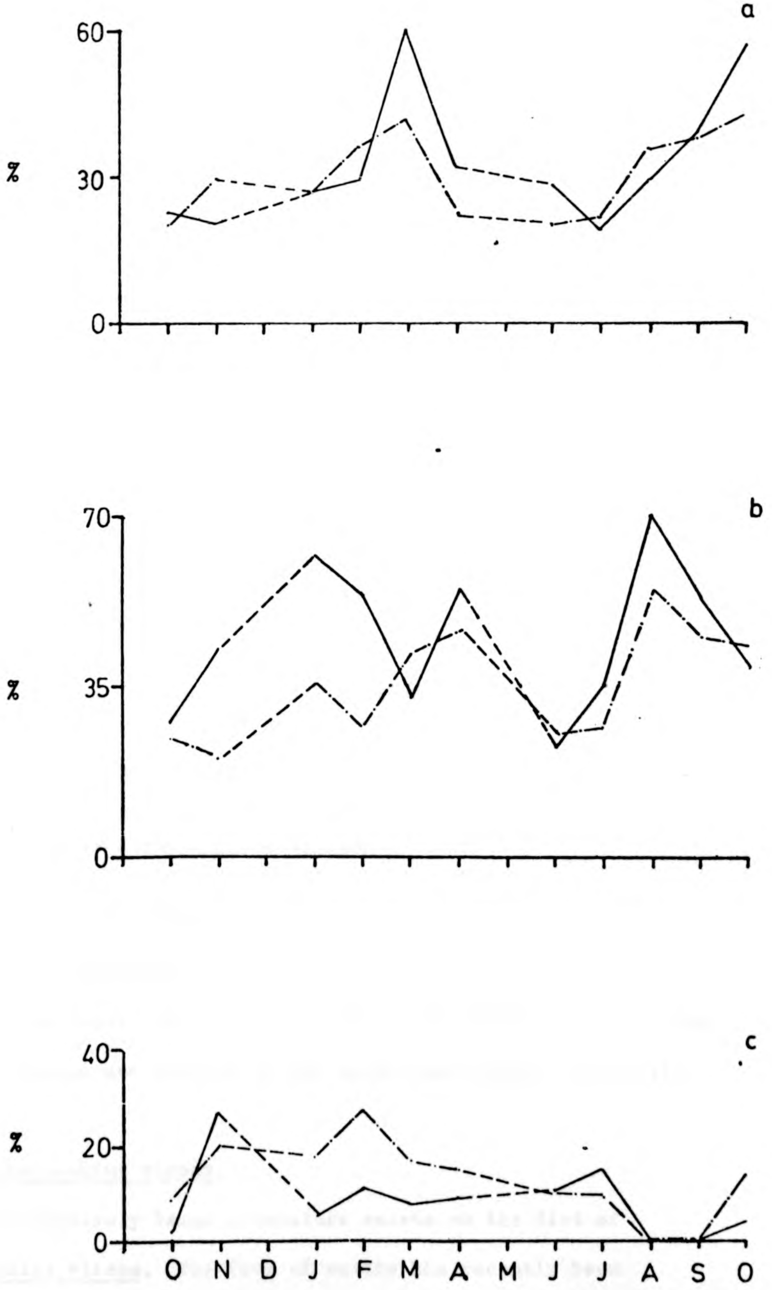
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Table 30. The food composition and the relative importance of various food groups in the diet of *Platichthys flesus*.

	PO	PP
CRUSTACEA		
AMPHIPODA	34	43
Ampelisca sp	7	8
Gammaridae	19	12
Talitridae	2	3
Corophium sp	62	70
Microprotopus sp	2	1
Nototropis sp	1	1
Indet Amphipos	8	5
ISOPODA	10	4
Idotea sp., *Jaera* sp.		
MYSIDACEA	3	5
Praunus sp., *Leptomysis* sp., Indet. Mysida		
DECAPODA	2	2
Crangon sp., Pilumnus hirtellus, indet. crabs		
CIRRIPEDIA	<1	<1
Adult barnacle		
COPEPODA	<1	<1
Harpacticoid copepods		
ANNELIDA	28	31
Polychaeta, *Arenicola* sp., Nereidae, Sabellidae, Aphroditidae, indet. polychaetes		
Oligochaeta	2	2
MOLLUSCA	11	7
Bivalves, *Ensis* sp, Indet. bivalves, Gastropoda, mollusc siphons.		
INSECTA	6	3
Terrestrial arthropods, Insect larvae		
NEMERTINI	1	1
TELEOSTEI	1	1
Juvenile flatfish, Indet. fish		
ACTINARIA	1	1
ALGAE	1	1
INDET. DIGESTED MATTER	1	1

had a high frequency of occurrence.

No seasonal trend was apparent in the monthly distribution of occurrence and amounts of the major food types. (Table 31*).

12. *Pollachius virens*.

A relatively large literature exists on the diet of *Pollachius virens*. The food of saithe has recently been comprehensively covered by Nagabushanam (1965). He mentions that this gadoid has a pelagic phase until they reach a length of 53 mm; between 53 and 70 mm they become bottom living. Up to 53 mm, saithe feed on calanoid copepods, euphausiid larvae, fish eggs, cladocerans and decapod larvae. In the demersal phase they take amphipods, isopods, mysids and polychaetes. In Loch Etive 149 specimens were caught, varying in length between 23-225 mm. The young fish under 53 mm were caught in May, June and July. Due to the absence or very low numbers of specimens caught in some months, the seasonal variation of the food types has not been treated in detail.

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* See Appendix

The results showed that unlike the food composition of most other fish species examined, no one food category had an exceptionally high percentage of occurrence. The highest PO value found was for copepods and was only 11%. Other food types which formed relatively large proportions of the total bulk of food were amphipods, decapods and polychaetes.

The saithe from Loch Etive were found to be mixed feeders, taking both planktonic and benthic food. In May, June and September the food was predominantly planktonic. Among the zooplankton taken, calanoid copepods, decapod larvae and

Table 32. The food composition and the relative importance of various food groups in the diet of *P. virens*.

	PO	PP
CRUSTACEA		
AMPHIPODA	7	18
Corophium sp	23	16
Gammarus sp	25	46
Hyale sp	15	15
Amphithoe sp	1	0.3
Caprella sp	3	1
Microprotopus sp	1	0.3
Nototropis sp	1	0.6
Indet. amphipods	31	18
ISOPODA	3	3
Idotea sp., *Jaera* sp., *Sphaeroma* sp.		
MYSIDACEA	2	5
Praunus sp., Indet. mysids		
DECAPODA	6	11
Crangon sp., *Eupagurus* sp., Indet. crabs, Decapod larvae		
CIRRIPEDIA	2	3
COPEPODA	11	28
Calanoid copepods, *pseudocalanus* sp., *Calanus* sp., *Temora* sp., *Centropages* sp	7	16
Harpacticoid copepods	4	12
Cyclopoid copepods, *Oithona* sp., Indet. cyclopoids	<1	1
CLADOCERA	5	9
OSTRACODA	<1	<1
MOLLUSCA	4	2
Gastropods, *Bittium reticulum*. *Littorina* sp., *Turitella* sp., Indet. Gastropods, Indet. Bivalves.		
ANNELIDA	5	12
Polychaeta, Phyllodocidae, Nereidae, Arenicolaidae, Indet. polychaetes		

Table 32. cont.

	PO	PP
INSECTA Adult insecta, insect larvae	2	1
TELEOSTEI Gobiidae, Indet. fish, Fish larvae	1	2
DIGESTED MATTER	5	3
PLANT MATTER	3	1

cladocerans were especially common; cirripede nauplii and cylopoid copepods occurred to a lesser extent.

Amphipods were most important in the summer and also in autumn, they were not well represented in the winter and were absent in spring. Among amphipods that could be identified, gammarids were of primary importance followed by Corophium sp and Hyale sp.

All polychaetes recorded were adult; no polychaete larvae was found among the planktonic food. Polychaetes became the most important food group in winter. They were also found in indignificant amount in autumn and summer but not in spring.

Among the decapods, shrimps were more common than crabs; in the months where planktonic food was taken, decapods consisted of larval forms.

Harpacticoid and cyclopoid copepods and ostracods were only found in smaller specimens caught between May–June. Feeding on planktonic organisms, although commonest in fish less than 49 mm in length,was not restricted to these smaller fish, because the September samples (size range 113–142 mm) consisted of fish which had been feeding entirely on planktonic food.

This may serve to demonstrate that planktonic feeding in saithe is not entirely dependent on fish size. Among the plankton eaten, fish larvae was taken by larger fish, perhaps indicating some size selection.

13. Gadus morhua.

The studies on the feeding habits of cod are numerous, although most of them deal with the food of adults. Nagabushanam (1965) gives a comprehensive list of the food of different sized cod. He found that young cod, up to 48 mm in length, feed on calanoid copepods and decapod larvae. Demersal fish of 44-370 mm length in shallow waters take mysids, euphausiids, amphipods, polychaete and fish.

In Loch Etive only 36 specimens with a size range of 31-104 mm were collected over the 13 month period. Since the size of monthly samples were too small to give a realistic indication of the seasonal variation in the type of food the data has been pooled.

Copepoda were the most important food group within the sample size range caught, calanoid copepods being the major component. Other significant food types in the cod's diet were amphipods and decapods. (Table 33).

14. Zoarces viviparus.

The diet of the viviparous blenny has been relatively well studied. Blegvad (1917) states that Zoarces viviparus in Danish waters feeds on bivalves, gastropods and small crustaceans, especially Gammaridae and Idothea sp. Larsen (1935) found that crustaceans, particularly Idothea sp and Leander sp make up the bulk of its food. Furthermore, small gastropods and fish were also taken. Muus (1967) mentions that Zoarces eats gammarids,

Table 33. The food composition and the relative importance of various food groups in the diet of *Gadus morhua*.

	PO	PP
CRUSTACEA		
AMPHIPODA	23	27
Ampelisca sp	8	20
Corophium sp	24	17
Gammaridae	20	10
Hyale sp	8	7
Caprellids	4	4
Nototrops sp	4	9
Indet. amphipods	32	32
ISOPODA	3	1
Jaera sp., *Sphaeroma* sp		
MYSIDACEA	5	3
DECAPODA	15	16
Crangon sp	6	9
Indet. crabs	4	5
Decapod larvae	5	2
CIRRIPEDIA	3	2
COPEPODA	30	39
Calanoid copepods	16	20
Harpacticoid copepods	10	12
Cyclopoid copepods	6	7
CLADOCERA	5	3
OSTRACODA	3	1
EUPHAUSIACEA	3	1
INSECTA	2	1
Adult insecta, Insect larvae		
ANNELIDA	3	1
POLYCHAETA		
TELEOSTEI	1	5
Pomatoschistus minutus		

molluscs, Nereis sp and young gobies.

181 specimens were caught in Loch Etive. Although the monthly sample sizes were often large the number of fish with empty stomachs was very high throughout the sampling period (see section on the seasonal variation in the quantity of food p 104)for this reason the results have been pooled. (Table 34).

The main food of Zoarces viviparus was amphipods, isopods and crabs. 80% of the amphipods in fish stomachs were in a broken condition and could not be identified; the relative frequencies of the different species therefore has not been estimated. The proportion of highly digested matter in fish stomachs was higher than in all the other fish species examined.

15. Crenilabus melops.

Blegvad (1917) has found that this species feeds on Idotea sp, Gammaridae, Crangon sp, small molluscs and insect larvae. The young stages feed on copepods.

23 specimens were caught and their stomach contents examined. (Table 35).

Crenilabrus melops from Loch Etive was essentially a crustacean feeder. Amphipods, isopods and ostracods constituted

Table 34. The food composition and relative importance of various food groups in the diet of *Zoarces viviparus*.

	PO	PP
CRUSTACEA		
AMPHIPODA	37	37
Ampelisca sp., *Corophium* sp., Gammaridae, *Hyale* sp., *Microprotopus* sp., indet. Amphipods		
ISOPODA	13	14
Jaera sp		
DECAPODA	10	9
Carcinus maenas, indet. crabs		
CIRRIPEDIA	4	2
COPEPODA	3	2
Harpacticoid copepods		
OSTRACODA	4	3
CUMACEA	2	2
MOLLUSCA	3	2
Bivalves, Gastropods		
ANNELIDA	2	5
Polychaeta		
INSECTA	5	4
Insect larvae, Adult insects		
ALGAE	7	6
INDET. DIG. MATERIAL	15	14

A large percentage of the diet. Among the amphipods that could be identified, *Microprotopus* sp was most frequent. Non-crustacean food consisted mainly of insect larvae and molluscs.

16. *Agonus cataphractus*

The occurrence of *A. cataphrachus* in the catches was rare. A total of 26 specimens were caught throughout the sampling period. (Table 36).

Table 35. The food composition and relative importance of various food groups in the diet of C. melops.

	PO	PP
CRUSTACEA		
AMPHIPODA	27	31
Gammaridae	4	6
Nototropis sp	4	2
Microprotopus sp	27	37
Caprellids	22	6
Corophium sp	4	8
Indet. Amphipods	36	41
ISOPODA	13	24
Jaera sp., *Idotea* sp		
DECAPODA	2	1
Indet Crabs		
OSTRACODA	24	21
COPEPODA	14	10
Harpacticoid copepods, Cyclopoid copepods		
INSECTA	6	3
Insect larvae, Terrestrial insects		
MOLLUSCA	13	9
Gastropods, Bivalves		

A. cataphractus was found to feed solely on crustacea. Two thirds of the total amount of food consisted of amphipods. Caprellids and *Microprotopus* sp. were the most common forms. Cumaceans were of secondary importance in the diet, although copepods occurred frequently.

17. *Hyperoplus lanceolatus*

Wheeler (1968) mentions that the food of *H. lanceolatus* consists of copepods, crustacean larvae, euphausiids and fish eggs.

Table 36. The food composition and the relative importance of various food items in the diet of *A. cataphractus*.

			PO	PP
CRUSTACEA	AMPHIPODA		49	67
		Caprellidae	19	24
		Microprotopus sp	21	24
		Ampelisca sp	6	9
		Gammaridae	9	13
		Iphimedia sp	2	1
		Nototropis sp	4	4
		Corophium sp	4	2
		Indet Amphipoda	30	17
	OSTRACODA		9	3
	COPEPODA		15	5
		Harpacticoida	11	4
		Cyclopoida	4	1
	DECAPODA		2	1
		Decapod larvae		
	CUMACEA		24	24

Table 37. The food composition and the relative importance of various food items in the diet of *H. lanceolatus*.

		PO	PP
CRUSTACEA	ISOPODA	2	2
	MYSIDACEA	1	2
	DECAPODA	19	21
	Decapod larvae		
	COPEPODA	48	50
	Calanoid copepods	42	45
	Calanus sp		
	Pseudocalanus sp		
	Temora sp		
	Acartia sp		
	Centropages sp		
	Harpacticoid copepods	2	1
	Cyclopoid copepods	4	4
	Oithona sp		
	CLADOCERA	218	23
ANNELIDA		1	<1
	OLIGOCHAETA		
PISCES		1	<1
	Fish larvae		

The stomach contents of 63 specimens from Loch Etive were examined.

Hyperoplus lanceolatus was a complete plankton feeder. Calanoid copepods made up the greatest bulk of the food. Temora sp, Pseudocalanus sp were the most commonly occurring species. Adult Calanus sp and Centropages sp rarely occurred. Cladocerans and decapod larvae were also present in large numbers. (Table 37).

18. Nerophis lumbriciformis

Wheeler (1968) gives the food of the adults of this species as larval and small crustaceans and larval fishes. The diet of this species has not been systematically studied. In Loch Etive 27 specimens were caught throughout the sampling period and stomach contents examined. (Table 38).

The food of this species in Loch Etive thus consisted mainly of ostracods, harpacticoids, amphipods and isopods.

19. Syngnathus sp

Two species of pipe fish was found in Loch Etive, Syngnathus rostellatus and Syngnathus acus. Some difficulty was experienced

Table 38. The food composition and the relative importance of various food groups in the diet of Nerophis lumbriciformis.

		PO	PP
CRUSTACEA	AMPHIPODA	17	13
	Caprellidae		
	Indet amphipods		
	ISOPODA	10	9
	MYSIDACEA	3	6
	COPEPODA	31	34
	Harpacticoid copepods		
	OSTRACODA	24	25
ANNELIDA		7	6
	POLYCHAETA		
	Polychaete tentacles		
MOLLUSCA		3	3
	GASTROPODA		
	INDET. DIGESTED MATTER	3	3

in distinguishing them, especially between the younger members of two species. In order to avoid any errors they were grouped as Syngnathus sp.

Wheeler (1968) lists the food of Syngnathus acus as small amphipods, isopods, small shrimps and crabs. Syngnathus rostellatus feeds on mysids, copepods and young decapods but take Amphipods and Isopods in lesser quantities.

21 specimens of Syngnathus were caught. The main food of this species was found to be mysids, harpacticoid copepods, amphipods. Decapod larvae, zoeae, ostracods and cumaceans were also frequent. Calanoid copepods, shrimps, isopods and cladocera occurred to a lesser extent. A well defined relationship between the fish size and prey size was apparent. Shrimps, mysids, amphipods occurred in the stomachs of larger specimens, whereas copepods, ostracods were common in smaller members. Among the amphipods members of the family Caprellidae were of frequent occurrence.

20. Anguilla anguilla.

Larsen (1935) found that the food of Anguilla anguilla consisted mainly of crustaceans among which Leander sp, Idotea sp and Gammarids were especially important.

Most individuals of this species were caught at Dail, the area with the lowest salinity of the three stations sampled. 17 specimens were caught and examined.

Amphipods, insect larvae and isopods were found to occur most frequently in the stomachs. Polychaetes were occasionally taken. Among the amphipods, the families Gammaridae and Corophidae were common.

21. Chirolophis Ascanii.

15 specimens were caught and examined in Loch Etive. This species is essentially a polychaete feeder, sabellid tentacles were very frequent in fish stomachs. Small bivalves and gastropods were occasional.

22. Salmo trutta

It had been mentioned in Table 1 that Salmo trutta, although a member of the inshore fish community, was not included in the analyses as its biology was being studied by another worker at the time of sampling, Pemberton (1975, in press). He found that crustaceans were the most prominent food component, followed by insects and fish. Among crustaceans, amphipods were particularly important. The food composition list of *S. trutta* shows that the majority of prey species in its diet, excluding fish, are common to several inshore fish covered in the present investigation. The extent to which each food group was taken by *S. trutta* was not worked out in detail; but the frequency of occurrence values for its main food components nevertheless suggest that the degree of utilization of different types of food are different from other fish (Crustaceans 43%, insects 31.1%, fish 30.6%). Thus the feeding habits of *S. trutta* appear to be similar to the rest of fish community examined, namely it utilizes approximately the same sources of food but to a different extent.

It is interesting to note that among the fish prey of *S. trutta*. ten of the species investigated here are listed, which suggests that *S. trutta* is a major predator of inshore fish and plays an important role in the economy of the fish community.

SEASONAL VARIATIONS IN THE TOTAL QUANTITY OF FOOD CONSUMED.

The seasonal changes in the amount of food eaten by each species was investigated by calculating a fullness index (F.I.) for each month as the mean number of points allotted/stomach for those species which had a relatively large sample size. The fullness index only gives an overall picture of the seasonal trend but does not show the variation of fullness in each monthly sample. To demonstrate this variation the frequency of stomachs that were empty, trace full, ¼ full, ½ full and full were also calculated.

For this purpose the stomachs were classified from empty to full as follows:

No. points allotted	Fullness category of stomach
0 - 0.5	Empty
0.6 - 3	Trace
4 - 7	¼ full
8 - 12	½ full
13 - 17	¾ full
18 - 20+	full

Seasonal changes in the feeding intensity of individual species

A clear seasonal pattern in feeding intensity was evident in most of the species examined. Since this was similar for all of them, only Spinachia is treated in detail in this respect. For the remainder general comments will be sufficient.

1) Spinachia spinachia

Fig 12a shows that the fullness index decreased slightly from October 1971 onwards and remained low during the months December, January and February, a small increase was found in March but this was not continued into April where the amount of food in fish stomachs was as low as January. From April to June the increase in the F.I. was quite marked; it decreased slightly in July, but in August was comparable to June values. The amount of food in the stomachs remained quite high in September and began to decline again in October.

Despite the slight variation it is clear from Fig 12a that the fluctuations in the percentage of empty stomachs and the F.I. show an opposite pattern. The percentage of empty stomachs was highest in the winter months whereas the fullness index was highest between May and September.

The number of fishes showing the different degrees of stomach fullness were also examined. Table 39* gives the number of stomachs in different fullness levels per month. It will be seen from Table 39 that completely empty and full

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* See Appendix

Fig. 12. The seasonal variation in the quantity of food consumed.

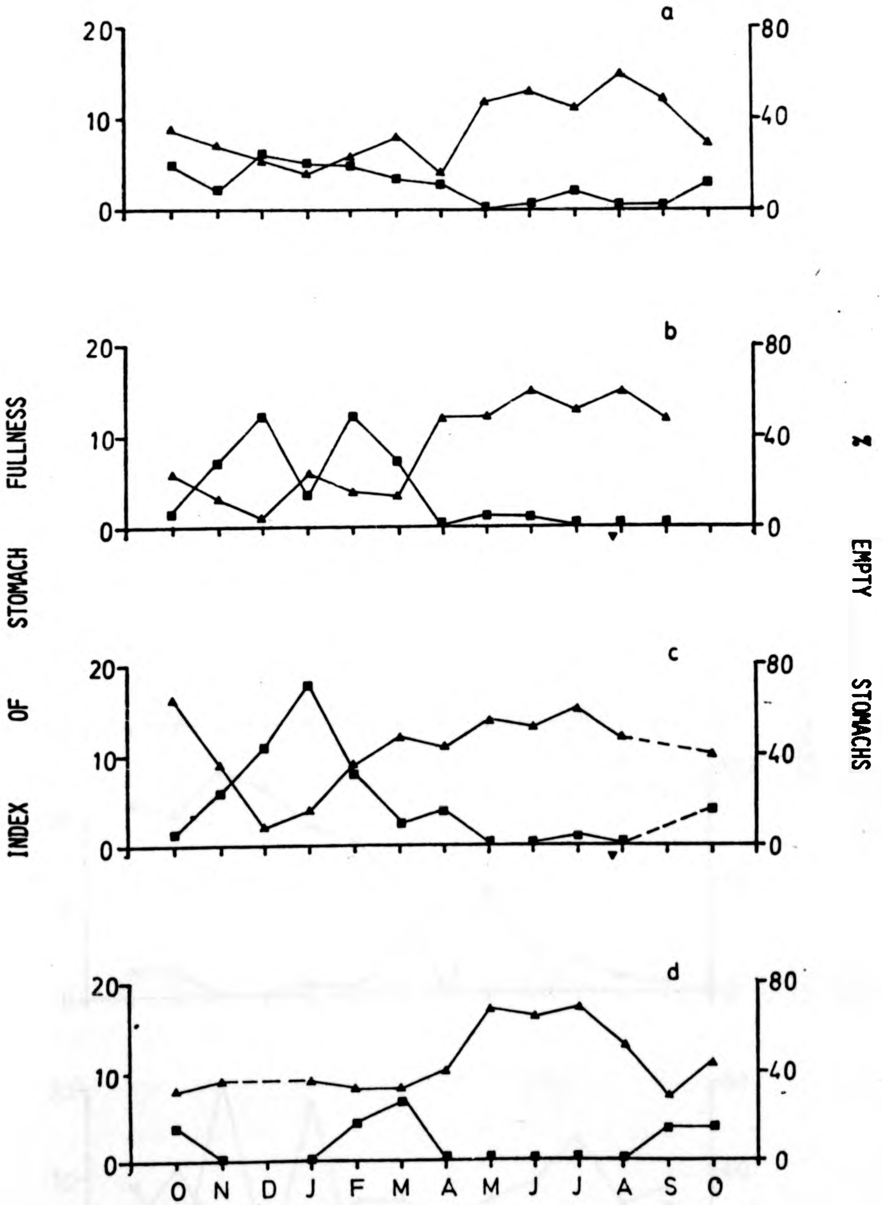
a) S. spinachia b) G. aculeatus c) M. scorpius

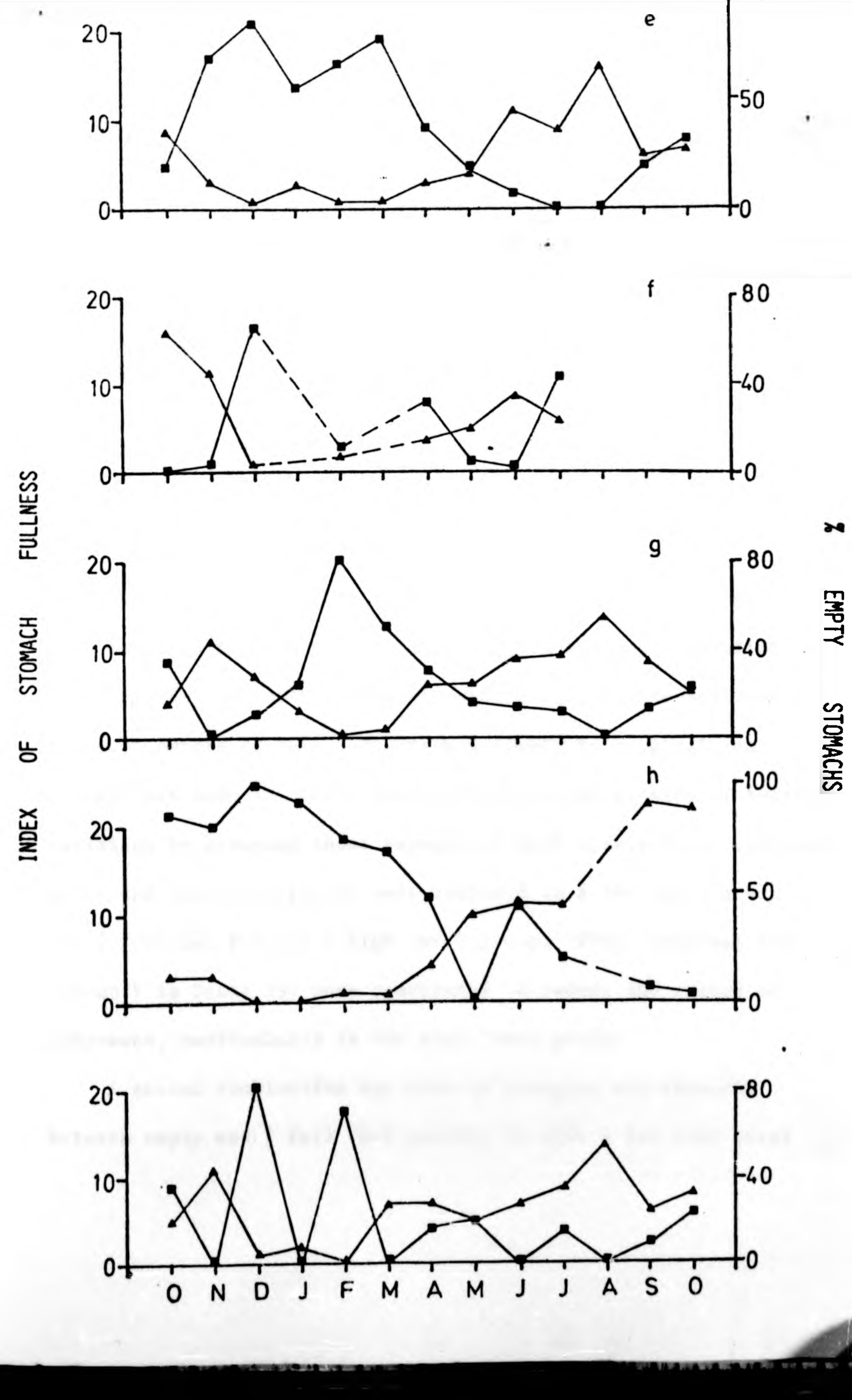
d) T. bubalis e) P. gunnellus f) A. presbyter

g) P. minutus h) Z. viviparus i) C. flavescens

■ % Empty stomachs

▲ Fullness index, expressed as mean points/stomach.


INDEX OF STOMACH FULLNESS
% EMPTY STOMACHS
a
b
c
d
20
10
0
80
40
0
O
N
D
J
F
M
A
M
J
J
A
S
O


e
f
g
h
INDEX OF STOMACH FULLNESS
% EMPTY STOMACHS
20
10
0
100
80
50
40
O
N
D
J
F
M
A
M
J
J
A
S
O

stomachs were present in almost every month, but their proportion in the summer and winter months was markedly different.

In order to follow in more detail the changes that took place in different fullness categories in successive months, it was necessary to calculate how much the different levels of fullness observed in one month differed from those observed in the following months. A statistical comparison of monthly fullness categories was therefore performed.

As mentioned earlier, errors in fullness estimation may have occurred from month to month, e.g., a stomach classified as ¾ full in one month may be classified as full the next month. Although errors of this sort are not likely to be great, an attempt was made to reduce their effect on the pattern of seasonal variation by grouping those categories most likely to be confused. Empty and trace categories were combined as a low level group and ¾ full and full as a high level group. These combinations (Group 1 in Table 39) were considered to reduce the errors of judgement, particularly in the high level group.

A second combination was made by grouping all stomachs between empty and ¼ full (0-7 points) to give a low food level

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class and $\frac{1}{2}$ full to full (8-20 points) to give a high food level class. The second grouping included all the fishes in a months sample and would further decrease the possible errors introduced by inaccurate estimation of fullness categories (Group 2 in Table 39).

Monthly differences in fullness in both groups were compared by a χ^2 test after applying Yates correction. The results for Groups 1 and 2 are given in Tables 40 and 41 respectively.

From the results given in Table 40 the following conclusions can be made:

1. Consecutive months are rarely different except November and December; April and May and August and September. Therefore, the increase or decrease in fullness levels is gradual.
2. Greatest differences (i.e., highest significance levels) occur when summer and winter months are compared.

Table 41 demonstrates essentially the same points except that the decrease from November to December become more gradual and February and March appear more markedly different from the low food level months, December, January and April.

Both of the comparisons showed that in April the fishes

Table 40. S. spinachia. Comparison by the X^2 test of the proportion of empty and trace full stomachs and ¼ full to full stomachs in each month. The X^2 values for each comparison are given in the right hand portion of the table and the significance levels in the left hand portion -, proportion was not significant at 5% level, + proportion significant at 5% level, ++ at 1% level, +++ at 0.1% level.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	
Oct		0.15	4.83	0.68	0.63	0.51	6.60	2.52	2.41	11.38	9.56	2.29	1.23	Oct.
Nov	-		6.77	0.70	0.34	0.24	12.73	6.32	6.35	21.39	18.88	7.19	4.39	Sept.
Dec	++	+		1.18	1.99	2.29	31.99	19.47	22.78	44.70	41.52	27.04	21.52	Aug.
Jan	++	++	-		0.06	0.01	8.94	4.54	6.02	13.98	12.04	5.22	3.85	July
Feb	-	-	-	-		0.06	14.34	6.17	6.17	20.73	18.38	7.82	5.38	June
Mar	-	-	-	-	-		6.25	2.91	4.08	9.99	9.95	3.25	2.29	May
Apr	+	-	-	-	-	-		0.34	1.30	0.52	0.15	3.52	5.00	April
May	-	-	++	++	+	-	+		0.14	1.89	1.12	0.81	1.51	March
June	+	++	+++	+++	+	+	+++	-		3.22	2.18	0.23	0.85	Feb.
July	+	+	+++	+++	+	+	++	-	-		0.01	7.85	10.30	Jan.
Aug	+++	+++	+++	+++	+++	+++	+++	-	-	-		6.11	8.36	Dec.
Sept	+	++	+++	+++	+	+	+++	-	-	-	++		0.40	Nov.
Oct	-	-	++	+++	-	-	++	-	-	-	+	-		Oct.
	Oct	Sept	Aug	July	June	May	Apr	Mar	Feb	Jan	Dec	Nov	Oct	

Table 41. S. spinachia. Comparison by the X^2 test of the proportion of empty to ¼ full and ½ full to full stomachs in each month. The X^2 values for each comparison are given in the right hand portion of the table and the significance levels in the left hand portion. -, proportion was not significant at 5% level, + proportion significant at 5% level, ++ at 1% level, +++ at 0.1% level.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	
Oct		0.47	7.40	2.84	0.37	0.03	8.33	0.01	0.65	13.09	8.54	0.84	1.50	Oct.
Nov	-		6.13	2.22	0.02	0.12	16.56	2.74	3.52	27.32	20.59	13.28	7.11	Sept.
Dec	+	-		0.25	4.82	4.79	34.14	12.88	6.23	48.83	41.02	33.76	23.90	Aug.
Jan	++	++	-		1.99	1.40	14.47	5.16	6.15	20.29	17.60	11.35	7.61	July
Feb	-	-	+	++		0.11	13.12	2.17	2.49	20.58	14.90	8.37	4.58	June
Mar	-	-	-	+	-		5.85	0.87	0.80	10.36	7.49	3.08	1.53	May
Apr	+	-	-	-	+	+		3.96	6.10	0.03	0.33	3.47	5.57	April
May	-	-	++	++	-	-	+		0.03	6.36	3.27	0.47	0.01	March
June	+	++	+++	+++	-	-	+++	-		10.63	6.18	1.46	0.18	Feb.
July	++	+++	+++	+++	+	+	+++	-	-		0.85	7.10	10.62	Jan.
Aug	+++	+++	+++	+++	+++	+++	+++	+	+	-		3.08	5.85	Dec.
Sept	+	+++	+++	+++	-	-	+++	-	-	-	+		0.89	Nov.
Oct.	-	-	+	+++	-	-	++	-	-	-	++	-		Oct.
	Oct	Sept	Aug	July	June	May	Apr	Mar	Feb	Jan	Dec	Nov	Oct.	

stomachs were present in almost every month, but their proportion in the summer and winter months was markedly different.

In order to follow in more detail the changes that took place in different fullness categories in successive months, it was necessary to calculate how much the different levels of fullness observed in one month differed from those observed in the following months. A statistical comparison of monthly fullness categories was therefore performed.

As mentioned earlier, errors in fullness estimation may have occurred from month to month, e.g., a stomach classified as ¾ full in one month may be classified as full the next month. Although errors of this sort are not likely to be great, an attempt was made to reduce their effect on the pattern of seasonal variation by grouping those categories most likely to be confused. Empty and trace categories were combined as a low level group and ¾ full and full as a high level group. These combinations (Group 1 in Table 39) were considered to reduce the errors of judgement, particularly in the high level group.

A second combination was made by grouping all stomachs between empty and ¼ full (0-7 points) to give a low food level

Table 40. S. spinachia. Comparison by the X^2 test of the proportion of empty and trace full stomachs and ½ full to full stomachs in each month. The X^2 values for each comparison are given in the right hand portion of the table and the significance levels in the left hand portion -, proportion was not significant at 5% level, + proportion significant at 5% level, ++ at 1% level, +++ at 0.1% level.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	
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Nov	-		6.77	0.70	0.34	0.24	12.73	6.32	6.35	21.39	18.88	7.19	4.39	Sept.
Dec	++	+		1.18	1.99	2.29	31.99	19.47	22.78	44.70	41.52	27.04	21.52	Aug.
Jan	++	++	-		0.06	0.01	8.94	4.54	6.02	13.98	12.04	5.22	3.85	July
Feb	-	-	-	-		0.06	14.34	6.17	6.17	20.73	18.38	7.82	5.38	June
Mar	-	-	-	-	-		6.25	2.91	4.08	9.99	9.95	3.25	2.29	May
Apr	+	-	-	-	-	-		0.34	1.30	0.52	0.15	3.52	5.00	April
May	-	-	++	++	+	-	+		0.14	1.89	1.12	0.81	1.51	March
June	+	++	+++	+++	+	+	+++	-		3.22	2.18	0.23	0.85	Feb.
July	+	+	+++	+++	+	+	++	-	-		0.01	7.85	10.30	Jan.
Aug	+++	+++	+++	+++	+++	+++	+++	-	-	-		6.11	8.36	Dec.
Sept	+	++	+++	+++	+	+	+++	-	-	-	++		0.40	Nov.
Oct	-	-	++	+++	-	-	++	-	-	-	+	-		Oct.
	Oct	Sept	Aug	July	June	May	Apr	Mar	Feb	Jan	Dec	Nov	Oct	

(Group 1, column a)and in the number of stomachs with low amounts of food (Group 2, column a) from October to January. They both

Table 40. S. spinachia. Comparison by the X^2 test of the proportion of empty and trace full stomachs and ¼ full to full stomachs in each month. The X^2 values for each comparison are given in the right hand portion of the table and the significance levels in the left hand portion –, proportion was not significant at 5% level, + proportion significant at 5% level, ++ at 1% level, +++ at 0.1% level.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	
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Nov	–		6.77	0.70	0.34	0.24	12.73	6.32	6.35	21.39	18.88	7.19	4.39	Sept.
Dec	++	+		1.18	1.99	2.29	31.99	19.47	22.78	44.70	41.52	27.04	21.52	Aug.
Jan	++	++	–		0.06	0.01	8.94	4.54	6.02	13.98	12.04	5.22	3.85	July
Feb	–	–	–	–		0.06	14.34	6.17	6.17	20.73	18.38	7.82	5.38	June
Mar	–	–	–	–	–		6.25	2.91	4.08	9.99	9.95	3.25	2.29	May
Apr	+	–	–	–	–	–		0.34	1.30	0.52	0.15	3.52	5.00	April
May	–	–	++	++	+	–	+		0.14	1.89	1.12	0.81	1.51	March
June	+	++	+++	+++	+	+	+++	–		3.22	2.18	0.23	0.85	Feb.
July	+	+	+++	+++	+	+	++	–	–		0.01	7.85	10.30	Jan.
Aug	+++	+++	+++	+++	+++	+++	+++	–	–	–		6.11	8.36	Dec.
Sept	+	++	+++	+++	+	+	+++	–	–	–	++		0.40	Nov.
Oct	–	–	++	+++	–	–	++	–	–	–	+	–		Oct.
	Oct	Sept	Aug	July	June	May	Apr	Mar	Feb	Jan	Dec	Nov	Oct	

Table 41. *S. spinachia*. Comparison by the X^2 test of the proportion of empty to ¼ full and ½ full to full stomachs in each month. The X^2 values for each comparison are given in the right hand portion of the table and the significance levels in the left hand portion. -. proportion was not significant at 5% level, + proportion significant at 5% level, ++ at 1% level, +++ at 0.1% level.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	
Oct		0.47	7.40	2.84	0.37	0.03	8.33	0.01	0.65	13.09	8.54	0.84	1.50	Oct.
Nov	-		6.11	2.22	0.02	0.12	16.56	2.74	3.52	27.32	20.59	13.28	7.11	Sept.
Dec	+	-		0.25	4.82	4.79	34.14	12.88	6.23	48.83	41.02	33.76	23.90	Aug.
Jan	++	++	-		1.99	1.40	14.47	5.16	6.15	20.29	17.60	11.35	7.61	July
Feb	-	-	+	++		0.11	13.12	2.17	2.49	20.58	14.90	8.37	4.58	June
Mar	-	-	-	+	-		5.85	0.87	0.80	10.36	7.49	3.08	1.53	May
Apr	+	-	-	-	+	+		3.96	6.10	0.03	0.33	3.47	5.57	April
May	-	-	++	++	-	-	+		0.03	6.36	3.27	0.47	0.01	March
June	+	++	+++	+++	-	-	+++	-		10.63	6.18	1.46	0.18	Feb.
July	++	+++	+++	+++	+	+	+++	-	-		0.85	7.10	10.62	Jan.
Aug	+++	+++	+++	+++	+++	+++	+++	+	+	-		3.08	5.85	Dec.
Sept	+	+++	+++	+++	-	-	+++	-	-	-	+		0.89	Nov.
Oct.	-	-	+	+++	-	-	++	-	-	-	++	-		Oct.
	Oct	Sept	Aug	July	June	May	Apr	Mar	Feb	Jan	Dec	Nov	Oct.	

had very small amounts of food in their stomachs. Food measures for this month were as low as January and December. This could not be explained by small sample size or a change that might have taken place in the type of food consumed (see Table 11) or a sudden change in temperature as no such drop in temperature was recorded. The food composition was not significantly different from the previous or following months. Most adults had very mature gonads in this month but the presence of full intestines showed that feeding had not ceased. The high number of stomachs either empty or with trace amount of food is thought to be a result of highly digested state of food in the guts.

The percentage of stomachs corresponding to the high and low level fullness categories in Group 1 and Group 2 are also given in Table 39.

It is clear from the seasonal variation in the percentages of stomachs in Group 1 and Group 2 that percentages follow the same trend as the χ^2 values given in Table 40 and 41. They show the progressive increase in the number of empty stomachs (Group 1, column a)and in the number of stomachs with low amounts of food (Group 2, column a) from October to January. They both show the January minimum, the July-August maximum and that autumn and spring values were intermediate between winter and summer. In both cases the inverse relationship between summer and winter stands out quite sharply.

It can be concluded, therefore the although statistical comparison of high and low food levels between months gives a more detailed account of the changes that take place, the consideration of percentages is probably sufficient to follow the general pattern and statistical comparisons of this sort for the other species were not made.

2) Gasterosteus aculeatus

The seasonal pattern of variation in feeding intensity of this species (Fig 12b, Table 42*) was similar to that of Spinachia except that the increase in feeding appeared to start somewhat earlier and remained more or less constant for most of the spring and summer.

3) Myoxocephalus scorpius

Here again the general trend of high feeding intensity in summer and low intensity in winter was apparent (Fig 12c, Table 43*), but this species seems to have a shorter period of low level feeding (Dec-Jan) than most others.

4) Taurulus bubalis

The number of individuals of this species caught in most months was usually small. The variation inherent in small samples

* See Appendix

inevitabley affects the estimation of seasonal trends in the amount of food consumed (Table 44*) but in spite of this a seasonal pattern was nevertheless apparent.

5) Pholis gunnellus

The quantity of food consumed by P. gunnellus also showed a very clear seasonal trend. (Fig 12e, Table 45*).

The winter decline in the feeding of P. gunnellus is strongly influenced by the onset of the spawning season which takes place in January and February (Qasim 1957, Wheeler 1969). Wheeler states that in winter, most females and some males guarding eggs cease feeding. Smith (1887) states that the breeding season in this species lasts from February to April. Quasim (1957) found that in North Wales feeding intensity reached a high level in April and May and remained so until October. In Loch Etive the fish stomachs still had very small amounts of food in April. It is apparent, however, that the general trend shown by fish in Loch Etive is comparable to that found by Qasim in North Wales

6) Atherina presbyter

Although no samples were obtained for August, September, October 1972, the pattern of monthly variation in the F.I. of this species appeared to be slightly different from the fishes considered previously. (Fig 12f, Table 46*).

