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STUDIES ON THE FEEDING BEHAVIOUR OF FLATFISH

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Studies on the feeding behaviour of flatfish

A thesis submitted for the degree of Doctor of Philosophy

Ray Holmes

(Dunstaffnage Marine Research Laboratory, Oban)

ABSTRACT

The feeding tactics of seven species of flatfish have been described by sequential analysis of their behaviour. The species studied were turbot, brill, Z. punctatus, P. regius, plaice, flounder and sole. Their feeding behaviour was observed in the laboratory using five different prey species, namely mysids, shrimps, corophiids, gammarids and enchytraeid worms. Forty-eight different elements of behaviour were recognised; the bothids had the most diverse behavioural repertoire, exhibiting 43 elements, the soleids were least diverse exhibiting 24 different elements and the pleuronectids occupied an intermediate position with 30. Frequencies and durations of behavioural elements were analysed and transition matrices and flow charts were presented to demonstrate the quantitative behavioural differences between families and species.

Elements of behaviour were categorised as water column activity, bottom activity or inactivity. The bothids, particularly turbot, performed more water column activity than the other two families. The proportion of bottom activity and inactivity was dependent on whether frequencies or durations formed the basis for comparison. The frequency

of elements of bottom activity was higher than that of inactivity but the durations of elements of inactivity were higher than the durations of bottom activity. This relationship was attributed to the elements of bottom activity being high in frequency but short in duration whereas the reverse situation applied to the elements of inactivity.

The tactics of the species differed considerably and were found to be dependent on prey species, the tactics of the bothids involved much more hunting and stalking because their prey were more mobile. In contrast, the tactics of the pleuronectids and soleids, whose natural prey are less mobile, could be described as hunting and cropping. The elements of behaviour exhibited made this very apparent.

The observations on the feeding behaviour of turbot were used to determine the importance of various prey stimuli in prey recognition. The response to selectively presented models and food cues was assessed quantitatively by a simple scoring method. Turbot preferred moving prey with a ratio of vertical:horizontal components of body shape of about 1:10. These attributes correspond well with those of the natural prey which constitutes the fishes' diet. Appendage movements were also found to be important but the general characteristics of body shape were unimportant. Inconspicuous cryptically coloured and translucent models were preferred to conspicuous ones. Turbot were found to be visual feeders and olfaction was unimportant in recognising prey. These results are discussed in relation to other work on flatfish and sticklebacks.

INTRODUCTION

Seven species of flatfish have been chosen from the three major taxonomic groups of the Pleuronectiformes:

1)	Bothidae	turbot	Scophthalmus maximus (L.)
		brill	Scophthalmus rhombus (L.)
		topknot	Zeugopterus punctatus (Bloch)
		Bloch's topknot	Phrynorhombus regius (Bonnaterre)
2)	Pleuronectidae	plaice	Pleuronectes platessa (L.)
		flounder	Platichthys flesus (L.)
3)	Soleidae	sole	Solea solea (L.)

Figure 1 is a simplified representation of the important factors operating in a laboratory based feeding system. For the purposes of this study, this integrated system is broken down into internal (that is, processes that originate from within the organism) and external components. The external component is the experimental environment. It can be conveniently subdivided into three categories: the food stimulus, conditioning and all other aspects of the environment.

1) The food (prey) stimulus has physical and chemical attributes such as colour, shape, size and odour. The prey stimulus also has behavioural attributes such as its locomotion, how well it conceals itself in its environment, specialised defence traits and its life processes such as feeding activities which make it vulnerable to predators. All these attributes may play a role in alerting predators to its potential as a food source.

2) Conditioning can often elicit a feeding response. In terms of classical conditioning, an unconditioned stimulus (the presence of food in the tank) evokes a response (initiation of the feeding response

FIGURE 1 FACTORS OPERATING IN A LABORATORY BASED FEEDING SYSTEM

EXTERNAL

1) ENVIRONMENT

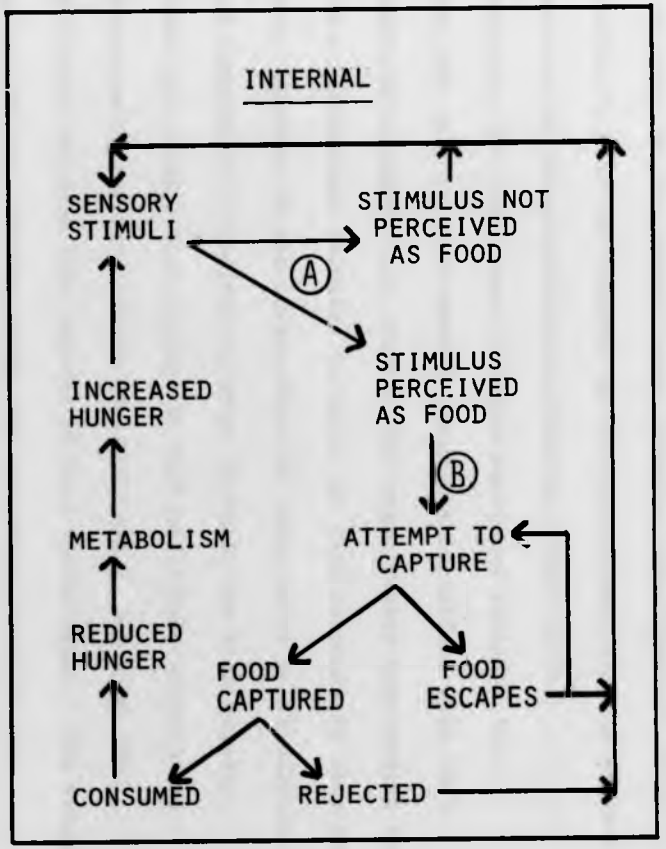
2) CONDITIONING

3) FOOD STIMULUS

(PREY/FOOD CHARACTERISTICS)

I. PHYSICAL & CHEMICAL
- -COLOUR
- -SHAPE
- -SIZE
- -ODOUR

II. BEHAVIOURAL ATTRIBUTES
- -NATURE OF LOCOMOTION
- -SPEED OF LOCOMOTION
- -CONTRAST WITH SURROUNDINGS
- -SPECIALIZED TRAITS
- -LIFE PROCESSES



in this case). If another stimulus (called the conditioned stimulus) is given prior to the unconditioned stimulus, the fish will learn by association to make the response to the conditioned stimulus without the presence of the unconditioned stimulus. Under normal circumstances the conditioned stimulus would not initiate the response but only does so through repeated associations with the unconditioned stimulus (i.e. food). The experimenter approaching the tank is a conditioned stimulus to which the fish responds by searching for food. Removal of the covers from the tanks prior to feeding is another example of a conditioned stimulus which the fish quickly associate with food. The response to the conditioned stimulus is maintained and reinforced by the constant association with the unconditioned stimulus (the arrival of food in the tank). The response to the conditioned stimulus would soon be extinguished if the association between the two types of stimulus were not constantly reinforced. Conditioning is a real difficulty when working with flatfish since they seem to make such associations quite quickly. It is a problem that must be constantly borne in mind when designing experiments.

Conditioning is not only a problem with flatfish. Nakamura (1962) observed rapid conditioning in skipjack tuna by the association of food with observers and to slapping of the water as a feeding signal. Olla, Katz and Studholme (1970) reported that bluefish became excited prior to feeding if they saw the observers.

3) In this category of the fishes' external environment are all the remaining considerations that have not been covered by the food stimulus and conditioning. Factors of the external environment may inhibit or promote the feeding response. Intensity of illumination,

for example, plays and important role in determining feeding activities (Verheijen and de Groot, 1967). The activity of plaice and sole was observed to increase as intensity of illumination decreased, passing through a 'bottom search for food' phase then to a prolonged 'swimming in the water column' during the dark period. As light intensity increased, the fish returned to the food searching pattern on the bottom and finally entered a phase of inactivity as light intensity reached its maximum.

Temperature is another factor of the environment which influences feeding activity. At high temperatures ($20^{o}C$) the rate of passage of food through the alimentary canal of plaice was found to be quicker than at lower temperatures (Edwards, 1971). A more rapid metabolism at higher temperatures leads to a higher food requirement and consequently increased feeding activity.

Prey population factors such as density are also to be included here. The relationship between predation rates and prey density has been studied for vertebrates by Tinbergen (1960) for songbirds, Smith (1974) for European thrushes, Ware (1972) for rainbow trout and Holling (1965) for a generalised predator. Ware reports that if the capture rate fell below "0.058 captures sec^{-1}, substrate orientated search preceeded to wane" and suggests that foraging behaviour in laboratory tanks may be controlled by a critical rate of food capture.

There are many ways in which the environment acts upon an organism to influence its feeding behaviour, some of which have been mentioned above. All these interactions should be held constant in optimum conditions, or eliminated in order to carry out investigations of the feeding behaviour.

There is a growing body of literature concerning the factors

operating in the internal environment of the fish. Much work has been done on motivational states with respect to hunger and satiation and how this state affects the feeding behaviour. A comprehensive survey of studies on aspects of feeding motivation is given by Colgan (1973) and will not be reiterated here except to say that the survey is organised into four sections: 1) homeostasis 2) deprivation and satiation 3) systemic need versus gastric volume and 4) preference and selectivity.