80% of stomachs were ½ full or completely full in October 1971 which was similar to the summer maximum found for the other species previously discussed. No empty, trace full or ¼ full stomachs were found and the F.I. for the month was very high (17).

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* See Appendix

Spawning in these fishes takes place in mid-summer (Wheeler 1968) and this may have a depressing effect on feeding. Atherina presbyter is a shoaling fish feeding on plankton; low amounts of food found in July and very high amounts observed in October, November could also be due to patchiness of the food.

7) Pomatoschistus minutus

With the exception of October 1971 and November the quantity of food in the stomach of P. minutus appeared to change seasonally in a consistent pattern (Fig 12g, Table 47*). The F.I. decreased sharply in December and was very low from January to March. It then began to rise in April, increasing steadily until a peak was reached in August, declining again in September and October 1972.

As mentioned earlier, most monthly samples were collected at low tide. Healey (1970) found that feeding activity had a tidal rhythm, most feeding taking place at high tide. If this feeding rhythm is also present in Loch Etive fish, then most -

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* See Appendix

monthly fullness index values are probably under-estimates of the actual amounts present.

8) Zoarces viviparus

Zoarces viviparus stomachs in Loch Etive were characterized by very low levels of food found throughout the year (Fig 12h).

As will be apparent from Table 48*, the percentage of empty and trace full stomachs was particularly high in the winter. Although an increase in feeding intensity occurred in April, it still remained relatively low during the summer. There was no sample for August. Even in June and July when the largest amounts of food were found in the stomachs, 55% of stomachs were empty to trace full.

The high percentage of empty stomachs in the winter could be explained by cessation of feeding during the breeding season. The presence of low food levels during the warmer months suggests, however, that some other factor apart from the temperature and breeding season may be responsible for these values, possibly a strong tidal or nocturnal feeding rhythm. If the fishes fed mostly at high tide or at night, a large percentage of empty stomachs would have been found at low tide and during the day,

* See Appendix

when most of the fishes were caught. The fact that in all months some food was found in the intestines may support this view.

9) Chaparrudo flavescens

The seasonal change in the stomach contents of C. flavescens does not show much deviation from the general pattern of high levels of food in the summer and low levels in the winter. (Fig 12i, Table 49*).

It is worth mentioning that in November 1972 two samples collected on different days showed much variation in fullness. One sample had nearly all empty to ¼ full stomachs whereas in the other sample 80% of the stomachs were ¾ full to completely full, similar to those values found in the summer months. Chaparrudo flavescens is a shoaling fish and the food in November consisted of zooplankton. It is possible that the sample with full stomachs were caught immediately after the shoal had fed on a plankton patch. Patchy feeding could be a potential source of error in the months where the greatest percentage of food was planktonic but the overall seasonal pattern was consistent.

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* See Appendix

10-14). Pleuronectes platessa, Platichthys flesus, Pomatoschistus microps, Gadus morrhua, Pollachius virens.

Most of the monthly samples for these five species were very small, the samples for cod being particularly scanty. Tables 50-54* show, however, that following the general trend of all other species stomach contents were low during winter months and high in the summer.

The figures in the tables suggest that feeding intensity began to rise in April in P. platessa, P. microps, P. virens and in May in P. flesus.

SUMMARY AND DISCUSSION OF VARIATIONS IN FEEDING INTENSITY

In most of the species examined a well marked seasonal variation in the feeding intensity was found.

The general pattern, as demonstrated for example by Fig 12 and Tables 39-54 was the presence of low levels of food in the winter and high levels in the summer. The trend was apparent even in those species where the monthly samples were relatively small.

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* See Appendix

The low food content of fish stomachs in the winter appears to be a common phenomenon and has been demonstrated in many different species by various workers. Ball (1961) found similar results in trout in a Welsh lake, Skazkina and Kostyuchenko (1968) in the Azov goby, Tyler (1973) in the demersal fishes of Passamaquody Bay, Lande (1973) in plaice of Borgenfjorden and Hunt and Jones (1972) in brown trout.

High food levels in the summer seems to be correlated with increasing daylength and more significantly with increasing temperature. Ball (1961) found a close correlation between the food quantities and temperature and daylength in brown trout. Hathaway (1927) demonstrated experimentally in Eupomotus gibbosus (L), Lepomis incisor, Micropterus salmoides that food intake increases three fold when the temperature is raised from 10 to 20°C. He found that moderate changes in illumination produced no perceptible effect on food consumption. Skazkina and Kostyuchenko (1968), and Tyler (1973) also found correlations between increasing quantities of food in stomachs and a rise in temperature. Swift (1955) maintains that the activity and appetite of trout increases with increasing temperature and daylength resulting in an increased food level. Internal factors such as the onset of the breeding season, as well as environmental factors, undoubtedly play an important role in the changes that occur in feeding intensity.

THE RELATIONSHIP BETWEEN FISH SIZE AND PREY SIZE

The results of the food analyses suggested that the size of the prey found in a fishes stomach was often related to its body size. In some fishes there was evidence for the existence of a clearly defined size-related feeding heterogeneity (Tyler, 1972) i.e., the food changes from one type to another over a certain range of body lengths. These changes were most ovious in those fishes which fishes which had a large size range. For example, in *M. scorpius* where the length range was between 24–230 mm and in *S. spinachia* where it was between 35–134 mm. The differences were more obscure in species which did not reach a large size as in *P. minutus* which had a size range of 31–78 mm over a year.

This relationship between prey size and body size will be discussed for individual species below.

1) S. spinachia

In S. spinachia harpacticoid copepods increased in importance in the diet of those months when juvenile fishes began to appear in the samples, reaching their peak of importance in July when the majority of fishes were very young; the range of total lengths for July being between 35-57 mm. The seasonal abundance of ostracods was similar to harpacticoids. Their overall importance in the diet was low except in very small fishes. Ostracods, harpacticoids and calanoid copepods were important in the diets of fish $<$ 70 mm total length. Insect larvae, although occurring throughout the size range, were similarly found in largest quantities in fish below 70 mm.

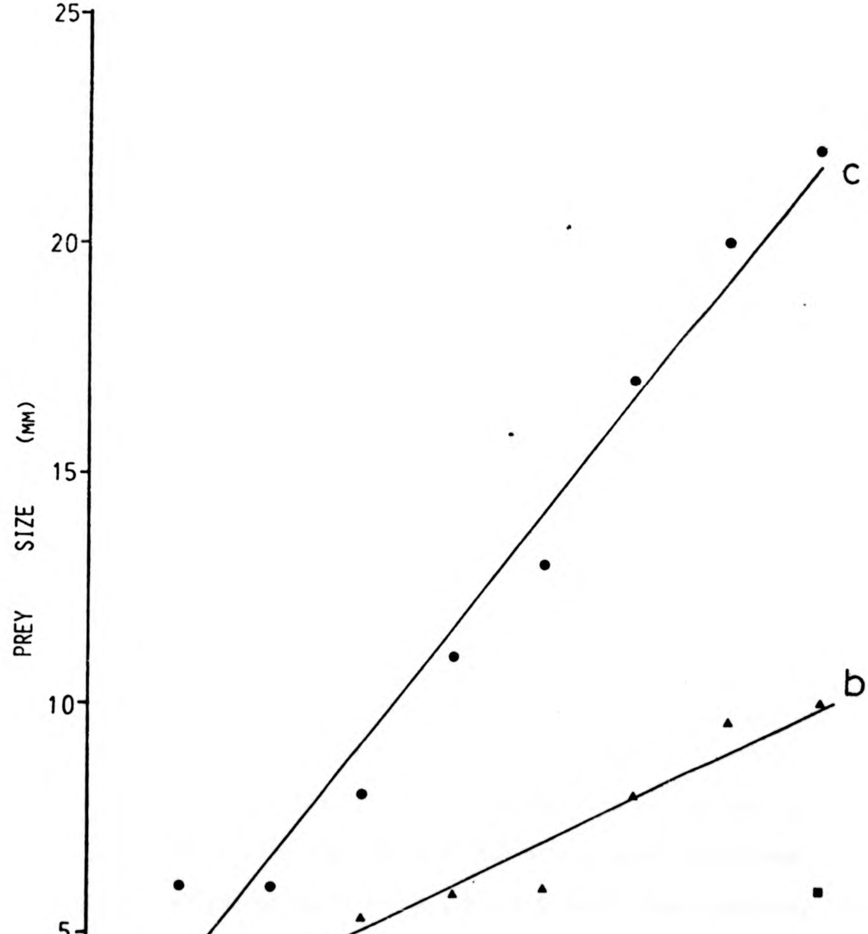
Amphipods as a group had comparable frequency of occurrence values throughout the whole fish size range examined, but the actual size of amphipods in the fishes stomachs clearly varied with the predator size. Fig 13 shows the relationship found between body length of amphipods and that of S. spinachia. The correlations between the mean maximum amphipod length (line C in Fig 13), mean amphipod length (line B in Fig 13) and fish size

Fig. 13. The relationship between the size of prey (amphipods) and the body length of S. spinachia.

Line a_1 = mean minimum prey size, r = 0.718

Line b = mean mean prey size , r = 0.979

Line c = mean maximum prey size, r = 0.985.


PREY SIZE (MM)
25
20
15
10
5
0
FISH SIZE (CM)
4
5
6
7
8
9
10
11
12
c
b
a1
a2

were highly significant (p 0.001). The mean minimum amphipod size also increased with increasing fish size (line A, in Fig 13), but the relationship was not as pronounced as in the case of mean maximum amphipod length and mean amphipod length ($p = 0.05$). If line A, in Fig 13 is examined, it will be seen that mean minimum prey size remained relatively unchanged over the greater part of the predator size range, between 50–110 mm, a considerable increase being noticeable only in the 120 mm predator size group. When the mean amphipod length for this size group was excluded from the calculations, the correlation between the mean minimum amphipod length and predator length was no longer significant. (Line A_2, Fig 13). This suggested that the observed relationship between the mean amphipod length and fish size was mainly due to an increase in maximum size of prey taken rather than an increase in minimum size, the slopes of the lines A_1, B and C further demonstrating that the sharpest increase was observed in the mean maximum prey size and the least increase in mean minimum prey size. The size range of prey taken thus increases greatly as the fish size increases.

Although, as mentioned above, the occurrence of amphipods as a group did not change greatly throughout the fish size range, the importance of different species did vary with fish size. The larger amphipods, such as gammarids increased in importance as the fish size increased, and conversely the smaller bodied amphipods such as *Nototropis* sp and especially *Microprotopus* sp decreased. Table 55 shows the percentage quantities of common species of amphipods taken by different size groups of *S. spinachia*.

Table 55. Relative importance of different types of amphipods in different size groups of *S. spinachia*, expressed as a percentage of the total number of points gained by each species of family throughout the size range.

	Fish body length (cm)									
Amphipod type	3	4	5	6	7	8	9	10	11	12
Gammaridae	-	-	7	8	6	12	14	13	19	21
Corophium sp	-	-	-	-	9	14	16	11	35	15
Caprellidae	-	-	15	-	45	13	2	16	9	-
Hyale sp	-	-	26	32	14	9	4	8	5	2
Nototropis sp	-	21	35	23	11	4	1	3	2	-
Microprotopus sp	19	26	22	17	10	3	1	1	-	1

Like gammarids, mysids could also not be found in fish stomachs in July, although they were plentiful in the environment. When the occurrences of mysids in different fish size groups were calculated, it was found that feeding on mysids begins to be important above 70 mm total length, although they also occur occasionally in the 50 mm and 60 mm size groups. The lack of mysids in the fish stomachs in July was probably a result of the fishes being smaller (mean fish length in July was 42 mm) than the lowest total length at which mysid feeding begins to be important.

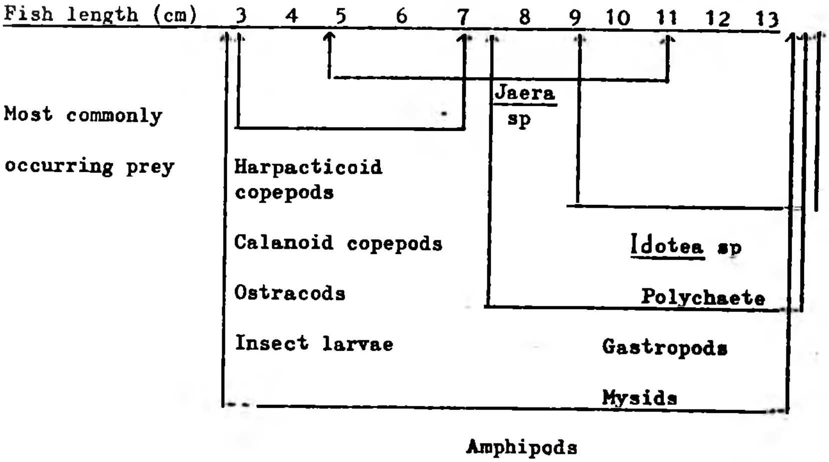
Among the isopods Idotea sp occurred in significant quantities above 90 mm total length. Smaller bodied Jaera sp occurred over a wider size range.

Fig. 14 summarises the relationship observed between food types and fish size.

2) Myoxocephalus scorpius

As suggested earlier, the amount of amphipods in the stomachs of M. scorpius was dependent on the total length of the fishes in the sample. Amphipods became important in June and July when juveniles appeared in the samples. They formed 98% of the food of the fishes with a total length between 27 and 50 mm.

Fig 14. The relationship between the fish length and type of food in S. spinachia.

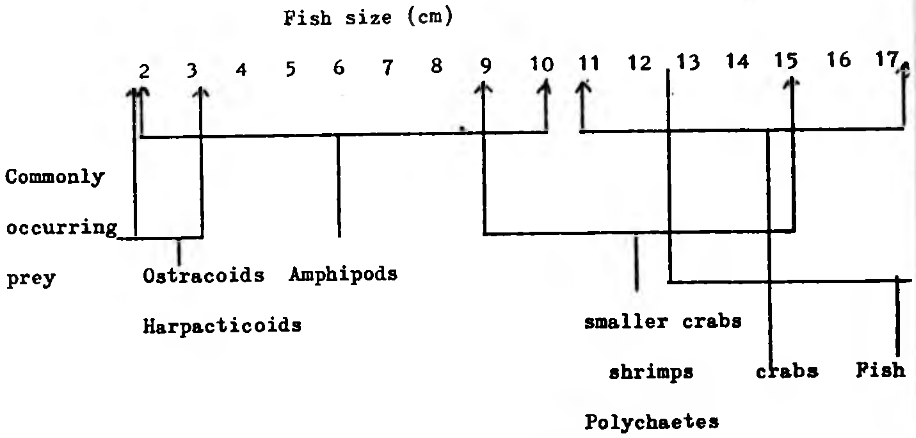

Fish length (cm) 3 4 5 6 7 8 9 10 11 12 13
Jaera sp
Most commonly occurring prey
Harpacticoid copepods
Calanoid copepods
Ostracods
Insect larvae
Idotea sp
Polychaete
Gastropods
Mysids
Amphipods

There was also a secondary division of amphipods which was related to the total fish length. In the 50+ mm size group, the commonest amphipods were gammarids. The PO and PP values for Ampelisca sp, Corophium sp, Nototropis sp and Microprotopus sp decreased in that order as the fish size increased from 20 mm to 50 mm. Lower proportions of smaller bodied amphipods were taken as the fish size progressively increased. Other smaller bodied prey, ostracods and harpacticoids were only important in the diet of the smallest fish with total lengths between 20-30 mm.

In the July samples most fish were juveniles. The food division within the fish size groups followed the same pattern as in June, that is, the largest fish fed primarly on large Carcinus. In the diets of intermediate sized fish, smaller crabs were important as well as shrimps and in the 9-10 cm group large amphipods, gammarids and Ampelisca sp began to gain importance. PO and PP values for both increased as the fish size progressively decreased while the proportion of smaller bodied amphipods Nototropis sp (mean total length, $\overline{TL}$ = 3 mm) Microprotopus sp ($\overline{TL}$ = 2 mm); Monoculopsis sp ($\overline{TL}$ = 2 mm) decreased with increasing fish size. The values for harpacticoids were similar to those of smaller amphipods. In August, adult M. scorpius were found once again to be feeding predominantly on shore crabs. Crabs or shrimps occurred extremely rarely in the fishes with a total length below or equal to 60 mm. Fish as prey only occurred in M. scorpius larger than 120 mm.

Fig 15 summarises the described selection in M. scorpius.

Fig 15. The relationship between fish size and the type of prey in M. scorpius.


Fish size (cm)
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Commonly occurring prey
Ostracoids
Harpacticoids
Amphipods
smaller crabs
shrimps
Polychaetes
crabs
Fish

It was concluded that there was a well defined size-related feeding heterogeneity in M. scorpius as the type and proportion of the food taken altered with the size of fish.

3) Taurulus bubalis.

On the whole, sample sizes and the size range of fish in the samples were smaller in T. bubalis than in M. scorpius. The size range of T. bubalis was 38-168 mm whereas in M. scorpius it was 24-230 mm. When similarly sized individuals were compared however, T. bubalis seemed to prefer smaller sized food than M. scorpius. This may explain the considerable difference found in the principal food types between the two species. As stated earlier, bulky crabs and shrimps form the main food of M. scorpius whereas amphipods, polychaetes and isopods are more important to T. bubalis. Other differences in the diet were probably related to habitat preferences of the fishes.

In the July samples, the number of juveniles of T. bubalis like those of M. scorpius, were large. Once again it appeared that among juveniles, smaller amphipods such as Microprotopus sp; (mean total length in juveniles stomachs = 1.5 mm); Urothoe sp ($\overline{TL}$ = 2 mm); Bathymedon sp ($\overline{TL}$ = 2 mm) were more frequent in juveniles. The small sample sizes precluded, however, any detailed size analysis. Larger bodied Isopods such as Idothea sp were found in higher proportions in larger juveniles. In smaller fish, only small sized Jaera sp were found.

Although selection of smaller prey by smaller fish was apparent in most fishes, size-related feeding heterogeneity was not always well defined. In Pomatoschistus minutus for example, the food of the fishes at both ends of the size range were markedly different. At one end, 7 cm fish were capable of taking shrimps, large proportions of *Ampelisca* sp and polychaetes. At the other end, 3 cm fish took more harpacticoids, ostracods and smaller amphipods, but the boundaries of the fish size groups where the changes from one type of food to another occurred were not clear. Both small and large food organisms appeared to be finally taken by all fish size groups between 3 cm and 7 cm. It was concluded, therefore, that in *P. minutus* size related food heterogeneity was not clearly defined.

Size dependent food selection was also clear in juvenile *G. morhua*, *P. virens*, *P. platessa*, *P. flesus*, *P. gunnellus* and *Syngnathus* sp, but less clear in the other species examined. Size selection was also apparent in plankton feeders; where in smaller members, small bodied species such as *Pseudocalanus*, *Temora*, *Paracalanus* and juvenile *Calanus* were abundant and larger prey such as adult *Calanus*, *Centropages* sp were rare. The proportion of the latter were much higher in the larger specimens. Also, in *A. presbyter* fish larvae were found only in the very large specimens and did not occur in others.

COMPARISON OF THE FOOD AND FEEDING RELATIONSHIPS OF THE INSHORE FISH OF LOCH ETIVE.

Most studies of the feeding habits of fishes imply that the fishes are generalists, emphasising the variety of prey found in their diets. Much of the earlier work on the fish communities was carried out in freshwater systems.

Hartley (1940) analysed the food of coarse fish in English waters and came to the conclusion that there were wide interspecific similarities among the fish concerned. Later Frost (1946) examined the food relationships of freshwater fish in Windermere; she found that the food requirements of most fishes are closely related and often overlap. In 1947 Hartley investigated the feeding habits of estuarine fishes. He reached the conclusion that there was some division of food among the fishes and classified them into four groups. 1. Fish without competitors, 2. Fish whose food consisted of organisms for which there was little competition, 3. Fish which fed on the commonest organisms but which had a wide choice of foods, 4. Fish which had many competitors for the bulk of their food. In 1948 he once again examined the feeding relationships in a community of freshwater fishes in Westmorland, showing that no two species had identical feeding habits and concluding that there was much competition between the fish.

More recently, Keast (1965) examined resource subdivision among the freshwater fish community in an Ontario Lake. He showed that the diets of fish overlapped only when food sources were abundant, otherwise there was a marked tendency for the fish to concentrate on different food organisms. He also found the competition between different size groups within the fish species was limited.

Zaret and Rand (1971) examined the food of nine freshwater fishes in a tropical stream in Panama. Their results were similar to those of Keast in that dietary overlaps were minimal when the food was least abundant, in this case, in the dry season.

Food resource partitioning among marine fish has been studied by several authors. Skalkin (1959) examined the flatfishes of a Northern Pacific locality and showed that related species had different predation tendencies in terms of their major prey. Richards (1963) investigated the food of juvenile fish populations of Long Island Sound, and found that different species of fish had different feeding habits. Nagabushanam (1965) examined the food of gadoids from the Isle of Man; he similarly found that the food resources were divided among the related species. Gibson (1968) investigated the food and feeding relationships of littoral fish in the Banyuls region. He found that the majority of fish species examined were carnivores feeding mainly on crustaceans. In 1972 he looked at the feeding relationships of intertidal fish on the Atlantic coast of France. He once again found that crustaceans, especially amphipods form a large part of the food in most species, although the importance of other groups varies considerably. Tyler (1972) found that marine demersal fishes showed relatively little overlap in their diets and that there was a division of food resources among the fishes.

In this section, the diets of all the species will be compared and an attempt will be made to assess the feeding niche each fills in the community as a whole.

COMPARISON OF MODES OF FEEDING.

The food analyses of the twenty two species showed that all species examined fed almost exclusively on animal food. Algae formed a very small fraction of the diet in most species and it is concluded that it was probably taken accidentally. The fish may be grouped into three categories according to their feeding habits.

1) Plankton Feeders

Atherina presbyter, *Chaparrudo flavescens* and *Hyperoplus lanceloatus* were predominantly plankton feeders. *Chaparrudo flavescens* took plankton in October, November, January, February, April, May, June but in December took a large proportion of benthic food in addition to plankton and in July fed completely on benthos. *Atherina presbyter* similarly took zooplankton in most months, but like *Chaparrudo flavescens* its food became predominantly benthic in December and July. Whether the observed change from planktonic food to benthos in the same two months in these fish was caused by a common environmental factor or was coincidental is not known. It is significant, however, in demonstrating that these plankton feeders are capable of benthic feeding under certain conditions.

2) Mixed Feeders.

G. aculeatus, though primarily a benthic feeder, took large proportions of planktonic food in spring, late summer, and especially in autumn. In September and October zooplankton became its primary food. It is likely that the small size of zooplankton and their increased abundance rendered them a suitable food at this time. Plankton feeding, however, was not as pronounced in spring. Similarly, juvenile Gadus morhua and Pollachius virens took planktonic food in some months. In Pollachius virens the food was predominantly planktonic in May, June and September. Gadus morhua took higher amounts of plankton than Pollachius virens, mostly in spring and early summer. There was no sample in autumn for this fish. In both fishes plankton feeding may thus be a reflection of increased zooplankton abundance following the spring and autumn blooms, as well as being dependent on the size of the fishes in the samples. Nagabushanam (1965) mentions that plankton feeding in gadoids occurs in juveniles in their pelagic phase and continues until they reach a length of 53 mm. In September, however, plankton was found to be the chief food of larger P. virens with a size range of 113-142 mm, which showed that plankton feeding may not entirely depend on fish size.

3) Benthos Feeders

The majority of the species examined belong to this category. Occasional planktonic food, especially calanoid copepods was taken in small quantities by otherwise essentially benthic feeders such as P. minutus, P. microps, P. gunnellus, A. cataphractus and S. spinachia. Generally the occurrence of planktonic food did not show a seasonal pattern but was associated more with the occurrence of smaller fish in the samples. This probably means only that small fish took calanoid copepods because they were suitably sized and occurred in shallow water around algae, rather than a distinct change of feeding habit. In September, however, a group of adult S. spinachia, which are true benthic feeders, were found to have been feeding on zooplankton. In this case zooplankton feeding was clearly not associated with small fish size. No planktonic food was ever found in the stomachs of M. scorpius and T. bubalis reflecting their truly demersal mode of life.

Insects of aquatic and terrestrial origin occurred in the diets of several species, although their proportions in the diet were often small. They were relatively well represented in the diet of G. aculeatus and also occurred to a much smaller extent in S. spinachia, P. gunnellus, P. minulus, P. microps, P. platessa, P. flesus, Z. viviparus and C. melops. Their occurrence in fish stomachs was irregular and often restricted to summer and autumn months. Although they never became an important part of the diet, they demonstrated the flexibility in the feeding habits of these species.

Fish were only found in any numbers in the diets of M. scorpius, T. bubalis , but were also present to a lesser extent in G. morhua, P. virens and P. flesus.

The examination of the food of different fish hence showed that although majority of fish found in the shallow waters of Loch Etive were essentially benthos feeders, a whole range of types exist whose feeding habits range from complete plankton feeding to complete bottom feeding.

DIVISION OF FOOD RESOURCES AMONG THE FISH POPULATION.

Among the 21 fish species examined, 27 major food groups (amphipods, isopods etc.) and 115 species were identified. The food composition lists for 18 species given earlier show that some food types are more extensively utilized than others. Crustaceans were by far the most common food in every fish species examined. This is similar to Gibson's (1968, 1971) results where he found crustaceans were the main food of both littoral fish of Banyuls region and intertidal fish of the Atlantic coast of France.

In Loch Etive the lowest values for crustacea were found in P. platessa, P. flesus and T. bubalis, although even there they made up from 49 to 62% of the total amount of food consumed. Values for crustacea as high as 91% and 93% were found in S. spinachia and H. lanceolatus, and A. cataphractus fed solely on crustacean food. The proportion of different major groups of crustacea showed, however, much variation between species and will be more fully discussed later.

Non-crustacean food which was relatively important belonged to the groups Polychaeta, Mollusca and Insecta. The group

Pisces, represented as fish, fish larvae and fish eggs was also not uncommon. Other food groups such as Nemertini, Hydrozoa, Chaetognatha, Ophiuroidea, Actinaria, and Rotifera were rare, occurring in three or fewer fish species.

In order to compare the diets of different species in more detail, the fish and the major food groups have been arranged as a partition plot in Table 56, following Tyler's (1972) method. The food groups which were considered to be most important in the diet of any one species were taken as those which had PO and/or PP values equal to or greater than 10%.

In Table 56 predators are arranged so that those which show the greatest similarity in their major food groups are adjacent to one another. The percentage overlap, or reoccurrence of food groups in more than one predator species, is calculated by the total number of reoccurrences of prey groups among predators divided by the total number of possible reoccurrences in the partition plot. One reoccurrence means that a prey group occurs in two predator species. The total number of possible reoccurences is calculated as the number

Table 56. Partition plot showing the major food groups of 18 fish species. An entry in the Table indicates that that particular food group had a PO and/or PP value equal to or greater than 10%.

Food Group \ Fish species	P.minutus	P.microps	S.spinachia	T.bubalis	Z.viviparus	M.scorpius	P.gunnellus	G.morhua	P.virens	A.presbyter	H.lanceolatus	C.flavescens	G.aculeatus	N.lumbriciformis	C.melops	A.cataphractus	P.platessa	P.flesus	Totals
Amphipoda	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	16
Isopoda			+	+	+	+								+	+			+	7
Mysidacea			+																1
Shrimps						+		+											2
Crabs				+	+	+													
Decapod larvae										+	+								2
Calanoid copepods								+	+	+	+	+	+						6
Harpacticoid copepods							+	+	+				+	+					5
Cladocera										+	+		+						3
Cirripedia													+						1
Ostracoda														+	+				2
Cumacea																+			1
Polychaeta	+	+	+						+	+							+	+	7
Mollusca															+		+	+	3
Insecta													+						
Total no of major food groups	2	2	3	4	3	3	3	4	4	5	3	2	5	4	4	2	3	4	60

of fish species minus one, multiplied by the number of major prey groups. In the present investigations, the number of reoccurrences between major food groups were 60, and the total possible number of reoccurrences 255, giving a percentage reoccurrence value of 23.5%. Table 56 shows at a glance that although the same food groups occur repeatedly in different fish species, when the overall distribution of these major food groups is compared the apparent similarity of diets is greatly reduced, suggesting a tendency for the food resources to be segregated.

The number of major food groups eaten by each species varied between 2 and 5 with a mean value of 3, showing that most fishes depended on relatively few food groups as their major food. It must be remembered that in the partition plot, food groups, instead of actual prey species are used and this grouping tends to reduce the differences between the predators' diet and to increase similarity. Regardless of this fact, Table 56 shows that, except for P. minutus and P. microps, no two species had exactly the same distribution of major food groups. This indicates that, even using this relatively crude comparison, the diets of these fishes are sufficiently different to prevent masking by the grouping of prey species. Judged by this method, both P. minutus and P. microps appeared to eat the same major food groups; namely amphipods and polychaetes. When the proportion of different amphipods species in both fishes are compared however, some differences become apparent. (See Tables 20 and 22).

Using partition plots to compare the similarity of diets of fishes Tyler (1972) found the percentage of reoccurrence of prey species was 24% in the winter and 16% in the summer. He concluded from his results that the fish were specialized predators in terms of their major preys. He also worked out partition plots from Nagabushanam's (1965) data on the food of gadoids and Skalkin's (1959) on the food of pleuronectids. He found only 10% at possible reoccurrences of principal prey among the pleuronectids and 15% in the gadoids. The results of the present study are thus comparable with their findings.

The significance of crustacean food in the fishes diet is also apparent from Table 56 as 49 out of the 60 major food groups belonged to crustacea. Among all crustacean, amphipods were the most important group. They occurred in all fishes with the exception of H. lanceolatus and were a major food group in all except Chaparrudo flavescens. The lowest value was found in Atherina presbyter where they made up only 10% of the total amount of food and consisted of both benthic and planktonic forms. In all other fishes they were present as benthic amphipods. PO and PP values were also relatively low in G. aculeatus, P. virens, G. morhua and N. lumbriciformis. The importance of amphipods in the diet of M. scorpius is also low but is masked in the overall food composition of the fish by the very high occurrence of amphipods in the large June and July samples. If the samples of these two months are excluded, amphipods make up only 10% of the total food in the remaining months.

There were also differences in the relative importance of different species of amphipods in different fishes. 22 species of amphipods were found to occur in 17 fish species but the types which were extensively utilized by the most fish were relatively low. The most commonly occurring amphipods were Gammarids, Corophium sp, Microprotopus sp, Nototropis sp, Ampelisca sp and the family Caprellidae. Amphithoe sp, Hyale sp were also found to occur frequently. Other species listed had occurrences common to 4 or fewer fish species.

Gammarids were often of primary importance in the diets; especially in S. spinachia, M. scorpius, T. bubalis, P. gunnellus, P. virens and to a lesser extent in G. aculeatus, P. flesus and G. morhua. Corophium sp was most important in P. flesus. G. aculeatus and P. microps, but also made up 10-24% of all amphipods in T. bubalis, G. virens, P. minutus, G. morhua, M. scorpius and P. platessa. Hyale sp was relatively important in G. virens, G. morhua and S. spinachia. Microprotopus sp, though common to most fish species and having a relatively high frequency of occurrence, usually made up only a very small proportion of the amphipods, except in plaice, P. gunnellus, P. minutus and P. microps. It gained primary importance only in C. melops and A. cataphractus. Caprellids similarly occurred in most fishes but in relatively small amounts except in A. cataphractus, C. melops and to a lesser extent in P. gunnellus. Ampelisca sp made up 56% of all amphipods in P. platessa, 38% in P. minutus,, 23% in M. scorpius and 20% in G. morhua but occurred in much smaller amounts in other fish.

If the relative proportions of different types of amphipods in different fish are examined, two generalisations can be made:

1. The number of different species of amphipods are large, but the ones which are extensively utilized by the majority of fish are relatively few; different fish take mostly similar types.

2. Although the same few species are repeatedly taken by different fish, the proportion of the different species in the diet of each predator is significantly different.

The second point above is clearly demonstrated when the relative proportions of different amphipod species are compared between predator species. The degree of overlap in terms of amphipods between fish species was calculated using the overlap measure of Morisita (1959) as modified by Horn (1966) and later by Zaret and Rand (1970). The similarity coefficeint (C_λ) varies from 0 when the samples are completely distinct (containing no amphipod species in common) to 1 when the samples are identical with respect to the proportion of amphipods.

For these calculations the percentage point values for each amphipod species in each fish diet were used. They were first converted to the actual proportion of the total amount of food in a fish diet. The similarity coefficient is calculated from the following formula:

$$C\lambda = \frac{2 \sum_{i=1}^{S} X_i \; Y_i}{\sum_{i=1}^{S} X_i^2 + \sum_{i=1}^{S} Y_i^2}$$

Where S is the total number of amphipod species, X_i is the proportion of amphipod i in the diet of species X, and Y_i is the proportion of amphipod i in the diet of species Y. Table 57 gives the results of these overlap calculations. Any value greater than or equal to 0.60 is accepted as showing significant similarity. (Zaret and Rand, 1970).

It is clear from the C λ values in Table 57 that the proportions of different species of amphipods taken by most fish are dissimilar for the majority of fishes, as in only 18 out of a total of 78 comparisons does C λ equal or exceed 0.60. S. spinachia, T. bubalis, M. scorpius, P. gunnellus and to a lesser extent P. virens take similar proportions of the same types of amphipods. Also the proportions of amphipods in the diet of P. minutus and P. platessa are similar. When C λ for pairs of related species are examined, it will be seen that the

Table 57. Results of Amphipod similarity calculations comparing the proportions of amphipods taken by different species. The figures in the Table are values for the similarity co-efficient ($C\lambda$) as calculated from the formula given in the text.

	M.scorpius	T.bubalis	P.gunnellus	P.minutus	P.platessa	P.flesus	G.morhua	P.virens	P.microps	C.melops	A.cataphractus	G.aculeatus
S.spinachia	0.79	0.91	0.97	0.17	0.11	0.28	0.36	0.63	0.25	0.17	0.39	0.43
M.scorpius		0.82	0.78	0.64	0.64	0.39	0.55	0.58	0.39	0.22	0.30	0.49
T.bubalis			0.88	0.30	0.19	0.56	0.40	0.65	0.55	0.25	0.39	0.61
P.gunnellus				0.18	0.14	0.23	0.26	0.55	0.21	0.24	0.54	0.37
P.minutus					0.19	0.52	0.47	0.23	0.51	0.19	0.37	0.25
P.platessa						0.28	0.48	0.11	0.29	0.23	0.40	0.18
P.flesus							0.36	0.44	0.97	0.19	0.13	0.52
G.morhua								0.60	0.42	0.22	0.23	0.73
P.virens									0.28	0.21	0.21	0.78
P.microps										0.30	0.20	0.60
C.melops											0.62	0.29
A.cataphractu												0.16
G.aculeatus												

extent of the use of different amphipods is significantly similar between M. scorpius and T. bubalis ($C\lambda = 0.92$) but the values of the similarity coefficient is much lower in other related species: $C\lambda = 0.60$ for cod and saithe, 0.52 for P. minutus and P. microps; 0.43 for S. spinachia and G. aculeatus and 0.28 for plaice and flounder.

The results in Table 57 indicate that sufficiently different proportions of amphipods are taken by predator species to reduce further the similarity between the fishes diets.

The second most important crustacean food was isopods, occurring in 17 predator species out of 18 and in 7 of them they became a major food group. (Table 56). They were particularly significant in S. spinachia, P. gunnellus, Z. viviparus, and C. melops. Relatively few species were identified, but as in the case of amphipods, there are indications that different species taken by different predators; for example P. gunnellus fed almost exclusively on Jaera sp, whereas M. scorpius mostly took Idotea sp.

Mysids occurred in 14 predator species but only once (in S. spinachia) did they become one of the major food groups.

Shrimps occurred in seven predators and crabs in 10, reaching significant amounts in the diets of M. scorpius and G. morhua in terms of shrimps and in M. scorpius, T. bubalis and Z. viviparus in terms of crabs. Decapod larvae were important in the diet of the two plankton feeders, Atherina presbyter and H. lanceolatus but were not utilized by Chaparrudo flavescens. They were also relatively important in partial plankton feeders such as cod and saithe, but not in G. aculeatus.

Calanoid copepods were the major food of all plankton feeders and were also important in the partial plankton feeders cod, saithe and G. aculeatus. Cladocerans were common to 8 fish species; their overall importance was not as high as calanoid copepods and highly seasonal. Harpacticoid copepods were found to occur in all fish species examined. The highest amounts were found in N. lubriciformis where they made up 34% of the total food; their proportion in other fish varied between 0.1% in T. bubalis to 12% in juvenile cod. They mostly occurred in the juvenile members of predators. Ostracods, like harpacticoids were common to most fish, occurring in small amounts. They became a major food group only in N. lubriciformis and C. melops. Except in these two instances, and like harpacticoids, their occurrence was highly correlated with small fish size. Cumaceans occurred in 9 fish species in minor amounts, gaining significance only in A. cataphractus.

Polychaetes were the most important non-crustacean food group common to 15 predator species out of 18. Their proportion in different fishes diets showed much variation, from 1% in cod to 34% in plaice. As might be expected they were most important in the diets of the truly benthic species, Plaice, flounder, P. microps, P. minutus and T.bubalis. In the diet of Atherina presbyter they were present as planktonic larvae. The commonest families, occurring repeatedly in many fishes were Nereidae and Phyllodocidae. As in the case of amphipods, there were indications of some families being more common in some predators than others. As most of the polychaetes could not be identified however, no comparison of similarity of diets with regards to their proportions was possible.

Molluscs, mainly gastropods and bivalves were also commonly taken by 15 species but their occurrences and relative amounts were often small. They became a major food group only in plaice, flounder and C. melops. Once again, some species, such as plaice, mainly took bivalves, and others like T. bubalis more gastropods, They were present in plankton feeders as planktonic larvae.

Insects, like molluscs and polychaetes were common to 15 predator species out of the 18 examined and were taken in varying proportions. Insect larvae were more common than the adults in the diets. Insects were a major food group in G. aculeatus where they comprised 21% of diet, but were also relatively important in P. microps, P. gunnellus, and S. spinachia.

This comparison of diets emphasises the conclusion reached earlier, namely that relatively few major food groups are used by predators and that the main differences between diets are caused by different degrees of utilization of the same group rather than feeding on entirely different groups. In this respect, no specialists, i.e., which use one food source exclusively were found among the fishes of Loch Etive. Within any one fish species the major types of food often did not alter throughout the year, although their relative importance sometimes changed. In T. bubalis, for example, polychaetes were more important in the winter months than the summer. Seasonal variation in the proportions of food taken may reduce the similarity of the diets between species even further.

It is also necessary to consider briefly the food division within a predator species. It has been mentioned earlier that in most species the food of juveniles differed considerably from that of larger individuals. As an example, juvenile *Spinachia* took many harpacticoids, ostracods and small amphipods, whereas larger specimens fed more on mysids, polychaetes and large amphipods. As the fish size changed, the proportion of different species of amphipods in the diet also changed. The difference in the diet of juveniles and adults were very marked in *M. scorpius*, *G. morhua*, *P. virens*, *P. platessa* and *P. flesus*. In *M. scorpius* smaller individuals fed almost entirely on amphipods, and the proportion of ostracods, harpacticoids decreased with increasing body length. In this species, once again, it was found that the type of amphipods eaten varied with fish size. Such differences in the diets of growth stages of a species are of course obscured when the diet of the species as a whole is considered. This clumping produces apparent similarities in the feeding habits of different species, but on closer examination these similarities are not as obvious and may completely disappear. For example, the diet of young M. scorpius is fairly similar to that of adult S. spinachia whereas the adults of these two species feed on very different types of food. Presumably the larger fish ignore the smaller food items because of the high energy outlay necessary to obtain sufficient quantities, or, in case of benthic animals, they may be harder to pick up from the bottom. On the basis of such observations it is suggested that the age groups of any one species are not or are in only limited competition with each other for food. When the diets of both young and adult fish are relatively similar as in the case of P. minutus intraspecific competition would still not be important as larger forms are capable of feeding on a wider variety of food than smaller specimens.

Taking all the above remarks into consideration, it is clear that the food resources available to a fish population are partitioned both inter-and intra specifically and that competition, if it exists at all, is most likely to occur between similar sized individuals of the same species, and possibly, also between different length groups of different species.

As a summary, it can be stated that in Loch Etive, between no two species was a true identity of feeding habits found when the proportions of different food types were considered. The differences between the diet of one species and another were often in the proportions in which the most commonly occurring food types were eaten rather than the exploitation of totally different sources of supply. It is thus thought that no true competition exists between the fish species in Loch Etive.

GENERAL INTRODUCTION

The results of the ecological work presented in Part I suggested the possibility that the fish were showing a certain amount of selection towards their food.

For example, a few prey species were dominant in the diet of most species. As discussed earlier, this was thought to be mainly due to the greater abundance of the dominant prey species in the environment. The possibility of some selection could, however, not be excluded.

It was also noticed that in a large number of species, that the size of prey taken was related to the size of the fish, larger prey being found in the stomachs of larger fish. Such observations are not uncommon in the study of the feeding habits of fish and several workers have demonstrated that prey size in fish stomachs correlates well with fish size (Kohler & Fitzgerald 1969; Schultz & Northcote 1972; Tyler 1972; Moore & Moore 1973). Such a relationship could be due either to an active selection for prey size or a function of prey catchability or both.

The ecological study further showed that most of the fish species examined were feeding on prey which was capable of movement. The percentage of fast moving prey such as mysids or amphipods was higher in the diet of some fishes than others, other fish species fed mainly on slow moving prey such as polychaetes. The proportion of sedentary prey, bivalves for example, was high only in the diet of a few fish species. It was considered that, in some fishes at least, the selection of moving prey could be either inherent or acquired by learning. This selection, if it existed might also be dependent upon the type and speed of the movement.

All these points suggested the importance of external features of prey such as size and movement which might influence the prey preferences.

The aim of the second part of the present work was to study experimentally the behavioural factors affecting the feeding in order to determine which external stimuli presented by the prey resulted in its selection by the fish.

Detailed descriptions of fish predatory behaviour under laboratory conditions are relatively rare. Tugendhat (1960) examined the feeding behaviour and the effects of satiation in the three spined stickleback Gasterosteus aculeatus. Brawn (1969) looked at the general feeding behaviour of cod Gadus morrhua. More recently Olla, Samet and Studholme (1972) have given a detailed account of the activity and behaviour of summer flounder Paralichthys dentatus and Chiszar and Windell (1973) analysed the components of feeding behaviour in bluegill sunfish Lepomis macrochirus.