Feeding motivation begins with hunger and is observable to the behaviourist as searching behaviour. Perception of potential prey stimuli occurs through the sensory systems of the fish and leads to either recognition of food, or rejection if the cues do not conform to intinsic criteria established by experience and/or genetic influences. Experiments with a variety of vertebrate predators have shown that foraging behaviour is modified by experience with prey; Ware (1971) for rainbow trout, de Ruiter (1952) for jays and chaffinches, Beukema (1968) for the three-spined stickleback, Holling (1959) for small mammals and Croze (1970) for carrion crows. Once a stimulus has been recognised as potential food, the organism may then proceed to capture the prey. If the prey is captured it is then either ingested or rejected if it is found to be unsuitable. The cycle continues if the fish is still hungry or ceases if enough has been consumed to satisfy the appetite.

This study is directed at investigating two of the links in the chain. The link labelled B (see Fig. 1) will be studied in Part Two. It describes the methods of prey capture or feeding strategies employed by the chosen species of flatfish. In Part Three, the link labelled A (how flatfish recognise their food) will be investigated

in depth for one species, the turbot, and some comparisons will be made with brill.

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PART ONE

THE NATURAL FOOD OF FLATFISH

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Data on the composition of the food in the stomachs of flatfish have been presented by a large number of authors. De Groot (1971) provides a comprehensive review of published work before the middle of the 1960's. Since this review further papers have been published by Jones (1973) for turbot; Macer (1967), Edwards and Steele (1968), Lande (1973), Braber and de Groot (1973), Thijssen, Lever and Lever (1974) for plaice; Moore and Moore (1976) for flounder; further accounts of food composition are to be found in Wheeler (1969).

Two facts emerge from all these stomach contents analyses. Firstly, that all species of flatfish are euryphagic predators, being able to utilise a wide range of prey forms as food and secondly that there can be large differences between the diets of populations of a species from different localities. It seems almost axiomatic to say that the diet reflects what is available rather than what the fish would prefer. There is therefore little evidence to suggest that there are well defined prey species that comprise typical diets of each species of flatfish. Certain species are, however, more suited to utilise particular prey types through modifications and adaptations of their feeding behaviour.

The flatfish can be broadly divided into three feeding categories with respect to their feeding habits which conform to the three major taxonomic divisions within the group:

1) Visual day feeders which find their quick-moving prey, such as fish, exclusively by visual means : Bothidae.

2) Visual day feeders which may use chemical as well as visual clues in their search for food in or near the bottom : Pleuronectidae.

3) Non-visual night feeders which feed on immobile or slow-moving invertebrates found in or near the bottom : Soleidae.

The prey organisms selected by flatfish can be divided into three morphological and behavioural groups:

1) Fast-moving prey organisms in the water column, mostly fish but also some crustaceans such as mysids.

2) Mobile bottom dwelling organisms such as amphipods, shrimps and crabs.

3) Sedentary or slow-moving bottom dwelling organisms such as polychaetes and molluscs.

The prey types of the three main taxonomic groups of flatfish correspond to the above groups. The bothids, turbot and brill, are large species which feed in the adult stages on fish. Gadoid and clupeoid fish form the main constituents of the diet and smaller flatfish are also eaten. The juvenile stages of turbot and brill feed on mysids, shrimps and sandeels. There is a gradual change in the diet as the fish mature corresponding to selection of progressively larger prey. The bothids, topknot and Bloch's topknot, are relatively small species and can only take very small fish or juvenile forms. Both topknots are predominantly crustacean feeders.

The pleuronectids plaice and flounder differ in their prey preferences. Flounders are crustacean feeders consuming gammarids, mysids and corophiids. Plaice, however, prefer more sedentary prey such as polychaetes (especially the tentacles of tube-dwelling forms) and molluscs (especially the siphons of bivalves).

The soleids are non-visual feeders using mainly olfaction to locate their food. Prey types eaten by soles are all sedentary organisms, molluscs and polychaetes comprising the majority of the diet.

The wide range of prey types consumed by the various flatfishes require widely differing hunting and capturing techniques. The next section attempts to describe and quantify the differences in feeding strategies of the seven chosen species.

PART TWO

THE FEEDING TACTICS

OF FLATFISH

1. INTRODUCTION

Because of their commercial importance, much of the literature relating to flatfish has been concerned with population structure, rates of recruitment, growth and mortality, migratory habits and many other aspects of the life history from egg to adult stages. Most of these studies have come from analysis of fishing catches. There have also been many laboratory studies describing the food, feeding habits, the use of various sensory systems and activity of flatfish (Bateson, 1890; Steven, 1930; Kruuk, 1963; de Groot, 1964, 1966, 1969, 1971; Verheijen and de Groot, 1967; Olla, Samet and Studholme, 1972; Stickney, White and Miller, 1973).

Although the feeding behaviour of certain species, notably the three-spined stickleback (Gasterosteus aculeatus L.; Tugendhat, 1960; Beukema, 1968) and the bluegill sunfish (Lepomis maciochirus, Rafinesque; Chiszar and Windell, 1973) has been investigated in detail, there are no accounts of the sequential analysis of such behaviour in flatfish.

This section is concerned with a descriptive observational analysis of the feeding strategies of seven species of flatfish. There were three main objectives of the study: 1) to identify the components of feeding behaviour 2) to determine the sequential relationships between the components and 3) to establish criteria for assessing the effectiveness of food cues and models in subsequent experiments designed to determine how flatfish recognise their prey.

2. METHOD

Stocks of seven species of flatfish (turbot, brill, topknot, Bloch's topknot, flounder, plaice and sole) were collected and held in laboratory tanks 120 x 54 x 18 cm with constant air and water flows. All species except sole were caught in the sea near the marine laboratory using either a beam trawl from a small boat, or a push net in shallow water. The sole were obtained from the Fisheries Laboratory at Port Erin, Isle of Man, where they had been reared.

The size (total body length) variation within each species was kept small in order to minimise variation in the feeding performance between individuals. Inter-specific variation in size was also minimised as much as possible, but because the species were different shapes, sole being very long and Bloch's topknot being a very small species, it was not possible to achieve complete uniformity of size between species. All the fish used were within the size range 8 - 23 cm making them either I- or II- group.

Each species was kept in a separate stock tank. All except the two topknot species were fed daily on an artificial diet of minced paste consisting of 3 parts trash fish (sprats and small gadoids) to 2 parts squid. The paste was extruded through a syringe with a 5 mm hole into 'worms' and dropped into the tanks. The topknots would not readily accept an artificial diet and were maintained on live mysids.

Observations of feeding behaviour were made in two clear perspex tanks with a bottom area of 175 x 30 cm filled to a depth of 24 cm with running sea water maintained at 15 $\pm$ 1°C (Fig. 2). Each tank was divided in half by an opaque perspex partition to provide a total of 4 separate enclosures, each 86 cm in length containing 1 fish. Suspended above each tank were 60 watt strip lights giving an

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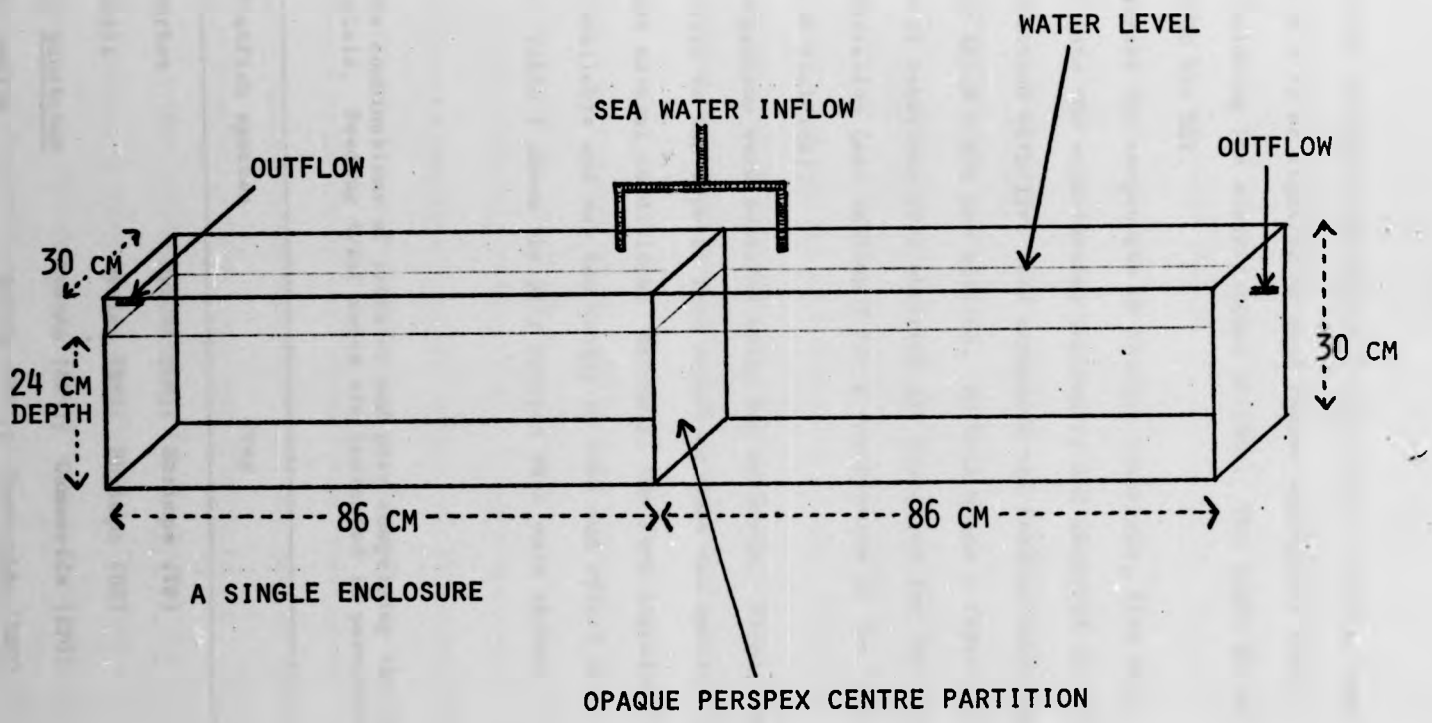
FIGURE 2 THE EXPERIMENTAL ENCLOSURE



illumination of 50 lux on the bottom of the tank. The fish were maintained in a 12 hr light/12 hr dark regime throughout their captivity including the observational periods. The light period began at 07.00 hrs BST.

To describe the components of feeding behaviour, fish were transferred into the experimental enclosures and observed in isolation. They were provided with live food organisms and feeding behaviour was observed for about 5 hrs per species. By this means a repertoire of 48 elements of behaviour were observed and described for the 7 species under consideration (see section 3 for a description of the behavioural repertoire of flatfish).

Prey organisms were selected using two criteria. First, they should be close to the type of food organisms that the species would consume under natural conditions. Secondly, the food organisms should be readily available and not too costly in time and effort of collection. Table 1 shows the prey species that were chosen.

Table 1 The combinations of predator and prey comprising the feeding trials. Feeding trial codes are indicated in parentheses.

Flatfish species	Prey
Turbot	Mysids (TM); Shrimps (TS)
Brill	Mysids (BM); Shrimps (BS)
Z. punctatus	Mysids (ZPM); Gammarids (ZPG)
P. regius	Mysids (PRM); Gammarids (PRG)
Plaice	Corophiids (PC); Enchytraeid worms (PW)
Flounder	Corophiids (FC); Enchytraeid worms (FW)
Sole	Enchytraeid worms (SW)

The mysids, Praunus flexuosus (Muller) and Neomysis integer (Leach), were found in the estuary of a small stream draining into Dunstaffnage Bay (O.S. Grid Reference NM882338). The mysids were captured in a hand net drawn through the stream whilst they were migrating in shoals up and down the estuary with the tidal cycle.

Shrimps, Crangon crangon (L.), were collected by push net in shallow water in Dunstaffnage Bay. Two types of amphipods were used, gammarids and corophiids. Gammarus marinus, being a gregarious species living amongst littoral weed was easily collected by disturbing boulders and stones. Corophium volutator lives in burrows in mud and was collected when the mud was uncovered at low tide. Individuals left their burrows in large numbers when the mud was disturbed by the movements of a collector and were easily picked from the surface using a spatula.

Acquiring a good supply of small polychaete worms proved rather difficult, mainly due to the problems of extracting the worms intact from their burrows. Typical food of young pleuronectids are polychaete tentacles and bivalve siphon tubes, but to set up tanks with bivalves and sedentary tube-dwelling worms in the numbers required would have been totally impractical. Enchytraeid white worms are probably rarely encountered by fish in the sea but they do fulfill all the criteria. These oligochaete worms are ubiquitous and large numbers could be obtained from rotting seaweed at the top of certain beaches near the laboratory. Extraction of the worms from the weed was relatively simple. Rotten weed was suspended on a 4 mm mesh in a tank of sea water. When covered by water the worms' response was to migrate downwards. In so doing they fell from the bottom of the mesh and accumulated at the bottom of the tank. After being left overnight the

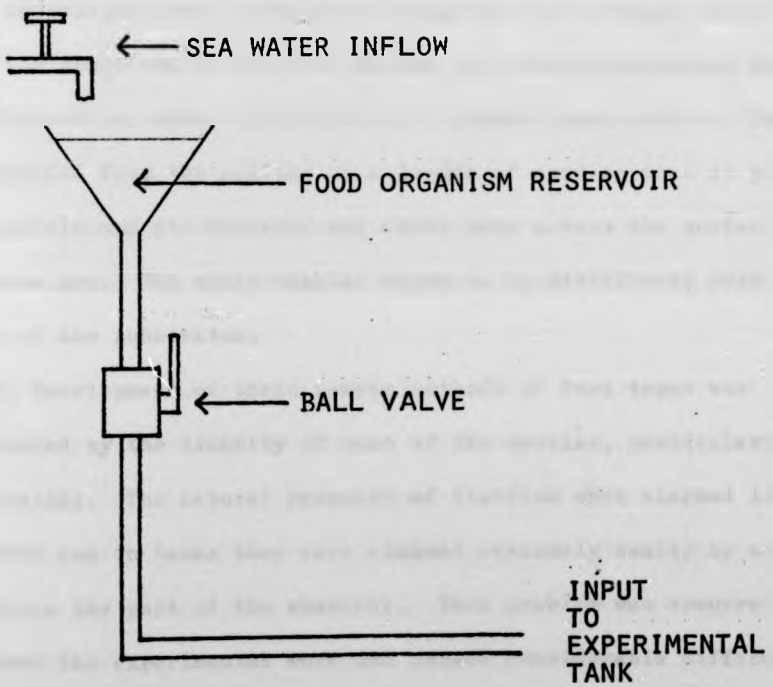
tank was drained and the worms were removed and washed to separate small fragments of weed which had fallen through the mesh. This method yielded large numbers of white worms Enchytaeus albidus and in addition small pink worms of the genus Lumbricillus. These two types of worms were readily eaten by soles, plaice and flounders. Enchytraeids were also found to be very acceptable to three-spined sticklebacks by Beukema (1968).

Mysids, shrimps, gammarids, corophiids and enchytraeid worms were the live prey organisms chosen as food. Although the species used in some cases were probably only rarely, if ever, encountered by the fish in their natural environment, they are at least close to the natural prey types eaten. All were found to be quite acceptable and served well as a food source upon which fish could be observed feeding.

Mobile organisms such as mysids, corophiids and gammarids were introduced into the experimental enclosure by means of a food dispenser (see Fig. 3). The food dispenser was found to be necessary for replacing consumed individuals so that the observer's attention could be fixed on the fish and not diverted by having to add more prey by some other method. Prey density was maintained at a constant level throughout the experimental period to provide constant conditions because there is evidence that prey density influences the feeding activity of fish (Ware, 1972). Fifty prey individuals per enclosure was chosen as a suitable density based on observation and experience of the feeding activity of flatfish. The dispenser consisted of a conical water reservoir into which the organisms were placed and then released into the tank via a ball valve. With practice, organisms could be introduced singly with a minimum of disturbance to the fish.

This method was not suitable for the enchytraeid worms which

FIGURE 3 THE FOOD DISPENSER SUITABLE FOR MOBILE ORGANISMS



tended to clump together into large balls if many individuals were left in close proximity. These large balls were not considered to be realistic prey stimuli, being merely the products of artificially high densities of individuals. In order to prevent the worms from clumping together, single individuals were introduced into the experimental tank from a shute inclined at 30^{o} to the horizontal. The shute consisted of 60 cm of 4 cm diameter perspex tubing. Using a pipette, 2 or 3 individuals were transferred from the worm storage vessel to the top of the shute where they were washed into the experimental tank with 5 - 10 mls of sea water squirted from a plastic wash-bottle. The shute was suspended from the ceiling by a length of cord so that it pivoted in the middle and its downward end would move across the surface of the tank in an arc. The shute enabled worms to be distributed over the surface of the substratum.

The development of these remote methods of food input was necessitated by the timidity of some of the species, particularly the pleuronectids. The natural response of flatfish when alarmed is to bury themselves and in tanks they were alarmed extremely easily by a slight movement on the part of the observer. This problem was recurrent throughout the experimental work and caused considerable difficulty. Burying in response to fright would often last for 10 - 20 minutes or even hours. Inactivity of the fish after burying led to much time being lost in carrying out observations. The fish did tend, however, to settle down after spending some time in their new tank environments. Five days was found to be the best compromise between time allowed for the fish to settle down and time being lost through not being able to make observations. Even so, many fish had to be rejected because they were found to be too timid to feed under the experimental conditions.

In an attempt to overcome the difficulty of alarming the fish, experiments were designed to examine the feasability of isolating them from the observer. There were inevitably instances when the experimenter needed access to the tanks for the introduction of prey etc. and this had to be considered whilst designing the methods of such experiments. Two designs were tested. First, a screen was positioned between the tank and the observer. Without the screens in place, the fish became used to the experimenter and after a while did not respond to his presence. With the screens in place, however, this did not seem to occur. In fact, the fish reacted with even more alarm to any slight vibrations or visual disturbance. Clearly this was no solution to the problem. A second attempt to solve the problem was made by enclosing the tanks in black polythene so that the fish could not see out at all. Mirrors were positioned above the tanks inclined at an angle so that the fish could be observed. Total enclosure of the tanks in this way completely inhibited feeding (data not included) and was clearly not a suitable solution either.

On balance it was decided that the experiment should be performed without any isolating mechanism, relying on the fishes' tendency to be less alarmed as they became accustomed to the observer. During the 5 days acclimation period before the fish were used in experiments they were exposed to the observer's presence whilst being fed and the tanks were positioned so that the fish could see the experimenter going about his work. By these means sufficient fish were ready after 5 days to feed well enough so that data could be collected to study their feeding tactics.