Studies of the many different aspects of prey selection are also rare. Early studies mainly investigated the ability of fish to respond to different pairs of stimuli. Rowleys (1934) found that goldfish could differentiate between two circles one 10% larger than the other. Hafen (1935), measuring the responses of Phoxinus laevis to different colours, showed that they preferred yellow and green to red, blue and violet. If, however, the same fish was fed on red meat, they later preferred red, demonstrating the effect of learning on colour discrimination. Zunini (1937) investigated size discrimination in the same fish. Hager (1938) examined contrast preferences and pattern recognition in Phoxinus laevis and Eupomotis gibbosus (L.). Meesters (1940) made some observations on size preference in Phoxinus laevis. He also investigated shape recognition by offering the fish triangles and squares in different orientations or presenting the fish with figures on uniform or patterned backgrounds. In addition he found that untrained Gasterosteus aculeatus gave the maximum response to shapes which were closest to their natural food. His experiments on the effects of movement showed that the speed of movement which the fish found most attractive corresponded closely to the speed of movement of their natural prey. Kettner (1948) investigated the colour discrimination in different species and divided them into different groups according to their ability to differentiate between colours. He found that different species differed widely in their colour recognition. Herter (1953) examined spontaneous and trained responses of fish to different shapes and shades and found that most fishes could differentiate between different shapes and shades.

In most of the above studies, the workers did not use enough subjects or a sufficiently rigorous experimental design to allow firm conclusions to be drawn. Their results, nevertheless, are interesting in that they show the wide differences that exist in the responses of different species to visual stimuli.

As it was not possible to investigate factors affecting food selection in all the fishes covered in the ecological studies, three species were chosen to act as representatives. These were Spinachia spinachia; Pholis gunnellus and Myoxocephalus scorpius. Spinachia spinachia is a midwater fish feeding almost exclusively on small crustacea. Pholis gunnellus is a bottom living fish with similar food habits as Spinachia. Myoxocephalus scorpius is also a bottom living fish with entirely different feeding habits from the first two species. All three species could be found in reasonably large numbers throughout the year and detailed information on their natural diets was already available. It was considered that a study of the behavioural aspects of feeding under laboratory conditions of these species could contribute to a better understanding of their feeding habits in the field; whether, for example, they showed any form of prey selection or whether they were exclusively opportunistic.

From a behavioural point of view, no studies on Spinachia or Pholis exist in the literature although there is a large amount of published work on the several aspects of behaviour in Gasterosteus aculeatus, a stickleback related to Spinachia (Tugendhat 1960; Beukema, 1968).

Before any experimental analysis of the effects of various visual stimuli on the feeding of these three species could be conducted, it was necessary to determine and describe their general pattern of feeding behaviour.

The three species were initially kept in tanks and general observations on their behaviour were made. Myoxocephalus scorpius was later abandoned as it was found to be behaviourally very inactive.

Once a knowledge of their general feeding behaviour had been gained, the response of Pholis and Spinachia to prey size and movement were examined experimentally. For Spinachia only the effects of shape and shade were further studied.

Finally, the results obtained from both species were compared.

FEEDING BEHAVIOUR OF S. SPINACHIA.

Methods:

A group of locally caught Spinachia spinachia were kept in a large circular tank for some weeks. Eight fishes of total length 80-110 mm were then placed into separate perspex tanks of 45 l capacity and observed individually..

The tanks were covered on three sides and at the bottom with graph paper so that the angles and distances could be measured. A black screen with a slit was placed in front of the tanks. The fishes were observed through these slits and with the help of mirrors arranged above the tanks at an angle of 45°.

The food offered consisted of chopped mussel gonads, squid pieces; freshly killed or thawed frozen mysids, live mysids and live adult Artemia which were grown on algal cultures to a suitable size of 6-10 mm in total length.

The sequence of actions during feeding and the various positions of the body in relation to food and to the tank boundaries were recorded on a tape recorder. The tapes were later transcribed for analysis.

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The sequence of actions during feeding and the various positions of the body in relation to food and to the tank boundaries were recorded on a tape recorder. The tapes were later transcribed for analysis.

BEHAVIOUR DURING ADAPTATION TO TANK CONDITIONS

When an individual S. spinachia was first placed in the rectangular tank, it kept close to the walls and corners of the tank. Swimming was very fast and the fish appeared to be very agitated. The pectoral fins were fanned rapidly (about 80 times/min), the head was turned from side to side and the fish repeatedly collided head first with the tank walls and corners, sometimes hitting them with great force. The number of times the walls were hit was quite high in the initial stages up to 48 times/min. Hitting of the walls and corners decreased later as the fish spent more time in the tank.

The fish mostly swam very close to the tank walls describing an eliptical course or a horizontal figure of eight which was repeated a number of times. It repeatedly swam to the bottom of the tank and then upwards in a circular course, almost touching the walls and giving the impression of chasing a moving object. The pattern of swimming and wall-hitting suggested that the fish might be reacting to its own reflection. This suggestion is supported by the fact that most of the swimming was done close to the front wall which was covered with a black screen and was more likely to act as a mirror than the other walls which were lined with white graph paper. As mentioned before, when the fish was first placed into the tank, it appeared very agitated. It seems unlikely however that agression would be displayed when the fish was stressed. The hitting of the front wall at these initial stages might therefore be due to the fish trying to escape through the only wall which looked transparent. This swimming close to tank walls persisted however and the repeated swimming up and down close to a wall on a more or less circular course was termed "reflection-chasing". The dorsal fin was erected occasionally during "reflection chasing". This and wall-hitting also suggested a defensive or agressive behaviour.

If conspicuous palatable prey was put into the tank when the fish was engaged in "reflection-chasing" and wall-hitting, no interest in the food was shown. Even if a lime prey, suspended from a long transparent tube was brought within 1-2 cm of a hungry fish, it was completely ignored.

When the fish stopped reacting to the tank boundaries, swimming became slower, regular and more random instead of the previous very rapid repetition of a pattern. The fish also began to accept food readily. When this state was reached the acclimatization period was considered to be complete. The time for adaptation to tank conditions was variable, but usually took 3-4 days.

"Reflection-chasing" and wall hitting were occasionally observed with acclimatized fish but such behaviour did not last for long periods. Whenever "reflection-chasing" or wall hitting were performed, no feeding took place, suggesting that the occurrence of one excluded the other.

BEHAVIOUR AFTER ADAPTATION IN THE ABSENCE OF FOOD

Once the fish stopped reacting to the tank boundaries it either swam or remained suspended in midwater. The fish could remain suspended motionless in the water for long periods either horizontally or almost vertically. The pectoral fins were moved slowly, about 48 times/min and the caudal fin undulated gently. The number of eye movements was low and a wide opening of the mouth was occasionally observed.

When swimming, the fish either moved horizontally or almost vertically. Most of the swimming was done in a relaxed fashion. It swam downwards head first with slow movements of the pectorals. The body usually assumed a narrow angle with the bottom of the tank though there were instances where it approached the bottom almost vertically, head downwards. It then changed direction and swam upwards again, approaching the surface through an angle or almost vertically. There was no fixed course which the fish repeated, swimming appeared to be random. It also swam at the same level, usually describing a circle by a full turn. Half turns by which the fish changed direction also took place.

Faster swimming in all planes occurred in short outbursts and was not continuous. Full turns and half turns were sometimes observed. The pectoral fins were fanned with great speed and the caudal fin also moved very fast.

"Yawning" (a wide gaping of the mouth) took place occasionally and was a distinct act. Yawning has been described for a number of other fishes. In pinfish Lagedon rhomboides it occurred together with strong erections of the dorsal fins and was found to be correlated with pressure changes (McCutcheon, 1966) Olla et al. (1972) hold the opinion that yawning is generally associated with the changes in activity. They found that in summer flounder, yawning preceeded some form of activity. Rasa (1971) similarly found that in yellow tail demoiselle, *Microspathodon chrysurus* activity increased following yawning. Tugendhat (1960) mentions that yawning occurs in *Gasterosteus aculeatus* in combination with erection of the dorsal fins and calls it a comfort movement. Morris (1958) in his studies of reproductive behaviour of ten spined stickleback, *Pygosteus pungitius*, called yawning a comfort movement and commented that yawning was most frequent when the fish was otherwise unoccupied.

In *Spinachia* yawning was not frequent. It occurred either singly or in succession, about 6-9 times in 30 mins. This is much less frequently than Olla, Samet. Studholme (1972) found for summer flounder, where up to 33 yawns were recorded in 30 min period. In *Spinachia* as in pinfish, three spined stickleback and ten spined stickleback yawning was frequently accompanied by the erection of the dorsal fins.

It was not clear from the observations whether yawning preceeded more intense activity or was in anyway associated with the position of the fish on the bottom of the tank or high in the water, i.e., in relation to pressure. For example it was not noticed that yawning took place specifically before the fish began to swim after having been suspended motionless or before a change in swimming speed or after a change in depth.

The speed and type of fin movements were naturally related to the movement of the fish, whether it was stationary or swimming; but in addition the speed with which the pectoral fins were moved was thought to serve as an expression of a particular state. For example, during the fixation of its reflection in the tank wall by a stationary fish, the pectoral fins would begin to beat very rapidly giving the fish an excited appearance.

The pectoral fins were usually beaten alternately with varying speeds. In certain states they were moved backwards and forwards in unison.

Erection of the dorsal fin was observed both during swimming and when the fish was motionless. Tugendhat (1960) states that in the three spined stickleback erection of the dorsal spines was associated with an abrupt stopping of movement. As mentioned above, McCutcheon (1966) commented on the association of yawns with pressure changes. In Spinachia erection of the dorsal fin frequently accompanied a yawn or occurred when the fish stopped swimming. Fin erection also occurred independently of yawns, however, during reflection-chasing, after swallowing too large a food or during swimming. Fin erection was probably involved in maintaining stability. Dorsal fin erection in Spinachia is thus performed for a variety of reasons.

In general it was possible to recognise three states typified by the various combinations of the actions described above. The states are summarised in Table . 58 .

Searching behaviour

When searching for food, the fish would swim horizontally with pectoral fins beating slowly and regularly. It would approach the bottom of the tank from the horizontal by tilting the head downwards and forming a narrow angle with the bottom. The angle of approach varied between 10-90° but usually was 45-65°. The eyes would move to examine the bottom, the head

Table 58 . Description of different "emotional" states observed in S. spinachia using various body actions as criteria.

Action State	Swimming	Pectoral Movement	Yawns	Dorsal Fin Erection
Relaxed	Slow, continuous regular or absent	Moved alternately 0.5-1 times/sec	Occasional	Occasional-rare
Excited	Fast, discontinuous	Moved alternately 2.1-2.8 times/sec	Rare	Rare
Stressed	Slow, jerky	Moved alternately or synchronously slow	Occasional	Occasional

would also be turned slightly. The fish then swam upwards, the area being examined all the time by eye movements and slight head turns. Changing of direction by full turns and half turns of the body also took place.

The fish was not able to see prey above or below it, neither did it respond to prey close to, but behind it, suggesting that the field of vision is fairly restricted and that vision plays the dominant role in food selection. Once the prey had been seen, the fish was able to capture it from the surface, the bottom or suspended in midwater.

Description of prey capture and feeding sequence

The feeding sequence began when the prey animal was sighted by the fish. If the fish was interested it orientated towards the prey (O), that is, it changed its body direction towards prey. The prey was then visually fixated (Fi) by converging both eyes upon it.

Fixation was followed by an approach towards the prey in a straight line (AP). Alternatively the fish could stop (ST); move on (MO) past the prey with a slight change of direction, or turn away from the prey (TA) with a full turn of the body.

ST could occur before the fish approached the prey or before it turned away and moved on. An approach was either followed immediately by an attack (AT); defined as a sudden dart towards the prey, or by a ST for a few seconds. If the fish stopped, the rate of movement of pectoral and caudal fins would increase to a maximum and the body would assume a typical S shape, called the S bend (SB) before attacking. Occasionally after stopping and showing an SB the fish would back (B), that is, swim backwards a short distance still facing the prey. If the fish backed, it could either reapproach the prey, move on or turn away.

If the attack was successful, the prey was grasped (GR) in the jaws by the head or sideways. If unsuccessful, a miss was recorded (M). If the prey was missed, the fish might either reorient, fixate approach and repeat the attack or it could move on in the same direction.

Once the prey was grasped, whether it was immediately ingested or not depended on the prey size. If the prey was of a suitable size it would be ingested (I), that is, be completely taken into the mouth either head first or if grasped sideways,from the middle of body by folding it into half.

If the prey was too large, it would be held between the jaws, (hold, H) while the fish swam round. The fish pressed its jaws tightly while holding the prey thereby killing it. The prey might then be spat out (SP) and the AT → GR → I sequence repeated. Alternatively, the fish might move on or turn away.

With palatable prey of a suitable size, ingestion resulted in swallowing (SW) and although there was no recognisable act which marked swallowing, a prey was considered to be swallowed when the fish began hunting again or engaged in other activities.

If the prey was large, chewing movements (CH) were observed before swallowing. Chewing usually implies crushing prey between the teeth, but in this case the movement suggested that the fish was breaking the prey by grating it against the gill rakers. The teeth of Spinachia are small and are grasping rather than biting teeth. (See Fig. 33).

The prey might then be swallowed or spat out whole or in 2-3 pieces. The fish then either regrasped the prey after repeating the O ⟶ P ⟶ AP ⟶ AT cycle and H was finally swallowed or abandoned.

After swallowing, regurgitation of prey (R) sometimes took place. R was differentiated from SP by the time interval passing after I. SP was usually instantaneous or preceeded the chewing movements. R, if it occurred, took place after the fish had swam for sometime or even captured another prey. After regurgitation the fish usually left the prey and moved on, turned away or in some instances it was regrasped, ingested and swallowed.

All the observed feeding acts and their relationships with one another are given in Fig 16. The left hand column in the figure with seven steps from 0 to SW shows the basic feeding sequence. Providing the fish was hungry, prey size and taste were suitable and the fish did not miss the prey during the attack stage, the feeding from 0 to SW could be completed without a break within a few seconds.

Deviations from the basic feeding sequence; sequence complexity and length.

Several factors appeared to effect the feeding sequence complexity. They were

a) hunger level of the fish

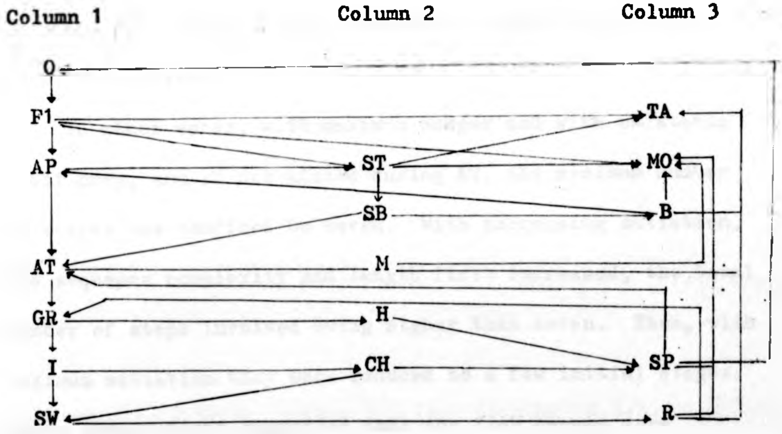
b) prey size

c) prey palatability

d) prey movement

a) With gradually increasing satiation, the basic chain might

Fig 16 . Diagram of the steps in the feeding sequence of Spinachia and their interrelationships. Those in column 1 represent the basic sequence, which involves actions towards prey; Column 2 shows intermediate actions; Column 3 shows the actions that result in the fish being further away from the prey.


Column 1
Column 2
Column 3
O
F1
AP
AT
GR
I
SW
ST
SB
M
H
CH
TA
MO
B
SP
R

break at any point before the swallow stage, and some of the steps shown in Fig 16 would be repeated, thereby increasing the total number of acts performed in the feeding sequence. As satiation increased, the chain was usually broken at progressively earlier stages, that is at AT, AP, FI, O stages. There was also an increased number of stops, turn aways and move ons. Finally, with complete satiation the feeding sequence would go no further than the first step, orientation.

In other words, with maximum hunger and with palatable small prey, and if not missed during AT, the minimum number of stages was confined to seven. With increasing satiation, the sequence complexity and length first increased, the total number of steps involved being higher than seven. Then, with maximum satiation they were reduced to a few initial stages. These observations suggested that the fish became more selective but not less responsive with decreasing hunger.

b) With large prey the basic feeding chain was mostly affected at the grasp stage with an increase in the number of holds, spits and grasps. Chewing movements were commonly observed after ingesting a large prey. The fish might also exhibit the stress condition at this stage by swimming very slowly, occasionally erecting the dorsal fins or laying on the bottom. The prey might be regurgitated after sometime and either swallowed again or abandoned.

c) The effect of less tasteful food of suitable size on the feeding chain was similar to that of large prey. A stale piece of food might be spat out, grasped and ingested a number of times. Chewing movements were sometimes observed as if the fish was having difficulty in swallowing the food, which might eventually be either swallowed or rejected. Regurgitation seemed to occur more frequently with less tasteful or very large food than with palatable small food.

d) Movement of prey affected the feeding acts before and after the attack stage. The increased movement of the pectoral fins accompanied by the S-bending of the body were consistently observed before the fish attacked a live prey, but were less frequently seen with dead prey.

The S-bend seemed to be an action performed before the fish made a sudden attack at an object which it anticipated capable of movement. The fact that S-bends were sometimes observed before the fish started hitting its own reflection on the tank walls supported this view. Also after the fish had been feeding on live animals, a dead mysid or Artemia lying on the bottom of the tank initially evoked an S bend but after one or two attempts the fish stopped showing S bends to dead animals, indicating some degree of learning.

Movement of the prey also increased the number of misses, causing a restart of the feeding sequence, hence increasing the sequence complexity. The attacks made to non moving prey were more successful than those made to moving prey.

PREY SIZE SELECTION IN S. SPINACHIA

Introduction

As discussed earlier in the ecological survey it was noticed that the size of prey in S. spinachia stomachs varied with the fish size. As the fish size increased, the size of the prey in the diet became progressively larger. The same phenomenon was repeatedly observed in the other fish species studied and was more marked in some species than others.

The behavioural nature of prey size selection, although frequently observed in the studies of fish feeding, is not well documented although there are a few laboratory observations which suggest the degree of predation is influenced by prey size. (Zunini 1937; Olla, Katz and Studholme 1970; Ware 1972).

The aim of this part of the work was to determine experimentally whether size selection is an innate behaviour pattern of the species, whether it is solely or partially a function of prey availability or whether selection is determined by the mouth size of the fish.

Choice of prey for the experiments.

Before the size dependent selection of food by Spinachia could be studied, it was necessary to decide on the food to be used in the experiments.

A group of freshly caught Spinachia were kept in a large circular tank for 6 to 8 weeks, fed on a mixed diet of chopped mussel, squid pieces, thawed frozen mysids and live mysids, *Neomysis integer*.

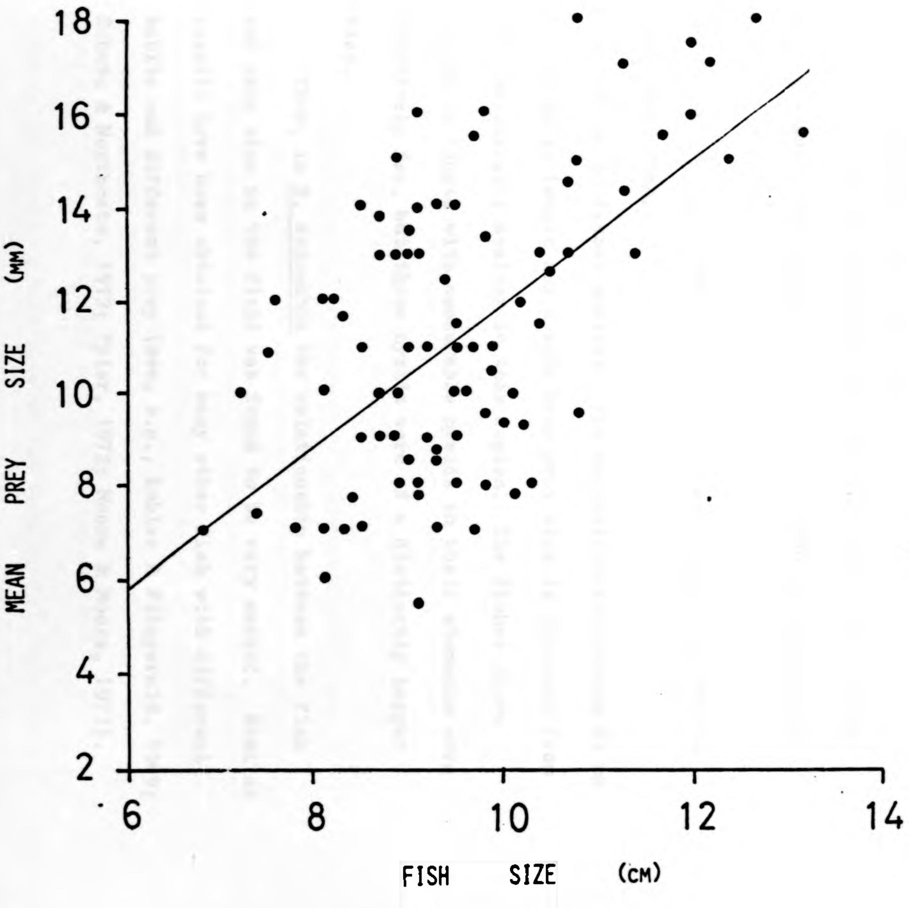
Swimming mysids were found to be taken markedly in preference to mussel, squid pieces and also thawed frozen mysids. As mentioned previously, Spinachia feeds primarily on amphipods, and mysids are not the most important food item of their diet in the field. Mysids were, however, found to be very readily taken by captive fish and compared to amphipods they could be collected in large numbers from the mouth of a nearby stream. They were also easy to keep alive in the laboratory. Mysids were therefore chosen as the prey organisms for the experimental work.

The relationship between mysid size and fish size in the field.

In the field fish were collected from Loch Etive, using a beach seine net or a push net in a depth of less than 8 m. The sampling period was October 1971 to October 1972. After capture, the fish were immediately preserved in 70% alcohol. They were later dissected under a binocular microscope, the stomach contents were identified and the total length of any mysids present recorded.

The results of the mysid size analysis for the fishes caught in the field are given in Fig 17. The frequency of occurrence of mysids is relatively low and when they are present it is usually in low numbers. In addition, mysids are soft-bodied animals and are frequently broken in fish stomachs;

Fig. 17. The relationship between the length of S. spinachia (cm) and mean length of mysids (mm) found in the stomachs of fish caught in the sea.


MEAN PREY SIZE (MM)
18
16
14
12
10
8
6
4
2
6
8
10
12
14
FISH SIZE (CM)

this further reduces the number of mysids available for any size analysis since only intact prey whose size could be reliably measured were included.

Regardless of these factors, however, Fig. 17 shows that a significant correlation exists between the mysid size and fish size in the field ($r = 0.60$; $n = 83$; $P < 0.001$). Each point on the graph represents the mean prey size for an individual fish.

Out of 83 fishes analysed, the majority were between 85 mm to 105 mm in length and a wide mean prey size is apparent from the considerable scatter in this region. The fishes above 110 mm in length with measurable mysids in their stomachs were relatively few, but these mysids were of a distinctly larger size.

Thus, in S. spinachia the relationship between the fish and prey size in the field was found to be very marked. Similar results have been obtained for many other fish with different habits and different prey (see, e.g., Kohler & Fitzgerald, 1969; Schutz & Northcote, 1972; Tyler, 1972; Moore & Moore, 1973).

The relationship between mysid size and fish size in the laboratory using free swimming mysids.

Two experiments were conducted with free swimming mysids. The purpose of the first experiment was to determine whether size selection similar to that found in the field could be observed in the laboratory under simulated field conditions. By field conditions it is meant that a dense *Neomysis integer* population with a natural size distribution should be present in the tank with differences in swimming speed and tail flip i.e., with differences in their capacity to escape predation. Since *Neomysis integer* swarm and shoal in shallow water in nature, this is not such an artificial situation as it might appear.

In Experiment 1 the response of a group of different sized fishes to different sized prey was observed in order to see whether size selection could be reproduced in the laboratory with free swimming mysids. A dense population of mixed sized *Neomysis integer* were kept in a tank 90 x 45 x 45 cm. The size distribution of mysids in the tank was assumed to reflect that in the field at this time of the year (July), but the size-frequency distribution was not determined. According to

Mauchline (1971) Neomysis integer has a size distribution within the range of 5-18 mm, with a mean of 12 mm in July. Thirteen fish, brought directly from the field were deprived of food for 48 h and then put into the tank. After 2 h the fish were killed and stomach contents were analysed.

Line a in Fig. 18 shows the relationship between the fish size and prey size under such conditions. The number of predators was relatively few but they had a wide size range, between 50 to 123 mm. A very strong correlation was found between Spinachia size and the prey size ($r = 0.98$; $n = 13$, $p < 0.001$).

In the above experiment the frequency of different size groups in the mysid population was not measured, so that, if very few large and small mysids were present in the tank the mean prey size taken by the large and small fish could approach one another so reducing the difference in chosen mean prey size. Experiment 2 was carried out to see whether size selection became more evident when the numbers of smaller and larger mysids were increased in the tank.

Experiment 2 was otherwise similar to Experiment 1, but this time the relative abundance of different mysid size

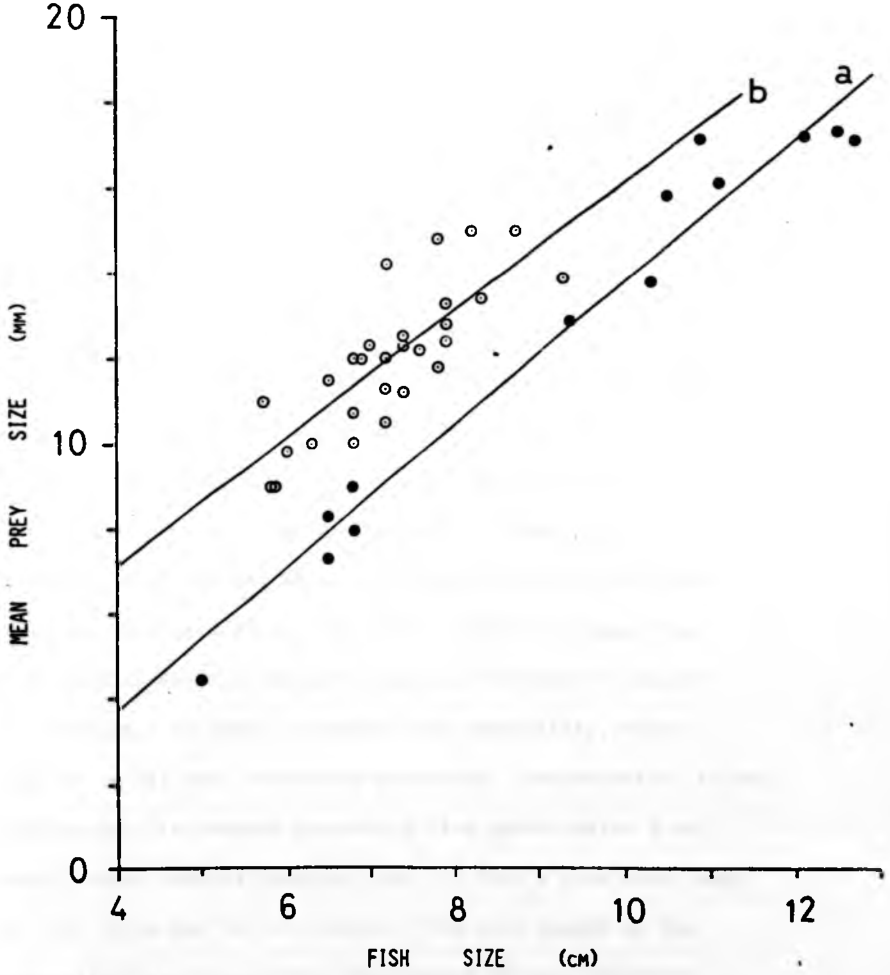


Fig. 18. The relationship between length of S. spinachia and mean prey size (mm) in the laboratory. Line a) Expt. 1 with an uncontrolled mysid population. Line b) Expt. 2 with a controlled mysid population (see text).

groups was strictly controlled in order to diminish any modification of size selection which could be caused by differences in the numerical availability of mysid size groups. Mysids of all sizes were not present in equal numbers in Experiment 1. This difference in abundance of the size groups could affect the number of large and small mysids caught by the fish, thereby affecting the mean prey size taken. For example, if there were only a few small mysids in the tank, a small fish might be more likely to take larger prey and thereby increase its mean prey size. Similarly, the virtual absence of large mysids could reduce the mean prey size of a large fish. This could cause the relationship between the prey size and fish size to appear less marked. In order to reduce this possibility, equal numbers of all prey sizes were presented. Unfortunately it was not possible to measure accurately live mysids below 9 mm total length without damaging them, so that a prey size range of 9 to 23 mm had to be selected. The mean length of the controlled mysid population (Experiment 2) was, therefore much higher than the uncontrolled population (Experiment 1).

Twenty mysids in each mm length group were measured, put into the tank, and allowed to settle. Twenty seven freshly caught fish were deprived of food for 30 h and then transferred to the mysid tank, allowed to feed for 3 h, killed and the mysids in their stomachs were measured. Line b in Fig. 18 shows the relationship between fish size and prey size when equal numbers of prey in each mm size group were present. Again, as in Fig 18 line a, each point on the figure represents the result for an individual fish.

It is apparent from line b (Fig 18) that when the numbers and the sizes of the mysids were controlled, the positive correlation between the fish size and prey size still holds ($r = 0.78$; $n = 27$; $\rho = < 0.001$). Furthermore, the slopes of the two lines are not significantly different ($\rho > 0.10$) suggesting the relationship between the prey size and fish size is in both cases similar, i.e., a given change in fish size is accompanied by a constant change in prey size, implying that, for example, a fish 1 cm larger than another will on average have a mean prey size $\approx$1.5 mm larger, whatever the range of prey size available. The fact that the relationship is similar shows that line a is not an incidental result of unequal numerical availability of smaller and larger mysids. A comparison of lines a and b also indicates that size selection did not become sharper with increased number of larger mysids.

The intercepts of two lines are statistically different ($p < 0.001$) because the smallest mysid size group present was 9 mm in Experiment 2, much higher than those in Experiment 1. The difference indicates that the fish can alter their average prey size according to the range of prey available, so long as the available range is within the limits of their own range of selection. For example, the mean prey size for a 60 mm fish in Experiment 1 was 7 mm whereas in Experiment 2 when mysids below 9 mm were not available, it was 10.2 mm.

None of the fish stomachs had any mysids above 18 mm although equal numbers of larger mysids up to 23 mm were also present in Experiment 2.

Observations in the laboratory of the relationship between S. spinachia and mysid size when both were free swimming show a close similarity to the field results. When the only prey available was larger than they would normally take in the field, the fish take the nearest size they can find within their preferred range, but do not consume much larger prey even if its abundance is high (Experiment 2).

The relationship between mysid size and fish size in the laboratory using stationary mysids.

In the experiments described above, escape movements of prey were not restricted. Also, a group of mixed sized fishes were used which were likely to differ in their swimming speed and perhaps in visual acuity. All these factors would affect the prey discovery and capture efficiency of fishes. Experiments 1 and 2 did not therefore distinguish between the possibilities that,

a) different fish of different lengths respond differently to different sized prey; or

b) fish responded to all prey but only larger fish could catch large prey due to the differences in fishes swimming speed, mouth size and possibly, visual acuity.

If assumption (a) is true, then selection should be demonstrated when all prey are equally catchable, but if assumption (b) be true, then no selection would be found in the above conditions. To determine which of these assumptions was correct, it was necessary to perform an experiment (Experiment 3) in which all prey were equally available hence maximising the capture efficiency of different size predators.

In Experiment 3 fish were placed into Perspex tanks of 47 x 31 x 31 cm, arranged on a bench. The tanks were divided into a small resting compartment and a larger feeding compartment separated by a sliding door. The tanks were covered on three sides so that once the fish was in the feeding compartment, it could not see outside the tank. In order to minimize disturbance by the observer, mirrors were arranged at 45° above the tanks and the front walls of the tanks covered with a black screen. The fish were observed through a slit in the screen and with the aid of mirrors. The tanks were so arranged that their illumination did not differ significantly. The temperature of water varied between 10–12°C. Prior to experiments the fishes were kept singly in these tanks for a minimum of 8 weeks and fed on mysids during this time.

In Experiment 3 only the responses of fish to prey of different sizes was under investigation and it was, therefore, necessary to eliminate the differences in the availability of different sized prey. The object of the experiment was to present to each fish a set of food which could be seen equally and also equally easily taken in order to equalize the chances of discovery and capture for all the prey presented.

The mysids were presented to the fish attached to the ends of fine transparent tubes, 1 mm in diameter. The position of the tubes were adjustable so that the mysids could be presented all at the same level and with equal distances between them. The food was suspended from the ends of the tubes in a loop of very fine nylon fishing line. Preliminary observations showed that four tubes at 5 cm intervals, arranged in a straight line 10 cm above the bottom of the tank and facing the resting compartment at a distance of 25 cm was the best arrangements,where all the prey could be equally seen. Preliminary observations also showed that immobilized living mysids were taken in preference to the same sized dead mysids. Living mysids were therefore used to keep the feeding responses at the optimum level.

Neomysis integer were caught and kept alive in a separate tank. For each presentation they were caught, their total length measured, and they were then looped to the ends of the tubes. At each presentation, four mysids of two different sizes were arranged as a set. The difference in size between the two pairs of mysids was kept as near 5 mm as possible. They were arranged in different orders at each presentation to eliminate the effect of conditioning to a particular arrangement. When two of the same size or a single mysid remained in the set, a new set was presented. The presentations continued until the fish stopped feeding.

Ten fishes between 72 mm and 124 mm, observed singly, were used for this part of the study. The deprivation time was 24 h and was kept constant throughout the experiments. Experiments were always conducted at the same time of the day. The sequence in which prey were taken and the time taken to respond to each prey was recorded. The response to prey was recorded as either positive or negative. Positive responses were the complete feeding responses beginning with an approach to the prey and resulted in swallowing, or in some cases ending in persistent strong attack. Negative responses were ones in which the fish did not attack or swallow the prey.

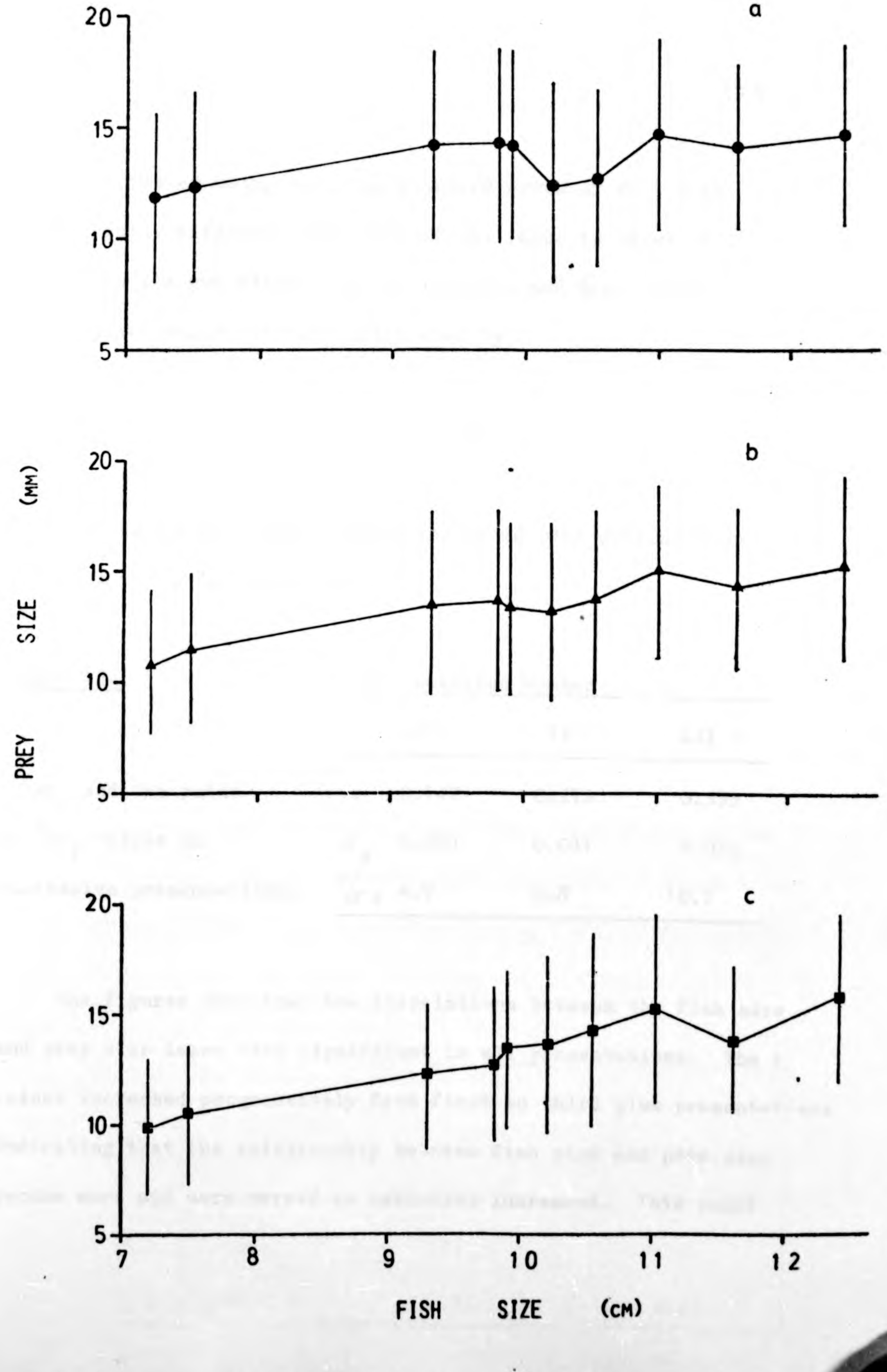
The first time the fish was presented with a set of four mysids after 24 h deprivation is called the first presentation. The first presentation has certain characteristics, namely, the time for the fish to respond to all four prey was shorter than the subsequent presentations and unless some mysids were too large to be taken, they were usually taken in a row indicating indiscriminate feeding. By indiscriminate feeding is meant that the fish moved down the line of tubes taking one mysid after another. The percentage of negative responses in the first presentation was also very small.

The effect of satiation on the fish-mysid size relationship.

Fig 19 shows the changes observed in the fish mysid size relationship for 10 fishes in successive presentations. After the third presentation the fish were not hungry and the number of positive responses was low. Because of this and their similarity, the third and subsequent presentations are combined as "third plus" prsentations.

In Fig 19 the mean prey size taken ∓ 1 standard deviation in each presentation is shown for 10 fish. As it will be seen from the legend to Fig 19 the total number of prey taken was extremely large in all presentations hence the values of the correlation coefficient, r for the relationship between fish and mysid size could not be tested using standard statistical tables. The significance of r was

Fig. 19. The relationship between the length of *Spinachia* and mean prey size in the laboratory in successive presentations. a) First presentation, b) Second presentation c) Third plus presentations. The points plotted are the means ± 1SD.


a
b
c
20
15
10
5
PREY SIZE (MM)
7
8
9
10
11
12
FISH SIZE (CM)

therefore tested using σr, the standard error of r. r is significantly different from zero if its value is three or more times its own standard error (Simpson and Roe, 1939). The standard error of r was calculated by

$$\sigma r = \frac{1 - r^2}{N} \quad \text{where } N = \text{number of observations.}$$

r values for first, second and third plus presentations are given below in Table 59.

Table 59.

r, σ_r and the ratio of r/σ_r values in successive presentations.

	Presentation Number		
	I	II	III +
r	0.147	0.272	0.353
σ_r	0.003	0.031	0.033
r/σ_r	4.9	8.8	10.7

The figures show that the correlations between the fish size and prey size taken were significant in all presentations. The r values increased progressively from first to third plus presentations indicating that the relationship between fish size and prey size became more and more marked as satiation increased. This point was further tested by comparing the regression coefficients of each line in order to see whether the observed increase in prey size with fish size in each presentation were significantly different from one another. The regression coefficients were compared by using the formula:

$$t = \frac{b_1 - b_2}{\text{standard error of the difference between } b_1 \text{ \& } b_2}$$

Where b_1 and b_2 are the regression coefficients of the lines being compared (Quenouille, 1950).

The results of this comparison are given below.

Table 60. Comparison of the regression coefficients of the successive presentations (I) = first presentation, (II) = second presentation, (III+) = third, plus presentations; DF = degrees of freedom. P = probability.

	Comparison of presentations		
	(I) & (II)	(I) & (III+)	(II) & (III+)
t	2.6714	4.576	2.205
D.F.	1946	1744	1548
P	< 0.01	< 0.001	< 0.05

The t values showed that the fish - mysid size relationship was significantly different between successive presentations. The greatest difference was found between first and third plus presentations and the least difference between second and third plus presentations.

The results suggested that increasing satiation produces a more selective response to prey size. A similar relationship between the degree of hunger and selectivity has been demonstrated for other fishes. (Ivlev 1961; Chiszar and Windell 1973).

Fig 19. also shows the standard deviations for the mean prey size taken by each fish in each presentation. The standard deviations decreased from the first to "third plus" presentation for each fish except for the 106 and 110 mm fishes. The decrease was, however, not very marked except for the smaller fishes. This suggested that the spread about the mean was quite wide in all presentations, showing that the prey size ranges taken in different presentations overlapped considerably.

The pattern of prey size selection in successive presentations for individual fishes.

The numerical availability of different size groups were not equal in different presentations and the number of prey taken reflected in some cases only the availability of a particular size group and could not be attributed to selection. In order to follow the changes which occurred with different presentations it was necessary to consider the proportion of prey taken out of the total number of prey offered in each size group.