Two different size groups of brill and turbot were selected for observations on mysids and shrimps. Larger fish were used to observe

feeding behaviour on shrimps so that more prey could be consumed in a session without the fish becoming quickly satiated. Table 2 shows the mean, size range and standard deviations of the groups of fish used for the different prey organisms.

Each feeding session consisted of 30 minutes of continuous observation of a single fish feeding on a particular prey type. The session began when prey were introduced into the experimental enclosure. At the onset, the experimental tank was stocked with 50 prey organisms (but only 10 in the case of shrimps which were considerably larger than the other prey types) and a commentary was given on the behaviour of fish in terms of the behavioural elements described in section 3. The commentary was recorded onto magnetic tape using a portable cassette recorder. The click of a stopwatch started at the beginning of the session was taken as a reference point for the beginning of the session when played back. As prey organisms were consumed, replacements were added until 30 minutes had elapsed.

At playback the elements of behaviour were written onto character punch sheets and then transferred on to data cards. At the onset of each new element of behaviour, the elapsed time from the beginning of the session was noted. Shown below is an example of the data collected over 30 seconds in one session:

CR	SP	TN	SK	AR	LG	MS	TN	SF	PS
8:57	9:03	9:12	9:14	9:16	9:17	9:18	9:19	9:24	9:26

The top line is the element code, the lower line is the elapsed time from the onset of the session in minutes and seconds. Each element begins at the time value stated and continues until the next element begins.

Once punched on the data cards, this information for all the

Table 2 The size characteristics of fish used for observations of feeding tactics on various prey organisms.

Fish species	Prey organism	SIZE OF FISH Mean(cm)	St. dev.	Range(cm)	Number of sessions
Turbot	Mysids	12.0	0.64	10.9 - 13.0	10
	Shrimps	20.8	1.16	19.1 - 22.7	8
Brill	Mysids	11.5	0.75	10.4 - 12.7	20
	Shrimps	20.2	0.95	19.0 - 22.5	17
Z. punctatus	Mysids	12.4	1.68	10.1 - 15.5	11
	Gammarids	13.1	2.76	10.1 - 15.5	3
P. regius	Mysids	9.8	0.98	8.1 - 11.1	9
	Gammarids	9.8	1.53	8.1 - 11.1	3
Plaice	Enchytraeid worms	10.4	0.49	9.8 - 11.1	5
	Corophiids	11.4	0.99	10.4 - 13.3	8
Flounder	Enchytraeid worms	10.3	0.78	9.5 - 11.5	6
	Corophiids	10.8	1.64	8.7 - 12.2	4
Sole	Enchytraeid worms	18.1	1.84	14.8 - 21.6	19

sessions was analysed by several Fortran computer programmes written by the author (see Appendices 10, 11 & 12). The behavioural analysis was based on 51,000 paired data values. The objectives of the analysis were 1) to describe the sequential relationships between the behavioural elements for each species of flatfish in order to define the feeding strategies 2) to provide a means of comparing and contrasting the differences in feeding strategies of the seven species 3) to investigate the effect of prey type on the feeding behaviour and 4) to provide a means of assessing the effectiveness of food cues and models presented to the fish in the later experimental work.

3. THE ELEMENTS OF FEEDING BEHAVIOUR

The behaviour of a fish, or any organism, consists of a series of integrated motor patterns. In a behavioural study the degree of resolution can be made at any level of complexity that seems appropriate to the objectives of the work. In order to describe the feeding behaviour of flatfish the degree of resolution should be such that distinct units of behaviour can be recognised visually. Each unit or element of behaviour consists of a series of motor patterns which when combined together are recognised as discrete acts. Elements of behaviour are themselves ordered into a temporal sequence of events by which the fish perceive and procure food.

Forty-eight elements of behaviour have been recognised for the seven species of flatfish under consideration. Thirty-two are simple elements which occur singly and the remaining sixteen are complex, being formed from two of the simple elements occurring simultaneously. The elements are described below.

TURN (TN) - Fish, on the substratum, changes the direction of the body axis by between 0 - 90° (see Fig. 9). No distinction has been made between left and right turns.

SWIVEL TURN (SV) - Fish, on the substratum, changes the direction of the body axis by more than 90° (see Fig. 9). Again no distinction has been made between left and right turns.

TURN AWAY (TA) - Fish, on the substratum, changes the direction of the body axis by between 0 - 90° and in so doing turns away from a potential prey organism.

LEAVE (LV) - Fish, on the substratum, does not continue to pursue the prey stimulus. This is more of a comment from the observer than a true element of behaviour. Leave is usually associated with a PAUSE or

FIGURE 4 ARC PERFORMED BY TURBOT

A - INITIALLY THE ANTERIOR OF THE BODY IS LIFTED UP FROM THE SUBSTRATUM TOWARDS THE PREY, THIS PATTERN IS SIMILAR TO THE ELEMENT CALLED HEAD-RAISE.

B - THE WHOLE BODY IS PROPELLED UPWARDS TO CAPTURE THE PREY, THEN FLEXES DOWNWARDS TO RETURN TO THE SUBSTRATUM AFTER CAPTURE.

A

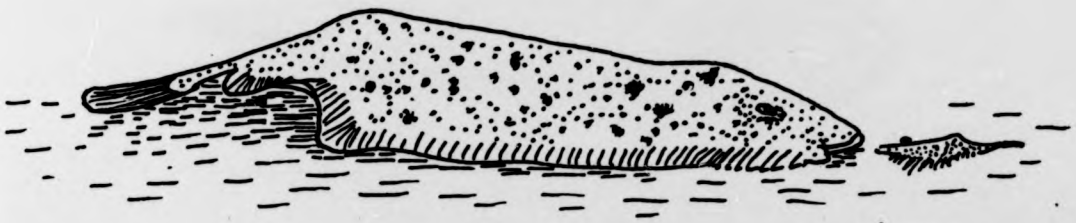
B

FIGURE 5 ARCH & LUNGE PERFORMED BY TURBOT

A - ARCH SEEMS TO REPRESENT A TENSING OF THE BODY MUSCULATURE IN PREPARATION FOR PREY ATTACK.

B - THE FISH LUNGES FORWARD VERY RAPIDLY WITH THE LARGE MOUTH FULLY EXTENDED TO CAPTURE THE PREY.

A



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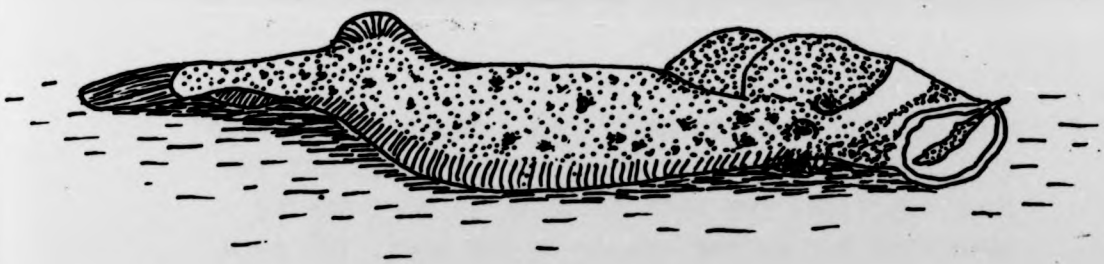


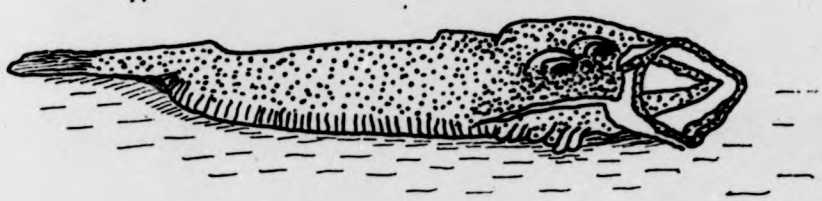
FIGURE 6 YAWN & ARCH PERFORMED BY BRILL.

A - YAWNING OCCURS IN ALL SPECIES OF FLATFISH STUDIED AND SEEMS TO BE ASSOCIATED WITH A TONING OF THE BODY PRIOR TO PERFORMING ACTIVITY. THE MOUTH IS OPENED WIDELY FOR THREE OR FOUR SECONDS.

B - ARCHING PERFORMED BY BRILL HAS A SLIGHTLY DIFFERENT APPEARANCE TO THAT OF TURBOT, ALTHOUGH IT HAS THE SAME FUNCTION. THE ARCH OF BRILL IS MORE GENTLE INVOLVING THE ENTIRE LENGTH OF THE BODY. THE ARCH OF TURBOT INVOLVES ONLY THE POSTERIOR PORTION OF THE BODY (COMPARE WITH FIGURE 5A).

C - BRILL ARCHING, VIEWED FROM THE REAR.

A



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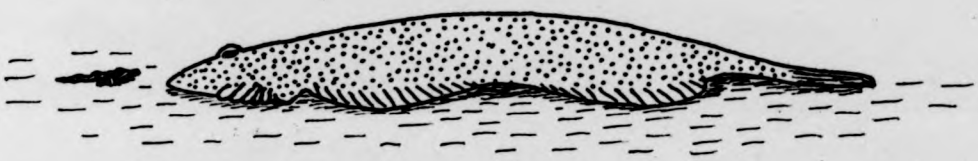


C

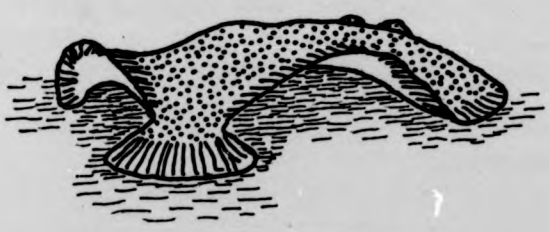


FIGURE 7 PAUSE, FORWARD & ARCH PERFORMED BY PLAICE.