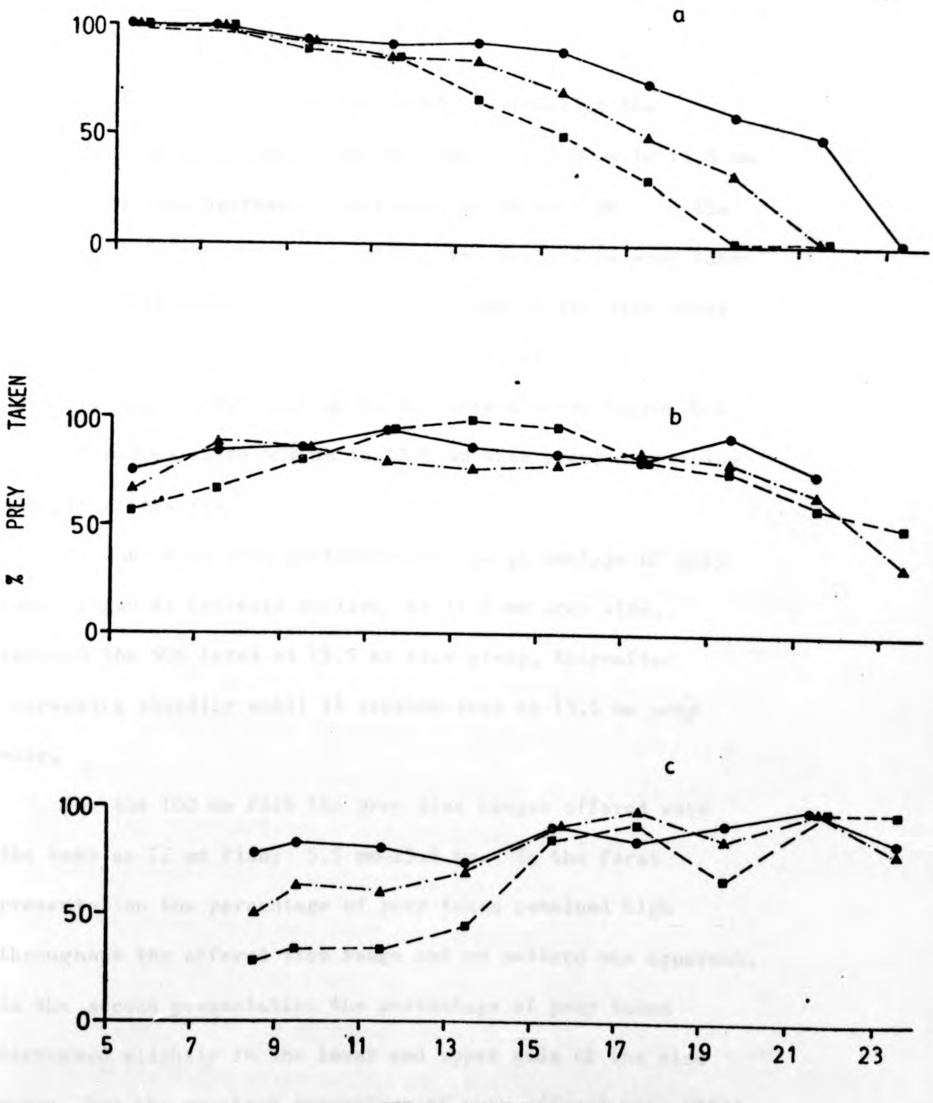
Fig 20 shows the different degrees of size selection operating at each presentation for three individual fishes with total lengths of 72, 102, 124 mm. The figure demonstrates the different patterns observed in three of the 10 fishes examined. The results for the remaining seven fish are given in Table 61.

In Fig 20 the prey taken in each size group is expressed as the percentage of the total number of prey presented in that size group.

The first point that is apparent from Fig 20 is that the proportion of prey taken out of the total number of prey offered is different in different size groups and a pattern is apparent in each fish which indicates selective feeding.

Fig. 20. The change in the pattern of size selection with increasing satiation for three Spinachia of a) 72 mm, b) 102 mm and c) 124 mm.

● First presentation; ▲ second presentation; ■ third plus presentations.


a
b
c
100
50
0
% PREY TAKEN
5
7
9
11
13
15
17
19
21
23
PREY SIZE (MM)

For the 72 mm fish in the first presentation the percentage of prey taken remained high from 5.5 mm to 15.5 mm prey size, then decreased reaching zero at 23.5 mm. In the second and third plus presentations the percentage prey taken remained still very high at the lower end of the size range but decreased steadily at the larger prey size groups. The decrease began after 13.5 mm in the second presentation but still remained above 50% up to 17.5 mm size group decreasing sharply afterwards.

In the third plus presentations the percentage of prey taken began to decrease earlier, at 11.5 mm prey size, reached the 50% level at 15.5 mm size group, thereafter decreasing steadily until it reached zero at 19.5 mm prey size.

For the 102 mm fish the prey size ranges offered were the same as 72 mm fish; 5.5 mm-23.5 mm. In the first presentation the percentage of prey taken remained high throughout the offered size range and no pattern was apparent. In the second presentation the percentage of prey taken decreased slightly in the lower and upper ends of the size range, but the greatest percentage of prey offered were still taken between 7.5 mm to 21.5 mm, indicating very little size discrimination within this range. The clearest pattern was observed in the third plus presentations where the percentage of prey taken increased steadily from 5.5 mm to 13.5 mm and decreased from 13.5 mm onwards.

For the 124 mm fish prey size range available was 7.5 mm to 23.5 mm.

In the first presentation, as in the other fishes, the percentage of prey taken did not vary significantly with prey size and remained at a high level for all size groups offered. In the second and subsequent presentations a pattern opposite to that shown by the 72 mm fish was observed, that is, the percentage prey taken decreased with decreasing prey size and as before the greatest decrease occurred in the third and following presentations. The percentage of prey taken remained below 40% at the smaller end of the size range up to 13.5 mm, then increased gradually remaining at a high level between 15.5 mm to 23.5 mm.

If Table 61 is examined, it will be seen that for most fish in the first presentation the percentage of prey taken out of the total number of prey offered remains high throughout

Table 61 . Variation in the proportion of prey taken in different size groups in successive presentations.

Fish size (mm)	Presentation number		PREY SIZE GROUP (mm) 5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22	23-24	25-26
75	I	Number presented	6	4	12	9	9	14	10	3	4	1	-
		Number taken	6	4	11	8	7	10	6	1	2	-	-
		No.negative responses	-	-	1	1	2	4	4	2	2	1	-
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$	100	100	92	89	78	71	60	33	50	0	-
75	II	Number presented	4	3	17	11	8	8	6	3	2	2	-
		Number taken	3	3	16	9	6	6	3	1	-	-	-
		No.negative responses	1	-	1	2	2	2	3	2	2	2	-
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$	75	100	94	82	75	75	50	25	0	0	
75	III+	Number presented	5	5	17	5	8	7	5	2	2	2	-
		Number taken	5	5	17	4	6	3	2	-	-	-	-
		No.negative responses	-	-	-	1	2	4	3	2	2	2	-
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$	100	100	100	80	75	43	40	0	0	0	-

Table 61 . cont.

Fish size (mm)	Presentation number		PREY SIZE GROUP (mm)										
			5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–26
93	I	Number presented		15	20	21	22	21	13	9	8	6	1
		Number taken		9	18	21	21	19	13	8	7	4	1
		No.negative responses		6	2	-	1	2	-	1	1	2	-
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$		60	90	100	95	90	100	89	88	67	100
93	II	Number presented		8	20	10	12	12	12	8	5	1	4
		Number taken		8	17	10	12	10	11	6	4	1	1
		No.negative responses		-	3	-	-	2	1	2	1	-	3
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$		100	85	100	100	83	92	75	80	100	25
93	III+	Number presented		6	10	8	10	6	8	13	2	4	1
		Number taken		6	10	8	7	4	2	3	1	-	-
		No.negative responses		-	-	-	3	2	6	10	1	4	1
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$		100	100	100	70	67	25	23	50	0	0

Table 61. cont.

Fish size (mm)	Presentation number		PREY SIZE GROUP (mm)										
			5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22	23-24	25-26
99	I	Number presented		12	17	21	21	24	12	13	9	7	-
		Number taken		9	17	21	18	21	10	10	6	5	-
		No.negative responses		3	-	-	3	3	2	3	3	2	-
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$		75	100	100	86	88	83	77	67	71	-
99	II	Number presented		8	24	15	9	16	12	10	7	3	-
		Number taken		6	22	14	9	13	9	7	3	1	-
		No.negative responses		2	2	1	-	3	3	3	4	2	-
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$		75	91	93	100	81	78	70	43	33	-
99	III+	Number presented		4	15	9	10	9	12	10	4	1	-
		Number taken		4	14	9	9	7	8	5	1	-	-
		No.negative responses		-	1	-	1	2	4	5	3	1	
		$\frac{\text{No,taken}}{\text{No.presented}} \times 100$		100	93	100	90	78	67	50	25	0	

Table 61 cont.

Fish size (mm)	Presentation number		PREY SIZE GROUP (mm)										
			5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–2
106	I	Number presented	8	10	17	18	19	16	12	9	3		
		Number taken	6	9	16	17	18	15	11	7	2		
		No.negative responses	2	1	1	1	1	1	1	2	1		
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$	75	90	94	94	95	94	92	78	67		
106	II	Number presented	8	10	15	12	18	22	13	8	6		
		Number taken	5	7	12	10	16	20	12	7	4		
		No.negative responses	3	3	3	2	2	2	1	1	2		
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$	63	70	80	83	89	91	92	88	67		
106	III+	Number presented	7	6	13	12	17	18	14	10	8	3	
		Number taken	4	4	10	10	14	16	11	7	5	2	
		No.negative responses	3	2	3	2	3	2	3	3	3	1	
		$\frac{\text{No.taken}}{\text{No.presented}} \times 100$	57	67	77	83	82	89	79	70	63	67	

Table 61 cont.

Fish size (mm)	Presentation number		PREY SIZE GROUP (mm)										
			5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–26
110	I	Number presented		12	17	23	22	23	16	12	11	5	3
		Number taken		11	16	21	21	23	15	12	10	4	2
		No.negative responses		1	1	2	1	–	1	–	1	1	1
		$\frac{\text{No.taken}}{\text{No.presented}}$ x 100		92	94	91	95	100	94	100	91	80	67
110	II	Number presented		7	17	18	20	28	18	17	9	5	1
		Number taken		5	14	16	19	26	17	15	7	3	–
		No.negative responses		2	3	2	1	2	1	2	2	2	1
		$\frac{\text{No.taken}}{\text{No.presented}}$ x 100		71	82	89	95	93	94	88	78	60	0
110	III+	Number presented		7	17	19	17	24	19	11	11	8	6
		Number taken		4	12	14	14	21	15	8	7	4	3
		No.negative responses		3	5	5	3	3	4	3	4	4	3
		$\frac{\text{No.taken}}{\text{No.presented}}$ x 100		57	71	74	82	88	79	73	64	50	50

Table 61 . cont.

Fish size (mm)	Presentation number		PREY SIZE GROUP (mm)										
			5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–26
116	I	Number presented		6	20	23	21	24	19	11	7	1	
		Number taken		5	19	21	21	23	18	10	6	1	
		No.negative responses		1	1	2	–	1	1	1	1	–	
		No.taken / No.presented x 100		83	95	91	100	96	95	91	86	100	
116	II	Number presented		6	20	18	19	21	16	12	3	1	
		Number taken		4	15	14	16	20	15	11	3	1	
		No.negative responses		2	5	4	3	1	1	1	–	–	
		No.taken / No.presented x 100		66	75	78	84	95	94	92	100	100	
116	III+	Number presented		6	21	20	20	26	13	6	3	1	
		Number taken		3	16	16	17	24	12	5	2	1	
		No.negative responses		3	5	4	3	2	1	1	1	–	
		No.taken / No.presented x 100		50	76	80	85	92	92	83	67	100	

the size range offered for most fishes. As the fishes become more satiated, a preferred size range within which the highest proportion of offered prey is taken begins to be apparent.

Fig 20 and Table 61 show that the overall size range of prey that could be taken is quite wide.

During the observations it was noticed that when four prey of different sizes, two large and two small were offered as a set, the fishes generally took the prey in a row in the first presentation. The fish appeared to be much more discriminating in its choice of prey in the second and subsequent presentations. It was therefore considered that the order of choice could offer a good measure of selection.

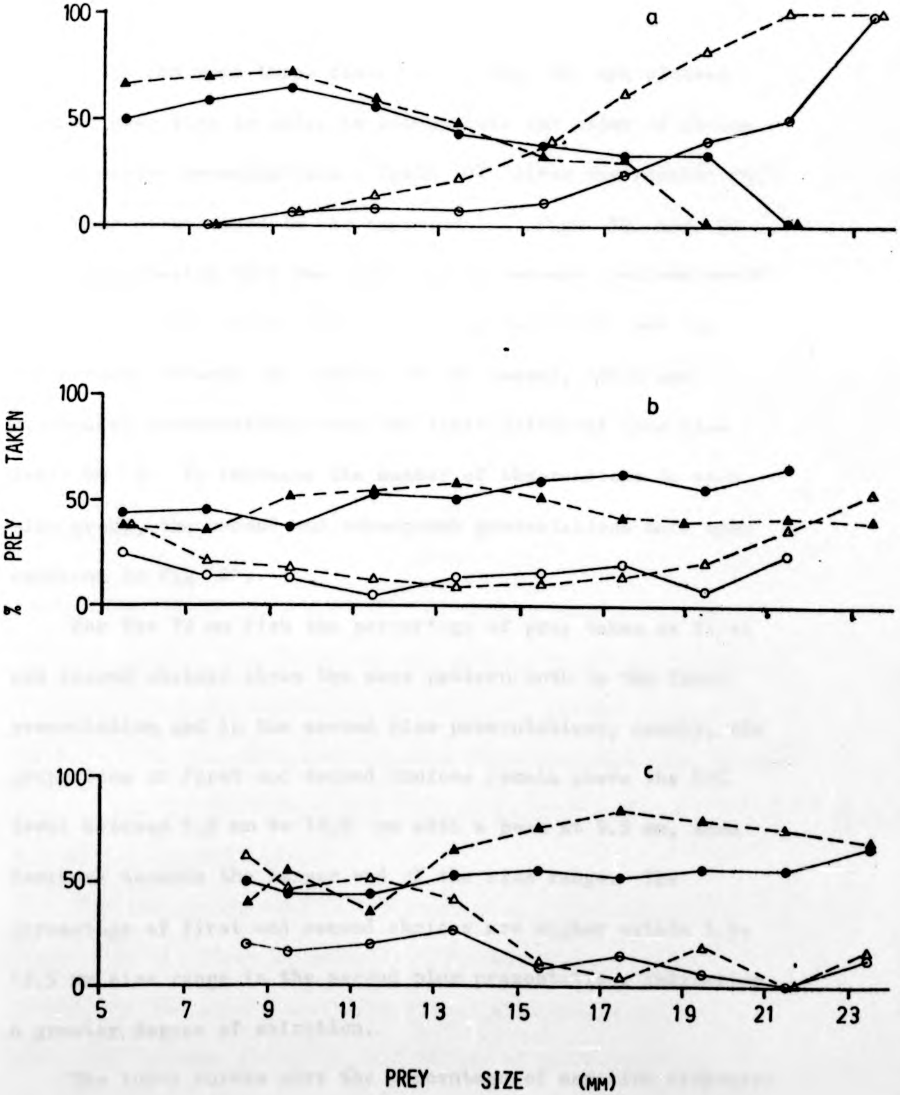
If size selection were operating and there are four mysids in two different size groups to choose from, all equally available, then the first and the second choices would be the most important indicators of selection. On the other hand, if prey were taken indiscriminately, then one would not expect the ratio of first and second choices to third and fourth to differ greatly from unity.

In Fig . 21 the percentage of prey taken as first and second

Fig. 21. The percentage of prey taken as first and second choices in the first and second plus presentations for 3 Spinachia of

a) 72 mm, b) 102 mm and c) 124 mm.

Closed symbols are positive responses; open symbols negative responses. Circles indicate first presentations and triangles represent second plus presentations.


a
b
c
100
50
0
% PREY TAKEN
5
7
9
11
13
15
17
19
21
23
PREY SIZE (MM)

choices by the same three fishes as in Fig 20 are plotted against prey size in order to demonstrate the order of choice in successive presentations. Table 62 gives the results for the other fishes used in the experiments. Figs 19 and 20 both demonstrated that the relationship between fish and mysid size become more marked with increasing satiation, but the differences between the results of the second, third and subsequent presentations were the least different (see also Table 60). To increase the number of observations in each size group, the second and subsequent presentations have been combined in Fig 21.

For the 72 mm fish the percentage of prey taken as first and second choices shows the same pattern both in the first presentation and in the second plus presentations, namely, the proportion of first and second choices remain above the 50% level between 5.5 mm to 12.5 mm with a peak at 9.5 mm, then decrease towards the larger end of the size range. The percentage of first and second choices are higher within 5.5-12.5 mm size range in the second plus presentations indicating a greater degree of selection.

The lower curves give the percentage of negative responses in the first and second presentations. Negative responses in both cases increased in the region where the proportion of prey taken as first and second choices dropped. Once again, the increase in the percentage of negative responses is greater at the higher end of the size range in the second plus presentations when compared to the first presentation.

For the 102 mm fish the percentage at first and second choices were below 50% up to 11.5 mm and above 50% from 11.5 mm to 21.5 mm, no obvious pattern being apparent in the first presentation. In the second plus presentations the percentage of first and second choices presented a clear pattern. They were under 40% in the 5.5 mm to 7.5 mm prey size group, from 7.5 mm onwards they increased and were above 50% level between 9.5 mm to 15.5 mm, decreasing to 40% level between 17.5 mm to 23.5 mm. The percentage of negative responses were high at the smaller and larger ends of the size range in both first and second plus presentations.

For the 124 mm fish the percentage of first and second choices in the first presentation fluctuated around 50% throughout the size range. The values were slightly under 50% level between 7.5 mm to 13.5 mm and slightly above it

Table 6.2 . The degree of preference shown for different prey size groups in the "first" and "second plus" presentations.

Preference is expressed as

$$\frac{\text{No. prey taken in a size group as first, second choices}}{\text{Total number offered in that size group}} \times 100\%$$

Negative responses are expresses as

$$\frac{\text{No. of negative responses shown to prey in a size group}}{\text{Total number offered in that size group}} \times 100\%$$

Fish size (mm)	Presentation number	Prey size group (mm)	5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22	23-24
75	I	Number offered	6	4	12	9	9	14	10	3	4	1
		No.taken as 1st,2nd choices	3	2	7	5	4	6	3	0	1	-
		No.taken as 3rd,4th choices	3	2	4	3	3	4	3	1	1	-
		% taken as 1st,2nd choices	50	50	64	63	57	60	50	0	50	-
		No.negative responses	-	-	1	1	2	4	4	2	2	1
		% negative responses	-	-	8	11	22	29	40	66	50	100

Table 6 2 cont.

Fish size (mm)	Presentation number	Prey size group (mm)	5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–26
		Number offered	9	8	34	16	16	15	11	5	4	4	
		No.taken as 1st,2nd choices	5	6	23	9	5	4	2	–	–	–	
75	II+	No.taken as 3rd,4th choices	3	2	10	4	7	5	3	1	–	–	
		% taken as 1st,2nd choices	63	75	70	69	42	44	40	0	0	0	
		No.negative responses	1	–	1	3	4	6	6	4	4	4	
		% negative responses	11	0	3	19	25	40	54	80	100	100	
		Number offered		15	20	21	22	21	13	9	8	6	1
		No.taken as 1st,2nd choices		5	10	11	10	9	6	3	3	2	–
93	I	No.taken as 3rd,4th choices		4	8	10	11	10	7	5	4	2	1
		% taken as 1st,2nd choices		56	56	53	48	47	46	38	43	50	0
		No.negative responses		6	2	–	1	2	–	1	1	2	–
		% negative responses		40	10	–	5	10	–	11	13	33	0

Table 62 cont.

Fish size (mm)	Presentation number	Prey size group (mm)	5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–26
93	II+	Number offered		14	30	18	22	18	20	21	7	5	5
		No.taken as 1st,2nd choices		10	19	16	16	10	5	3	0	0	0
		No.taken as 3rd,4th choices		4	8	2	3	4	8	6	5	1	1
		% taken as 1st,2nd choices		71	70	89	84	71	38	33	0	0	0
		No.negative responses		-	3	-	3	4	7	12	2	4	4
		% negative responses		-	10	-	14	22	35	57	29	80	80
98	I	Number offered		11	17	12	14	17	10	12	6	6	-
		No.taken as 1st,2nd choices		6	10	6	6	8	5	6	3	2	-
		No.taken as 3rd,4th choices		4	6	6	7	7	4	4	2	3	-
		% taken as 1st,2nd choices		60	63	50	46	53	56	60	60	40	-
		No.negative responses		1	1	-	1	2	1	2	1	1	-
		% negative responses		9	6	-	7	12	10	17	17	17	

Table 62 cont.

Fish size (mm)	Presentation number	Prey size group (mm)	5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–26
98	II+	Number offered		14	35	26	27	20	14	14	10	4	–
		No.taken as 1st,2nd choices		7	17	15	14	10	5	4	2	–	–
		No.taken as 3rd,4th choices		5	13	8	9	7	6	6	4	1	–
		% taken as 1st,2nd choices		58	57	65	61	59	45	40	33	0	–
		No.negative responses		2	5	3	4	3	3	4	4	3	–
		% negative responses		14	14	11	15	15	21	29	40	75	–
99	I	Number offered		12	17	21	21	24	12	13	9	7	
		No.taken as 1st,2nd choices		6	7	11	8	12	6	5	4	3	
		No.taken as 3rd,4th choices		4	10	10	10	9	4	5	2	2	
		% taken as 1st,2nd choices		60	41	55	44	57	60	50	67	60	
		No.negative responses		2	–	–	3	3	2	3	3	2	
		% negative responses		25	0	0	14	13	17	23	23	29	

Table 62 cont.

Fish size (mm)	Presentation number	Prey size group (mm)	5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22	23-24
		Number offered		12	39	24	19	25	24	20	11	4
		No.taken as 1st,2nd choices		6	21	13	12	13	8	5	1	-
99	II+	No.taken as 3rd,4th choices		4	15	10	6	7	9	7	3	1
		% taken as 1st,2nd choices		60	58	57	67	65	47	42	25	0
		No.negative responses		2	3	1	1	5	7	8	7	3
		% negative responses		17	8	4	5	20	29	40	64	75
		Number offered	8	10	17	18	19	16	12	9	3	-
		No.taken as 1st,2nd choices	3	4	9	9	10	8	5	3	1	
106	I	No.taken as 3rd,4th choices	3	5	7	8	8	7	6	4	1	
		% taken as 1st,2nd choices	50	44	56	53	56	53	45	43	50	
		No.negative responses	2	1	1	1	1	1	1	2	1	
		% negative responses	25	10	6	6	5	6	8	22	23	

Table 62 cont.

Fish size (mm)	Presentation number	Prey size group (mm)	5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24
106	II+	Number offered	15	16	28	24	35	40	27	18	14	3
		No.taken as 1st,2nd choices	4	5	12	13	20	23	12	5	3	-
		No.taken as 3rd,4th choices	5	6	10	7	10	13	11	9	6	2
		% taken as 1st,2nd choices	45	45	55	65	67	64	52	36	33	0
		No.negative responses	6	5	6	4	5	4	4	4	5	1
		% negative responses	40	31	21	16	14	10	15	22	36	33

between 13.5 mm-23.5 mm. In the second plus presentations the percentage of first and second choices was around 43% in the region of 9 to 11.5 mm prey size, then increased from 11.5 mm prey size remaining above 50% in the higher part of the size range. Also the percentage of negative responses were highest in the lower end of the size range. The pattern of negative responses were similar in both first and second plus presentations but the pattern was more accentuated in the second plus presentations.

Table 62 shows that for some of the fishes a size range where most of the prey were taken as first and second choices was already apparent in the first presentations but became more clearly expressed in the second plus presentations. For the remaining fishes the percentage of prey taken as first and second choices fluctuated around 50% level with no apparent pattern in the first presentations; a range where this percentage was highest being only apparent in the successive presentations.

Fig 21 and Table 62 once again suggested that the fishes had a preferred prey size range, which became more apparent in successive presentations.

The preferred size range as estimated from the results of the experiments given in Fig 20, Table 61. and Fig 21. and Table 62 agreed closely, although the maxima were not always found in the same size group.

Estimation of the maximum swallowing capacity of the mouth.

Figs 20, 21 and Tables 61, 62 indicated that there was a preferred size range within the range of prey sizes offered to the fish. It was however not known whether this preferred range reflected to some extent the capacity of the mouth of the fish, prey only being taken within the size range that the fish could swallow, with negative responses being shown to prey which was too large. It was of interest therefore to compare the maximum size of the prey that could be taken by the fish with the size group for which they showed the highest preference.

The size range offered to the fishes had to be chosen according to the availability of size groups of mysids in the field and, as mentioned earlier, it was difficult to find very large mysids. For this reason the maximum prey size which fishes were capable of taking could not be estimated from the laboratory observations, because the results, especially in the case of larger fish might well only reflect the upper limit of the size range offerred to that fish.

Field results and laboratory observations showed that Spinachia took mysids whole and usually did not break them into pieces. If the maximum mouth gape of the fish was known, it would then be possible to calculate the maximum size of prey they could swallow whole.

60 fishes with total length varying from 74 to 118 mm were caught and killed by immersing in 70% alcohol for a few minutes. They were then immediately removed from the alcohol to prevent the jaws stiffening. The mouth capacity was measured by inserting fine drills of gradually increasing diameter into the mouth. When a drill could not be eased any further into the mouth, its thickness was considered to be equal to the maximum mouth capacity.

Fig 22. shows the relationship found between the fish size and maximum mouth capacity. The correlation was found to be significant at the 0.1% level ($n = 60$, $r = 0.874$).

From the regression line in Fig 22 it was possible to predict the maximum thickness of any prey the fishes were

Fig. 22. S. spinachia. The relationship between the fish length and maximum mouth gape.

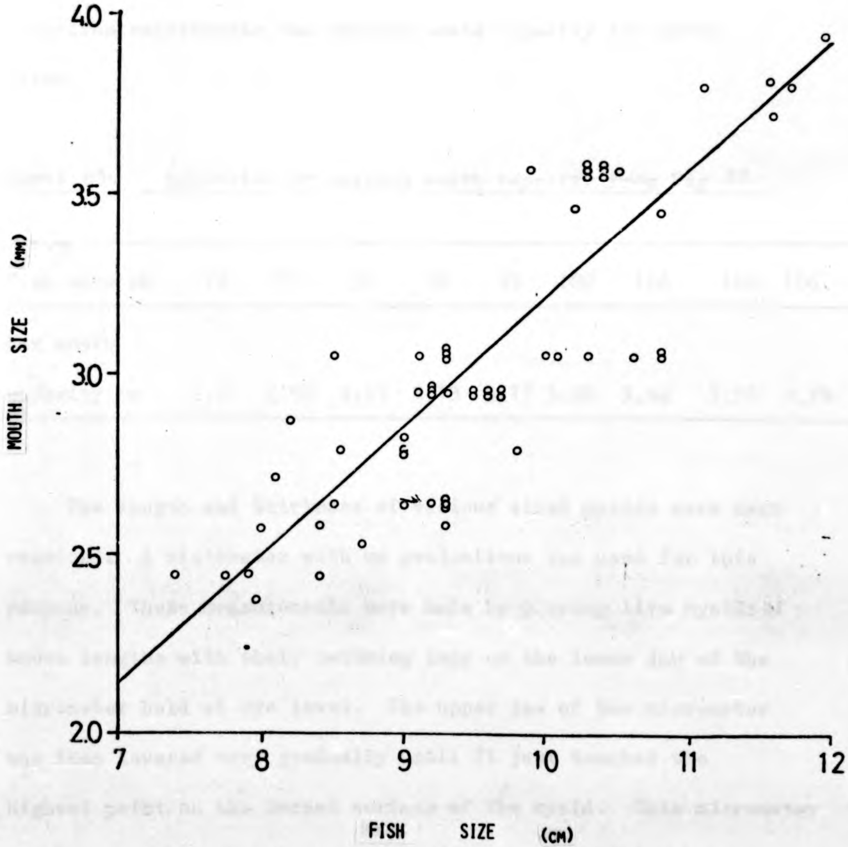
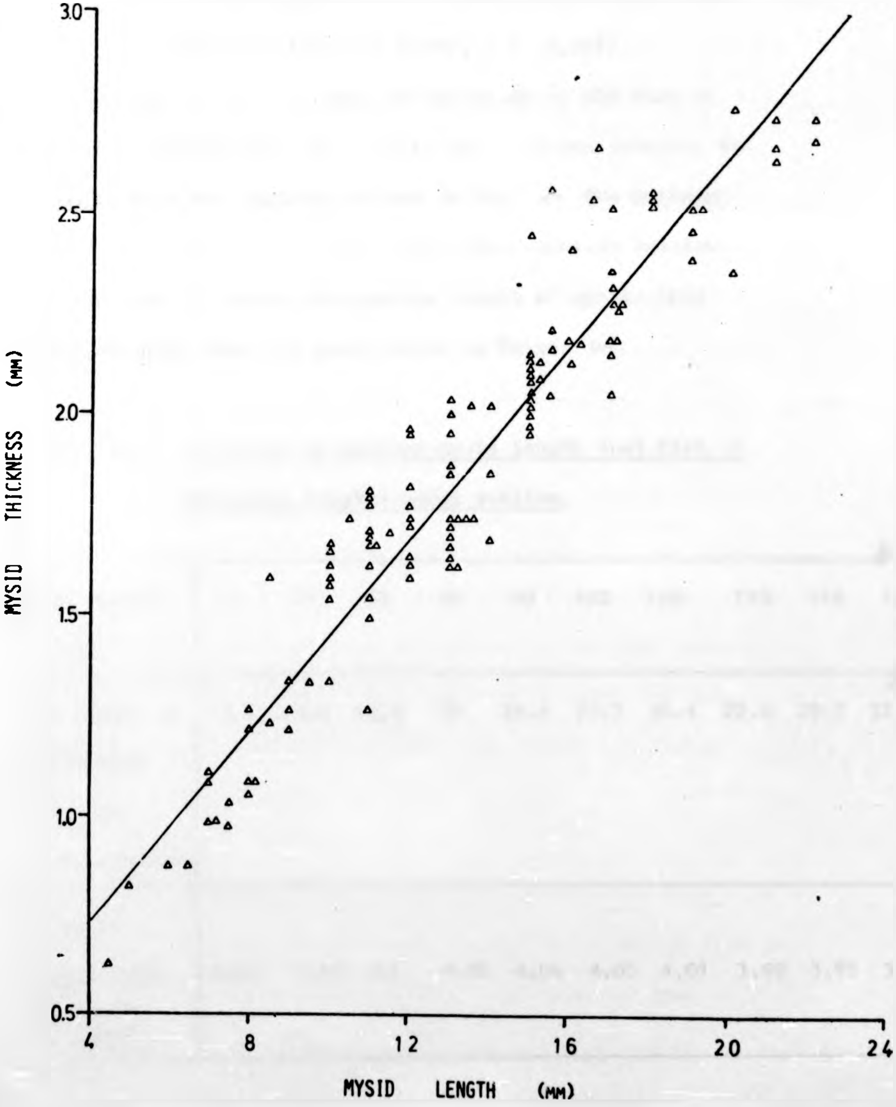

4.0
3.5
3.0
2.5
2.0
MOUTH SIZE (MM)
7
8
9
10
11
12
FISH SIZE (CM)

Fig. 23. The relationship between the length and maximum body thickness of mysids.


3.0
2.5
2.0
1.5
1.0
0.5
MYSID THICKNESS (MM)
4
8
12
16
20
24
MYSID LENGTH (MM)

5 mm to 22 mm. Once again the correlation was found to be very significant ($n = 110$, $r = 0.957$, $p = 0.001$).

Knowing the maximum gape of the mouth of the fish of different lengths (Fig 22 Table 63) it was possible to estimate from the regression line in Fig 23 the maximum length of mysids any one fish could theoretically swallow. For the same 10 fishes the maximum length of mysids they could possibly take are given below in Table 64

Table 64 Estimates of maximum mysid length that fish of different lengths could swallow.

Fish length (mm)	72	75	93	98	99	102	106	110	116	124
Max length of mysid that could be swallowed (mm)	18.1	19.0	22.6	24	24.4	25.3	26.4	27.6	29.5	31.8
Ratio of fish length / max mysid length	3.98	3.95	4.1[illegible]	4.08	4.06	4.03	4.01	3.99	3.93	3.91

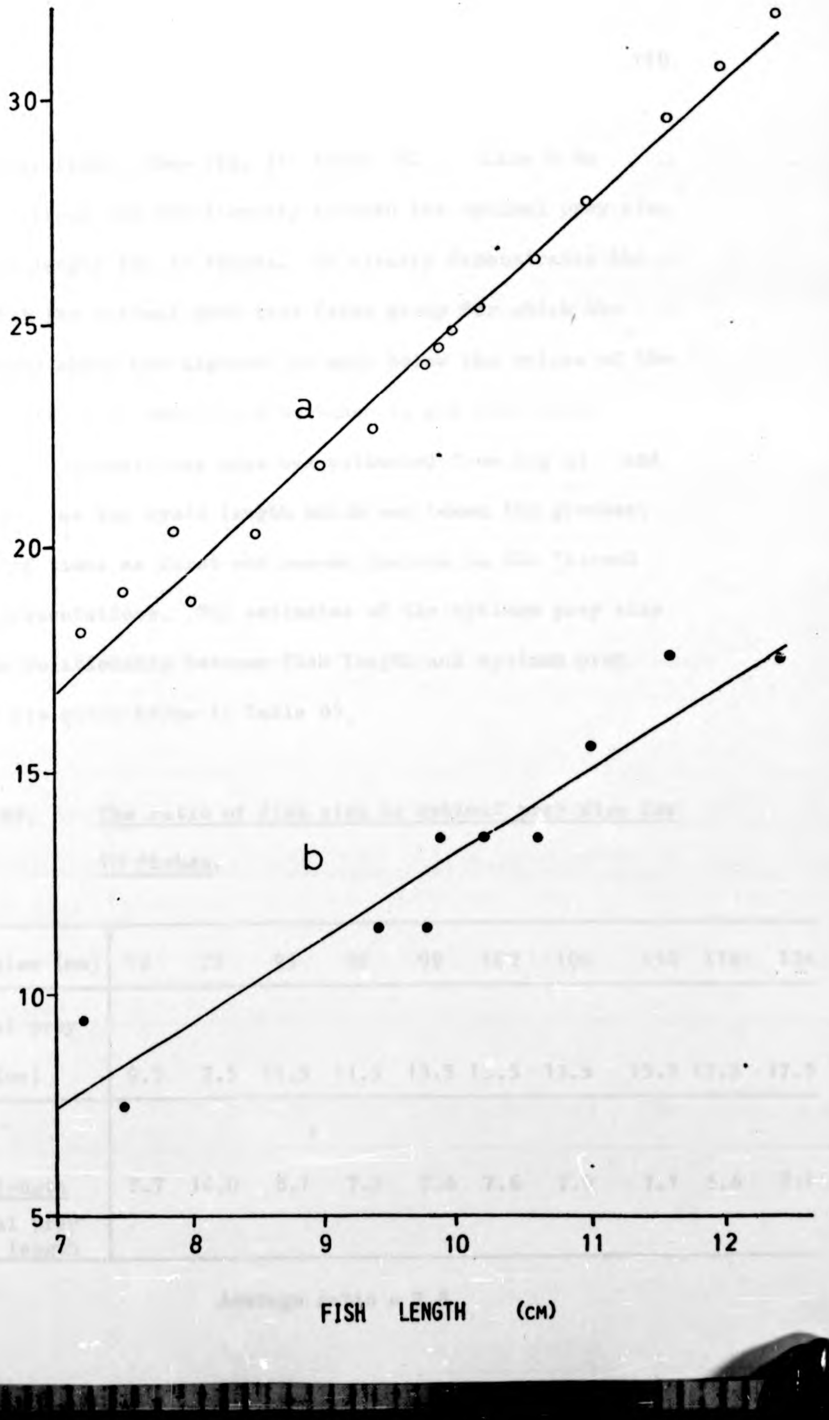
The figures in Table 64 show that the maximum size of mysids the fishes were capable of swallowing was approximately $\frac{1}{4}$ of their total length, and the ratio $\frac{\text{fish length}}{\text{max. mysid length}}$ is independent of fish length.

It will be seen from these figures that the size range offerred to the fishes used in size selection experiments covered the maximum size of the whole mysid that could be swallowed for 72, 75, 93, 98 mm fishes but the offered ranges did not include the upper limit of mysid size which could be swallowed for the remainder.

In Fig 24 the maximum and optimum prey size groups are plotted against the fish size. Line a in Fig 24 shows the maximum possible size of mysid that fish could take whole. Apart from the mysid sizes corresponding to the fish sizes used in the experiments, calculated maximum mysid sizes for the fishes of 80, 85, 90, 100, 120 mm total length are also included to obtain a more accurate regression line. (For line a, $n = 15$, $r = 0.994$, $\rho = < 0.001$.)

In the second and subsequent presentations the prey size where the percentage of prey taken as first and second choices was maximum was taken as the optimal prey size for that

Fig. 24. S. spinachia. The relationship between maximum prey size (Line a), optimal prey size (Line b) and fish length.


MYSID LENGTH (MM)
30
25
20
15
10
5
a
b
7
8
9
10
11
12
FISH LENGTH (CM)

particular fish. (See Fig. 21 Table 62 , Line b in Fig 24 shows the relationship between the optimal prey size and fish length for 10 fishes. It clearly demonstrates the fact that the optimal prey size (size group for which the preference shown was highest) is much below the values of the maximum prey size that could be taken in all fish sizes examined. Optimal prey size was estimated from Fig 21 and Table 62 as the mysid length which was taken the greatest number of times as first and second choices in the "second plus" presentations. The estimates of the optimum prey size and the relationship between fish length and optimum prey length are given below in Table 65.

Table 65. The ratio of fish size to optimal prey size for 10 fishes.

Fish size (mm)	72	75	93	98	99	102	106	110	116	124
Optimal prey size (mm)	9.5	7.5	11.5	11.5	13.5	13.5	13.5	15.5	17.5	17.5
Ratio $\frac{\text{Fish length}}{\text{Optimal prey length}}$	7.7	10.0	8.1	7.3	7.6	7.6	7.9	7.1	6.6	7.1

Average ratio = 7.8

The ratio of fish size to optimal prey size (Table 65) fluctuated around the mean value of 7.8 and was not found to be as constant as the $\frac{\text{fish length}}{\text{max. prey length}}$ ratio. These figures suggest that the optimum size of mysid which fishes select is around $\frac{1}{8}$ of the fishes total length.

If the thickness of optimal prey is estimated from the regression line in Fig 23 for the 10 fishes used in the experiments and related to the mouth capacity, the following $\frac{\text{prey size}}{\text{mouth size}}$ ratios are obtained (Table 66).

Table 66. Ratios of optimal $\frac{\text{prey size}}{\text{mouth size}}$ for fish of different lengths.

Fish size (mm)	72	75	93	98	99	102	106	110	116	124
Mouth size (mm	2.41	2.52	2.95	3.13	3.17	3.28	3.42	3.56	3.78	4.06
Optimal prey size (mm) (thickness)	1.38	1.14	1.62	1.62	1.86	1.86	1.86	2.10	2.35	2.35
Optimal $\frac{\text{prey size}}{\text{mouth size}}$	0.57	0.45	0.55	0.52	0.59	0.57	0.54	0.59	0.62	0.58

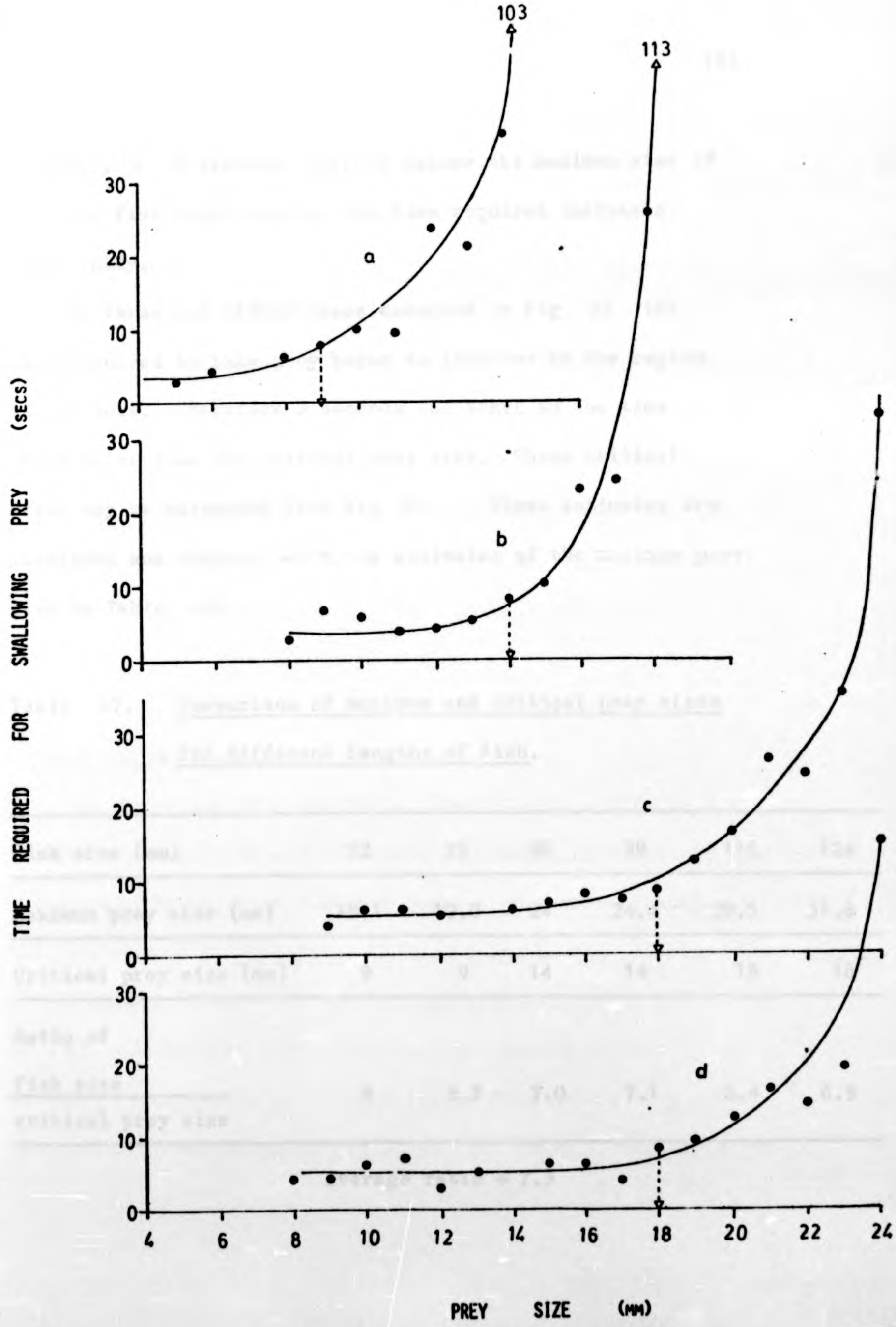
It is interesting to note that Werner (1974) found that in two species of sunfishes the optimal prey size occurs at a prey size to mouth size ratio of 0.59 regardless of fish size. Werner (1974) also measured the prey size as the maximum depth of prey in the dorso-ventral plane.