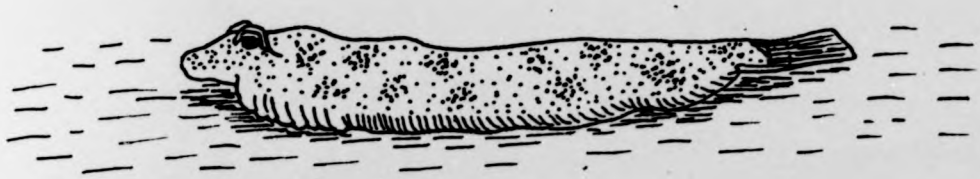
A - WHEN ALERT AND ENGAGED IN FEEDING PLAICE PAUSE IN A POSITION CHARACTERISTIC OF ALL PLEURONECTIDS, WITH THE HEAD HELD ABOVE THE SUBSTRATUM SUPPORTED BY THE ANTERIOR PORTIONS OF THE DORSAL AND ANAL FINS. IN THIS POSITION PLAICE COMMAND A GOOD VIEW OF THE SURROUNDING SUBSTRATUM ENABLING THEM TO LOCATE PREY.

B - PREY HAS BEEN LOCATED AND APPROACHED. THE FISH PAUSES BEFORE MAKING AN ATTACK.

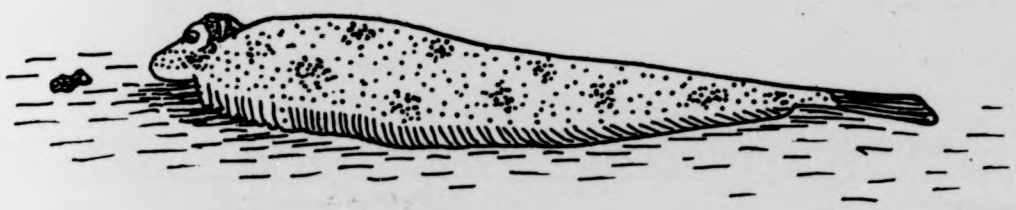
C - THE TYPICAL ELEMENT OF ATTACK EXHIBITED BY THE PLEURONECTIDS IS FORWARD. THIS IS EQUIVALENT IN FUNCTION TO THE LUNGE OF THE BOTHIDS, ALTHOUGH IT IS NOT AS RAPID. THE SMALL PROTRUSIBLE MOUTH IS BROUGHT DOWN ONTO THE PREY SO THAT IT CAN BE SUCKED UP. COMPARISON WITH FIGURE 5B ILLUSTRATES THE DIFFERENCE BETWEEN PREY CAPTURE IN THE BOTHIDS AND THE PLEURONECTIDS.

D - ARCHING BY PLAICE INVOLVES ONLY THE ANTERIOR OF THE BODY (COMPARE WITH FIGURES 5A, 6B & 6C). ARCHING BY PLAICE IS NOT SUCH A COMMON ELEMENT AS IT IS BY THE BOTHIDS. ARCHING IN THIS WAY IS WELL SUITED TO SNATCH UP PARTIALLY BURIED RELATIVELY IMMOBILE PREY.

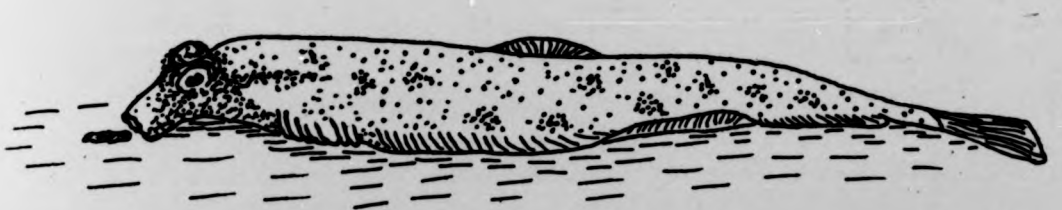
A



B



C.



D

FIGURE 8 PALPATION & BITE PERFORMED BY SOLE.

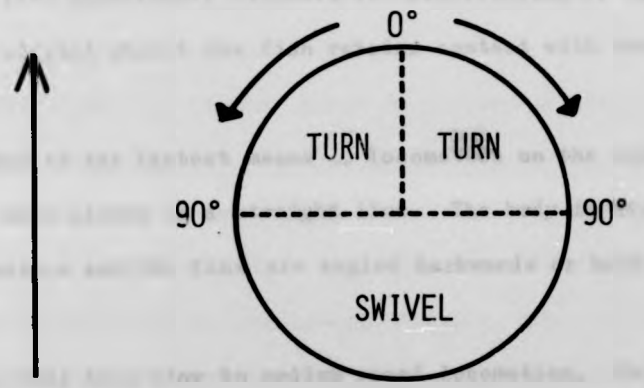
A - SOLE LOCATE THEIR FOOD BY SMELL AND TOUCH. PALPATION DESCRIBES THE INVESTIGATION OF POTENTIAL PREY BY THE VILLIFORM PAPILLAE LOCATED ON THE BLIND SIDE OF THE HEAD.

B - IF THE PREY IS RECOGNISED AS FOOD THE SOLE GRASPS IT BY A SWIFT DOWNWARD MOVEMENT OF THE HEAD WITH THE MOUTH OPEN, FOLLOWED BY AN UPWARD JERK OF THE HEAD. PRESUMABLY THIS UPWARD JERK IS AN ADAPTATION IN THE FEEDING BEHAVIOUR TO EXTRACT A WORM FROM ITS BURROW.

A

B

FIGURE 9 AN ILLUSTRATION OF THE DIFFERENCE BETWEEN TURN AND SWIVEL.



a TURN AWAY.

PALPATION (PP) - Fish, on the substratum, pushes its head down onto the substratum and appears to be sensing for the presence of food. This element of behaviour is only exhibited by soles, see Fig. 8A.

SWIM (SW) - The conventional method of propulsion by fish through the water column. There is never any contact with the substratum.

DOWN (DN) - The fish comes to rest on the substratum after activity in the water column. This element terminates all the elements in which the fish is not in contact with the substratum.

The next five behavioural elements are descriptions of the methods of locomotion adopted whilst the fish retains contact with the substratum:

SKIM (SK) - This is the fastest means of locomotion on the substratum. It is a rapid dart always in a straight line. The body is held in a streamlined posture and the fins are angled backwards or held flat to the body.

SHUFFLE (SF) - This is a slow to medium speed locomotion. It can vary between the fish almost 'hopping' along the substratum to seemingly 'walking' on its lateral fins. There is a sharp distinction between SHUFFLING AND SKIMMING because the body and fins are used in a different manner. While shuffling the head is held above the substratum and the whole impression from watching this behaviour is of unhurried, wandering locomotion. This is the most common form of locomotion in flatfish and is usually associated with searching for prey organisms. The speed of movement has an upper limit of about 10 cm per second compared with a SKIM, which would have a lower limit of about 15 cm per second. During SHUFFLING the eyes move independently scanning the environment.

CREEP (CR) - In contrast to SHUFFLE this behaviour gives an impression of extreme intensity of purpose and is always associated with stalking prey. At its fastest it would not exceed 1 cm per second but commonly it would be of the order of 1 mm per second, and sometimes movement becomes almost imperceptible. While CREEPING, the head is brought right down onto the substratum and both eyes are fixed on the prey.

FORWARD (FD) - This is a very brief forward movement whilst the fish is on the substratum. By definition it does not exceed half a body length in distance travelled; if it did it would become a SHUFFLE. It is characteristic of pleuronectids and can often have an equivalent function to LUNGE, that is, to move the fish forward to grasp the prey, see Fig. 7C.

REVERSE (RV) - Reverse moves the fish backwards and in appearance is somewhere between a backwards CREEP and a very slow SHUFFLE. The fish appears to 'walk' backwards on its lateral fins.

PAUSE (PS) - The fish ceases what it was doing and remains inactive on the substratum.

The next four behavioural elements are probably aberrations caused by the artificial tank environment:

SETTLE (ST) - Settle is equivalent to DOWN with the difference that the fish comes to rest on a vertical wall of the tank.

FLAP (FP) - The body and fins move as if the fish were swimming by flapping movements but the fish's snout is pressed against the wall of the tank and it remains in contact with the substratum.

FLAP-SWIM (FS) - This is another particular aberrant form of behaviour. It is like a FLAP only the fish does not remain on the substratum, but lifts itself into the water column. The only explanation that can be

offered to account for FLAP and FLAP-SWIM is that because the fish can see through the tank walls, which are clear perspex, it persistently tries to swim or move thrcugh them but of course it cannot.

UNDULATE (UN) - Undulation of the body is a form of behaviour observed only in sole. It is performed either when the fish is on the substratum or while it adheres to a vertical wall of the tank. Undulation of the body begins at the head and travels to the tail and during the process the fish remains in contact with the base on which it was resting. When the base is a vertical tank wall the behaviour may help the fish to retain its vertical position.

BURY (BY) - Flatfish are well adapted in colouration and morphology to lie still in the sand when alarmed or in danger and to be almost totally inconspicuous. Their natural cryptic appearance is complemented by their behaviour of burying themselves in the sand, a process which Kruuk (1963) described as "digging-in" behaviour. Burying is brought about by a rapid beating of the body downwards on the substratum so that the water currents waft sand from beneath the body up onto the dorsal surface. The body movement may last up to 2 seconds but the state of being buried may last seconds, minutes or hours. In this description it was not felt necessary to distinguish between the body activity and the resultant quiescent state. BY, when referred to, begins with the body activity, includes the period of inactivity and terminates when the fish carries out its next action.

YAWN (YN) - Yawning has been thoroughly investigated in the Jewel fish, Microspathodon chrysurus, by Rasa (1971). In flatfish a YAWN is a slow, purposeful protrusion of the jaw apparatus (see Fig. 6A); the head and tail are elevated slightly from the horizontal plane giving the body a bowed appearance. Flatfish do not stretch their fins to the extent that

Rasa describes for the Jewel fish. Further comment on yawning will be deferred until the discussion.

OMEGA JUMP (JP) - The omega jump is a behaviour characteristic of sole. It has been fully described by Kruuk (1963) who presents a series of photographs describing stages of behaviour. The jump usually occurs as sole emerge from the sand. Initially the head is lifted and then the tail is raised so that the body forms a U shape, remaining in contact with the substratum in the middle. A powerful down beat of the tail is followed by a downwards movement of the head propelling the body forwards and upwards into the shape of the Greek letter omega. The fish finally lands on the substratum completely uncovered.

Next come nine behavioural elements that are always associated with feeding:

BODY ARCH (AR) - This behaviour occurs prior to attack, especially in the bothids. The head is lowered and the dorsal and anal fins are braced against the substratum ready to push when the moment for attack is appropriate. The midline of the body is arched, supported by the dorsal and anal fins, and the cavity formed between the body and the substratum presumably aids in giving the fish forward thrust for its attack. The angle and amount of body that is arched differ slightly between species, but they all share a common recognisable appearance and the function seems to be the same, see Figs 5A, 6B and 6C.

Although pleuronectids have been seen to use the above posture when feeding on mobile prey, they sometimes perform a different form of ARCH. The front end of the body is raised up from the substratum whilst the tail remains in contact with it. The whole body is arched so that the head makes an angle of 50 - 60° with the substratum, see Fig. 7D. The attack is made from this position after one or two

seconds by bringing the head directly down onto the prey. This type of BODY ARCH seemed to be particularly well-suited to 'browsing' on sedentary worms that were partly emerged from the sand.

BODY RELAX (RX) - Body relax is the reverse of BODY ARCH and is the process of relaxation by which the body reverts to a more relaxed posture.

ARC (AC) - The fish propels itself into the water column describing a profile similar to a 'normal' curve (as in the statistical sense). At the peak of the curve, the fish attacks a prey organism and then returns to the substratum. The peak of the ARC is usually between 4 - 10 cm off the bottom. This behavioural element is confined to brill and to a lesser extent turbot (see Fig. 4).

HOVER (HV) - This occurs when the fish is poised motionless in the water column. It can occur at any height above the substratum. It usually occurs when the fish is selecting a prey organism to attack.

LUNGE (LG) - Lunge is the final element in a feeding sequence and represents the attack stage. The fish gives a vigorous thrust with its tail and moves forward very rapidly. As this occurs the jaw apparatus opens the mouth into a protrusible tube; this action creates a partial suction and, coupled with the forward motion of the fish, sucks the prey organism into the buccal cavity, see Fig. 5B.

BITE (BT) - Bite describes the successful ingestion of the prey into the buccal cavity, see Fig. 8B.

MISS (MS) - In some instances the prey escapes being engulfed by the fish. The result of such a sequence is a MISS.

CHEW (CW) - This element is a repeated opening and closing of the jaw apparatus. Although it appears to an observer similar for all the species, it probably has differing functions depending on the species

concerned. The jaw adaptions and positions and the nature of the teeth vary considerably between the species. Chew is probably either for mastication or for swallowing prey, but further comment upon its function will be deferred until the discussion of results.

SPIT (SP) - Spit occurs if the food particle is too large or otherwise unsuitable for swallowing. Sometimes the food is taken back into the buccal cavity after a spit in a further attempt to consume it. On other occasions the particle is disregarded as if the fish did not find it palatable.

HEAD RAISE (HR) - The head is raised up from the substratum while the tail and body remain flat. The head can be angled up to 80^{o} from the horizontal, see Fig. 4A.

HEAD LOWER (HL) - Head lower can be either the reverse of HEAD RAISE, returning the body to a more normal posture where the head is held very slightly above the substratum supported by the body musculature, the anterior portions of the dorsal and anal fins and the blind side pelvic and pectoral fins, or if the body was already in this posture, head lower can be the lowering of the head right onto the substratum.

QUIVER (QV) - This is a rare form of behaviour in topknots occurring whilst the fish are stalking prey. It is the anterior portions of the dorsal and anal fins that tremble and quiver.

The remaining sixteen behavioural elements are composites of two of the elements described above occurring simultaneously. They need very little extra description because all of the separate parts have already been described. There are eight types of complex behaviour including SWIM as one of the components:

SWIM-TURN (STN)

SWIM-TURN AWAY (STA)

SWIM-LEAVE (SLV)

SWIM-LUNGE (SLG)

SWIM-BITE (SBT)

SWIM-MISS (SMS)

SWIM-CHEW (SCW)

SWIM-YAWN (SYN)

The purpose of these complex elements is to differentiate between activities that occur in the water column and on the substratum.

ARCH is a body posture that often has a long duration and there are six elements that have been seen to occur whilst ARCH is in progress. They are:

CREEP-BODY ARCH (CAR)

TURN-BODY ARCH (TAR)

ARCH-TURN AWAY (ATA)

ARCH-REVERSE (ARV)

ARCH-HEAD RAISE (AHR)

ARCH-HEAD LOWER (AHL)

The remaining two complex behaviours are:

REVERSE-CHEW (RCW)

HEAD RAISE-CHEW (HCR)

4. RESULTS AND DISCUSSION

There are numerous different ways of analysing series of behavioural elements. This section compares and contrasts the feeding tactics adopted by the seven species of fish investigated. It deals with the gross differences between species and with those within a species as it feeds on different types of prey organisms. Table 2 (page 22) gives details of the thirteen different feeding trials, each involving one flatfish species and one prey species.

For convenience, the analysis of the data has been divided into eleven subsections. The early sections deal with the frequencies of performance and the duration of the behavioural elements. The final four sections deal with prey capture efficiency, analysis of the elements immediately prior to attack, transition probability and behaviour flow charts.

4.1. Comparison of the proportions of the main categories of behaviour performed by the families.

One of the main behavioural features of all flatfish is that they spend a large proportion of their time in contact with the substratum. When they are active their behaviour may be defined as on or off the bottom. This section compares the proportion of behaviour spent in these broad categories, namely inactivity, activity on the bottom and activity off the bottom. It attempts to describe the differences between families. The analysis of the data was therefore designed to provide answers to the following questions: 1) What proportion of the behaviour consists of active elements, opposed to inactive ones? 2) What proportion of the active elements are performed on the bottom? Both questions may be answered in terms of the relative frequencies and durations of the behavioural elements. Frequencies and durations are expressed as percentages. For example, the percentage frequency figure for activity was calculated as:

$$\frac{\text{Number of active elements per trial}}{\text{Total number of elements in trial}} \times 100$$

and the percentage duration figure for activity as:

$$\frac{\text{Time active per trial}}{\text{Total time of trial}} \times 100$$

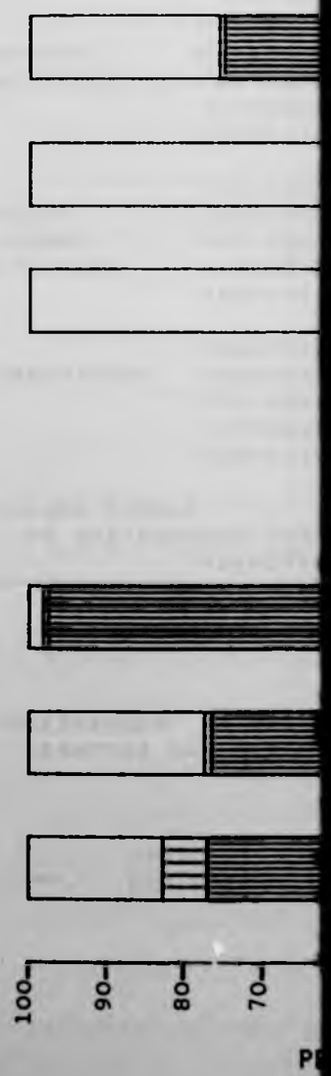
Figure 10 summarises the results. The frequencies of elements comprising behavioural categories were analysed statistically using a multi-way chi-squared test (Table 3). A parametric two-way analysis of variance would have been a concise means of analysing the durations of the behavioural categories but unfortunately the data did not fulfill the necessary criteria for this procedure. Instead the more cumbersome approach of testing categories separately between test groups by a Kruskal-Wallis analysis of variance was adopted and the

FIGURE 10 PERCENTAGE FREQUENCY HISTOGRAMS SHOWING THE PARTITIONING OF BEHAVIOURAL CATEGORIES BASED ON FREQUENCIES AND DURATIONS OF ACTIVITY WITHIN AND BETWEEN FAMILIES.