It will be seen from Table 60 that this ratio for Spinachia is very close to Werner's value of 0.59. The question remains as to whether this similarity is pure coincidence or whether it has a wider application. The question cannot be answered without examining more species which also show size selection.

Estimation of critical prey size and its relationship to mouth size.

It was clear from the observations that the time a fish takes to swallow a prey is dependent not only on the absolute size of the prey but also on the size of the prey taken previously. For example, if a small fish swallows a large prey the time taken to swallow a subsequent small prey is greater than if the small prey had been swallowed first, therefore, in order to determine the time taken to swallow prey of different sizes in different sized fish, only the prey taken as the first choice in the first presentations were included. Fig 25 shows the mean time taken for fish to swallow the first prey in the first presentation for the smallest, medium sized and the largest fishes used in the size selection experiments. The results for 72 and 75 mm fish and 98-99 mm fish are combined to increase the number of observations. All four curves in Fig 25 show essentially the same pattern, namely, the time taken for a fish to swallow a prey is short at the lower end of the size range for all fishes and it does not vary greatly with the fish size. When, however, the prey reaches a critical size, the mean time for the fish to swallow the prey suddenly increases; in other words, it becomes mechanically more difficult to swallow the prey at a certain prey size. The point at which the time required to swallow the prey suddenly increased (8 secs. see below) was called the critical prey size. As the fish size increases, the values for critical prey size also increases. Of the four curves, the one for 72-75 mm fishes is the most complete as it includes the maximum size of the prey the fish are capable of of swallowing. This curve demonstrates that over most of the preferred prey size range the time required to take prey was

Fig. 25. *S. spinachia*. The mean time required by the fish to swallow prey of different sizes. a) 72 & 75 mm, b) 98 & 99 mm, c) 116 mm.
Vertical arrow indicates estimated critical prey size (see text p. 193 for definition).


103
113
a
b
c
d
TIME REQUIRED FOR SWALLOWING PREY (SECS)
0
10
20
30
4
6
8
10
12
14
16
18
20
22
24
PREY SIZE (MM)

generally $<$ 10 seconds, whereas nearer the maximum size of prey the fish could swallow the time required increases drastically.

In three out of four cases examined in Fig 25 the time required to take prey began to increase in the region of $\geq$ 8 secs. Therefore 8 seconds was taken as the time which determines the critical prey size. These critical sizes may be estimated from Fig 25. These estimates are tabulated and compared with the estimates of the maximum prey size in Table 67.

Table 67. Comparison of maximum and critical prey sizes for different lengths of fish.

Fish size (mm)	72	75	98	99	116	124
Maximum prey size (mm)	18.1	19.0	24	24.4	29.5	31.8
Critical prey size (mm)	9	9	14	14	18	18
Ratio of $\frac{\text{fish size}}{\text{critical prey size}}$	8	8.3	7.0	7.1	6.4	6.9

Average ratio = 7.3

It is clear from these figures that if 8 seconds is accepted as the time which determines critical prey size then it becomes difficult for the fish to swallow prey when their prey size exceeds approximately 1/7 of the length of the fish i.e. when the ratio of fish size/critical prey size is greater than 7. Table 67 also demonstrates that maximum prey size that can be taken is much higher than critical prey size. Fig 25 shows that below the critical prey size all sizes offered to the fish are almost equally easy to take and that the time required to take these prey is independent of fish size.

Summary and discussion.

The selection of a particular prey size by a fish of a certain size is a commonly observed phenomenon in the field and the results of the food analyses demonstrated the existence of this phenomenon in Spinachia. (Fig 17 and Section I, Fig 13).

A number of theories may be suggested concerning the nature of such selection in fishes such as that the visual acuity and swimming spped may be greater in larger fish making them more successful in capturing larger prey. For example, Blaxter &

Jones (1967) showed that the visual acuity in herring increased with fish size. Similarly, Baerends et al. (1960) demonstrated that in trained young cichlids the ability to distinguish between 2 close stripes improved with increasing body length. Bainbridge (1958) observed a nearly linear dependence of swimming speed on body length, and, Ohlmer & Schwarzkopff (1959) in a different species found a nearly linear relationship with the square root of body length.

Several workers have demonstrated experimentally the existence of a well-defined response to prey size. Zunini (1937) found in minnows that the selection of a food item was related to its size. Hester (1968) has demonstrated from the principles of visual mechanics that in visual-feeders such as goldfish, large objects have a higher risk of discovery, which was verified by Ware (1972) who showed that in rainbow trout larger prey evoked stronger feeding responses. Similarly Olla, Katz & Studholme (1970) showed that in bluefish increasing the prey size produced an increase in feeding motivation.

Laboratory observations with free swimming mysids showed that a prey-fish size relationship similar to that found in the field could still be observed under experimental conditions. (Experiment 1). Other experiments demonstrated that the fish could alter their average prey size within the limits of their own range of selection (Fig 18 line a) but did not take much larger prey even if it was abundant.

The laboratory experiments demonstrate that when the capture efficiency of S. spinachia is maximized by rendering different sized prey all equally available, the mean size of prey taken still varies with the fish size; the results are comparable to those found in the field.

A comparison of successive presentations indicated that increasing satiation produced more selective response to prey size. The results agree with the findings of Ivlev (1961) and Chiszar & Windell (1973) who found a similar relationship between the degree of hunger and selectivity of fishes.

When different sized S. spinachia were examined individually, it was found that a wide range of prey size could be taken by a fish of a particular size, indicating that when prey availability is maximum and escape mechanisms are eliminated, the fish are capable of taking larger prey than they would normally take in the field. This suggests that while part of any size selection in S. spinachia is affected by the swimming speed and escape mechanisms of the prey, it is not completely determined by them. The prey size range of a fish could overlap with that of a different sized fish but within the range there is a preferred region.

Estimation of the maximum swallowing capacity of the mouth of Spinachia showed that the fish were capable of swallowing whole mysids whose size was $\frac{1}{4}$ of their total length (Table 64). The optimal prey size as determined from the results of Experiment 3 suggested that the fish showed highest preference for prey size around $\frac{1}{8}$ of their total length. (Table 65). It was therefore concluded that the size selection observed in the experiments was not a reflection of mouth size.

On the basis of these studies it appears that there is an innate tendency in S. spinachia for the selection of a certain size range. Smaller fish preferred smaller prey even when the difference in the availability of different sized prey were eliminated. The range of prey size taken, however, increases under such conditions. The results suggest that in S. spinachia prey size selection is not purely a result of prey availability or of mouth size. In the field the maximum size of prey that can be caught is determined by the ability of the fish to catch prey, so that innate size selection is affected and modified by the differences in the swimming speeds of different sized fish and prey.

THE EFFECT OF MOVEMENT ON FEEDING OF SPINACHIA.

Introduction

The important role of movement as a stimulus for fish which are visual feeders is well known and is commonly applied to the design of baits for catching fish. Bateson (1889) commented on the well marked response to movement in visual fishes such as wrasse and mullet. Fulton (1904) and McKenzie (1935) similarly observed that captive cod were strongly attracted to food falling through the water. Meesters (1940) found that the movement of the food item was of decisive importance in the feeding of pike. Tester (1963) concluded from his experiments on tuna that the most efficient baits were the most mobile ones and movement was the most important stimulus. Differences in size, shape and colour of the baits had no significant effect on their efficiency. Brawn (1969) found that she could evoke a feeding response in captive cod by moving a fingertip along the glass front of their tank or by moving paper discs in the water.

During the preliminary observations on the general feeding behaviour of Spinachia it was noticed that moving particles and air bubbles would often evoke a feeding response such as fixating, approaching the objects and, sometimes attack, ingestion and ejection. Preliminary observations also showed that moving palatable prey were preferred in all instances to non-moving palatable prey. Also, if the fish, after being kept for sometime on palatable non-moving food such as chopped mussel gonads, were offered unfamiliar moving prey such as adult Artemia with their usual food, they still showed a clear preference for the moving food.

When Artemia were presented for the first time with freshly killed mysids to which the fish were accustomed, artemia were taken preferentially. These and similar observations strongly suggested that movement was likely to be a very important visual stimulus initiating feeding in Spinachia.

All the findings of previous workers and the results of preliminary observations on feeding of Spinachia point to the significance of movement in the feeding behaviour of visual fishes. In view of this, a knowledge of the responses to movement in Spinachia was considered to be of some value in the analysis of factors affecting food selection. A study of the effects of movement on feeding of Spinachia was therefore undertaken.

The study aimed to answer four questions:

(1) Is moving food taken in preference to stationary food and are there any differences in responses shown to food moving at different speeds?

(2) How does the movement affect the feeding response and what changes, if any, does it cause in the feeding sequence?

(3) Are there any differences in responses to prey moving with different types of movement?

(4) What are the relative strengths of two feeding stimuli, size and movement?

Table 69 . The number of prey taken as first, second, third and fourth choices at 5 speeds. Combined results for 6 fish.

Speed	State	Choice				Totals			Comparison of (a) & (b) X^2	P
		1st	2nd	3rd	4th	1st + 2nd (a)	3rd + 4th (b)	Total (a)+(b)		
0.2 cm/sec	Moving	21	13	14	19	34	33	67	0.01	> 0.80
	Stationary	16	23	17	12	39	29	68	1.47	> 0.30
1 cm/sec	Moving	26	24	9	9	50	18	68	15.06	< 0.001
	Stationary	11	13	22	21	24	43	67	5.39	< 0.05
1.9 cm/sec	Moving	37	31	11	8	68	19	87	27.59	< 0.001
	Stationary	8	15	28	26	23	54	77	12.48	< 0.001
2.9 cm/sec	Moving	28	27	4	3	55	7	62	37.16	< 0.001
	Stationary	4	4	24	24	8	48	56	28.57	< 0.001
3.9 cm/sec	Moving	29	26	7	2	55	9	64	33.06	< 0.001
	Stationary	5	8	22	24	13	46	59	18.46	< 0.001

The effect of movement on the response to prey.

The aim of the first part of the experiments was to show whether or not moving food was taken in preference to stationary food.

Six fishes, varying in size between 93 to 124 mm were used. They were kept singly in the glass tanks of 47 x 31 x 31 cm used in the size selection experiments. The arrangement of tanks and physical conditions such as light temperature were as before (see p 171). The results were recorded on a tape recorder for later analysis. Neomysis integer were used as food in these experiments.

The food was presented to the fish as a set. The apparatus consisted of a 40 cm long, 5 cm wide flat piece of perspex to which transparent glass tubes could be attached at required intervals. An electric motor was attached ½ way along the perspex strip and a 15 cm piece of perspex rod was then attached to the motor spindle. The speed of the motor could be varied between 0 and 3.9 cm/sec by means of a variable power supply.

As in the size selection experiments, live mysids were suspended at the end of transparent tubes of 1 mm in diameter, by fishing line.

Two tubes with suspended mysids were arranged on the main perspex frame at 5 cm intervals, these held the stationary food. Another two tubes were attached to the arms of the movable piece of perspex, separated by 10 cms so that when the motor was switched on, a smooth directional movement of the food could be sustained in a circular orbit of 31 cm. All four mysids, both moving and stationary were kept at the same height.

Four mysids of the same size were presented to the fish at each presentation. The size of the food offered to different fishes was determined according to the optimal prey size in the size selection experiments. (See Table 65). The size range of the food offered to each fish was kept constant throughout the experiments.

The following prey size ranges were used for each fish (Table 68).

Table 68. The food size ranges offered to the fishes of varying lengths in the movement experiments.

Fish size (mm)	93	98	99	110	116	124
Food size range offered (mm)	10-12	12-14	12-14	14-16	16-18	16-18

The first few observations with speeds from 0 to 3.9 cm/sec showed that the initiation of a feeding response for moving prey was earlier at some speeds than others, suggesting the fish responded differently to different speeds.

Five different speeds were used to test the differences in response to varying speed. At each presentation two moving and two stationary mysids of the same size, all equally visible, were offered to each fish and the sequence in which the prey were taken recorded. Observations began after a 24 h deprivation period and continued until the fish stopped feeding.

Experiment 4 was designed to determine whether moving food provided a stronger stimulus for feeding than stationary food when palatability, size, colour, shape and availability of prey were the same.

The preference for stationary or moving food was determined by considering the order of choice. Following the same argument used in the size selection experiments; when four prey, two moving two stationary, otherwise equal in other visual characteristics were available, the first two choices would indicate whether or not a preference for any state existed. That is, if moving and stationary prey were taken indiscriminately the ratio of first and second choices to third and fourth choices would not differ greatly from 1.

Table 69 shows the number of prey taken as first, second, third and fourth choices at five different speeds for six fishes.

The results indicated that at all speeds above 0.2 cm/sec first and second choices differed significantly from third and fourth choices, that is, above 0.2 cm/sec there was always preference for the moving food. Moving prey were usually taken first and stationary prey later.

The number of times when moving food was taken as third and fourth choices i.e. incidents of no selection for movement was low in all cases between 1.0-3.9 cm/sec but was lowest at 2.9 cm/sec.

Table .70. compares the preference (measured as the sum of first and second choices) shown for moving and stationary food at different speeds by means of the X^2 test. A clear selection for the moving food is evident between 1.0 and 3.9 cm/sec, the highest preference for movement being shown at 2.9 cm/sec.

In Fig 26 the percentage of moving prey taken as first and second choices are plotted against speed. It was found that the responses to movement increased from 1 cm/sec up to 2.9 cm/sec then decreased slightly at 3.9 cm/sec but still remained at a high level. Because of the limitation of motor it was not possible to test the responses to higher speeds.

Table 71 . gives the results for the comparison of responses to prey moving at different speeds. The first and second choices which were used as the indicators for preference were summed for moving and stationary prey at each speed. The differences in responses to moving and stationary prey between varying speeds than were compared

Table 70 .. The differences in responses to moving and stationary prey at different speeds.

Speed	No. moving prey taken (a)	No. stationary prey taken (b)	Total	% Moving	% Stationary	Comparison of (a) & (b) χ^2	P
0.2 cm/sec	34	39	73	47	53	0.34	0.70
1 cm/sec	50	24	74	68	32	9.14	0.01
1.9 cm/sec	68	23	91	75	25	22.25	0.001
2.9 cm/sec	55	8	63	87	13	35.06	0.001
3.9 cm/sec	55	13	68	81	19	25.94	0.001

Fig. 26. *S. spinachia*. Variation in preference shown for prey moving at different speeds. (Combined results for 6 fishes).

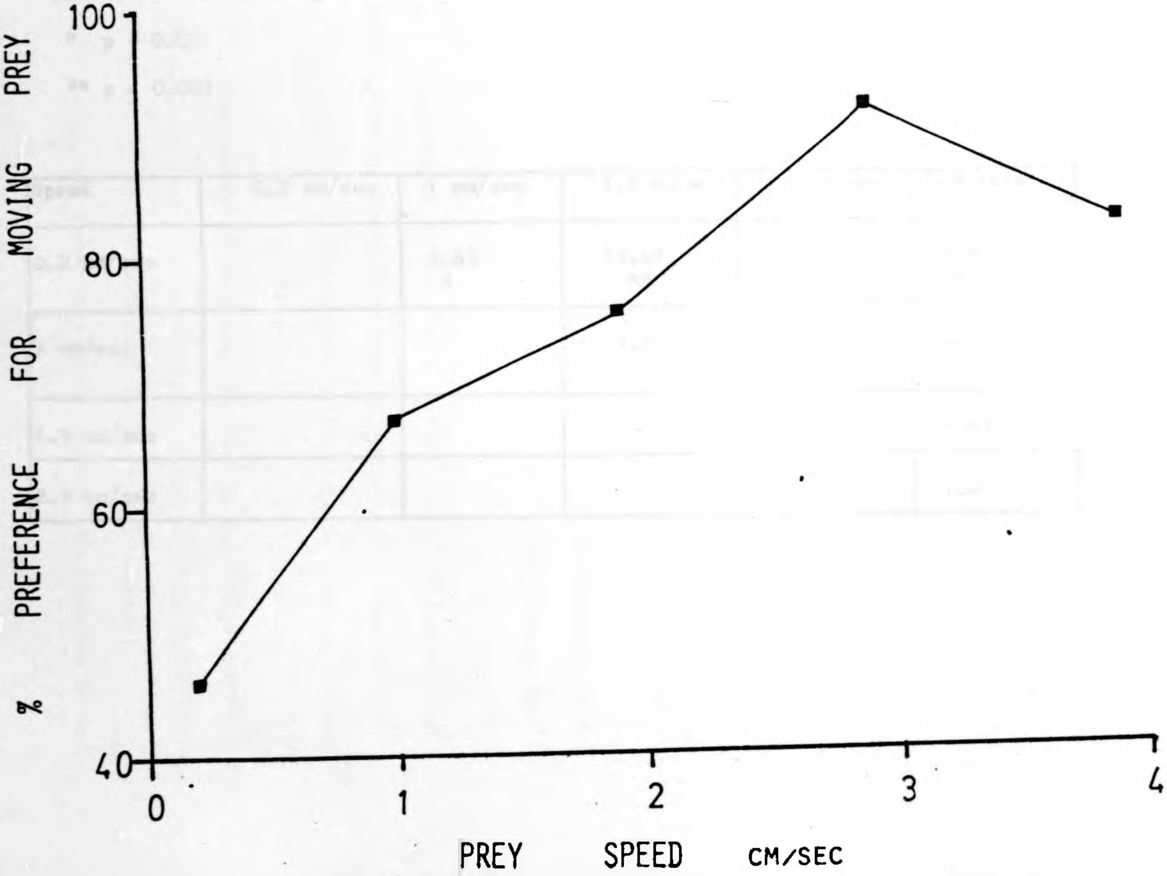

% PREFERENCE FOR MOVING PREY
100
80
60
40
0
1
2
3
4
PREY SPEED CM/SEC

Table 7: χ^2 values for the comparison of responses shown to prey moving at different speeds.

* $p < 0.01$

** $p < 0.001$

Speed	0.2 cm/sec	1 cm/sec	1.9 cm/sec	2.9 cm/sec	3.9 cm/sec
0.2 cm/sec		6.63 *	13.65 **	24.80 **	17.8 **
1 cm/sec			1.03	7.4 *	3.3
1.9 cm/sec				3.66	0.84
2.9 cm/sec					1.00

by the χ^2 test.

The χ^2 values show that the responses to prey moving very slowly with a speed of 0.2 cm/sec were significantly different from the responses shown to prey moving at higher speeds, which means that prey moving at the lowest speed were hardly perceived as moving prey. When the prey speed reached 1cm/sec however, there was a considerable increase in the selection of moving prey. As the speed increased further, the preference for moving food became more marked but when the speed of prey reached 3.9 cm/sec a slight drop in the responses to movement were observed. This drop suggested that the optimal speed has already been reached.

The number of responses to food moving at 1cm/sec did not differ markedly from prey moving at 1.9 cm/sec or 3.9 cm/sec but was significantly different from responses shown to prey moving with the optimal speed of 2.9 cm/sec.

The number of responses to prey moving with a speed of 1.9 cm/sec were not significantly different from those moving with speeds of 2.9 cm/sec or 3.9 cm/sec. Also no difference was found between the number of responses shown to 2.9 cm/sec prey speed and 3.9 cm/sec speed.

This analysis showed that although the difference in responses to stationary and moving prey was maximum at 2.9 cm/sec; the increase in preference for movement after 1.9 cm/sec was not significant. After the critical speed of 1 cm/sec was exceeded, movement of the prey was perceived and moving prey was selected.

The effect of movement on the feeding sequence.

The purpose of the next set of experiments was to determine the degree and the type of change in feeding responses brought about by movement. From the time measurements with stationary prey it was known that when a fish was offered a mysid of optimal size after 24 hr food deprivation, feeding was completed within 8 secs. (Fig 25).

In these experiments (Experiment 5) single mysids were attached to the movable arm of the motor and offered to the fish as stationary food. Once again optimal prey sizes were used for each fish. The presentation of stationary food continued until the fish did not complete the feeding sequence (i.e. did not swallow the prey) within the first minute. All responses to prey were recorded. The motor was then switched on to move the uneaten food at a speed which was known to produce the greatest response (2.9 cm/sec) and any changes occurring in the feeding response were recorded. After this another stationary food was offered and if uneaten within a minute was moved once again, noting any changes in responses and so on. The observations ended when the fish showed no interest to the same food in both moving and stationary states. In this way the changes in the nature of the feeding responses induced by movement could be assessed.

A control experiment (Experiment 6) was then performed to test whether the responses to movement could be produced in the absence of food, that is when no visual clues from prey were available. After the initial deprivation period the fishes were first shown the same stationary glass tubes and responses, if any, were recorded. The tubes were then moved at the optimal speed of 2.9 cm/sec and any further responses to the moving tubes were noted.

The number of changes in feeding responses brought about by movement of food are given in Table 72. As mentioned

Table 72 The number and type of changes in the feeding responses caused by the movement of prey.

Row number	Stage observed while prey stationary	Positive changes (more stages added)	Number of times observed	% of total (65)	No changes (same stage observed)	Number of times observed	% of total (32)	Negative changes (an earlier stage observed while prey moving)	Number of times observed	% of total (10)
1	F1	+ AP	8	12	→ F1	17	53	Not applicable	-	-
		+ AP + AT	11	17						
		+ AP+AT+SW	21	32						
2	F1+AP	+ AT	7	11	→ F1+AP	11	34	→F1 only	5	50
		+ AT+SW	6	9						
3	F1+AP +AT	+ SW	12	18	→ F1+AP + AT	4	13	→F1 only	2	20
								→AP only	3	30
TOTAL			65			32			10	

previously on p.158 a completed feeding response consisted of the basic

$O \rightarrow PI \rightarrow AP \rightarrow AT — GR \rightarrow I \rightarrow SW$ sequence

with free swimming prey. (Fig. 16). By using mysids of optimal size attached to the tubes, the necessity for orientation was eliminated and $GR \rightarrow I \longrightarrow SW$ stages occurred simultaneously as one step; the feeding sequence was therefore reduced to four stages; $PI \rightarrow AP \rightarrow AT \longrightarrow SW$.

Any changes in the stages that occurred towards the completion of the feeding were recorded as positive changes and those from an advanced stage such as attack to initial stages (AP, PI) were considered negative changes.

The total number of positive changes caused by movement were found to be significantly higher than no changes, negative changes and the sum of the latter two when compared by a χ^2 test. χ^2 values for these tests were 11.23, 40.01 and 4.94 respectively.

The movement of the prey induced positive feeding responses in 61% of cases. The proportion of no changes were 30% and negative changes 9%.

When the total number of positive changes are considered, the highest number of positive changes were found to occur between the stage of fixating when prey was stationary and swallowing if moved. The proportion of changes from attack to swallow and Fixate to Approach were also high.

It has been mentioned in the general description of feeding behaviour (p 158) that as the fish gets less hungry the feeding chain stops at earlier stages. By this criterion the observations in the lowest row of the Table 72 where the responses to stationary prey stopped at AT level corresponds to a higher hunger level of the fishes and observations in the first row where the responses to stationary prey stopped at F1 stage to a lower hunger level.

In general, the motivation necessary to induce the fish to approach a prey must be stronger than that necessary to fixate and similarly the stimulus to induce attack must be stronger than that necessary to approach. Therefore it can be assumed that the intensity of responses increases from F1 to SW i.e.,

$$\mathrm{F1} < \mathrm{F1} \longrightarrow \mathrm{AP} < \mathrm{F1} \longrightarrow \mathrm{AP} \longrightarrow \mathrm{AT} < \mathrm{F1} \longrightarrow \mathrm{AP} \longrightarrow \mathrm{AT} \longrightarrow \mathrm{SW}$$

The fact that the highest proportion of positive changes at a lower hunger level was from F1 stage to the completion of feeding and not simply to AP stage indicates that the movement of prey must provide a very strong stimulus for further feeding.

The highest number of no changes were recorded at Fixate stage which was a reflection of a high degree of satiation. The number of no changes at Approach stage were also high but they were relatively few at an advanced feeding stage such as Attack. The number of no changes increased as the hunger level of the fishes decreased.

The total number of negative changes was very low. They mostly consisted of fish approaching the food when stationary and fixating only if moved, indicating once again a high satiation level.

The number and type of changes and no changes when no visual stimuli from prey were present are given in Table 73.

The total number of no changes in this case were found to be significantly higher than number of positive changes brought about by movement. ($\chi^2 = 5.03$, significant at 5% level).

The highest number of positive changes took place

Table 73 . The number and type of changes in feeding responses caused by movement of tubes only. (Control experiment).

Stage observed when tubes stationary	Positive changes (more stages added)	No.	% of total	No changes (same stage observed)	No.	% of total
F1	+ F1 + AD	33	80	→ F1	44	69
	+ F1 + AP + AT	5	12			
F1 + AP	+ F1 + AP + AT	3	7	→ F1 + AP	13	20
F1 + AP + AT	Not applicable	-		→ F1 + AP + AT	7	11
Total		41			64	

Total no of observations: 107.

between stages Fixate and Approach which showed that the movement alone did not stimulate feeding as strongly as movement and prey. Only in a relatively few number of cases did movement promote the feeding response as far as the attack stage.

The number of no changes were highest at F1-F1 stage, that is the fish mostly looked at the tubes both when stationary and moving and showed no further response. The percentage of no changes at the attack stage was lowest. No negative changes were found in these observations, i.e., after approaching or attacking a stationary tube, the fish showed either the same response or advanced to the next stage in the feeding sequence.

The effect of the type of movement on the feeding response and sequence.

The object of the next set of observations was to determine the fishes responses to prey with different types of movement at a high satiation level. The effects of two types of movement, directional and vibratory were tested.

The fishes were first fed on stationary mysids. When the feeding stopped they were offered moving prey of the same size. In directional movement a single prey was moved linearly in front of the fish at a speed of 3 cm/sec and whether or not the fish responded was recorded (Experiment 7). To test the effect of vibratory movement, a glass tube with a prey suspended from its end was attached to a set used in the size selection experiments and was placed at a distance of 20 cm facing the fish. It was then vibrated by moving it 1 cm backwards and forwards 7 times/sec. Any responses shown to prey were recorded. (Experiment 8).

Table 74 summarises the results for responses shown to directional and vibratory movement of prey at a high satiation level. Forty four and forty two observations were made for each type of movement. The figures in Table 74 show that if only the number of positive changes and not the types of changes are considered, the number of feeding responses induced by each type of movement did not differ significantly (χ^2 value for the comparison of the number of positive changes evoked by directional and vibratory movement was 0.36).

Also the number of responses shown to moving prey were

Table 74 .. The number and type of responses shown to prey with directional and vibratory movement at a high satiation level.

Type of movement	Directional					Vibratory				
Type of changes	F1 to AP	F1 to AT	F1 to SW	Total positive changes	Total no changes	F1 to AP	F1 to AT	F1 to SW	Total positive changes	Total no changes
Number	21	1	2	24	20	13	4	3	20	22
%	88	4	8	54	46	65	20	15	48	52

not significantly different from the number of no responses (no changes) in each case. (χ^2 values were 0.36 for directional movement and 0.09 for vibratory movement). This suggested that at a very high satiation level, movement did not provide a high feeding motivation and this was probably independent of the type of movement of prey.

If the proportion of different type of responses evoked by each type of movement were examined, most of the responses were found to take place between F1 ⟶ AP stages for both types of movement which was likely to be a reflection of very low hunger level of the fishes.

The proportion of responses which advanced further to AT and SW stages were low in both cases but were higher in vibratory movement than directional movement. This could imply although the total number of responses induced by each type of movement were not different, vibratory movement could affect the feeding more strongly than smooth directional movement. However, the number of responses at AT, SW stages are too low to reach firm conclusions.

The relative strengths of size and movement as stimuli for eliciting the feeding response.

Lastly the relationship between the two feeding stimuli, movement and prey size was investigated. Two fishes of 93 and 124 mm total length were used in these observations. (Experiment 9).

At each observation the fish were offered two stationary prey of preferred size and two moving prey within the size range that could be taken but would have been taken secondarily if stationary.

It was known from the size selection experiments (Experiment 3) that when stationary prey was used 93 mm fish preferred a size range of 7.5 to 15.5 mm (with a peak at 11.5 mm) to larger prey and 124 mm fish preferred a size range of 15.5 to 23.5 mm (with a peak at 17.5 mm) to smaller prey. In Experiment 9 the 93 mm fish was presented simultaneously with a set of stationary near-optimum size prey (10-12 mm) and a set of moving above-optimum size prey (17-19). The moving prey was rotated at a speed of 2.9 cm/sec. The same size ranges were used for 124 mm fish, this time keeping the large prey stationary and the smaller prey moving. The number of times each prey size group were taken as first, second, third and last choices was recorded.

The results of Experiment 4 demonstrated that moving prey were chosen in preference to the same sized stationary prey. In Experiment 9 prey of preferred size were offered as the stationary prey and secondarily selected size as the moving prey. There were two possibilities (1) If the effects of either positive stimulus did not overrule the effect of another, no preference would be shown for either of them, i.e., the number of prey taken as first, second, third or fourth choices would not differ significantly in both moving and preferred sized prey groups. (2) If preference for movement was stronger than preference for size, then the number of moving prey taken as first and second choices would be significantly higher than the number of first and second choices of preferred (stationary) prey size.

The results of Experiment 9 are tabulated in Table 75 for each fish. The first thing that is apparent from Table 75 is that the pattern of responses shown to moving

Table 75 . Number and proportion of first, second, third and fourth choices of movement and size at three hunger levels for two fish.

Fish size	Type of stimulus	Movement					Preferred size				
	Choice	1st	2nd	3rd	4th	Total	1st	2nd	3rd	4th	Total
93 mm	I.presentation	11	8	9	4	32	7	9	9	10	35
	%	34	25	28	13		20	26	26	29	
	II.presentation	13	8	8	6	35	5	10	10	10	35
	%	37	23	23	17		14	29	29	29	
	III.presentation	12	5	5	2	24	2	9	8	7	26
	%	50	21	21	8		8	35	31	27	
	ΣI+II+III	36	21	22	12	91	14	28	27	27	96
	%	40	23	24	13		15	29	28	28	

Table 75 . cont.

Fish size	Type of stimulus	Movement					Preferred size				
	Choice	1st	2nd	3rd	4th	Total	1st	2nd	3rd	4th	Total
	I.presentation	10	7	6	3	26	3	6	7	10	26
	%	38	27	23	12		12	23	27	38	
124 mm	II.presentation	10	4	7	5	26	3	9	6	8	26
	%	38	15	27	19		12	35	23	31	
	III.presentation	15	7	9	4	35	5	13	11	10	39
	%	43	20	26	11		13	33	28	26	
	I+II+III	35	18	22	12	87	11	28	24	28	91
	%	40	21	25	14		12	31	26	31	

or preferred sized prey remained the same in all presentations for each fish i.e., if there was a selection for movement or size, it did not alter with satiation or the fish size.

When the data and the sums of individual choices are considered, the number of first choices for movement were found to be significantly higher than the number of first choices for size in both fishes. ($\chi^2 = 9.68$, $p < 0.01$; $\chi^2 = 15.08$, $p < 0.001$ for the 93 mm and 124 mm fish respectively). These results indicated that initial preference was shown for movement and not for the preferred prey size.

The sum of first and second choices for movement were consistently higher than the sum of first and second choices for size in all presentations for each fish, but the difference did not reach a statistically significant value in any one of them. This contrasted with the results presented in Table 70 where, for equal sized prey moving at speeds > 1 cm/sec, the sum of first and second choices was always significantly higher than the sum of the first and second choices for stationary food. The results in

Table 75 implied that when the stationary preferred prey size and moving secondarily preferred size were offered to the fish, preference for movment did not completely overrule the preference for size.

The number of second and third choices for movement did not differ significantly from the number of second and third choices for size. The number of last choices indicating the least preference was always significantly higher for size than movement. This meant that when the fish encountered moving prey of secondarily preferred size and stationary prey of preferred size, it first reacted to movement, but it did not necessarily select the remaining moving prey second.

Table 76 shows the number of times that movement and preferred size were taken in a particular order. For example in the moving prey group 1,2 means the moving prey were taken as first and second choices; 1,3 first and third choices; 1,4 first and last choices and so on. The figures verify the same points shown in Table 75 namely that in all presentations most of the moving prey were taken either as first and second (1,2) or first and third (1,3)

Table 76 . Number and times the movement and preferred size taken in a particular order for two fish

Fish size	Type of stimulus	Movement									Size								
	Order of selection	1.0	2.0	1.2	1.3	1.4	2.3	2.4	3.4	Total	1.0	1.2	1.3	1.4	2.3	2.4	3.0	3.4	Total
93 mm	No	5	2	12	13	6	5	3	4	50	2	4	4	4	11	13	1	11	50
	%	10	4	24	26	12	10	6	8		4	8	8	8	22	26	2	22	
124 mm	No	5	–	10	13	7	6	4	1	46	–	1	4	6	12	14	1	9	47
	%	11		22	28	15	13	9	2			2	9	13	26	30	2	19	

choices. Most of the preferred sized food were taken as second and fourth (2,4); second and third (2,3) and third and fourth (3,4) choices. Once again the initial selection for movement is clear.

Summary and discussion : Experiments 4-9.

Experiment 4 demonstrated that Spinachia shows a very strong preference for moving prey. Also there was a threshold speed of prey above which all moving prey were chosen in preference to stationary prey.

Experiment 5 showed that even when the hunger level was not high the movement of the prey induced further feeding. Part of this response was due to the movement of tubes holding the prey (Experiment 6) but this movement alone did not stimulate a feeding response as strongly as when prey were also available, even though the hunger level was higher than in Experiment 5.

At a very high satiation level, movement of prey could still evoke feeding responses from the fish (Experiments 7,8) but its effect on feeding was much less than that found at lower satiation levels (Experiment 5). Also, at a low hunger level, no difference between the two types of movement was found though there were indications that vibratory movement was more effective than directional movement. (Experiments 7, 8).

The observations on size-movement comparison (Experiment 9) showed that the fish initially responded to prey movement and not prey size and this was independent of hunger levels. However, it did not completely ignore the size cue from the prey once it was in the vicinity of suitably-sized prey. The effects of size and movement were therefore additive, movement being the stronger stimulus.

The above results agree in general with those of other workers (Bateson 1889; Fulton 1904; McKenzie 1935; Brown 1969) in that movement is indeed a strong feeding stimulus to visual fish which feed on moving prey. Tester (1963) found in tuna that the effect of the movement of prey completely overruled the other external features of prey. In *Spinachia* although movement has priority, the size of the prey is still important. This suggests that food selection in *Spinachia* is probably a result of several factors.

THE EFFECT OF SHAPE AND SHADE ON THE SELECTIVE FEEDING OF SPINACHIA.

Introduction

Many authors hold the view that movement and size of the prey are of primary importance for feeding of visual predators. Other external prey features such as colour and shape are generally thought to be of secondary importance. The primary importance of prey movement has often been demonstrated experimentally, for example by Martin et.al. (1974) who showed the significance of prey movement in feeding of newts. De Groot (1971) in the feeding of flatfishes, Smith (1973) in the feeding of shrikes.

On the other hand, the influence of colour and shape on food selection has been well established for some fishes. Certain species react maximally to a certain colour which is usually the colour of their natural food and many marine fish are able to distinguish between the different shapes of models (Protasov 1970; Herter 1940).

It has already been mentioned in the general feeding behaviour section that *Spinachia* attacked mysids from the side and swallowed them head first. Directing attacks at the head of prey is a common feature among predatory animals. The predator could react either instinctively or by experience to the specific cues associated with the head or to the anterior end of the body, that is, react to one particular portion of the body in relation to the rest of the body or to a combination of these two factors. If the head is recognised as the anterior end of the body, head discrimination could be a function of prey movement. Smith (1973) has suggested that the forward motion of body may direct the predator's attack to the foremost part of the body i.e., the head.

In addition, it was also noticed during the observations on Spinachia that when darker coloured mysids were put into the tank together with transparent mysids, the fish responded to the dark mysids first. The responses to darker coloured prey were not as frequent as the attacks to prey heads, nevertheless they suggested that mature Spinachia could discriminate between different shades.

Attacks directed at the head of the prey appeared to be a consistent feature of feeding; responses to dark mysids also occurred quite frequently. Such observations suggested that on investigation of the relative importance of shape and shade in evoking feeding responses in Spinachia would be of some value.

Questions that arose were whether head attack was solely due to the movement of prey and if not, which cues in the head made it more attractive to the fish than other parts of the body. If the effects of shape and shade stimuli could be established, then the role of these external prey features in the selective feeding of Spinachia could be evaluated in greater detail.

Feature of the attack on stationary mysids.

The aim of the first part of the experiments was to see whether the fish would discriminate between different parts of the prey body when the prey was stationary. Neomysis integer was used as prey. (Experiment 10).

A group of mysids were kept in a glass tank for six weeks and due to colour adaptation they became opaque white in appearance. The stalked eyes were large, black and very conspicuous in the head. The darkly pigmented stomach under the carapace was also quite conspicuous from the dorsal view in the anterior third of the body. Two rows of dark pigment bands extended from head to tail. The pigmentation at the tail segments was slight. The overall picture of the mysid consisted of a darker head region tapering towards a lighter mid-part and tail.

Single live mysids within the predators preferred size range were offered to the fish, held stationary by attaching them to the glass tubes used in the size selection experiments. The mysids were suspended from the tubes in such a way that the fish have a broadside view. Five fishes of 72, 75, 102, 106, 110 mm total length were used in these experiments. The number of times the fishes attacked the various parts of the mysid body are given in Table 77.. .

The results showed that the number of attacks directed at the head were very significantly higher than the number of attacks made to the middle of body and to tail. They were also significantly higher than the sum of attacks to middle and tail combined. It may be concluded therefore the head was clearly differentiated from the rest of the

Table 77. Comparison of the regions of attack of mysids

A = number of attacks made on different body regions

B = χ^2 and ρ values for comparison of attacks between different body regions.

χ^2 value at ρ = 0.001 level is 10.83.

	A				B			
Body Region	Head(H)	Middle(M)	Tail(T)	Total	(H)X(M)	(H)X(T)	(M)X(T)	(H)X(M &
Number of Attacks	181	28	33	240	112.0	106.13	0.15	70.21
Percentage	75	12	13		0.001	0.0001	0.70	0.001

body, even when stationary.

The number of attacks made to the middle region of the body did not differ significantly from those made to tail. The fact that the middle part was not differentiated from the tail which is the posterior end of the body showed that head selection could not be solely based on recognising the ends of the body in a stationary prey.

The possible cues present in the mysid head which could contribute towards the recognition of this part of the body as head when stationary are:

1. Overall shape of the head region together with shape of antennae, eyes, carapace and legs;

2. Thickness of the head region compared to tail;

3. Overall differences in shade caused by the black eyes, dark alimentary tract, pigmentation at the base of the legs and opaqueness of the head region in contrast to the transparency of tail;

4. Movements of legs, antennae.

The head recognition would be due to the combined effects of 1 to 4. For example, the head could be distinguished as the thicker, darker end of the body with moving extensions.

Comparisons between body regions and colour.

In the second set of experiments (Experiment 11) Praunus flexuosus was used as prey because Praunus was found to show a higher degree of colour adaptation than Neomysis.

A group of Praunus were kept in white tanks to reduce their colour as much as possible. When colour adaptation was maximum only the black eyes, alimentary tract and the pigments at the base of the legs contrasted with the remaining part of the body which was uniformly transparent.

A second group of mysids were kept in black tanks to darken their colour maximally. Even when they were at their darkest, the contrast between the black eyes and the rest of the body was still noticeable. In order to eliminate this contrast the whole animal was darkened with finely powdered animal carbon. Mysids were rolled in the powder until the whole body acquired a very darkly pigmented appearance.

A complete set of comparisons were carried out between the various combinations of head, tail, black and white. (Experiment 11).

The fish were presented with two choices at a time, a white head and black head for example and the number of times each one was selected were recorded.

The portions offered were kept equal in length but although the head of a smaller mysid was offered together with the tail of a larger mysid in order to equalise the thickness of the parts, small differences in the thickness of the head and tail still existed.

Head portions and whole animals were not compared because although their length could be equal, their thickness could never be, and vice versa.

By using dead animals and as near as possible equally sized portions, the effects of thickness and moving parts, such as legs, were eliminated from the list of possible cues for the recognition of head given earlier. The observations, therefore should test the effect of shape and shade.

Table .78 gives the number of times that heads, tails, black and white were selected and the total number of of observations in each comparison.

At each comparison it was assumed that there was no selection between different parts and colours offered, the null hypothesis being that equal numbers of each choice were likely to be taken in each set of observations. If the null hypothesis was correct then the number of choices in each category for each comparison would not differ significantly.

Table 78 . Comparison of the choice between prey body regions and colour.

Comparison number	Type of comparison		Number of tests	X^2	P
1	Black whole 60	White whole 34	94	6.48	< 0.02
2	Black head 49	White head 27	76	5.80	< 0.02
3	Black tail 36	White tail 26	62	1.31	> 0.20
4	White head 37	White tail 19	56	5.16	< 0.05
5	Black head 34	Black tail 16	50	6.48	< 0.02
6	White head 51	Black tail 34	85	3.01	> 0.05
7	Black head 58	White tail 33	91	6.33	< 0.02
8	Black whole 43	White tail 22	65	6.15	< 0.02
9	White whole 45	Black tail 32	77	1.87	> 0.10
10	White whole 49	White tail 29	78	4.63	< 0.05
11	Black whole 41	Black tail 26	67	3.36	> 0.05

On the basis of the results given in Table 78 it appeared that the head was dominant to tail and black was dominant to white. The degree to which each characteristic was selected seemed to depend on the presence and absence of other characteristics. For example, black heads and black whole animals were selected in preference to white head and white whole animals but this selection for black colour was not as strong when only black and white tails were present.

A scheme was devised to describe the selection mechanisms that were thought to be operating. Arbitrary cue strengths were chosen for each body part and colour. It was assumed that the order of dominance was Black > Head > White > Tail.

Black was given a cue strength of 4, head 3, white 2, tail 1.

Using these arbitrary cue strengths it was possible to predict the outcome of any comparison by comparing the difference in scores of the two choices offered, the choice with the higher score of cue strength being preferred. For example a black head (score : 4 + 3 = 7) should be taken more often than a white tail (score: 2 + 1 = 3) and so on.

Table 79 lists the comparisons and their predicted outcomes.

In 8 out of 11 comparisons the actual outcomes matched the predictions but there were three outcomes which did not agree with the predictions.

First, if black colour was always dominant to white and was independent of the part of the body, it would have been expected that black tails would have been preferred to white tails. Although the number of black tails taken was higher than the number of white tails, the difference was not statistically significant. (Table 79, , comparison 3).

Secondly, when white whole animals were compared with black tails, although whole animals, which contained the preferred characteristic "head", were taken in higher numbers the difference once again was not significant (Table 79, Comparison 9).