KEY TO FIGURE

SD - SOLEIDS / DURATION ANALYSIS
PD - PLEURONECTIDS / DURATION ANALYSIS
BD - BOTHIDS / DURATION ANALYSIS

SF - SOLEIDS / FREQUENCY ANALYSIS
PF - PLEURONECTIDS / FREQUENCY ANALYSIS
BF - BOTHIDS / FREQUENCY ANALYSIS



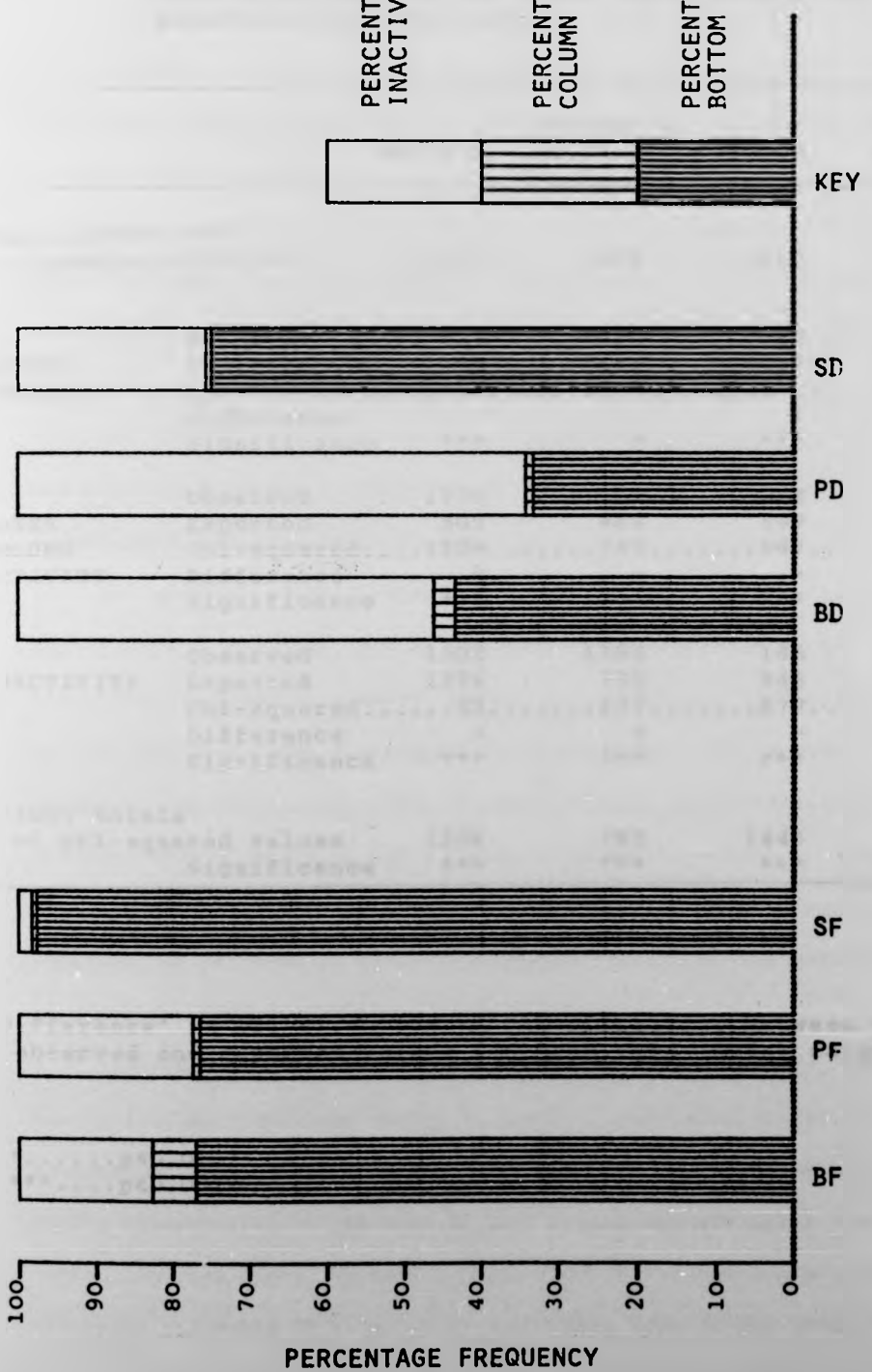

PERCENTAGE INACTIVITY
PERCENTAGE WATER COLUMN ACTIVITY
PERCENTAGE BOTTOM ACTIVITY
KEY
SD
PD
BD
SF
PF
BF
100
90
80
70
60
50
40
30
20
10
0
PERCENTAGE FREQUENCY

Table 3 A statistical comparison of the differences between the flatfish families for the frequencies of elements comprising each of the three broad categories of behaviour (see Fig. 10).

		Bothids	Pleuro-nectids	Soleids	Row Totals
Total number of elements exhibited		11078	6376	8210	25664
BOTTOM ACTIVITY	Observed	7819	5010	8012	20841
	Expected	8996	5178	6667	20841
	Chi-squared	154	5	271	430
	Difference	-	-	+	
	Significance	***	*	***	***
WATER COLUMN ACTIVITY	Observed	1750	64	52	1866
	Expected	805	464	597	1866
	Chi-squared	1109	345	497	1951
	Difference	+	-	-	
	Significance	***	***	***	***
INACTIVITY	Observed	1509	1302	146	2957
	Expected	1276	735	946	2957
	Chi-squared	43	437	677	1157
	Difference	+	+	-	
	Significance	***	***	***	***
Column totals of chi-squared values		1306	787	1445	3538
	Significance	***	***	***	***

'Difference' is the direction of the difference between the observed and expected values for each behavioural category

*.....$p<0.05$
***....$p<0.001$

differences between categories within groups were tested by a Friedman two-way analysis of variance.

The frequencies of performance of all behavioural categories differed significantly between families ($p \ll 0.001$, Table 3). Within all families the performance of behavioural categories also differed significantly ($p \ll 0.001$). Bothids perfomed more water column activity ($p \ll 0.001$), more inactivity ($p \ll 0.001$) but less bottom activity ($p \ll 0.001$) than expected. Pleuronectids performed more inactivity ($p \ll 0.001$) but less water column activity ($p \ll 0.001$) than expected. Pleuronectid bottom activity was only slightly less than expected ($p < 0.05$). Soleids performed more bottom activity ($p \ll 0.001$) but less water column activity ($p \ll 0.001$) and less inactivity ($p \ll 0.001$) than expected.

The duration of performance of inactivity between families was highly significant ($p < 0.001$) as was that of bottom activity ($p < 0.001$). Water column activity, however, showed no significant difference between families. The discrepancy in significance between the frequency and duration of water column activity can be explained by the fact that elements of water column activity are large in frequency for bothids but relatively short in duration. Within all families the durations of performance of water column activity, bottom activity and inactivity differed significantly ($p < 0.001$).

Although these results represent very broad differences, they are nonetheless important and should be borne in mind when comparing and contrasting the behaviour of the three families. The differences are partly attributable to the type of prey organisms upon which the various species feed. Whereas bothids feed on fast-moving prey in mid-water and would be expected to spend more time in the water column,

at the other extreme soleids feed on slow-moving benthic organisms and have little need to leave the bottom to feed. Also bothids feeding on active prey would be expected to spend more of their feeding activities in pursuit of the prey than would the pleuronectids whose prey are considerably slower moving. Soleids, too, spend much time engaged in active searching rather than in pursuit of prey like the bothids, presumably because their olfactory method of prey location restricts their range of detection.

4.2. Comparison of the proportions of the main categories of behaviour performed by the species.

This section looks in more detail at the differences between species within the families. The data was analysed using the statistical methods described in the previous section and Table 4 gives the results of this analysis. Clearly water column activity, bottom activity and inactivity are all highly significantly different between feeding trials. The variation between the observed and expected frequencies of the behavioural categories within trials as well as the levels of significance are clearly indicated in Table 4 and need no further comment. In all cases the frequencies of the three behavioural categories are highly significantly different within feeding trials.

The statistical analysis of the behavioural categories within and between feeding trials with respect to durations of activity are shown in Table 5. Most of the comparisons show a high level of significance.

The results of the statistical analysis on frequencies and durations of activity of the behavioural categories within and between feeding trials gives strong support to the conclusions set out in the following discussion.

Bothids

How do the tactics of the four bothid species differ when feeding on mysids? Activity/inactivity partitioning for frequencies and durations shows that turbot are markedly different from brill and the two species of topknots (Figs. 11 and 12). Turbot spent more of their time active than the other three species, but it was the high proportion of water column activity which really set turbot apart from the other three species. Turbot are highly active in the water column

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Bothids

How do the tactics of the four bothid species differ when feeding on mysids? Activity/inactivity partitioning for frequencies and durations shows that turbot are markedly different from brill and the two species of topknots (Figs. 11 and 12). Turbot spent more of their time active than the other three species, but it was the high proportion of water column activity which really set turbot apart from the other three species. Turbot are highly active in the water column

Table 4 A statistical comparison of the differences between feeding trials for the frequencies of elements comprising each of the three broad categories of behaviour (see Fig. 11).