Thirdly, when black whole animals with the preferred "head" cue were compared with black tails, higher number of whole animals were taken than the tails but the difference did not reach the 5% significance level. (Table 79, Comparison 11.

Table 79 .. Comparison of the actual and predicted outcomes of prey choices based on the differential "cue strength" hypothesis. (See p).

Comparison number	Comparisons with assigned cue strengths for each characteristic		Score difference	Prediction	Prediction correct at $p < 0.05$
1	Black (Head + tail) 4 + 3 + 1 = 8	White (Head + tail) 2 + 3 + 1 = 6	2	BHT > WHT	✓
2	Black head 4 + 3 = 7	White head 2 + 3 = 5	2	BH > WH	✓
3	Black tail 4 + 1 = 5	White tail 2 + 1 = 3	2	BT > WT	×
4	White head 2 + 3 = 5	White tail 2 + 1 = 3	2	WH > WT	✓
5	Black head 4 + 3 = 7	Black tail 4 + 1 = 5	2	BH > BT	✓
6	White head 2 + 3 = 5	Black tail 4 + 1 = 5	0	WH = BT	✓
7	Black head 4 + 3 = 7	White tail 2 + 1 = 3	4	BH > WT	✓

Table 79 cont.

Comparison number	Comparisons with assigned cue strengths for each characteristic	Score difference	Prediction	Prediction correct at $\rho < 0.05$
8	Black (Head + tail) 4 + 3 + 1 = 8 White tail 2 + 1 = 3	5	BHT > WT	✓
9	White (Head + tail) 2 + 3 + 1 = 6 Black tail 4 + 1 = 5	1	WHT > BT	×
10	White (Head + tail) 2 + 3 + 1 = 6 White tail 2 + 1 = 3	3	WHT > WT	✓
11	Black (Head + tail) 4 + 3 + 1 = 8 Black tail 4 + 1 = 5	3	BHT > BT	×

The overall trend of the results suggested that the scheme of black being dominant to white and head dominant to tail was probably correct, although the three wrong predictions may indicate that the relative strengths of different cues were slightly different from those allocated. For example, the actual strength of the black cue was not one cue strength unit more than the strength of the head, twice the strength of white or four times the strength of the tail cue. Also the effect of combining a number of sign stimuli may not necessarily be simply additive in an arithmetical sense.

The nonsignificant differences obtained in comparison of whole animals with tails could also be partly due to the unequality of the thickness of portions. A smaller whole animal was presented together with the tail of a larger mysid to equalise the parts as much as possible, but there still could be differences in the actual thickness of the two choices. If one of the recognisable characteristics of head was its thickness, a thicker tail could have some of the attractiveness of head, hence a greater number of tails would be selected than in straightforward head and tail comparisons. In support of this view, it was noticed that the fish attacked the anterior, thickest part of the tail portion throughout the observations.

Comparison of size and colour stimuli.

It has been mentioned above that head and whole animal comparisons were not attempted when testing the effect of colour and shape, because the thickness and length of the two portions could never be equalised. They were used in comparison of the relative stimulus strengths of size and colour. (Experiment 12).

Two fishes of 72 mm and 102 mm total length were used. Each fish was presented with head portions and whole mysids of the same thickness but of different lengths and alternate colours. The length of the head portion was 7 mm and of the whole mysid 14 mm. Fig 20 Fig 21 show that the length of the head portion was within the optimal size range of 72 mm fish while that of the whole mysid was secondarily selected. Similarly the size of whole mysid was optimal for 102 mm fish and head portion was of secondarily selected size. The number of times head and whole animals were selected were recorded. The null hypothesis here was that an equal number of each choice were likely to be taken in each set of observations by each fish. The results of the outcomes are tabulated in Table 80.

Table 80. Comparison of the choice between prey colour and size for two individual fishes.

Comparison Number	Fish size (mm)	Type of Comparison		Number of Tests	χ^2	P
1	72	White Head 24	Black Whole 12	36	4.0	<0.05
2	72	Black Head 22	White Whole 8	30	6.53	<0.025
3	102	White Head 21	Black Whole 46	67	9.32	<0.005
4	102	Black Head 14	White Whole 27	41	4.1	<0.05

The comparisons of size and black, white colour were found to be significantly different in all cases and the null hypothesis was rejected.

The results show that both fishes in each set of comparisons took a significantly higher number of their preferred size, regardless of its colour. This showed that size stimulus was stronger than the stimulus provided by colour.

Earlier comparisons suggested that black was a stronger stimulus than white (Table 78). For both fishes χ^2 values of the comparisons where the preferred sized food colour was black were higher than when it was white. (Table 80 comparisons 2, 3). This may indicate the additive nature of colour and size stimuli; which suggests that if a food is both of preferred size and black, the selection for it is stronger than if it is of preferred size and white.

GENERAL SUMMARY AND DISCUSSION OF THE EXTERNAL FACTORS AFFECTING PREY SELECTION BY SPINACHIA.

The results of Experiments 1-3 deomonstrated that size cue of prey was significant in the selection of food by Spinachia. For each fish size, an optimal prey size range was found. (Experiment 3). This preferred range became more marked as the fish became more satiated. The trend of increasing selection for size with a high degree of satiation was demonstrated both when the number of negative responses were considered (Fig 20 , Table 61) and when the percentage of first and second choices was examined (Fig 21 , Table 62). Meesters (1940) mentioned in his work with Phoxinus laevis that when the fish were hungry, they preferred bigger objects, and on the whole, they were less selective. Ivlev (1961), Protasov (1968), Ware (1972) similarly hold the view that fish become more selective with regards to prey as the hunger level decreases. The earliest experimental evidence for the selection of a preferred size is given by Herter (1929). He trained Phoxinus laevis to respond to small and large shapes and found that the response to smaller objects was highest. He did not measure the responses to a graded series of sizes so that the smaller size his fishes selected was presumably closer to their optimal size. Unfortunately he does not give the size of the preferred shape or of the fish which would enable us to work out the relationship between the fish size and preferred size. His observations do, however, suggest the presence of an optimal size in this fish. Zunini (1937) similarly demonstrated experimentally in Phoxinus laevis, by offering the fish wax globules of varying size, that the size of object selected depended on the size of the fish.

No optimal prey size determinations are found in the literature until quite recently. Werner & Hall (1974) showed the existence of an optimal prey size in blugill sunfish under experimental conditions and discussed size selection in relation to searching and handling time.

Experiments 4-9 examined the importance of movement as a feeding stimulus in Spinachia. When the fishes were hungry, moving prey was always preferred to stationary prey. Also when the hunger level was lower, movement provided strong motivation for further feeding and this was apparent from the analysis of feeding stages, but when the satiation was complete, movement of food no longer stimulated feeding.

Meesters (1940) showed that in pike, moving prey stimulated feeding much more strongly than stationary prey. Tester (1963) showed the importance of movement of prey in his research into bait selection by tuna. Brawn (1969) found for cod that a feeding response could be evoked by moving inedible objects. Experiments with Spinachia using moving tubes without prey (Experiment 6) showed that although movement alone could evoke feeding responses, they were not as strong as movement and prey combined, suggesting that visual cues from the prey as well as movement were important in food selection. In this respect Spinachia is different from tuna in which Tester (1963) showed that size, shape and colour of bait did not affect the feeding response.

Experiments with moving prey showed that in Spinachia there was an optimal speed of prey movement. This is similar to Meesters (1940) findings with minnows. He found that the number of attacks made on a wavy thread moving at different speeds was dependent upon the frequency of the thread's movement, up to a maximum of 1.5 movement/sec. This optimal speed was similar to the frequency of movement of the fishes natural prey (Enchytraeus). When the frequency of movement was higher than 1.5 mov/sec, the attack rate dropped. In Spinachia the highest number of responses were shown to prey moving at 2.9 cm/sec. The swimming speed of their natural prey, such as amphipods and mysids, were not measured but optimum speed to which the fish responded most strongly is probably related to the speed of their natural prey.

Experiments 4 and 5 demonstrated the importance of size and movement of prey in evoking feeding responses. A comparison of the relative strengths of size and movement stimuli demonstrated that the fish responded initially to movement and moving prey was selected first, regardless of it's size. It was also found that the movement of prey, though dominant, did not completely overrule the size stimulus. (Experiment 9).

General observations on the feeding behaviour of Spinachia showed that attacks to the head of moving prey were much more frequent than attacks to any other part of the body. Meesters (1940) similarly observed that pike usually attacked roach at the head end. Observations with stationary prey in Spinachia (Experiment 10) demonstrated that head attack persisted even when the prey was stationary and thus could not be solely a result of prey movement. This suggested the possibility of the existence of shape recognition in Spinachia which might be combined with shade recognition as the dark eyes of the prey provided a sharp contrast to the colour of the body. Zunini (1937) found that Phoxinus laevis preferred objects with irregular surfaces more than those with flat smooth surfaces. If such recognition applied to other fishes it could provide another explanation for the recognition of head portion of prey by Spinachia. The tails of the mysids used as prey have smooth flat surfaces whereas the surface of the head portion is more irregular with extensions and protrusions such as antennae, legs and eyes. Hager (1938) found that when both Phoxinus laevis and Eupomotis gibbosus were presented with flat surfaces of the same size and shape, but one with uniform colour and the other divided into different patterns such as squares, the plain surface was much less preferred than the one divided into patterns. If such a preference also applies to Spinachia it could also contribute towards explanation of the selection of mysid heads which, as well as being more irregular in structure, have a less uniform colour than the tail. When different body portions of same colour were offered to Spinachia, it was found that head was preferred to tail. Similarly black was found to be dominant to white. The outcome of comparisons of different body parts with different shades suggested a relationship between head, tail and black, white as follows:

Black > Head > White > Tail

The results suggested that shape and shade stimuli were possibly additive but not in a straight-forward arithmetical sense. This phenomenon may be another case of the general principal of the "heterogeneous summation" of stimuli. (Hinde, 1966).

The selection of black colour over white is to be expected as the black colour increases the contrast of prey with the environment; but black preference over white does not appear to be general. Herter (1953) found among six species of fish he examined four selected white in preference to black, and two preferred black to white. Furthermore he found in some species that this colour selection could be modified by association with other fish; in other words, those fishes which selected black over white individually, after being kept for a month or so with fish which selected white over black changed their preference. Black preference persisted in one species even when kept with fishes which preferred white. In another set of observations he offered Phoxinus laevis black and white shapes on contrasting backgrounds and found that white was selected more when the background of aquarium was black. This suggests that the contrast between the prey and background is more important than the actual colour. Hager (1938) similarly found in Eupomotis gibbosus L. a black square with white stripes was preferred to a white square with black stripes as white on black background offered a stronger contrast than black stripes on white background.

The relative strengths of colour and size stimuli were tested in Spinachia by offering the fish black and white prey of preferred and secondarily preferred size. (Experiment 12). It was found that regardless of colour, both fishes of different size, selected their preferred size, whether it was black or white. When the food was both black and preferred size, the selection for it was more marked, which suggested that although size is dominant to colour, the two stimuli could be additive.

The relative stimuli of shape and size were not compared, but as colour is a stronger stimulus than shape, and size stronger than colour, it could be predicted that size is probably dominant to shape.

The results suggested that in Spinachia the importance of the various sign stimuli presented by prey have the following relationship

Movement > Size > Colour > Shape

(Shade)

Meesters (1940) found that when the responses of three spined sticklebacks to a motionless wavy thread were compared with those to a motionless straight thread, the fish preferred the wavy thread, indicating shape recognition in this fish. When the straight thread was moved however, the responses to it increased up to a maximum and then declined with a further increase in the speed of movement. His results suggested that the stimulus for movement is stronger than that of shape, as well as demonstrating the presence of an optimal speed of prey movement.

Movement, size, colour and shape of prey all contribute towards making the prey more visible to a predator, hence it can be expected that they should be significant in prey selection.

Experiment 3 clearly showed that an optimal size range exists for each fish size in Spinachia. Since a large prey is both more conspicuous and beneficial fot the fish than a small one, one would not expect the selection of a particular size under experimental conditions where small and large prey were rendered equally catchable. The results showed that even with stationary prey, a small fish does not take the biggest prey it is capable of swallowing but selects a certain size. If size selection exists, it must have a practical value for the fish. Thus it is necessary to consider what benefit the fish could derive from selecting an optimal size range, for it is logical to assume that natural selection will necessarily favour those foraging patterns in a species that are most economical.

If all prey were equally easy to find, capture and swallow; then the biggest prey will be more beneficial to fish than smaller ones i.e., the fish obtains a larger benefit (food intake) at a smaller cost (energy output); therefore the prey size which gives the smallest "$\frac{\text{cost}}{\text{benefit}}$" ratio will be most advantageous for the fish (Werner and Hall, 1974).

In the field with free swimming prey, the cost of obtaining prey will consist of the energy expanded in searching and pursuit i.e., the time required for the predator to find and capture the prey, together with handling time, defined as the time required to swallow the captured prey.

Fig 25 shows that below a critical size all prey size groups had approximately the same handling time (5 secs). Thus it will be most beneficial for the fish to swallow the largest prey nearest to and below this critical size, thereby maximising the cost/benefit ratio. If this assumption is correct then one would expect that the optimal prey size for the fish, as estimated from the previous experiments, should lie close to the critical size after which handling time begins to increase rapidly. As explained earlier, the critical size was taken as the point at which handling time became consistently 8 secs, as it was in this region that handling time began to increase in 3 out of 4 cases illustrated in Fig 25. Comparisons of the estimates of critical size for each case in Fig. 25 with the estimated optimum size are shown in Table 81.

Table 81. Comparison of preferred prey size range and critical prey size for fishes of different sizes.

Fish size	Preferred prey size range			Critical prey size (mm)
	Minimum (mm)	Optimum (mm)	Maximum (mm)	
72	< 5.5	9.5	11.5	9.0
75	< 5.5	7.5	11.5	9.0
98	7.5	11.5	15.5	14.0
99	7.5	13.5	15.5	14.0
116	13.5	17.5	21.5	18
124	13.5	17.5	23.5	18

It will be seen from Table 81 that optimum prey size and the estimated critical prey size are in close agreement and in all cases the critical prey size lies well within the preferred range. Hence the hypothesis put forward above to account for the existence of an optimal prey size may be considered valid.

LABORATORY OBSERVATIONS ON PREY SIZE SELECTION BY PHOLIS GUNNELLUS

Introduction

The results of the gut content analyses showed P. gunnellus in the field fed primarily on small crustacean and, like S. spinachia, amphipods were the main food item in the diet. (Tables 18, 19).

There were also indications of size related feeding heterogeneity, that is, the type of food in the fishes stomachs varied with the size of fish. This relationship between food types and fish size however, was not as well defined as in S. spinachia, but was most apparent at both ends of fish size range. For example, crabs and fish were taken by the largest fish and the importance of small crustacea such as harpacticoids in the diets of the fish increased markedly in the summer months when most fishes examined were juveniles. This suggested the possibility of prey size selection in P. gunnellus. It was not known whether the fish actively sought a prey of a certain size or whether any division of prey sizes in fish stomachs arose as a result of the fishes ability to catch and swallow prey.

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The aim of the laboratory observations on P. gunnellus was to determine whether or not there was an instinctive or learned preference for a particular size of prey in different sized fish.

The relationship between fish size and prey size in the laboratory.

Methods: A group of 8 fishes with a total length varying between 80-170 mm were used. They were caught in the field and kept in the tanks for 4-6 weeks prior to the experiments. Trials with various food items showed that they readily took a variety of food both familiar and unfamiliar such as mysids, live *Artemia*, chopped mussel and squid pieces. Both dead and live mysids were found to be highly palatable to the fish although the fish had difficulty in capturing the swimming mysids. Mysids were chosen as the food objects for the size selection experiments to enable a direct comparison with the results obtained with *S. spinachia* where live mysids were also used as prey.

The fishes were placed in the same perspex tanks used in the *Spinachia* experiments. The fish were observed singly. The physical conditions in the tanks were as described for *S. spinachia*. The apparatus used to offer the fish the prey of different sizes were the same as that described in pp.172 except that to render all prey equally visible to the fish and facilitate capture, the tubes to which prey were attached extended to the bottom of the tank.

Preliminary observations showed that after the initial food deprivation period when the fish was released into the feeding chamber, it swam directly ahead to the food and apparently did not see all the four prey presented, reacting at most to two adjacent preys. This was especially true in smaller fishes. In order to enable the fish to see the prey equally, only two prey at a time were presented.

The size range of the mysids used in the observations was 4-27 mm. During the course of the experiment it became clear that the fish, particularly the larger ones, would respond to prey larger than 27 mm. Since mysids larger than 27 mm were not available, shrimps (Crangon crangon) were used to extend the available prey size range up to 60 mm.

At each presentation one large and one small mysid were offered to the fish and the prey to which is first responded i.e., attacked, bit off a part or swallowed was recorded. The steps before AT stage in the basic ~~feeding~~ chain (i.e., FI, AP) were not included as positive responses. The number of first and second choices for each 2 mm prey size group were recorded.

Decription and feeding behaviour of P. gunnellus

P. gunnellus is a bottom living fish and extremely flattened laterally. In the tanks the fish could swim both vertically and along the bottom of the tank. When swimming, it moved its body from side to side in a sinusoidal wave, rather like an eel. The fish remained mostly stationary with body curled. It seemed to prefer places where the body in the resting postion could be in maximum contact with the surface of the substrate, corners of the tank were favourite locations. When there were more than one fish in the tank they did not choose separate corners but remained in the same corner. When searching for the food, the head was directed forward and lifted by propping on pectoral fins, the tank area being searched by the eyes. This lifting of the head, propped up on the pectoral fins, which was typical of the searching behaviour of this fish, appears to be common among bottom feeders. Both M. scorpius and T. bubalis were found to display pectoral fin propping in the tanks. Stickney (1973) gives a description of similar behaviour observed in flat fishes.

P. gunnellus could move its eyes without head or body movements, turning of the head from side to side was also commonly observed. There were sudden outbursts of rapid swimming, the fish would then stop, both eyes fixed binocularly on the potential food object; then make an attack towards it. The basic feeding sequence was similar to that of S. spinachia, that is,

Fixation → Approach → Stop → Attack → Ingest.

Stopping before attacking seemed to occur more frequently than in S. spinachia. A mysid could be ingested both from head onwards or from the side, folded into two. Biting pieces from a large food item was also common. P. gunnellus was able to take food from tank surface by swimming upwards, but was more efficient when taking food from the bottom.

Yawning activity was observed mostly in the resting position and appeared to be more frequent than in S. spinachia.

Results:

Since there were only two choices at each presentation, the preference shown for each size group was determined by the extent to which it was selected as the first choice, i.e., the number of prey attacked first is expressed as a percentage of the total number of prey presented in that size group.

The percentage preference shown for different size groups were similar in the first and subsequent presentations. When the number of first and second choices in the first presentations were compared by the χ^2 test with those in the subsequent presentations in each size group, 6 out of 8 fishes showed no differences in preference between the presentations.

For the two fish that did show differences, the number of first and second choices in the first presentations were found to be different from those in following presentations at the 5% significance level in 5 out of 12 size groups examined. As the majority of the fish did not show significant differences in number of first and second choices in the first and subsequent presentations, the pooling of the results for each fish was considered to be valid.

The percentage preference shown for different size groups of prey offered are given for each fish in Fig 27 and Table 82.

The prey size groups above 26.5 mm correspond to observations where shrimps were used, as it was not possible to collect mysids larger than 27 mm. The observations suggested that the use of shrimps did not affect the pattern of responses. It was assumed that the fish continued to respond to the size of prey and not other visual clues such as colour and shape that differ from mysids.

Fig 27 shows the variation in percentage preference with

Fig. 27. *P. gunnellus*. The percentage preference shown for different prey size groups for 3 fishes of a) 80 mm, b) 120 mm, c) 155 mm.

Prey sizes are in 2 mm groups up to 36 mm, thereafter they are in 5 mm groups. The dotted lines on the right hand part of the figures indicate the change in prey from mysids to shrimps.

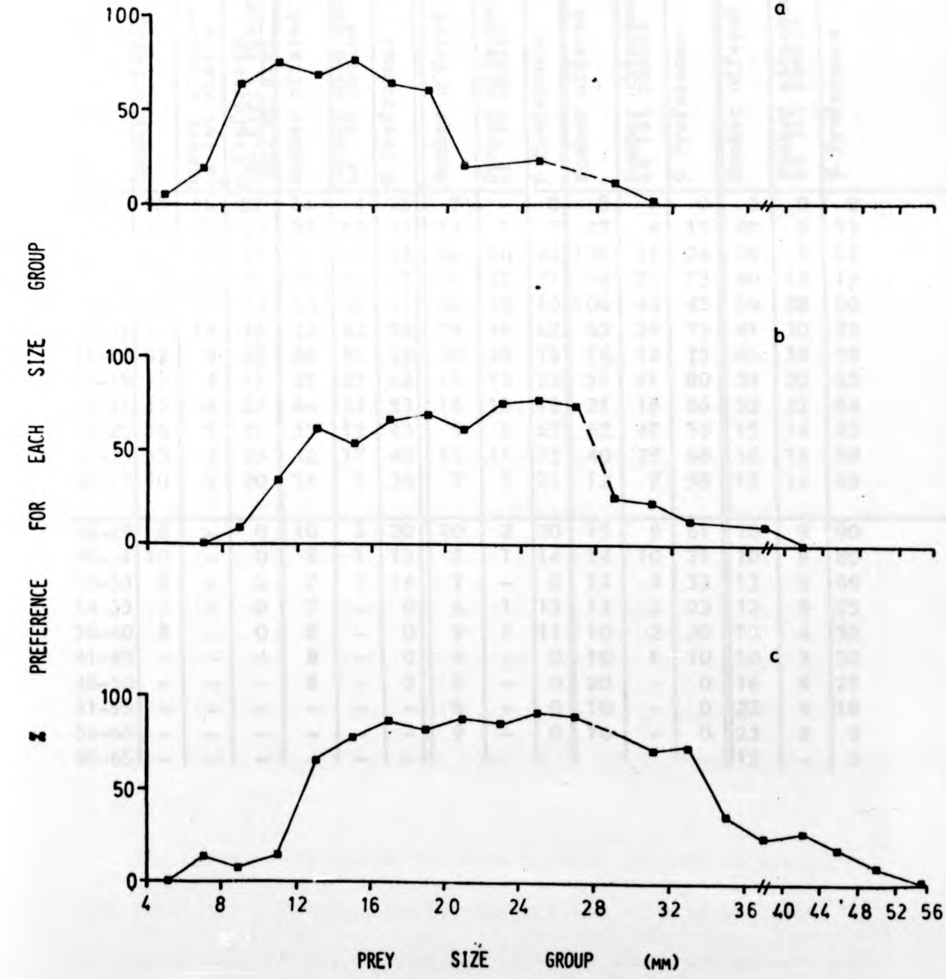

a
b
c
100
50
0
% PREFERENCE FOR EACH SIZE GROUP
4
8
12
16
20
24
28
32
36
40
44
48
52
56
PREY SIZE GROUP (MM)

Table 82. The relationship between the percentage preference and different prey size groups. The top half of the table refers to mysids, the bottom half to shrimps.

	FISH SIZE (mm)														
	50			90			110			135			170		
Prey size (mm)	Number offered	Number attacked as 1st choice	% Preference (No. first choice x 100) / No. offered	Number offered	Number attacked as 1st choice	% Preference	Number offered	Number attacked as 1st choice	% Preference	Number offered	Number attacked as 1st choice	% Preference	Number offered	Number attacked as 1st choice	% Preference
4–5	28	16	57	16	4	25	7	–	0	8	–	0	2	0	0
6–7	37	23	62	32	10	31	14	1	7	27	4	15	40	5	13
8–9	43	25	58	92	35	38	46	10	22	130	31	24	39	5	13
10–11	96	63	66	176	00	57	101	37	37	59	31	53	90	13	14
12–13	36	16	44	63	32	51	50	30	60	106	46	43	56	28	50
14–15	37	14	38	72	42	58	74	46	62	65	36	55	41	30	73
16–17	32	9	28	86	51	59	50	38	76	16	12	75	46	36	78
18–19	13	4	31	27	27	63	18	13	72	51	41	80	24	20	83
20–21	15	4	27	64	34	53	18	13	72	21	18	86	32	27	84
22–23	16	5	31	35	15	43	9	6	67	62	47	76	15	14	93
24–25	13	3	23	42	17	40	15	11	73	40	27	68	18	16	89
26–27	10	2	20	14	5	36	7	5	71	12	7	58	15	14	93
28–29	8	–	0	10	2	20	10	2	20	15	9	61	10	9	90
30–31	10	–	0	8	1	13	7	1	14	14	10	71	70	8	80
32–33	6	–	0	7	1	14	7	–	0	12	4	33	13	9	69
34–35	7	–	0	7	–	0	8	1	13	13	3	23	12	9	75
36–40	8	–	0	8	–	0	9	1	11	10	2	20	12	4	33
41–45	–	–	–	8	–	0	9	–	0	10	1	10	10	3	30
46–50	–	–	–	8	–	0	8	–	0	20	–	0	16	4	25
51–55	–	–	–	–	–	–	8	–	0	10	–	0	22	4	18
56–60	–	–	–	–	–	–	9	–	0	10	–	0	23	2	9
61–65	–	–	–	–	–	–							12	–	0

different sizes of prey in 80, 120 and 155 mm fish.

The three fishes show essentially the same trend, namely, the percentage preference is low in the lower end of the size range, its values being much below the 50% level. When the prey size reaches a certain value, the percentage preference increases above the 50% level and remains high and relatively unchanged over a wide size range. As the prey size continues to increase, the percentage preference falls sharply below the 50% level once again and remains low until it finally reaches zero.

In the 80 mm fish, the percentage preference increased rapidly with prey size above 6-7 mm prey size group; remained above 60% up to 18-19 mm, decreased sharply with a further increase in prey size and tailed off to zero at 30-31 mm.

In the 120 mm fish the percentage preference increased more gradually in the lower end of the size range, exceeding the 50% level at 12-13 mm. It remained high up to 27 mm, then fell sharply at 28-29 mm.

The 155 mm fish showed the same plateau pattern as the 80 mm fish where the percentage preference was low at both the lower and higher ends of the size range. Between these low preference zones, there was a well defined high preference region which remained relatively unchanged.

It will be seen from the data in Table 82 that the remaining five fishes exhibited the same pattern, this being most clearly demonstrated by the 110, 135, 170 mm fishes.

In the 50 mm fish the percentage preference for the smallest prey size group offered, 4-5 mm, is above 50%, which suggests that the high preference region starts at a lower prey size. The percentage preference begins to decrease after 10-11 mm prey size.

Also in the 90 mm fish the plateau pattern is not as clearly defined as in other fishes but a size range where the percentage preference is higher than the remaining size groups is nevertheless apparent.

Fig 28 examines the size range where the percentage preference was consistently high for 8 fishes. The lower and upper ends of this preferred size range were taken as those size groups which were consistently above 50% at both ends of the prey size range offered. The lower end of the preferred size range for the 50 mm fish could not be determined as no prey below 4 mm was available.

The minimum values of the preferred prey size range increased with the fish size up to 110 mm. They then remained relatively

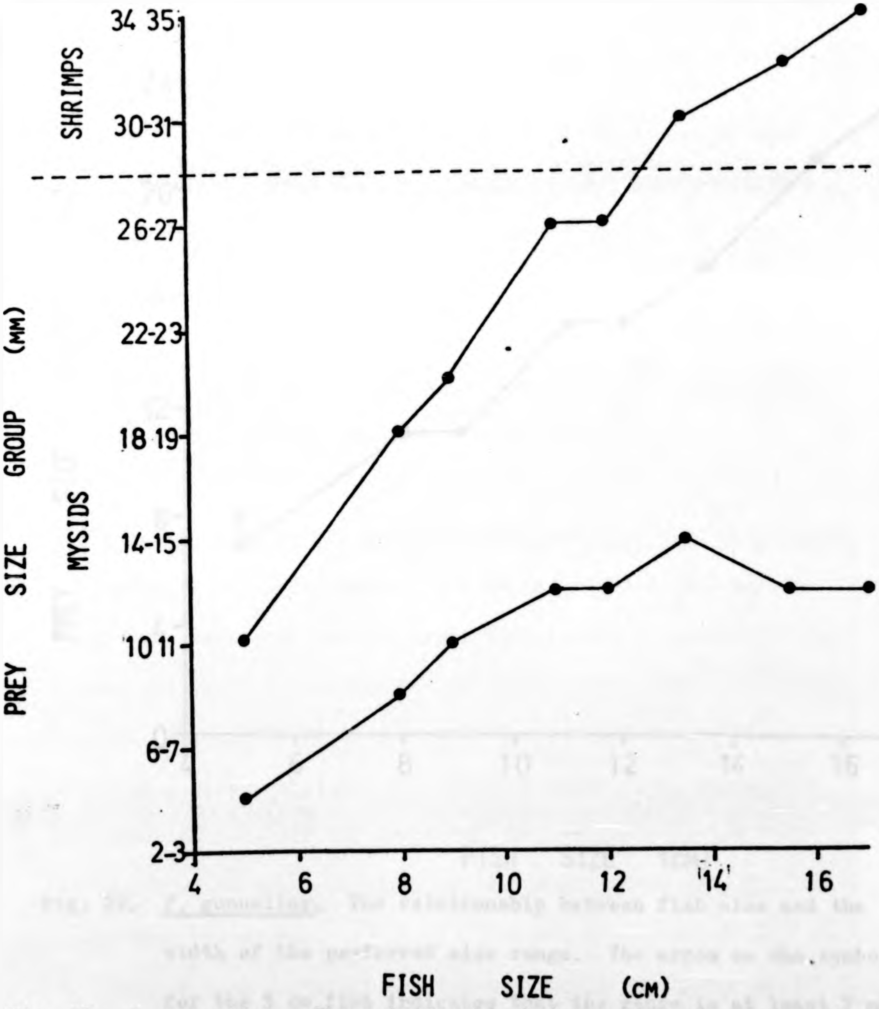


Fig. 28. P. gunnellus. The relationship between fish size and preferred prey size range. Upper and lower lines show the upper and lower limits of the preferred prey size ranges respectively. Points above the horizontal broken line are those in which shrimps instead of mysids were used as prey.

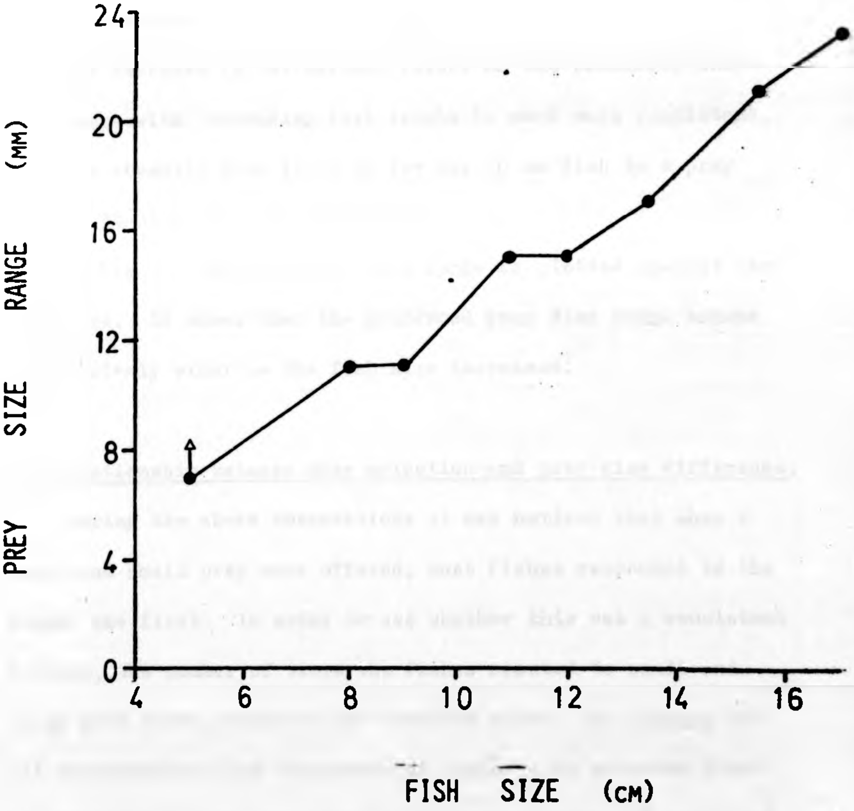


Fig. 29. **P. gunnellus**. The relationship between fish size and the width of the preferred size range. The arrow on the symbol for the 5 cm fish indicates that the range is at least 7 mm.

unchanged between 110 mm and 170 mm.

The increase in the maximum values of the preferred prey size range with increasing fish length is much more consistent. It rises steadily from 10-11 mm for the 50 mm fish to a prey size of 34-35 mm for the 170 mm fish.

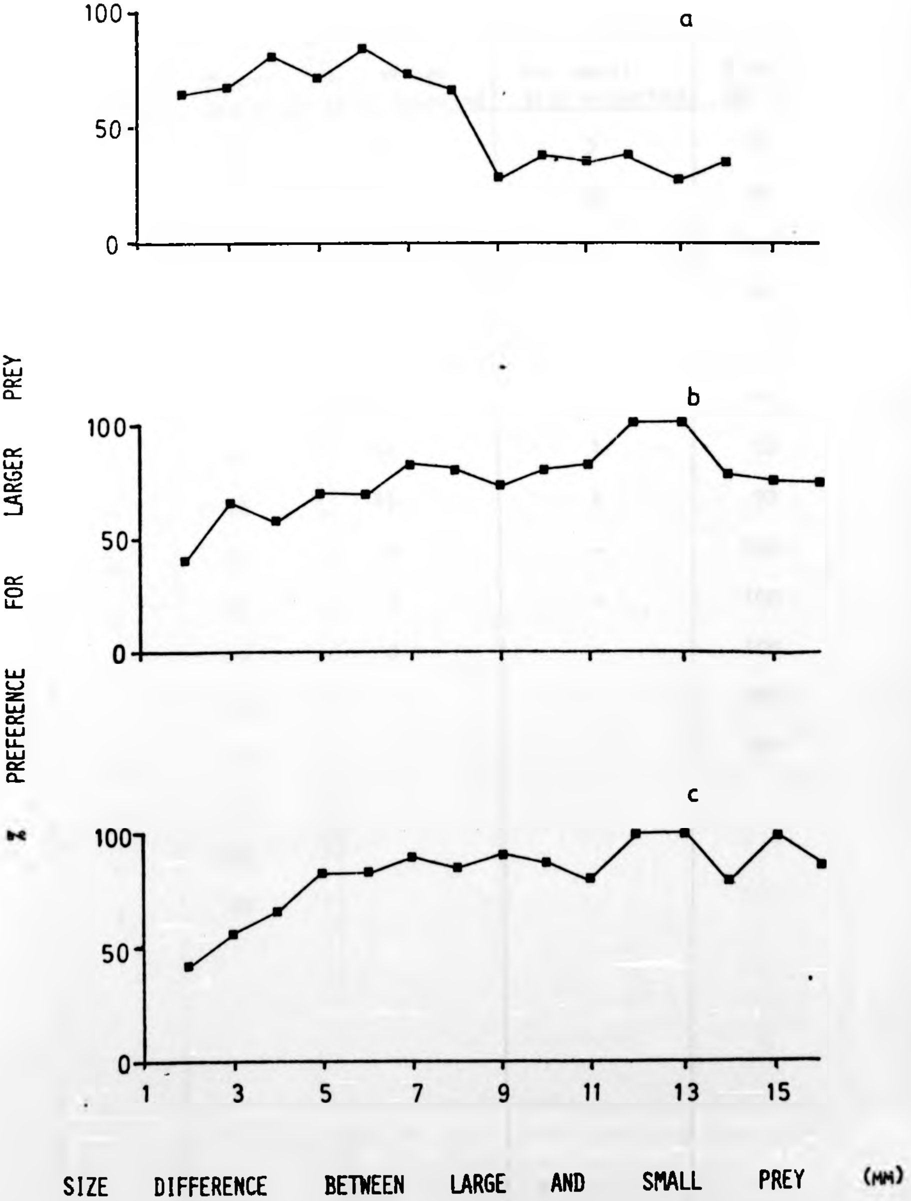
In Fig 29 the preferred size range is plotted against the fish size. It shows that the preferred prey size range became progressively wider as the fish size increased.

The relationship between prey selection and prey size difference.

During the above observations it was noticed that when a large and small prey were offered, most fishes responded to the larger one first. In order to see whether this was a consistent feature, the number of times the fishes reacted to small and large prey first, whatever the absolute sizes, was summed for all presentations and the number of larger prey selected first is expressed as the percentage of the total number of small and large prey selected.

Fig 30 and Table 83 show for 8 fish the variation in percentage preferences for the larger prey with increasing difference in length between the two prey presented. The results

Fig. 30. P. gunnellus. The relationship between the percentage preference for larger prey and prey size contrast for 3 fishes of a) 80 mm, b) 120 mm, c) 155 mm.



a
b
c
100
50
0
1
3
5
7
9
11
13
15
% PREFERENCE FOR LARGER PREY
SIZE DIFFERENCE BETWEEN LARGE AND SMALL PREY (MM)

Table 83 The relationship between percentage preference for larger prey nd prey size contrast.

mm	50			90			110			135			170		
Prey size difference	No. of large prey selected	No. of small prey selected	% preference larger prey	No.large prey 1st selected	No. smll prey 1st selected	% pref. lge prey	No.of lge prey	No.smll prey	% pref. lge prey	No.of lge prey	No.smll prey	% pref. lge prey	No. of lge prey selected	No. small prey selected	% pre lge
2	4	3	57	1	2	33	2	3	40	9	12	43	4	3	57
3	7	6	54	5	5	50	10	4	71	4	6	40	5	2	71
4	11	7	61	15	4	79	19	5	79	11	5	69	9	4	69
5	10	18	36	26	21	55	24	7	77	16	8	67	21	3	88
6	13	17	43	31	20	61	27	7	79	22	10	69	16	7	70
7	9	10	47	29	20	59	15	4	79	19	6	76	37	4	90
8	3	7	30	17	9	65	10	3	77	11	2	85	14	1	93
9	3	8	27	11	16	41	16	4	80	21	3	88	13	1	93
10	2	4	33	20	22	48	14	3	82	30	9	77	9	-	100
11	8	10	44	9	12	43	3	1	75	22	5	81	2	-	100
12	3	5	38	8	9	47	6	-	100	9	3	75	8	-	100
13	3	6	33	9	7	56	-	-		9	4	69	9	-	100
14	1	6	14	7	8	47	5	1	83	10	4	71	6	-	100
15	-	2	0	4	4	50	2	-	100	15	3	83			
16	-	2	0	2	2	50	4	2	67	4	-	100			
17	-	2	0	1	2	33	3	1	75	5	1	83			

correspond only to observations where mysids were used as prey and hence covered a size range of 4-27 mm. Fig 28 shows that this range (23 mm) is outside the preferred range of the three smaller fishes of 50, 80, 90 mm total length but within the preferred range of all others.

For the 50 mm fish the percentage preference for the larger prey was above the 50% level when the contrast between large and small prey were 2, 3 and 4 mm (Table 83) but as the contrast increased further, the percentage preference for the larger prey decreased linearly, the smaller of the two prey offered usually being selected first. For this fish the correlation between the percentage preference for larger prey and contrast in prey size was negative and significant at the 2% level.

The preferred prey size range of the 50 mm fish was between 4-11 mm (Fig 28) which was much smaller than that offered to the fish, 4-27 mm. The selection of smaller prey by this fish was likely to be a result of it being offered prey which for the most part were outside its preferred range.

For the 80 mm fish the percentage preference for larger prey was above 50% level between 2-8 mm size contrast and dropped sharply below 50% above 9 mm contrast. The correlation between prey size contrast and percentage preference for larger prey was not significant between 2-8 mm contrast or 9-14 mm contrast. Percentage preference for larger prey was above 60% between 2-8 mm contrast and under 40% between 9-14 mm contrast. Once again it was likely that the results were affected by the offered prey size range being greater than preferred size range.

The 90 mm fish likewise did not show any clear relationship between the percentage preference for larger prey and prey size contrast, fluctuating between 30 and 60% over the whole range.

The remaining 5 larger fishes presented a consistent pattern. In each fish after a 2 mm contrast, the percentage of preference for larger food was always above the 50% level i.e., as the size contrast between the prey offered continued to increase the fishes consistently responded to the larger prey first. Moreover, the results suggested that the percentage preference for the larger prey at first increased with increasing contrast, then levelled off.

For 120, 135, 155 and 170 mm fishes a positive correlation was found between the percentage preference for larger prey and prey size contrast as the difference between large and small prey increased from 2 mm to 8 mm. The correlation coefficient was significant at $p < 0.01$ for all 4 fishes. As the size contrast increased further the preference for larger prey remained unchanged. No significant correlations between the percentage preference for larger prey and prey size difference were found for 9-17 mm contrast for the same fishes.

For the 110 mm fish, the preference for larger prey remained well above 50% level for 2 mm size contrast but did not show an initial increase with increasing contrast as in the case of 120, 135, 155 and 170 mm fishes. The correlation coefficient between the percentage preference for larger prey and increasing contrast was found to be nonsignificant between 2-8 mm contrast, 9-17 mm contrast and 2-17 mm contrast.

When the preference for larger prey is expressed as the percentage of total reference shown for small and large prey offered to the fishes in all size contrast groups, the following results were obtained.

Fish size	50	80	90	110	120	135	155	170
% preference for larger prey	40	57	54	78	73	73	82	87

For each of the 5 fishes (total length 110-170 mm) where the largest mysid size offered (27 mm) was within the limits of preferred size range (Fig 28) the percentage preference for larger prey was above 70%.

Summary and Conclusions

The results of ecological work on the diet of P. gunnellus suggested the possibility of some prey size selection by the fish and the laboratory observations with stationary prey supported this view.

Fishes of different sizes were not found to show preference for a prey of a particular size; instead a wide prey size range existed for which the fish showed higher preference. For example a fish of 17.0 cm did attack stationary prey of up to 60 mm, but it showed preference for a size range of 12-35 mm.

The width of the preferred size range increased with increasing fish size which was mainly due to the increase in the upper limit of the size range. (Fig 28). The lower limit of the preferred size range was found to be similar between 110-170 mm fishes.

The results did not indicate any difference between first and successive presentations, i.e., the preference shown for a prey size range did not alter markedly with hunger level as it did in

S. spinachia.

When the variation of preference for smaller or larger prey was examined with respect to the difference in prey size, it was found that in those fishes where the upper limits of the prey size range offered was within the preferred size range, the fishes more often selected the larger prey first in all size contrast groups except 2 mm. Also, 4 fishes out of five showed an increasing preference for larger prey until the contrast between small and large prey reached 8 mm, after 8 mm contrast it remained unchanged.

From these results it can be concluded that there is a selection of prey sizes in P. gunnellus when all sizes are equally catchable but this selection is not as well defined as in S. spinachia. There exists a wide preferred size range which increases with fish size. The fish is, however, not completely indiscriminate within its preferred range and the larger of the two preys offered is selected.

In the laboratory, the size of prey selected by P. gunnellus. within wide limits, does not seem to depend on the actual size of the prey but is based more upon the fishes ability to discriminate between large and small prey. This would imply that size selection observed in the field must be partly a result of fishes ability to capture prey rather than an instinctive selection for size.

THE EFFECT OF MOVEMENT ON THE FEEDING RESPONSES OF P. GUNNELLUS.

Observations on the general feeding behaviour of P. gunnellus in the laboratory showed that the fish readily took both moving and stationary prey if given separately; if given together the fish seemed to respond more to moving prey, though attempts to capture fast swimming prey were not always successful. Such observations suggested that moving prey might induce a stronger response than stationary prey. The following experiments were carried out to determine whether or not the preference shown for moving prey was significantly different from that shown for stationary prey.

Once again mysids were used as prey. The apparatus used was the same as that described for S. spinachia except that only one moving and one stationary prey were offered to the fishes at each presentation.

Six fishes ranging in total length from 90 to 170 mm were used in these experiments, the results were later combined.

The size of moving and stationary prey were kept equal throughout the experiments. The following prey size ranges were used for each fish. All prey used were within the preferred size range of the fishes.

Fish size (cm)	9.0	11.0	12.0	13.5	15.5	17.0
Prey size (mm)	12-14	12-14	12-14	14-16	14-16	14-16

There was also the possibility that the effect of movement on feeding was stronger at certain speeds than others. It was therefore necessary to test the feeding responses to prey at different speeds. Five speeds, varying between 0.2 cm/sec to 3.9 cm/sec were used.

At each presentation one moving and one stationary prey of equal size were offered to the fish and the number of times it first responded to each one (i.e., either attacked, bit off a portion or swallowed) were recorded. Table 84 gives the results of the preference shown for moving and stationary prey at different speeds. The difference in the number of responses shown to each state of prey was tested by the χ^2 test. (See also Fig. 31).

The χ^2 values show that when the prey was moving very slowly,

Table 84. The number of attacks to moving and stationary prey at 5 different speeds.

Speed (cm/sec)	No of moving prey attacked	No of stationary prey attacked	Total	% moving	% stationary	χ^2	P
0.2	62	53	115	54	46	0.7	0.05
1	62	26	88	70	30	14.73	0.001
1.9	59	21	80	74	26	18.05	0.001
2.9	62	18	80	78	22	24.20	0.001
3.9	54	42	96	56	44	1.51	0.05

Table 85. χ^2 values for the comparison of responses shown to prey moving at different speeds.

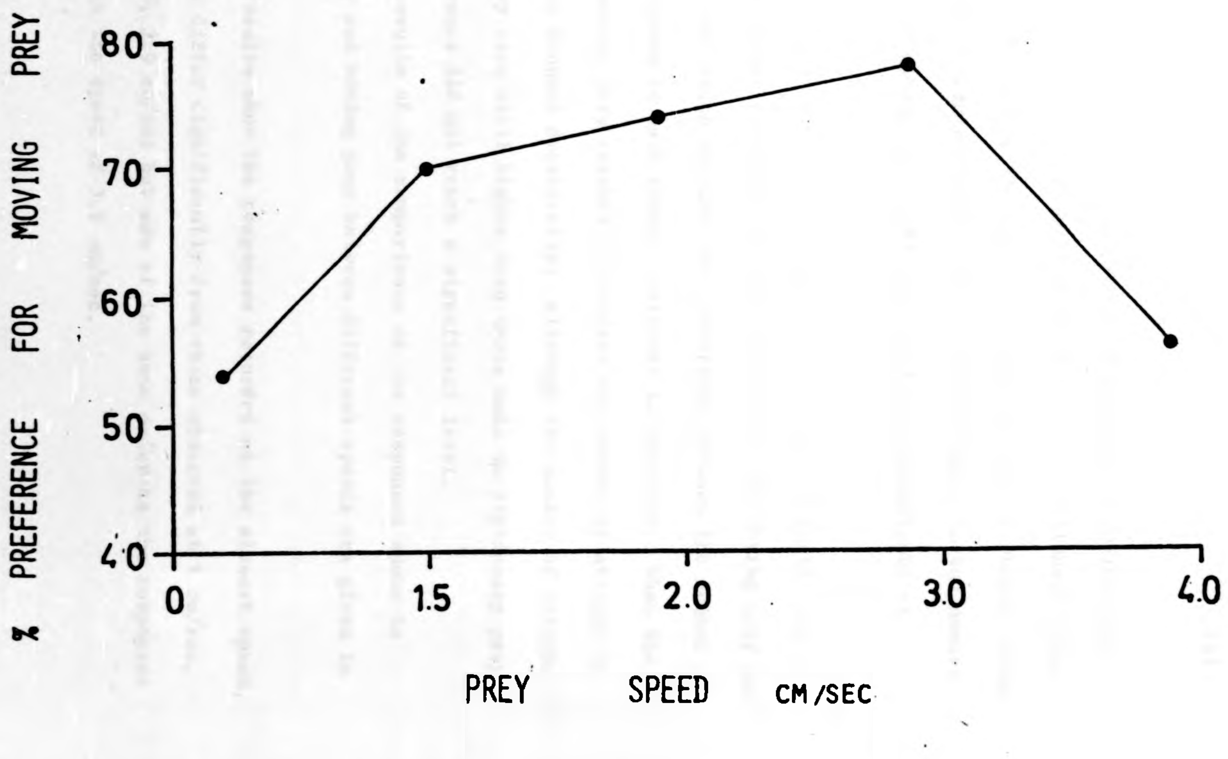
Speed	0.2 cm/sec	1 cm/sec	1.9 cm/sec	2.9 cm/sec	3.9 cm/sec
0.2		5.73*	7.88**	11.33***	0.11
1 cm/sec			0.22	1.07	3.97*
1.9 cm/sec				0.30	5.81*
2.9 cm/sec					8.76**
3.9 cm/sec					

* = p 0.05

** = p 0.01

*** = p 0.001

Fig. 31. P. gunnellus. The relationship between the percentage preference for moving prey and the speed of the prey.


% PREFERENCE FOR MOVING PREY
80
70
60
50
40
0
1.5
2.0
3.0
4.0
PREY SPEED CM/SEC

at a speed of 0.2 cm/sec, the number of attacks to moving prey did not differ significantly from those made to stationary prey. When the speed of prey increased to 1 cm/sec, the responses shown to moving prey suddenly increased. The difference in the number of attacks to moving and stationary prey was significant at $p < 0.001$.

As the speed of prey increased further to 1.9 cm/sec and 2.9 cm/sec the fishes continued to show preference for moving prey and the χ^2 values, which measure the difference between the number of responses shown to each state, continued to increase. When the speed of moving prey reached 3.9 cm/sec the number of attacks to moving prey dropped drastically; although the number of attacks to moving prey were still higher than those made to stationary prey, the difference did not reach a significant level.

The results of the comparisons of the responses shown to stationary and moving prey between different speeds are given in Table85.

The results show the responses recorded at the slowest speed, 0.2 cm/sec differ significantly from those observed at 1 cm/sec, 1.9 cm/sec, 2.9 cm/sec but are of the same order as the responses recorded at the speed of 3.9 cm/sec.

The responses at the speed of 1 cm/sec were not significantly different from those at 1.9 cm/sec, 2.9 cm/sec but the difference between the responses at 1 cm/sec and 3.9 cm/sec was found to be significant at the 5% level. (χ^2 test).

Similarly there was no difference between the responses observed at 1.9 cm/sec and 2.9 cm/sec but both were significantly different from those found at 3.9 cm/sec. The difference between the responses at 3.9 cm/sec and lower speeds increased with increasing speed from 1 cm/sec to 2.9 cm/sec.

The nonsignificant χ^2 values found for the comparisons between the speeds of 1 cm/sec and 2.9 cm/sec indicate that although the preference for moving prey increases from 1 cm/sec speed to 2.9 cm/sec speed, there is not one optimum speed which evokes the highest response from the fishes.

The results suggest that the speed of 0.2 cm/sec is the threshold speed above which the prey is perceived as moving. A high preference is shown for prey moving within the speed range of 1 cm to 2.9 cm/sec. When the speed of prey reaches to 3.9 cm/sec it becomes much too fast for the fish to follow and attack the prey and the preference for movement is reduced to the level found at 0.2 cm/sec.

The effect of movement on the feeding sequence at a low hunger level.

The next set of observations were made to test whether the movement of prey could produce feeding responses when the satiation level of the fishes was high.

The fishes were first fed on stationary mysids attached singly to a tube on the movable arm of the motor which could later be moved at a known speed. The size of the mysids offered in each presentation were once again kept constant.

When the fishes were hungry they responded to prey almost immediately, attacking, biting parts of the prey off or swallowing it completely. As the hunger level dropped the attacks and swallows did not occur as readily. If an attack or swallow did not take place within a minute, the stage of feeding was recorded which was either fixate or fixate + approach.

The same prey was then moved with a speed of 1.9 cm/sec by switching on the motor and whether or not any changes in feeding stages occurred were noted. Positive changes were those that took place from an earlier stage to a later stage in the feeding sequence.

If feeding responses shown to stationary prey stopped at the fixate stage, the possibilities of positive changes were from

a) Fixate to fixate + approach

b) Fixate to fixate + approach + attack

c) Fixate to fixate + approach + attack + swallow (wholly or partially).

If the feeding had stopped at the approach stage, the positive changes that could occur were

d) From approach to approach + attack

e) From approach to approach + attack + swallow

The number of times the changes a–e occurred were recorded as positive changes.

No change was recorded when the fishes only fixated or fixated and approached the prey in both stationary and moving states without showing any further responses.

The only possibility of negative responses were from approach to fixate stage i.e., when the fish approached the stationary prey but observed it without following when it began to move.

If a high degree of motivation was produced by the movement of prey, one would expect the number of positive changes to differ significantly from the number of no changes and number of negative changes. If the feeding motivation produced by moving and stationary prey were not different, the difference between the three categories should not reach significant levels.

Table 86 gives the number of positive, negative and no changes observed in these experiments.

The total number of positive changes were found to be significantly higher than no changes, negative changes and the sum of the two when compared by a χ^2 test. χ^2 values for these comparisons were 10.25, 65.01 and 4.31 respectively.

Out of 169 observations 58% were positive changes, 34% were no changes and 8% were negative changes.

Among positive changes a higher percentage occurred from the initial feeding stage (fixate) to subsequent (a-c) stages (60%) than from fixate + approach stages to later stages (d-e) (40%); the difference being significant at 5% level. (χ^2 = 4.08).

The lowest number of positive changes were recorded from fixate to fixate + approach stages (change a) which was significantly lower than the number of changes b and c. χ^2 values for the comparisons of a-b and a-c being 4.23 and 5.44 respectively. If the hypothesis that stronger motivation is necessary to induce an attack or swallow than to cause only an approach is accepted, then these results indicate that the movement of prey does indeed provide a strong feeding stimulus. The positive changes b and c or d and e did not differ significantly from one another.

Table 86. The number of type of changes in feeding responses caused by the movement of prey.

	+VE CHANGES						NO CHANGES			-VE CH	
	a	b	c	d	e		g	h		i	
Stage observed when prey stationary	F1	F1	F1	F1+AP	F1+AP	TOTAL	F1	F1+AP	TOTAL	F1+AP	
Stage observed when prey moving	F1+AP	F1+AP +AT	F1+AP+AT +SW	F1+AP+AT +SW	F1+AP+ AT+SW		F1	F1+AP		F1	
NUMBER	11	23	25	21	18	98	27	31	58	13	
PERCENTAGE	11	23	26	21	18		47	53			

Total no of Observations = 169

Table 87. The number and type of changes in feeding responses caused by the movement of the tubes only.

	+ VE CHANGES				NO CHANGES				-VE CHANGES			
Stage observed when tubes stationary	F1	F1	F1+AP	TOTAL	F1	F1+AP	F1+AP +AT	TOTAL	F1+AP	F1+AP +AT	F1+AP+ AT	
Stage observed when tubes moving	F1+AP	F1+AP +AT	F1+AP+AT		F1	F1+AP	F1+AP +AT		F1	F1+AP	F1	Z
NUMBER	33	8	6	47	37	23	8	68	5	1	6	6
PERCENTAGE	70	17	13		54	34	12		83	17		

Total no of Observations = 21

Table 88. The effect of movement of prey on preference shown for large prey for 2 fishes.

Fish Size		A			B		
	State	Stationary	Stationary	TOTAL	Stationary	Moving	TOTAL
	Prey Size	Large	Small		Large	Small	
15.5 cm	No Chosen	35	8	43	19	24	43
	%	81	19		44	56	
17 cm	No Chosen	42	7	49	17	28	45
	%	86	14		38	62	

No difference between the no change groups Fixate to fixate or Fixate + approach to Fixate + approach was found.

A control experiment was carried out to test whether feeding responses could be evoked in the absence of food solely by the movement of the tubes to which the mysids were attached.

After the initial deprivation period, the fishes were first shown the stationary glass tubes and any responses shown to them within 2 mins were recorded. The tubes were then moved with a speed of 1.9 cm/sec and the number of positive changes, no changes and negative changes were recorded.

Table 87 shows the number and type of changes observed by the movement of tubes alone. Out of 121 observations, 39% were positive changes, 56% were no changes and 5% were negative changes. The number of movements induced by movement were significantly lower than number of no changes ($\chi^2 = 3.84$ $p = 0.05$) and from sum of no changes and negative changes ($\chi^2 = 6.03$ $p < 0.02$).

Among the positive changes the percentage of changes from fixate to fixate + approach were highest (70%). The changes from fixate to Fixate + approach were significantly higher than changes from Fixate to fixate + approach + attack. ($\chi^2 = 11.9$ $p < 0.001$). This was a reverse situation to that found among positive changes induced by moving prey. (Table 86 , column a,b) which meant that although the fish do respond to the movement of the tubes alone, movement plus prey provides a stronger feeding motivation than movement of the tubes by themselves.

The highest number of no changes occurred at Fixate to fixate stages (54%). The number of negative changes were very low.

The effect of movement on selection of larger prey

One of the conclusions of the prey size selection experiments in P. gunnellus was that the fish showed preference for the larger of the two preys offered within its preferred size range and that this preference was independent of the fishes preferred size range. For example, if the preferred prey size range of a fish was 10 to 20 mm and if it could detect a difference of 5 mm in prey size, when offered preys of 10 and 15 mm, it would select the 15 mm prey. If, however, it was offered preys of 15 and 20 mm length, it would select the 20 mm prey.

Experiments with moving and stationary prey showed that the preference for moving prey was very high. The next set of observations were made to compare the effects of movement on prey contrast selection.

Two fishes of 15.5 cm and 17 cm were used. At each presentation one large (20 mm) and one small (12 mm) mysid, both stationary, were offered to the fishes and the number of times small and large prey were selected were recorded. The size of the mysids were within the preferred size range of fishes (see above).

In a second set of observations the large mysid was kept stationary and the small mysid was moved with the speed of 1.9 cm/sec, noting the number of times each one was selected. The sizes of mysids were the same as before.

Table 88 gives the percentage preference for larger prey when both were stationary and when the small prey was moving for each fish.

When both large and small prey were stationary (Group A) the preference for large prey was above 80% for each fish.

The number of small and large prey selected did not differ significantly between the two fishes. ($\chi^2 = 0.31 \quad p > 0.10$).

When the large prey was stationary and the small prey was moving (Group B) the preference for larger prey to less than 50% in both fishes.

The comparison of the number of large and small prey taken between Group A and B were significantly different for each fish at $p < 0.001$. The χ^2 values were 11.46 for the 15.5 cm fish and 23.6 for the 17 cm fish.

The results suggested that movement of the prey overrules the effect of size.

Summary and Conclusions

Observations with moving and stationary prey indicated that moving prey was selected in preference to stationary prey. By testing the responses to movement at varying speeds between 0.2 cm/sec - 3.9 cm/sec it was found that the effect of movement in producing responses varied with the speed of prey within these limits. The threshold speed was found to be 0.2 cm/sec, above which the movement of prey evoked significantly higher number of responses. The preference for movement increased slightly between 0.2 cm/sec to 2.9 cm/sec but the increase was not found statistically significant. The preference decreased markedly above 2.9 cm/sec (Tables 84 & 85) which suggested that the optimal speed of prey was between 1 cm/sec to 2.9 cm/sec.

A set of observations which examined the type and number of changes indiced by movement of prey showed that even at a high satiation level movement brought about a significantly higher number of changes. (Table 86).

A control experiment tested whether the movement of tubes normally used to hold prey could evoke feeding responses when the fishes were hungry i.e., when they were most responsive. It was found that tube movement alone could still induce a number of feeding responses which mainly consisted of following the tubes. The number of times the positive responses occurred were significantly less than incidents of no responses.

When two stationary prey, large and small were offered to the fishes, a high preference for the larger prey was found. (Table 88. Group A). If the small prey began to move the preference shown for large prey no longer existed which suggested that movement decreases the effect of the size stimulus.

From all these results it can be concluded that the movement is an important stimulus for feeding in P. gunnellus.

COMPARISON OF THE FEEDING BEHAVIOUR OF S. SPINACHIA AND P. GUNNELLUS

Both S. spinachia and P. gunnellus were found to show prey size selection under experimental conditions. The pattern of selection was, however, different in the two species.

When S. spinachia were offered prey of different sizes, most fish were found to select prey within a preferred size range, above and below which the fish tended to reject the offered prey. Selection became progressively more pronounced as the hunger level of the fish dropped. P. gunnellus on the other hand, responded to prey with a wider size range in all fish size groups examined and no clear indication of increasing selectivity with decreasing hunger was found. The fish still continued to attack prey sizes much outside their preferred size range, whereas in S. spinachia the number of positive responses to prey outside its preferred size range were considerably reduced at higher satiation levels.

The differences in the prey size range for the two species may be demonstrated by calculating the ratio of fish size to preferred prey size range. Table 89 shows these ratios for 10 S. spinachia and 8 P. gunnellus.

The table shows that the $\frac{FS}{PR}$ ratio was relatively constant in both species. The mean $\frac{FS}{PR}$ ratio was 10.98 for S. spinachia and 7.56 for P. gunnellus. It is thus clear that P. gunnellus prefers a wider size range than S. spinachia.

Table 89. The ratio of $\frac{\text{fish size}}{\text{preferred prey size range}}$ $(\frac{FS}{PR})$ for *S. spinachia* and *P. gunnellus*.

Species										
S. spinachia	72	75	93	98	99	102	106	110	116	124
width of preferred size range (mm)	7	7	9	9	9	7	9	13	11	11
$\frac{\text{Fish size}}{\text{preferred range}}$	10.3	10.7	10.3	10.9	11.0	14.6	11.7	8.5	10.5	11.3
P. gunnellus	50	80	90	110	120	135	155	170		
width of preferred size range (mm)	7	11	11	15	15	17	21	23		
$\frac{\text{Fish size}}{\text{preferred range}}$	7.0	7.3	8.2	7.3	8.0	7.9	7.4	7.4		

Furthermore, in *S. spinachia* an optimal prey size was found within the preferred size range for which the highest preference was shown. In *P. gunnellus* the preference shown for different size groups within the preferred size range did not differ markedly and no optimal prey size was apparent. The observations suggested that *P. gunnellus* selected the larger of the two preys offerred within the preferred size range regardless of their absolute size.

Such results implied that prey size selection demonstrated by *S. spinachia* under experimental conditions is more specific than that of *P. gunnellus*. It is possible that the observed differences in prey size selection may be a result of morphological differences in the shape and/or size of mouth and teeth between the two species. It has been mentioned earlier in the section describing the general feeding behaviour of S. spinachia that the fish took mysids whole and that biting off only a portion was rare. In P. gunnellus on the other hand, although the fish did usually swallow prey whole, biting parts off the prey body was much more frequent. It was considered that this biting habit might be related to the anatomy of the mouth and dentition. To elucidate this question, the mouth size (gape) and teeth of the two species were examined in more detail.

The mouth size measurements of S. spinachia were given earlier in Fig 22 . The mouth size of P. gunnellus was measured similarly, by inserting graduated drills of known size into the fishes mouth. 35 freshly killed fish with a size range of 59-156 mm were used for these measurements. The relationship between the mouth diameter and the total length of P. gunnellus is given in Fig32, Line A. For comparative pusposes, the regression line showing the relationship between mouth size and fish size of S. spinachia is also given on the same figure (Line B).

Fig32 shows that for a given length the mouth size of

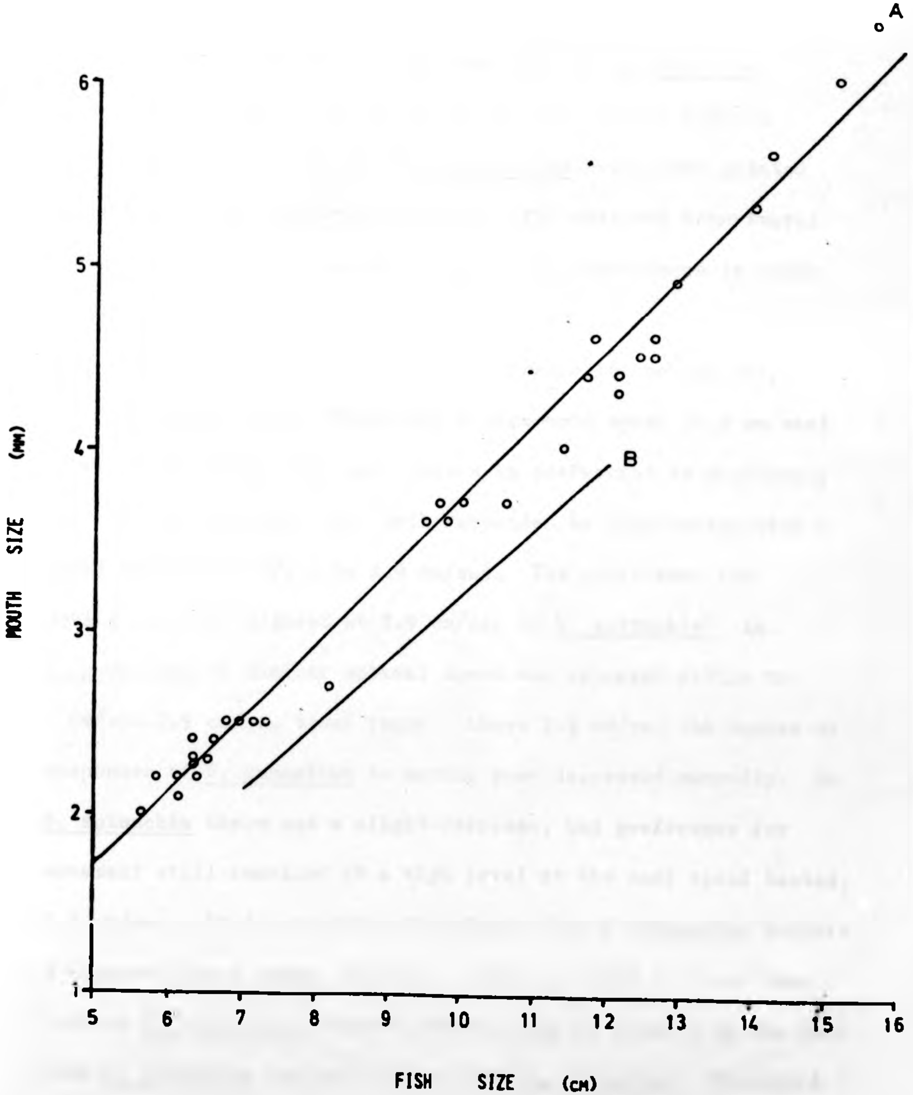


Fig. 32. P. gunnellus. The relationship between total length and mouth diameter (Line A). Line B is the regression line for the relationship in Spinachia and is included for comparison,

P. gunnellus is slightly larger than that of S. spinachia. Also the arrangement and the shape of teeth differ between the two species, the teeth of P. gunnellus being more pointed than those of S. spinachia. (Fig33). The observed behavioural differences might be therefore due to the differences in mouth size and teeth shape.

Both fish showed a distinct preference for moving prey over stationary prey. There was a threshold speed (0.2 cm/sec) above which moving prey were chosen in preference to stationary prey by both fishes. They both responded to prey moving with a speed between 1 cm/sec to 2.9 cm/sec. The preference for moving prey was highest at 2.9 cm/sec in S. spinachia; in P. gunnellus no similar optimal speed was apparent within the 1 cm/sec-2.9 cm/sec speed range. Above 2.9 cm/sec the number of responses of P. gunnellus to moving prey decreased markedly. In S. spinachia there was a slight decrease, but preference for movement still remained at a high level at the next speed tested, 3.9 cm/sec. It is concluded therefore, that P. gunnellus prefers a narrower speed range, the upper limit of which is lower than that of S. spinachia. This difference may be related to the fact that S. spinachia can swim faster than P. gunnellus. Blaxter &

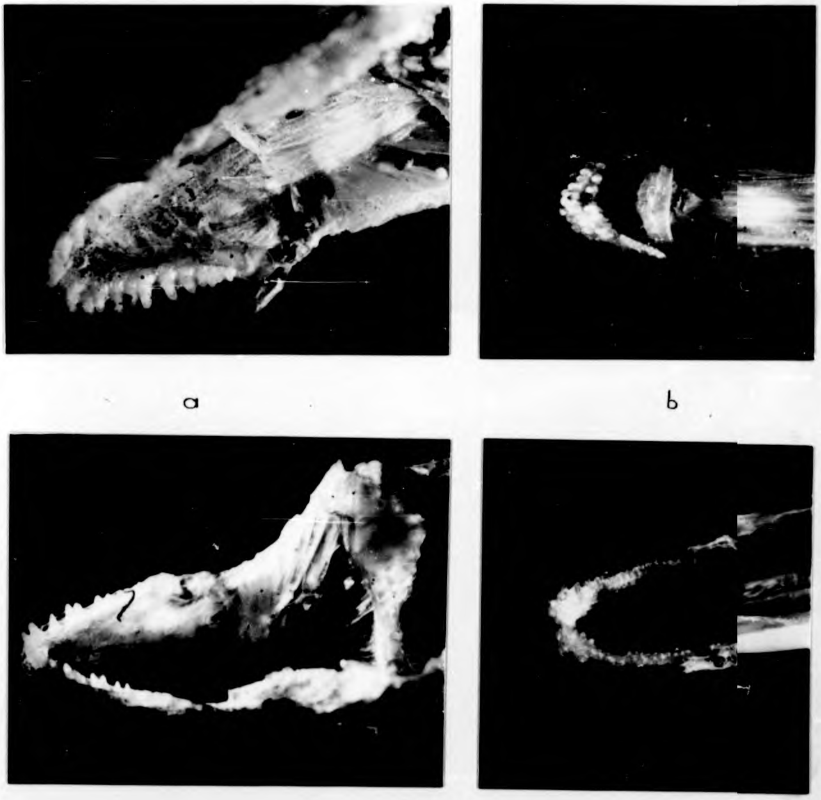


Fig. 33. Photographs of the jaws of a) P. gunnellus

b) S. spinachia.

Upper photographs are upper jaws and lower photogr

lower jaws.

Dickson (1958) give a maximum speed of 72 cm/sec for S. spinachia and 30 cm/sec for P. gunnellus.

In both species movement of the prey produced sufficiently strong motivation to induce further feeding at relatively high satiation levels. The type and the number of feeding responses evoked by the movement of prey were similar in both species.

The results of the comparisons of size and movement stimuli for both fish were also similar. In S. spinachia moving prey were taken in preference to optimal sized prey, but the size cue from the prey was not completely ignored. In P. gunnellus the preference for larger prey disappeared when the small prey was moving and the large prey was stationary. For both fishes, therefore, movement was the stronger stimulus of the two.

Finally, it must be considered how much the feeding ecology of the two species can be explained by the results of the observations on their feeding behaviour. In the field, S. spinachia was found to show a size related feeding heterogeneity. Observations in the laboratory with stationary mysids suggested that prey size selection had a behavioural basis; therefore, the division of different prey among different fish size groups found in the field must have been, at least partly, a result of fishes behaviour pattern and not entirely due to prey availability or catchability. In P. gunnellus the relationship between the fish size and prey size in the field was not as marked as that found in S. spinachia. These results were supported by the laboratory experiments where P. gunnellus showed a less well defined size selection.

The observations in the laboratory on both P. gunnellus and S. spinachia further indicated that the preferred prey size range increased with increasing fish size and this was paralleled in the field, where, as in the laboratory, the increase in the prey size range was due mainly to an increase in the upper limit of the preferred prey size range. The lower limit of preferred prey size range did not vary as markedly with increasing fish size.

Both S. spinachia and P. gunnellus attacked the head of the prey in preference to the rest of the body. This seems to be a common feature of predatory behaviour but may account for the presence of decapod heads in P. gunnellus stomachs. S. spinachia, as has already been mentioned, tended to swallow its prey whole. Apart from the differences in mouth size already referred to, mouth shape may also be important in this respect. S. spinachia's mouth is long and tubular whereas that of P. gunnellus is shorter and jaw muscles appear to be much more powerful.

In the laboratory it was observed that P. gunnellus took food most easily from the bottom although it could also take it from the surface. S. spinachia on the other hand could take food easily from all levels of water. Differences in diet between the two species may therefore also be attributable in some measure to their swimming habits and mode of life. P. gunnellus is negatively buoyant and almost entirely restricted to the bottom whereas S. spinachia is neutrally buoyant and can swim at any level with ease. For example, planktonic copepods were commoner in the diet of S. spinachia than in that of P. gunnellus where those copepods present consisted almost entirely of bottom living harpacticoids. Similarly, polychaetes were an imporant part of the diet in P. gunnellus but were rarely taken by S. spinachia.

As mentioned earlier, P. gunnellus was found to have a lower preferred prey speed range than S. spinachia. Some differences in the diet of the two species in the field might be a result of the fact that P. gunnellus prefers slower moving prey than S. spinachia. The speeds of movement of the various prey organisms in the field are not known; but although sedentary molluscs such as gastropods and bivalves were not very significant in the diet of either species, they occurred more frequently in P. gunnellus. This could be influenced by the speed preferences of the fishes.

They were also indications from the laboratory observations that S. spinachia exhibited shape and contrast discrimination; but it is not possible to infer to what extent these factors influence prey selection in the field. Comparable experiments were not carried out with P. gunnellus.

Although the effects on food selection of only a few visual cues were investigated in this work, some may be used to explain the natural feeding behaviour in general terms. Nevertheless, it would be an oversimplification to say that a complete interpretation of the field results is possible on the basis of few visual stimuli tested. A more detailed analysis of the fishes diet to determine the degree of preference shown for different food species as well as some measures of abundance and distribution of prey species in the sea would be required. Also, further laboratory observations on the rate of learning, taste discrimination and experiments with models of different shapes and colours would be necessary to gain a complete insight into the extent which the fishes behaviour determines the selection of its prey in the field.

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Appendix

a) Seasonal variation in the composition of the diet of individual species

Tables 11,13, 15, 17, 19, 21, 23, 25, 27, 29, 31.

b) Seasonal variation in the total quantity of food consumed.

Tables 39 and 42-54.

Table 11. The seasonal variation in the persentation composition of the diet of Spinachia spinachia

Month	October 1971				November			
Number examined	91				121			
Food Category	No. occurrences	% occ.	No. points allotted	% pts.	No. occ.	% occ.	No. pts.	% pts.
Amphipoda	42	24	261	33	64	31	285	35
Isopoda	28	16	126	16	77	37	347	42
Decapoda	22	13	125	16				
Euphausicea	5	3	35	4				
Mysidacea	30	17	163	21	19	9	93	11
Ostracoda	4	2	1	0.1	7	3	6	0.7
Calanoid copepods	10	6	9	1				
Harpacticoid copepods	7	4	4	0.5	1	0.5	0.5	0.1
Cirripedia	–	–	–	–				
Mollusca	2	1	1	0.1	12	6	18	2
Annelida	–	–	–	–	4	2	41	5
Insecta	12	7	30	4	4	2	1	0.1
Fish Eggs	–	–	–	–				
Nemertini	–	–	–	–	1	0.5	1	1.0
Hydrozoa	–	–	–	–				
Plant Matter	4	2	9	1	4	2	9	1
Digested Matter	7	4	17	2	17	8	23	3
Totals	173		781		207		824.5	

Month	December				January				February			
Number examined	54				49				46			
Food Category	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
Amphipoda	16	24	81	27	40	43	132	61	34	38	144	52
Isopoda	24	35	102	34	35	37	71	33	32	36	101	36
Decapoda												
Euphausicea												
Mysidacea	14	21	92	31	2	2	2	1	5	6	19	7
Ostracoda												
Calanoid copepods												
Harpacticoid copepods	1	1	1	0.3	1	1	1	0.5	1	1	0.2	0.1
Cirripedia												
Mollusca	6	9	11	4	5	5	2	1	12	13	9	3
Annelida	1	1	5	2								
Insecta					1	1	0.2	0.1	2	2	0.5	0.2
Fish Eggs												
Nemertini												
Hydrozoa												
Plant Matter	2	3	2	1	3	3	2	1	1	1	0.5	0.2
Digested Matter	4	6	6	2	7	7	5	2	3	3	4	1
Totals	68		300		94		215.2		90		278.2	

Month	March				April				May				
Number examined	21				26				15				
Food Category	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.
Amphipoda	16	43	117	73	20	39	86	79	14	36	96	63	24
Isopoda	11	30	32	20	11	22	10	9	9	23	16	10	16
Decapoda	1	3	2	1									
Euphausicea													
Mysidacea					1	2	2	2	5	13	17	11	5
Ostracoda									1	3	1	0.7	1
Calanoid copepods									1	3	1	0.7	4
Harpacticoid copepods	2	5	4	3	2	4	1	1	1	3	3	2	4
Cirripedia							1	1					
Mollusca	1	3	0.1	0.01									
Annelida													1
Insecta	3	8	4	3	8	16	5	5	7	18	19	12	8
Fish Eggs					2	4	2	2	1	3	0.2	0.1	
Nemertini													
Hydrozoa													
Plant Matter													
Digested Matter	2	5	2	1	5	10	2	2					
Totals	37	161.	161.1		51		109		39		153		6

ops

January				February				March				April				May				June				July				August				September				October			
49				46				21				26				15				34				12				54				65				25			
No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
40	43	132	61	34	38	144	52	16	43	117	73	20	39	86	79	14	36	96	63	24	38	215	50	6	32	36	27	46	32	267	32	39	30	313	40	23	38	65	38
35	37	71	33	32	36	101	36	11	30	32	20	11	22	10	9	9	23	16	10	16	25	93	22	3	16	21	16	39	27	264	30	35	27	200	25	16	26	50	29
								1	3	2	1																					1	1	3	0.3				
2	2	2	1	5	6	19	7					1	2	2	2	5	13	17	11	5	8	40	9					7	5	57	7	18	14	113	14	11	18	28	16
																1	3	1	0.7	1	1	1	0.2	1	5	2	2	3	2	1	0.1								
																1	3	1	0.7	4	6	34	8					2	1	1	0.1	15	12	100	13				
1	1	1	0.5	1	1	0.2	0.1	2	5	4	3	2	4	1	1	1	3	3	2	4	6	29	7	6	32	56	42	14	10	67	8	5	4	8	1	3	5	4	2
														1	1																								
5	5	2	1	12	13	9	3	1	3	0.1	0.01																	1	1	0.5	0.1					2	3	3	2
																				1	1	10	2					2	1	0.5	0.1					2	3	9	5
1	1	0.2	0.1	2	2	0.5	0.2	3	8	4	3	8	16	5	5	7	18	19	12	8	13	9	2	3	16	18	14	32	22	176	21	14	11	50	6	4	7	7	4
												2	4	2	2	1	3	0.2	0.1																				
																																1	1	2	0.3				
3	3	2	1	1	1	0.5	0.2																																
7	7	5	2	3	3	4	1	2	5	2	1	5	10	2	2																					1	1	5	3
94		215.2		90		278.2		37	161.	161.1		51		109		39		153		63		431		19		133		146		834		128		789		62		171	

Table 13. The seasonal variation in the percentage composition of the diet in *G. aculeatus*. There was no sample in December 1971 or October 1972

Month	October				November				January				February				March				April				May				June				
No. examined	74				33				18				4				10				9				15				41				
Food Category	No. occurrences	% occ.	No. points allotted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.
Amphipods	12	10	65	15	14	22	40	36	11	32	56	52	1	20	2	13	2	10	12	33	3	19	21	19	8	21	58	34	16	17	162	26	20
Isopods	3	2	2	0.5	5	8	29	26	10	29	28	26	1	10	0.1	0.6	1	5	0.5	1					2	5	5	3	15	16	55	9	11
Mysids	3	2	5	1																					1	3	12	7	1	1	7	1	
Decapods	1	1	1	0.2													1	5	0.5	1					2	5	1	0.6	1	1	4	1	3
Cirripede													1	10	1	6	1	5	0.5	1	2	13	1	1									
Calanoid copepods	51	40	174	41	16	25	10	9					2	20	4	25	1	5	0.5	1	2	13	3	3	6	15	21	12					
Harpacticoid copepods	5	4	4	1	5	8	2	2	1	3	1	1	2	20	6	38	3	15	3	8	2	13	3	3	6	15	25	15	5	5	12	2	
Cladocera																	1	5	0.5	1					3	8	11	6	2	2	6	1	
Cumacea	15	12	16	4																													
Ostracoda	6	5	7	2	2	3	1	1					1	10	1	6	1	5	0.5	1													
Mollusca					2	3	1	1																									
Insecta	4	3	4	1	12	18	9	8	2	6	4	4									1	6	1	1	2	5	2	1	13	14	60	16	10
Insect larvae	12	10	90	21					2	6	3	3					5	25	8	22	6	38	80	73	1	3	1	1	23	25	248	40	5
Polychaete	5	4	26	6					2	6	6	6					3	15	9	25					2	5	20	12	2	2	21	3	3
Oligochaete	5	4	20	5																					4	10	5	3	12	13	41	7	15
Nemertini	2	2	11	3																													
Fish	1	1	1	0.2																					1	3	7	4	1	1	4	1	
Plant Matter	1	1	1	0.2	1	2	2	2	1	3	1	1					1	5	1	3													
Digested Matter					8	12	18	16	5	15	8	7	1	10	2	13									1	3	3	2	3	3	6	1	1
Totals	126		427		65		112		34		107		10		16		20		36		16		109		39		171		94		628		6

age composition of the diet G. *aculeatus*. There was no sample in December 1971 or October 1972

	November				January				February				March				April				May				June				July				August				September			
	33				18				4				10				9				15				41				26				35				88			
ts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
15	14	22	40	36	11	32	56	52	1	20	2	13	2	10	12	33	3	19	21	19	8	21	58	34	16	17	162	26	20	29	139	40	5	7	44	9	12	11	73	7
.5	5	8	29	26	10	29	28	26	1	10	0.1	0.6	1	5	0.5	1					2	5	5	3	15	16	55	9	11	16	28	8	1	2	2	0.4				
1																					1	3	12	7	1	1	7	1												
.2													1	5	0.5	1					2	5	1	0.6	1	1	4	1	3	4	4	2					11	10	71	7
									1	10	1	6	1	5	0.5	1	2	13	1	1																				
41	16	25	10	9					2	20	4	25	1	5	0.5	1	2	13	3	3	6	15	21	12									4	6	18	4	28	26	311	29
1	5	8	2	2	1	3	1	1	2	20	6	38	3	15	3	8	2	13	3	3	6	15	25	15	5	5	12	2					8	12	37	7	19	18	249	23
													1	5	0.5	1					3	8	11	6	2	2	6	1					26	38	304	59	23	22	269	25
4																																								
2	2	3	1	1					1	10	1	6	1	5	0.5	1																								
	2	3	1	1																													6	9	13	3	5	5	63	6
1	12	18	9	8	2	6	4	4									1	6	1	1	2	5	2	1	13	14	60	16	10	15	99	29	3	4	7	1	2	2	5	0.5
21					2	6	3	3					5	25	8	22	6	38	80	73	1	3	1	1	23	25	248	40	5	7	21	6	14	21	86	17	5	5	23	2
6					2	6	6	6					3	15	9	25					2	5	20	12	2	2	21	3	3	4	10	3					1	1	5	0.5
5																					4	10	5	3	12	13	41	7	15	22	42	12								
3																																								
.2																					1	3	7	4	1	1	4	1												
.2	1	2	2	2	1	3	1	1					1	5	1	3																								
	8	12	18	16	5	15	8	7	1	10	2	13									1	3	3	2	3	3	6	1	1	2	2	1	1	2	2	0.4				
	65		112		34		107		10		16		20		36		16		109		39		171		94		628		68		345		68		513		106		1068	

Table 15. The seasonal variation in the percentage composition of the diet of M. scorpius. No. sample for September 1972.

Month	October				November				December				January			
No. examined	19				17				7				7			
Food Category	No. occurrences	% occ.	No. points allotted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
Amphipoda	7	18	40	13	8	33	22	14	1	9	3	18	1	20	1	4
Isopoda	2	5	1	0.3					1	9	1	6				
Mysidacea	5	13	28	9	2	8	3	2	1	9	1	6				
Decapoda	19	49	198	65	7	29	87	55	6	55	10	59	3	60	24	92
Mollusca	1	3	1	0.3	2	8	11	7	1	9	1	6	1	20	1	4
Polychaeta					2	8	2	1								
Copepoda																
Ostracoda																
Insect larvae																
Pisces	2	5	30	10	3	13	33	21								
Digested Matter	3	8	5	2					1	9	1	6				
Totals	39		303		24		158		11		17		5		26	

Month	February				March				April				May				
No. examined	26				12				12				11				
Food Category	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts	No. occ.
Amphipoda	5	15	27	12	2	11	10	8	3	15	13	10	4	21	23	15	20
Isopoda	1	3	0.5	0.2									1	5	4	3	2
Mysidacea	4	12	10	4	2	11	16	12	1	5	2	2					
Decapoda	14	41	128	55	7	37	58	45	8	40	68	50	9	47	85	56	9
Mollusca	1	3	0.5	0.2									1	5	1	1	
Polychaeta	2	6	26	12	2	11	17	13	1	5	5	4	1	5	8	5	
Copepoda													1	5	15	10	3
Ostracoda																	1
Insect larvae					1	5	1	1	1	5	5	1					
Pisces	2	6	18	8	2	11	6	5	4	20	26	19	2	11	16	11	
Digested Matter	5	15	21	9	3	16	21	16	2	10	21	15					2
Totals	34		231		19		129		20		136		19		152		37

ius.   No. sample for September 1972.

er		January				February				March				April				May				June				July				August				October			
		7				26				12				12				11				22				83				5				12			
No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
3	18	1	20	1	4	5	15	27	12	2	11	10	8	3	15	13	10	4	21	23	15	20	54	166	60	82	77	1047	85	2	25	10	16	5	24	17	14
1	6					1	3	0.5	0.2									1	5	4	3	2	5	6	2												
1	6					4	12	10	4	2	11	16	12	1	5	2	2									1	1	9	1								
10	59	3	60	24	92	14	41	128	55	7	37	58	45	8	40	68	50	9	47	85	56	9	24	59	21	6	6	80	7	4	50	45	73	9	43	88	74
1	6	1	20	1	4	1	3	0.5	0.2									1	5	1	1					4	4	7	1								
						2	6	26	12	2	11	17	13	1	5	5	4	1	5	8	5													2	10	3	3
																		1	5	15	10	3	8	20	7	4	4	8	1								
																						1	3	2	1												
										1	5	1	1	1	5	5	1									1	1	4	0.3	1	13	2	3				
						2	6	18	8	2	11	.6	5	4	20	26	19	2	11	16	11					3	3	60	5	1	13	.5	8	3	14	9	8
1	6					5	15	21	9	3	16	21	16	2	10	21	15					2	5	23	8	6	6	12	1					2	10	2	2
17		5		26		34		231		19		129		20		136		19		152		37		276		107		1227		8		62		21		119	

Table 17. Seasonal variation in the percentage composition of the diet of T. bubalis. No sample [illegible] for December 1971

Month	October				November				January				February				March				April				May				June				Jul	
Number examined	19				7				10				17				4				17				4				6				8	
Food category	No. occurrences	% occ.	No. points allotted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts	No. occ.	% occ
Amphipoda	9	25	38	25	5	29	23	37	7	23	37	36	8	24	58	42	3	38	23	82	11	22	61	29	3	25	15	22	6	50	73	74	7	35
Isopoda	5	14	5	3	1	6	1	2	6	19	7	7	5	15	11.5	8					3	6	7	3	1	8	2	3	2	18	13	13	3	15
Crabs	2	6	4	3	2	12	2	3	4	13	6	6	2	6	4	3					2	4	6	3	3	25	35	52					1	5
Shrimps	3	8	21	14					1	3	2	2									2	4	13	6										
Mysidacea	3	8	21	14	1	6	1	2																										
Cumacea																													1	9	2	2		
Harpacticoid																																	1	5
Polychaeta	2	6	9	6	3	18	20	32	7	23	27	27	4	12	32.5	24	2	25	2	7	6	12	78	37	3	25	6	9	2	18	10	10	2	10
Mollusca	3	8	3	2	3	18	12	19					5	15	14	10	1	13	1	4	2	4	1	0.5					1	9	1	1	1	5
Insecta	2	6	1	0.7																	2	4	2	1	1	8	3	5					2	10
Pisces	3	8	41	27	1	6	3	5	1	3	12	12									2	4	11	5									3	15
Digested Matter	4	11	9	6	1	6	1	2	4	13	10.5	10	8	24	17	12	2	25	2	7	8	16	29	14	1	8	6	9						
Plant Matter									1	3	0.5	0.5	1	3	1	0.7					1	2	7	3										
Totals	36		152		17		62				102		33		138		8		28		50		214		12		67		12		99		20	

bubalis. No sample[illegible] for December 1971

January 10			February 17				March 4				April 17				May 4				June 6				July 8				August 4				September 7				October 13			
% occ.	No. pts.	% pts.	No. occ.	% occ	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
23	37	36	8	24	58	42	3	38	23	82	11	22	61	29	3	25	15	22	6	50	73	74	7	35	91	68	3	60	36	70	6	60	30	77	5	22	32	24
19	7	7	5	15	11.5	8					3	6	7	3	1	8	2	3	2	18	13	13	3	15	11	8					2	20	3	8	4	17	5	4
13	6	6	2	6	4	3					2	4	6	3	3	25	35	52					1	5	7	5	1	20	9	18					4	17	28	21
3	2	2									2	4	13	6																					2	9	28	21
																			1	9	2	2																
																							1	5	1	0.8												
23	27	27	4	12	32.5	24	2	25	2	7	6	12	78	37	3	25	6	9	2	18	10	10	2	10	12	9	1	20	6	12	1	10	3	8	8	34	30	23
			5	15	14	10	1	13	1	4	2	4	1	0.5					1	9	1	1	1	5	1	0.8									1	4	1	0.8
											2	4	2	1	1	8	3	5					2	10	4	3									2	9	3	2
3	12	12									2	4	11	5									3	15	7	5									1	4	6	5
13	10.5	10	8	24	17	12	2	25	2	7	8	16	29	14	1	8	6	9																				
3	0.5	0.5	1	3	1	0.7					1	2	7	3																	1	10	3	8				
	102		33		138		8		28		50		214		12		67		12		99		20		134		5		51		10		39		23		133	

Table 19. The seasonal variation in the percentage composition of the diet of *P. gunnellus*. No sample for December 1971

Month	October				November				January				February				March				April				May				June				July		
No. examined	31				16				50				42				9				41				12				12				22		
Food Category	No. occurrences	% occ.	No. points allotted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts
Amphipoda	19	32	165	63	4	36	20	53	25	36	95	70	17	57	69	72	2	50	4	57	19	42	107	72	6	27	13	26	8	30	50	37	21	47	17
Isopoda	7	12	18	7	1	9	3	8	22	31	29	21	3	10	5	5					1	2	5	3	3	14	8	20	1	4	4	3	2	4	9
Mysidacea					1	9	5	13					1	3	5	5	1	25	2	29									1	4	20	15			
Natantia + Decapod larvae	4	7	12	5																	1	2	7	5	1	5	2	4							
Crabs	1	2	4	1																									2	11	23	17			
Calanoid Copepods									1	1	0.2	0.2													1	5	1	2	2	7	2	1	1	2	2
Harpacticoid copepods									5	7	2	2									12	27	15	10	3	13	2	4	4	15	8	6	11	24	22
Ostracoda	6	10	7	3	2	18	1	3	5	7	2	2					1	25	1	14	3	7	4	3	3	13	4	8	2	7	3	2	4	9	1
Cirripedia																					2	3	4	2											
Cumacea																																	1	2	
Insect larvae	5	8	11	4																					4	17	12	25	2	7	4	3	1	2	
Insect									1	1	0.1	0.1																					1	2	
Polychaeta	7	12	31	12	1	9	8	21	3	4	2	2	4	13	14	15					2	4	2	1	1	5	6	12	1	4	8	6	1	2	
Mollusca	1	2	2	1	2	18	1	3	4	6	3	2	2	7	1	1					1	2	1	1	1	5	0.5	1	1	4	1	0.7	2	4	1
Fish larvae																																	1	2	
Digested Matter	1	2	1	0.4					4	6	3	2	3	10	2	2					3	7	4						1	4	1	0.7			
Plant Matter	5	8	4	2																	1	2	1						1	4	10	7			
Total	59		261		11		38		70		136.3		30		96		4		7		45		149		23		48.5		27		134		42		1

of the diet of *P. gunnellus*. No sample for December 1971

ber		January				February				March				April				May				June				July				August				September				October		
		50				42				9				41				12				12				22				5				10				24		
No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts	No. occ.	% occ.	No. pts.	% pts	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts	% pts.	No. occ.	% occ.	No. pts.	% pts	No. occ.	% occ.	No. pts.
20	53	25	36	95	70	17	57	69	72	2	50	4	57	19	42	107	72	6	27	13	26	8	30	50	37	21	47	17	59	5	36	57	70	5	26	16	22	17	44	156
3	8	22	31	29	21	3	10	5	5					1	2	5	3	3	14	8	20	1	4	4	3	2	4	9	5	3	21	18	22	5	26	11	15	6	15	9
5	13					1	3	5	5	1	25	2	29									1	4	20	15													1	3	4
														1	2	7	5	1	5	2	4																	1	3	8
																						2	11	23	17													1	3	2
		1	1	0.2	0.2													1	5	1	2	2	7	2	1	1	2	2	1	2	14	2	2					2	5	2
		5	7	2	2									12	27	15	10	3	13	2	4	4	15	8	6	11	24	22	11	1	7	1	1					3	8	16
1	3	5	7	2	2					1	25	1	14	3	7	4	3	3	13	4	8	2	7	3	2	4	9	12	6									1	3	3
														2	3	4	2																							
																										1	2	4	2											
																		4	17	12	25	2	7	4	3	1	2	7	4	3	21	4	5	7	37	42	56	5	12	10
		1	1	0.1	0.1																					1	2	1	0.5					2	11	3	4	2	5	1
8	21	3	4	2	2	4	13	14	15					2	4	2	1	1	5	6	12	1	4	8	6	1	2	3	2									1	3	9
1	3	4	6	3	2	2	7	1	1					1	2	1	1	1	5	0.5	1	1	4	1	0.7	2	4	13	7					2	11	2	3			
																										1	2	8	4											
		4	6	3	2	3	10	2	2					3	7	4						1	4	1	0.7															
														1	2	1						1	4	10	7															
38		70		136.3		30		96		4		7		45		149		23		48.5		27		134		42		198		14		82		19		74		39		221

Table 21. The seasonal variation in the percentage composition of the diet of P.minutus.

Month	October				November				December				January				February				March				April				May				June		
No. examined	140				50				19				16				16				6				10				11				26		
Food Category	No. occurrences	% occ.	No. points allotted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No
Amphipoda	58	38	299	46	46	81	485	91	17	63	104	84	13	42	26	63	4	100	4	100	1	33	2	40	4	36	31	42	4	20	22	31	20	61	14
Isopoda	7	5	10	2									1	3	2	5									2	18	4	5	3	15	3	4	2	6	10
Mysidacea	5	3	19	3	1	2	12	2																									1	3	3
Natantia	7	5	43	7																					2	18	8	11	2	10	12	17	2	6	3
Crabs									1	4	3	2																							
Calanoid copepods	8	5	3	0.5					1	4	1	1																	3	15	17	24			
Harpacticoid copepods	11	7	7	1									2	6	1	2																			
Cumacea	8	5	5	1	2	3	2	0.4					2	6	1	2																			
Ostracoda									1	4	1	1																							
Cirripedia																													3	15	8	11			
Insecta	11	7	22	3	1	2	1	0.2					1	3	1	2																	1	3	
Mollusca	1	0.6	1	0.2					1	4	1	1	1	3	1	2																			
Oligochaeta																																			
Polychaeta	20	13	199	31	1	2	1	0.2					4	13	7	17									5	45	30	41					2	6	
Nematoda	1	0.6	1	0.2																															
Fish eggs																													3	15	4	6			
Plant Matter	2	1	4	0.6	1	2	5	1	2	7	4	3																							
Digested Matter	15	10	32	5	5	8	27	5	4	15	10	8	8	26	4	10								60					2	10	6	8	5	15	
Total	154		645		59		533		27		124		30		41		4		4		3		5		11		73		20		72		33		

Table 23. The s

January				February				March				April				May				June				July				August				September				October			
16				16				6				10				11				26				30				17				22				28			
No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
13	42	26	63	4	100	4	100	1	33	2	40	4	36	31	42	4	20	22	31	20	61	143	64	22	52	178	68	9	39	84	37	13	59	137	70	24	77	123	85
1	3	2	5									2	18	4	5	3	15	3	4	2	6	10	4	2	5	3	1	1	4	8	4								
																				1	3	3	1					3	13	28	12	3	9	18	9	2	6	8	6
												2	18	8	11	2	10	12	17	2	6	30	13	2	5	15	6					1	3	5	3				
																3	15	17	24																				
2	6	1	2																									1	7	10	4	1	3	3	2				
2	6	1	2																																				
																3	15	8	11																				
1	3	1	2																	1	3	4	2	3	7	6	2	3	13	58	26	2	6	2	1	1	3	1	0.7
1	3	1	2																																				
																																1	3	1	0.5				
4	13	7	17									5	45	30	41					2	6	25	11	3	7	18	7	2	9	19	8	4	13	28	14	2	6	9	6
																3	15	4	6																				
																								5	12	29	11									2	6	4	3
8	26	4	10								60					2	10	6	8	5	15	8	4	5	12	11	4	4	17	20	9	1	3	2	1				
30		41		4		4		3		5		11		73		20		72		33		223		42		260		23		227		32		196		31		135	

Table 23. The seasonal variation in the percentage composition of P. microps

Season	Autumn				Winter				Spring				Summer			
No. Examined	35				18				12				30			
Food Category	No. occurrences	% occ.	No. points allotted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
Amphipoda	16	43	125	57	12	46	71	58	3	18	21	25	17	28	174	47
Isopoda					3	12	9	7	3	18	8	10				
Mysidacea	1	3	5	2									3	5	34	9
Decapoda													2	3	7	2
Cladocera													3	5	16	4
Cyclopodia													1	2	3	1
Harpacticoida	1	3	7	3									12	20	30	8
Calanoida									1	6	2	2	2	3	3	1
Ostracoda					1	4	2	2					1	2	1	0.3
Cirripedia													4	7	8	2
Cumacea					2	8	12	10								
Mollusca													2	3	5	1
Oligochaeta													2	3	11	3
Polychaeta	9	24	56	26	3	12	24	20	4	24	30	36	6	10	55	15
Insecta	6	16	17	8	2	8	2	2	4	24	20	24				
Nemertini	1	3	3	1												
Fish eggs									2	12	3	4				
Plant Matter					1	4	1	1					2	3	11	3
Digested Matter	3	8	7	3	2	8	2	2					3	5	12	3
Total	37		220		26		123		17		84		60		370	

Table 25. The seasonal variation in the percentage composition of the diet of C. flavescens. No sample for March 1972

Month	October				November				December				January				February				April				May				June				July	
No. examined	39				120				30				10				7				16				15				62				13	
Food Category	No. occurrences	% occ.	No. points allotted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.
Amphipoda					2	1	5	0.5	3	33	13	72									4	17	5	4	2	7	4	5	2	1	5	1	11	42
Isopoda					3	2	4	0.4					1	6	1	4													7	4	9	2	5	19
Decapoda	3	9	4	2	1	0.6	3	0.3					1	6	2	7					1	4	7	6										
Mysidacea					1	0.6	1	0.1	2	22	3	17					1	50	2	50														
Calanoid copepods	21	64	177	86	119	65	998	92					10	56	19	69					3	13	10	9	12	40	40	48	50	27	99	21		
Harpacticoid copepods	2	6	6	3	4	2	3	0.3	3	33	1	6	3	18	2	7									1	4	3	4	11	6	34	7	3	12
Ostracoda	2	6	2	1	2	1	4	0.4																										
Cirripedia					2	1	2	0.2					1	6	2	7					12	50	71	63	8	28	18	21	19	10	26	6		
Cladocera																													42	23	87	19	1	4
Mollusca	2	6	3	2	29	16	36	3																					5	3	9	2	2	8
Polychaeta					14	8	30	3					1	6	2	7									2	7	6	7	8	4	8	2		
Insecta	1	3	1	0.5																	4	17	20	18	2	7	6	7	37	20	179	38	3	12
Fish Eggs																													1	0.5	6	1		
Fish Larvae																									3	10	6	7						
Digested Matter	2	6	12	6					1	11	1	6					1	50	2	50					-	-	-	-	1	0.5	8	2		
Total	33		205		182		1086		9		18		17		28		2		4		24		113		30		83		183		470		[illegible]	

of *C. flavescens*. No sample for March 1972

December				January				February				April				May				June				July				August				September				October			
30				10				7				16				15				62				13				9				33				35			
No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
3	33	13	72									4	17	5	4	2	7	4	5	2	1	5	1	11	42	54	45	2	6	7	6	4	8	18	9	3	4	8	3
				1	6	1	4													7	4	9	2	5	19	52	44												
				1	6	2	7					1	4	7	6																					2	3	3	1
2	22	3	17					1	50	2	50																					3	6	8	4	2	3	4	1
				10	59	19	69					3	13	10	9	12	40	40	48	50	27	99	21					9	29	71	52	30	61	160	79	27	38	158	56
3	33	1	6	3	18	2	7									1	4	3	4	11	6	34	7	3	12	5	4									2	3	4	1
																																5	10	7	3				
				1	6	2	7					12	50	71	63	8	28	18	21	19	10	26	6					7	22	15	12					19	27	83	29
																				42	23	87	19	1	4	1	0.8	8	26	20	16	2	4	2	1	2	3	2	1
																				5	3	9	2	2	8	2	2	5	16	11	9	3	6	4	2	14	20	21	7
				1	6	2	7									2	7	6	7	8	4	8	2																
												4	17	20	18	2	7	6	7	37	20	179	38	3	12	4	3					1	2	2	1				
																				1	0.5	6	1									1	2	2	1				
																3	10	6	7																				
1	11	1	6					1	50	2	50					–	–	–	–	1	0.5	8	2																
9		18		17		28		2		4		24		113		30		83		183		470		25		118		31		124		49		203		71		283	

of *C. flavescens*. No sample for March 1972

December				January				February				April				May				June				July				August				September				October			
30				10				7				16				15				62				13				9				33				35			
No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
3	33	13	72									4	17	5	4	2	7	4	5	2	1	5	1	11	42	54	45	2	6	7	6	4	8	18	9	3	4	8	3
				1	6	1	4													7	4	9	2	5	19	52	44												
				1	6	2	7					1	4	7	6																					2	3	3	1
2	22	3	17					1	50	2	50																					3	6	8	4	2	3	4	1
				10	59	19	69					3	13	10	9	12	40	40	48	50	27	99	21					9	29	71	52	30	61	160	79	27	38	158	56
3	33	1	6	3	18	2	7									1	4	3	4	11	6	34	7	3	12	5	4									2	3	4	1
																																5	10	7	3				
				1	6	2	7					12	50	71	63	8	28	18	21	19	10	26	6					7	22	15	12					19	27	83	29
																				42	23	87	19	1	4	1	0.8	8	26	20	16	2	4	2	1	2	3	2	1
																				5	3	9	2	2	8	2	2	5	16	11	9	3	6	4	2	14	20	21	7
				1	6	2	7									2	7	6	7	8	4	8	2																
												4	17	20	18	2	7	6	7	37	20	179	38	3	12	4	3					1	2	2	1				
																				1	0.5	6	1									1	2	2	1				
																3	10	6	7																				
1	11	1	6					1	50	2	50					-	-	-	-	1	0.5	8	2																
9		18		17		28		2		4		24		113		30		83		183		470		25		118		31		124		49		203		71		283	

ble 27. Seasonal variation in the food composition of the diet of *Atherina presbyter*. No samples for January 1972, March 1972 and August 1972 onwards.

Month	October				November				December				February				April				May				June				July			
No. examined	15				26				141				46				24				30				38				13			
Food Category	No. occurrences	% occ.	No. points alloted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
Amphipoda									14	20	50	40	8	9	6	6					4	5	21	15	4	6	11	3	6	31	54	48
Isopoda					3	4	7	2	4	6	11	9									2	2	4	3	2	3	6	2	2	11	5	6
Mysidacea																													2	11	3	4
Decapoda	2	7	7	3	10	12	32	11					25	28	21	21	4	9	7	8	19	21	22	16								
Calanoid copepods	15	54	156	65	25	32	147	52	15	22	23	17	26	29	30	31	17	38	24	28	21	24	28	20	29	46	159	49				
Harpacticoid copepods					1	1	2	1	6	9	7	6	5	6	3	3													1	5	1	1
Cladocerans	9	32	68	28													8	18	11	13	9	10	15	11	24	39	138	43				
Ostracoda					3	4	9	3																								
Cumacea									2	3	4	3	1	1	1	1																
Cirripedia					1	1	2	1	5	7	4	3					12	27	18	21	24	27	31	23								
Chaetognatha									1	1	2	2																				
Polychaeta	2	7	9	4	17	21	44	15	5	7	10	8	23	26	36	37					8	9	12	9					2	11	6	8
Mollusca	1	4	2	1	17	21	40	14	4	6	5	4	1	1	1	1																
Insecta					1	1	2	1	2	3	2	2									1	1	4	3	3	5	10	3	2	11	4	5
Fish Larvae																	4	9	25	29												
Digested Matter									11	17	6	5																	4	21	6	8
Total	29		240		78		285		69		124		89		98		45		85		83		137		62		248		19		79	

Table 29. The seasonal variation in the percentage composition of the diet of *P. platessa*. No sample for March and October 1972.

Month	October				November				December				January				February				April				May				June					
No. examined	19				15				5				5				9				8				10				13				55	
Food Category	No. occurrences	% occ.	No. points alloted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.
Amphipoda	10	50	54	68	4	29	15	21	1	13	3	18	2	40	5	50	5	42	9	25	2	13	1.5	2					10	33	103	43	39	36
Isopoda																					1	6	2	3					2	7	3	1	5	5
Decapoda																									4	16	40	27					13	12
Harpacticoida																																	1	1
Cladocera																																	9	8
Cumacea	1	5	1	1																													4	4
Ostracoda																									5	20	10	7					2	2
Oligochaeta																					3	19	12	17	10	40	61	42	10	33	98	41	21	20
Polychaeta	5	25	19	24	7	50	52	73	3	38	12	71	2	40	4	40	6	50	27	74	6	38	35.5	51	6	24	23	16	7	23	33	14	6	6
Mollusca	3	15	4	5	3	21	4	6	2	25	1	6	1	20	1	10					1	6	3	4	4	16	12	8					7	7
Insecta																	1	8	0.5	1	2	13	4	6										
Ophiura																																		
Actiniaria																																		
Rotifera									1	13	0.5	3																						
Nematoda									1	13	0.5	3																						
Plant Matter																					1	6	12	17					1	1	1	0.5		
Digested Matter	1	5	1	1																														
Total	20		79		14		71		8		17		5		10		12		36.5		16		70		25		146		30		236		107	

of the diet of *P. platessa*. No sample for March and October 1972.

er		December				January				February				April				May				June				July				August				September			
		5				5				9				8				10				13				55				4				7			
No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
15	21	1	13	3	18	2	40	5	50	5	42	9	25	2	13	1.5	2					10	33	103	43	39	36	311	49	4	40	24	38	5	55	25	60
																						2	7	3	1	5	5	6	1	1	10	1					
														1	6	2	3																				
																		4	16	40	27					13	12	69	11								
																										1	1	2	0.3								
																										9	8	15	2								
																										4	4	15	2								
																		5	20	10	7					2	2	16	3								
52	73	3	38	12	71	2	40	4	40	6	50	27	74	3	19	12	17	10	40	61	42	10	33	98	41	21	20	158	25	2	20	18	28	3	33	12	29
4	6	2	25	1	6	1	20	1	10					6	38	35.5	51	6	24	23	16	7	23	33	14	6	6	34	6								
										1	8	0.5	1	1	6	3	4	4	16	12	8					7	7	8	1								
														2	13	4	6																				
																														2	20	6					
		1	13	0.5	3																																
		1	13	0.5	3																																
																																		1	11	5	12
														1	6	12	17					1	1	1	0.5					1	10	16					
71		8		17		5		10		12		36.5		16		70		25		146		30		236		107		634		10		65		9		42	

Table 31. The seasonal variation in the percentage composition of *P. flesus*. No.sample for December 1971, May 1972.

Month	October				November				January				February				March				April				June				July				
No. examined	32				9				11				8				8				8				8				12				
Food Category	No. occurrences	% occ.	No. points allotted	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.
Amphipoda	11	24	55	27	2	20	21	43	8	36	50	62	3	27	19	54	5	42	13	33	6	46	41	55	5	25	23	23	8	26	49	35	6
Isopoda	3	7	3	1	2	20	1.5	3	4	18	4	5	1	9	2	6					2	15	2	3	3	15	20	20	3	10	5	4	1
Mysidacea	5	11	50	24																													
Shrimps	1	2	7	3																									2	7	5	4	
Crabs	1	2	9	4																													
Harpacticoida																									2	10	6	6					
Cirripedia																																	
Mollusca	4	9	2	1	2	20	13	27	4	18	5	6	3	27	4	11	2	17	3	8	2	15	7	9	2	10	11	11	3	10	21	15	
Oligochaeta																									2	10	7	7	3	10	16	11	
Polychaeta	9	20	48	23	3	30	10	21	6	27	22	27	4	36	10	29	5	42	24	60	3	23	24	32	4	20	29	29	6	21	27	19	4
Insecta	7	16	16	8																					2	10	5	5	3	10	14	10	
Pisces	1	2	3	1																									1	3	3	2	
Actinaria																																	
Nemertini	1	2	11	5																													
Digested Matter	1	2	1.5	1	1	10	3	6																									
Plant Matter	1	2	1.5	1																													
Total	45		207		10		48.5		22		81		11		35		12		40		13		74		20		101		29		140		1

e composition of *P. flesus*. No.sample for December 1971, May 1972.

November				January				February				March				April				June				July				August				September				October			
9				11				8				8				8				8				12				6				15				4			
No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.	No. occ.	% occ.	No. pts.	% pts.
2	20	21	43	8	36	50	62	3	27	19	54	5	42	13	33	6	46	41	55	5	25	23	23	8	26	49	35	6	55	69	70	11	46	85	53	3	43	19	39
2	20	1.5	3	4	18	4	5	1	9	2	6					2	15	2	3	3	15	20	20	3	10	5	4	1	9	1	1	1	4	2	1				
																																1	4	3	1				
																								2	7	5	4												
																				2	10	6	6																
																																1	4	5	3				
2	20	13	27	4	18	5	6	3	27	4	11	2	17	3	8	2	15	7	9	2	10	11	11	3	10	21	15									1	14	2	4
																				2	10	7	7	3	10	16	11												
3	30	10	21	6	27	22	27	4	36	10	29	5	42	24	60	3	23	24	32	4	20	29	29	6	21	27	19	4	36	28	29	9	38	63	39	3	43	28	57
																				2	10	5	5	3	10	14	10												
																								1	3	3	2												
																																1	4	2	1				
1	10	3	6																																				
10		48.5		22		81		11		35		12		40		13		74		20		101		29		140		11		98		24		160		7		49	

Table 39. S. spinachia. Numbers of fish stomachs showing different fullness levels and seasonal variation of the percentages of high and low food levels throughout the year.

	Fullness Category							Group 1 (Percentages)		Group 2 (Percentages)	
Months	Empty	Trace	¼ Full	½ Full	¾ Full	Full 18–22	Total	Empty – Trace-full %	¾ Full – Full %	Empty – ¼ Full %	½ Full Full %
Points	0–0.5	6–3	4–7	8–12	13–17	18–22		0–3	13–20	0–7	8–20
Oct	18	15	16	11	10	21	91	36	34	54	46
Nov	11	30	32	17	14	17	121	34	26	61	40
Dec	13	13	14	9	2	3	54	48	10	74	27
Jan	10	17	13	5	3	1	49	55	8	82	18
Feb	9	7	7	14	6	3	46	35	20	50	50
March	3	5	3	7	2	1	21	37	15	51	48
April	3	12	5	2	-	3	25	60	12	80	20
May	-	1	4	3	2	1	15	9	27	45	54
June	1	4	6	5	6	12	34	15	53	33	68
July	1	-	-	4	2	5	12	8	59	8	92
Aug.	1	2	4	7	9	31	54	6	73	13	86
Sept.	1	12	8	15	9	20	65	20	45	33	68
Oct.	3	2	5	5	4	6	25	20	40	40	60
							608				

Table 42. G. aculeatus. Number of fish stomachs in different fullness categories and percent variation of the high and low food levels in stomachs throughout the year.

	Fullness Category							Group 1 (Percentages)		Group 2	
	Empty	Trace	¼ Full	½ Full	¾ Full	Full	Total	Empty + Trace-full	¾ Full + Full	Empty + Trace + ¼ Full	½ Full + ¾ Full + Full
Points	0-0.5	0.6-3	4-7	8-12	13-17	18-22		0-3	13-20	0-7	8-22
Oct	5	29	23	6	6	5	74	46	15	77	23
Nov	10	14	6	2	1	-	33	72	3	90	9
Dec	1	1	-	-	-	-	2	100	-	100	-
Jan	3	3	5	5	2	-	18	34	2	61	39
Feb	2	-	1	1	-	-	4	50	-	75	25
Mar	3	4	1	2	-	-	10	70	-	80	20
April	-	2	1	1	2	3	9	22	55	33	66
May	1	2	2	3	3	4	15	20	47	33	66
June	2	4	2	11	9	13	41	15	54	20	80
July	-	1	5	5	4	10	25	4	56	24	76
Aug	-	1	5	5	7	17	35	3	69	17	83
Sept	-	5	8	12	15	48	88	6	72	15	85
							354				

Table 43. Number of fish stomachs in different fullness categories and percentage variation of high and low food levels throughout the year in *M. scorpius*.

	Fullness Category							Group 1 (Percentages)		Group 2 (Percentages)	
Points	Empty 0–0.5	Trace 0.6–3	¼ Full 4–7	½ Full 8–12	¾ Full 13–17	Full 18–22	Total	Empty + Trace 0–3	Full + ¾ Full 13–20	Empty – ¼ Full 0–7	½ Full to Full 8–20
Oct	1	2	2	4	2	8	19	15	52	25	73
Nov	4	5	1	2	2	3	17	53	21	59	42
Dec	3	2	2	-	-	-	7	72	-	100	-
Jan	5	-	-	1	1	-	7	71	-	71	28
Feb	8	4	3	6	2	3	26	46	20	58	42
Mar	1	2	1	3	2	2	2	11	27	36	63
April	2	-	1	5	1	3	12	16	33	24	75
May	-	1	2	1	3	4	11	9	63	27	72
June	-	1	1	5	5	10	22	5	69	10	92
July	3	2	5	11	14	48	83	7	75	13	88
Aug	-	-	-	3	1	1	5	-	40	-	100
Sept											
Oct	2	1	3	1	4	1	12	21	41	50	49
							232				

Table 44. Number of fish stomachs in different fullness categories and percentage variation of low and high food levels throughout the year in *T. bubalis*.

	Fullness Category							Group 1		Group 2	
								(Percentages)			
Points	Empty 0-0.5	Trace- 0.6-3	¼ Full 4-7	½ Full 8-12	¾ Full 13-17	Full 18-22	Total	Empty - Trace 0-13	Full - ¾ Full 13-20	Empty to ¼ Full 0-7	½ Full to Full 8-22
Oct	3	6	4	3	1	2	19	46	16	67	31
Nov	-	2	-	4	1	-	7	29	14	29	71
Dec											
Jan	-	1	3	3	2	1	10	10	30	40	60
Feb	3	3	2	4	4	1	17	36	30	48	54
Mar	1	1	-	1	1	-	4	50	25	50	50
April	-	6	2	3	1	5	17	38	37	44	56
May	-	-	-	1	2	1	4	-	75	-	100
June	-	-	-	1	2	3	6	-	83	-	100
July	-	-	1	1	1	5	8	-	76	13	89
Aug	-	-	1	1	-	2	4	-	50	25	75
Sept	1	2	2	2	-	-	7	43	-	86	29
Oct	2	1	3	2	2	3	13	23	38	46	53
							116				

Table 45. Numbers of stomachs in different fullness categories and percent variation of the low and high food levels in fish stomachs throughout the year in *P. gunnellus*.

	Fullness Category							Group 1 (Percentages)		Group 2	
	Empty	Trace Full	¼ Full	½ Full	¾ Full	Full	Total	Empty + Trace Full	¾ Full + Full	Empty to ¼ Full	½ Full to Full
Points	0-0.5	0.6-3	4-7	8-12	13-17	18-22		0-3	13-20	0-7	8-20
Oct	6	3	3	9	9	1	31	29	32	34	61
Nov	11	1	3	-	1	-	16	75	6	94	6
Dec	6	-	1	-	-	-	7	86	-	100	-
Jan	28	10	7	5	-	-	50	76	-	90	10
Feb	28	8	6	-	-	-	42	86	-	100	-
Mar	7	2	-	-	-	-	9	100	-	100	-
April	15	13	6	4	2	1	41	71	8	86	18
May	2	3	2	3	1	1	12	42	16	59	41
June	1	1	-	5	3	2	12	16	42	16	84
July	-	-	7	11	2	2	22	-	18	32	68
Aug	-	-	1	-	1	3	5	-	80	20	80
Sept	2	1	3	4	-	-	10	30	-	60	40
Oct	6	2	8	3	2	3	24	33	21	66	34
							281				

Table 46. Numbers of fish stomachs in different fullness categories and percent variation of the low and high full levels in fish stomachs throughout the year in *Atherina presbyter*.

	Fullness Category							Group 1 (Percentages)		Group 2	
	Empty	Trace	¼ Full	½ Full	¾ Full	Full	Total	Empty + Trace Full	¾ Full + Full	Empty to ¼ Full	½ Full to Ful
Points	0-0.5	0.6-3	4-7	8-12	13-17	18-22		0-3	13-20	0-7	8-20
Oct	-	-	-	3	3	9	15	-	80	-	100
Nov	1	2	6	6	7	4	26	12	42	35	65
Dec	94	36	4	4	3	-	141	91	2	94	6
Jan								-	-	-	-
Feb	6	26	14	-	-	-	46	68	-	99	-
Mar								-	-	-	-
April	8	17	6	3	-	-	24	63	-	88	13
May	2	11	10	4	3	-	30	46	11	76	23
June	1	4	11	13	7	2	38	13	23	42	59
July	6	3	1	-	-	3	13	69	23	77	23
							333				

Table 47. Numbers of fish stomachs in different fullness categories and percent variation of the low and high food levels in fish stomachs throughout the year in *P. minutus*.

	Fullness Category							Group 1 (Percentages)		Group 2	
	Empty	Trace	¼ Full	½ Full	¾ Full	Full	Total	Empty + Trace Full	¾ Full + Full	Empty to ¼ Full	½ Full to Ful
Points	0-0.5	0.6-3	4-7	8-12	13-17	8-22		0-13	13-20	0-7	8-20
Oct	53	30	24	16	11	7	140	59	14	76	25
Nov	2	5	8	17	17	1	50	12	38	30	70
Dec	2	5	5	4	2	1	19	37	16	63	37
Jan	4	10	2	-	-	-	16	88	-	100	-
Feb	13	3	-	-	-	-	16	100	-	100	-
Mar	3	3	-	-	-	-	6	100	-	100	-
April	3	1	3	1	2	-	10	40	20	70	30
May	2	1	4	3	-	1	11	27	9	63	36
June	4	2	5	6	5	4	26	23	34	42	57
July	4	3	3	10	7	3	30	23	33	33	66
Aug	-	2	4	4	3	4	17	12	42	35	66
Sept	3	2	4	7	6	-	22	23	27	41	59
Oct	6	9	6	7	-	-	28	53	-	74	25
							391				

Table 48. **Numbers of fish stomachs in different fullness categories and percent variation of the low and high food levels in fish stomachs throughout the year in *Z. viviparus*.**

	Fullness Category							Group 1		Group 2	
								(Percentages)			
	Empty	Trace	¼ Full	½ Full	¾ Full	Full	Total	Empty + Trace Full	¾ Full + Full	Empty to ¼ Full	½ Full Full
Points	0–0.5	0.6–3	4–7	8–12	13–17	18–22		0–3	13–20	0–7	8–20
Oct	6	-	-	-	-	1	7	86	14	86	14
Nov	12	-	-	1	2	-	15	80	13	80	20
Dec	1	-	-	-	-	-	1	-	-	-	-
Jan	11	1	-	-	-	-	12	100	-	100	-
Feb	26	5	1	2	1	-	35	88	3	91	9
Mar	11	3	2	-	-	-	16	88	-	100	-
April	12	-	4	8	1	-	25	48	4	64	36
May	-	1	1	1	-	1	4	25	25	50	50
June	6	1	1	2	2	1	13	54	23	62	38
July	7	2	-	1	3	3	16	55	39	55	45
Sept	18	-	-	-	2	-	20	90	-	90	10
Oct	15	1	-	1	-	-	17	94	-	94	6
							181				

Table 49. Numbers of fish stomachs in different fullness categories and percent variation of the low and high food levels in fish stomachs throughout the year in *Chaparrudd' flavescens*.

	Fullness Category							Group 1 (Percentages)		Group 2	
	Trace	Empty	¼ Full	½ Full	¾ Full	Full	Total	Empty + Trace Full	¾ Full + Full	Empty to ¼ Full	½ Full to Ful
Points	0-0.5	0.6-3	4-7	8-12	13-17	18-22	389	0-3	13-20	0-7	8-20
Oct	14	8	7	8	1	1	39	57	6	74	27
Nov	-	20	28	21	24	27	120	17	43	43	68
Dec	25	2	3	-	-	-	30	90	-	100	-
Jan	-	7	3	-	-	-	10	70	-	100	-
Feb	5	2	-	-	-	-	7	90	-	100	-
Mar							0				
April	3	5	2	3	-	3	16	50	19	63	38
May	3	7	2	2	1	-	15	67	7	80	20
June	-	13	24	16	4	5	62	21	15	60	41
July	2	-	5	4	-	2	13	15	15	53	45
Aug	-	-	-	2	3	4	9	-	77	-	100
Sept	3	6	9	10	4	1	33	27	15	54	45
Oct	8	2	5	7	4	9	35	29	37	43	57
							389				

Table 50. Number of stomachs in different fullness categories and seasonal variation of the percentages of high and low food levels in fish stomachs in *P. platessa*.

	Fullness Category							Group 1		Group 2
								(Percentages)			
	Empty	Trace	¼ Full	½ Full	¾ Full	Full	Total	Empty + Trace Full	¾ Full + Full	Empty to ¼ Full	½ Full to Ful
Points	0–0.5	0.6–3	4–7	8–12	13–17	18–22		0–3	13–22	0–7	8–22
Oct	9	2	4	3	1	–	19	58	21	79	21
Nov	5	4	2	3	1	–	15	60	27	73	27
Dec	1	2	2	–	–	–	5	60	–	100	–
Jan	3	–	2	–	–	–	5	60	–	100	–
Feb	2	3	3	1	–	–	9	55	–	88	12
Mar	1	1	–	–	–	–	2	100	–	100	–
April	–	2	1	3	1	1	8	25	26	38	64
May	–	–	–	4	3	3	10	–	60	–	100
June	–	–	–	2	3	7	13	–	77	8	92
July	2	4	7	24	12	6	55	11	33	24	77
Aug	–	–	–	1	1	2	4	–	75	–	100
Sept	1	4	–	–	2	–	7	71	29	71	29
							152				

Table 51. Number of fish stomachs in different fullness categories and seasonal variation of the percentages of high and low food levels throughout the year in *P. flesus*.

	Fullness Category							Group 1		Group 2	
								(Percentages)			
	Empty	Trace	¼ Full	½ Full	¾ Full	Full	Total	Empty + Trace Full	¾ Full + Full	Empty to ¼ Full	½ Full to Ful
Points	0-0.5	0.6-3	4-7	8-12	13-17	18-22		0-3	13-22	0-7	8-22
Oct	9	8	2	5	3	5	32	53	19	60	41
Nov	4	1	1	2	1	-	9	55	11	66	33
Dec	2	-	-	-	-	-	2	100	-	100	-
Jan	2	4	2	-	2	1	11	54	9	72	27
Feb	5	1	-	1	-	1	8	76	13	76	26
Mar	2	2	3	-	-	1	8	50	13	88	13
April	2	2	1	-	2	1	8	50	38	63	38
May											
June	1	1	-	1	1	4	8	26	63	26	76
July	2	1	1	3	3	2	12	25	42	33	67
Aug	-	-	-	1	1	4	6	-	83	-	100
Sept	4	1	1	5	1	3	15	34	29	41	60
Oct	-	1	-	1	1	1	4				
							123				

Table 52. Numbers of fish stomachs in different fullness categories and percent variation of the low and high food levels in fish stomachs throughout the year in *P. microps*.

	Fullness Category							Group 1		Group 2	
								(Percentages)			
	Empty	Trace	¼ Full	½ Full	¾ Full	Full	Total	Empty+ Trace Full	¼ Full + Full	Empty to ¼ Full	½ Full to Ful
Points	0-0.5	0.6-3	4-7	8-12	13-17	18-22		0-3	13-20	0-7	8-20
Oct	5	3	4	1	-	2	15	53	13	80	20
Nov											
Dec											
Jan		5	1	3	2	-	11	46	18	54	46
Feb	1	1	3	2	-	-	7	29	-	71	29
Mar	1	1	-	-	-	-	2	100	-	100	-
April	-	2	2	1	2	1	8	25	38	50	50
May	-	-	-	1	1	-	2	-	50	-	100
June	1	1	1	1	-	3	7	29	43	43	57
July	-	2	3	2	2	7	16	13	57	31	69
Aug	1	1	1	-	-	4	7	29	57	43	52
Sept	3	2	4	6	2	3	20	25	25	45	55
							103				

Table 53. Number of fish stomachs in different fullness categories and seasonal variation of th low and high food levels in fish stomachs in *Gadus morhua*.

	Fullness Category							Group 1		Group 2	
								(Percentages)			
	Empty	Trace	¼ Full	½ Full	¾ Full	Full	Total	Empty tc Trace Full	¾ Full to Full	Empty to ¼ Full	½ Full to Ful
Points	0-0.5	0.6-3	4-7	8-12	13-17	18-22		0-3	13-22	0-7	8-22
Oct	1	1	-	-	-	-	2	100	-	100	-
Nov	-	2	1	-	1		4	50	25	75	25
Dec	2	1	1	-	-	1	5	60	20	80	20
May	-	1	-	-	-	-	1				
June	-	-	2	4	1	2	9	-	43	29	72
July	-	1	1	8	3	1	14	7	58	14	85
Aug	-	-	-	-	-	1	1	-	100	-	100
							36				

Table 54. Number of fish stomachs in different fullness categories and seasonal variation of the low and high food levels in fish stomachs in *Pollachius virens*.

	Fullness Category							Group 1		Group 2	
								(Percentages)			
	Empty	Trace	¼ Full	½ Full	¾ Full	Full	Total	Empty to Trace Full	¾ Full + Full	Empty to ¼ Full	½ Full to Ful
Points	0-0.5	0.6-3	4-7	8-12	13-17	18-22		0-3	13-22	0-7	8-22
Nov	-	-	-	4	2	1	6	-	49	-	100
Dec	1	15	13	11	6	4	50	32	20	58	42
Jan	-	2	-	-	-	-	2	100	-	100	-
Feb	-	-	2	-	-	-	2	-	-	100	-
May	-	-	1	2	4	4	11	-	72	9	91
June	-	-	7	3	9	14	33	-	69	21	78
July	-	-	1	8	2	4	15	-	40	7	93
Aug	-	-	-	1	-	9	10	-	90	-	100
Sept				2	5	4	11	-	82	-	99
Oct	-	1	1	2	1	1	6	17	34	37	67
							146				