		TM	TS	BM	BS	ZPM	ZPG	PRM	PRG	PW	PC	FW	FC	SW	TOTAL
Total No. of elements		4740	1274	1640	905	1092	86	1171	170	2534	1878	454	1510	8210	25664
BOTTOM ACTIVITY	O	2731	1005	1305	694	890	62	987	145	2392	1282	355	981	8012	20841
	E	3849	1035	1332	735	887	70	951	138	2058	1525	369	1226	6667	20841
	C	325	0.9	0.5	2.3	0	0.9	1.4	0.4	54	39	0.5	49	271	745
	D	-	-	-	-	+	-	+	+	+	-	-	-	+	
	S	***	ns	ns	ns	ns	ns	ns	ns	***	***	ns	***	***	***
WATER COLUMN ACTIVITY	O	1602	76	34	36	0	0	2	0	20	4	0	40	52	1866
	E	345	93	119	66	79	6	85	12	184	137	33	110	597	1866
	C	4580	3	61	14	79	6	81	12	146	129	33	45	497	5686
	D	+	-	-	-	-	-	-	-	-	-	-	-	-	
	S	***	ns	***	***	***	*	***	***	***	***	***	***	***	***
INACTIVITY	O	407	193	301	175	202	24	182	25	122	592	99	489	146	2957
	E	546	147	189	104	126	10	135	20	292	216	52	174	946	2957
	C	35	14	66	48	46	20	16	1.2	99	654	42	570	677	2288
	D	-	+	+	+	+	+	+	+	-	+	+	+	-	
	S	***	***	***	***	***	***	***	ns	***	***	***	***	***	***
CHI^2 TOTAL		4940	18	127	64	125	27	98	14	299	822	75	664	1445	8719
	S	***	***	***	***	***	***	***	***	***	***	***	***	***	***

Key to abbreviations: O - Observed, E - Expected, C - Chi^2 value, D - the nature of the difference between observed and expected values, S - the level of significance where ***.....$p<0.001$, *.....$p<0.05$, ns..... no significant difference at $p=0.05$.

Table 5 Statistical analysis of the behavioural categories within and between feeding trials with respect to durations of activity.

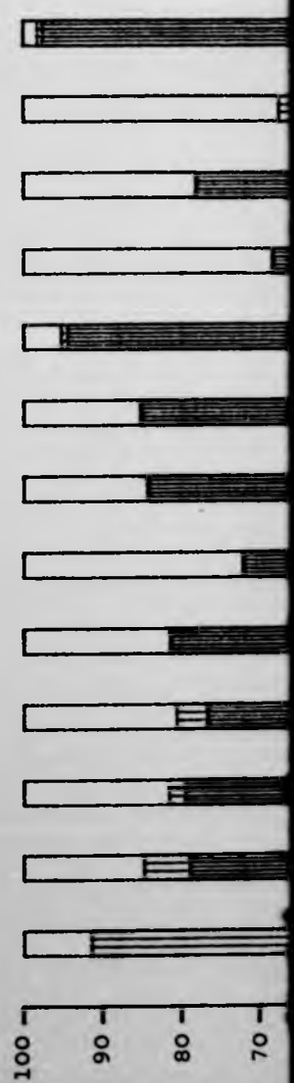
	Test group	Test statistic	Level of significance
Between trials	Water column activity	H=55.7	***
	Bottom activity	H=28.1	**
	Inactivity	H=33.3	***
Within trials	TM	Xr_2^2=14.6	***
	TS	Xr_2^2=12.2	***
	BM	Xr_2^2=25.8	***
	BS	Xr_2^2=27.1	***
	ZPM	Xr_2^2=12.0	**
	PRM	Xr_2^2=14.0	***
	PW	Xr_2^2= 6.3	ns
	PC	Xr_2^2=12.0	***
	FW	Xr_2^2= 4.0	ns
	FC	Xr_2^2= 8.0	**
	SW	Xr^2=21.3	***

ns.....no significant difference at p=0.05
**.....significant at p<0.01
***.....significant at p<0.001

FIGURE 11 PERCENTAGE FREQUENCY HISTOGRAMS SHOWING THE PARTITIONING OF BEHAVIOURAL CATEGORIES BASED ON FREQUENCIES OF ACTIVITY WITHIN AND BETWEEN FEEDING TRIALS.

KEY TO FIGURE

SW - SOLE / ENCHYTRAEID WORMS
FC - FLOUNDER / COROPHIIDS
FW / FLOUNDER / ENCHYTRAEID WORMS
PC - PLAICE / COROPHIIDS
PW - PLAICE / ENCHYTRAEID WORMS
PRG - P. REGIUS / GAMMARIDS
PRM - P. REGIUS / MYSIDS
ZPG - Z. PUNCTATUS / GAMMARIDS
ZPM - Z. PUNCTATUS / MYSIDS
BS - BRILL / SHRIMPS
BM - BRILL / MYSIDS
TS - TURBOT / SHRIMPS
TM - TURBOT / MYSIDS



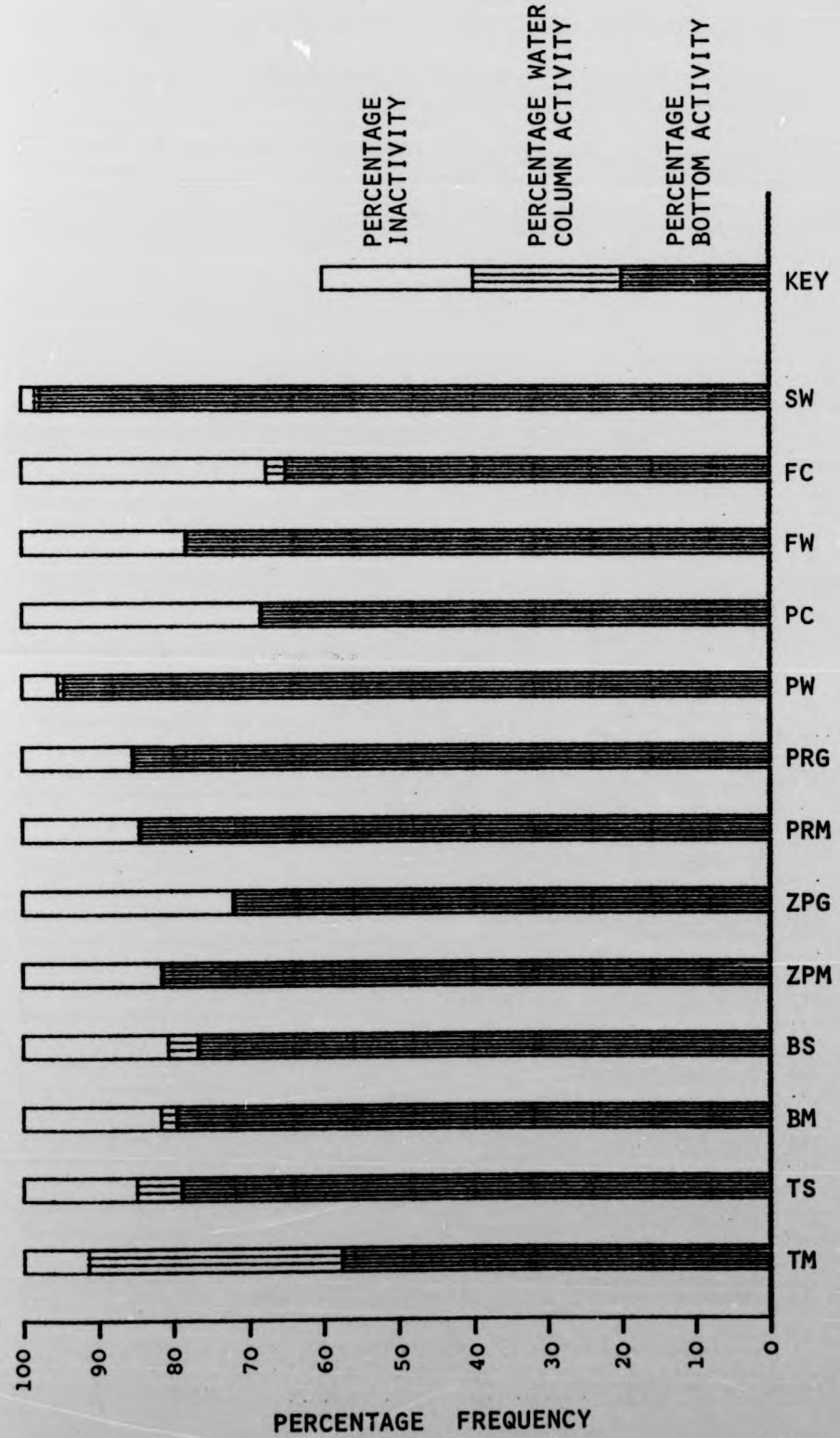
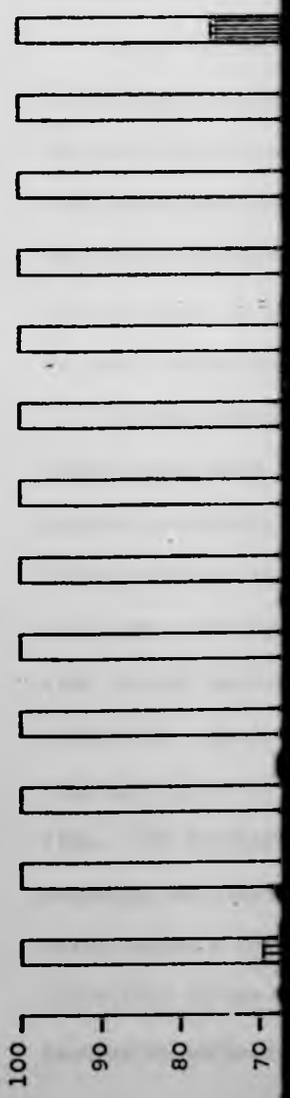
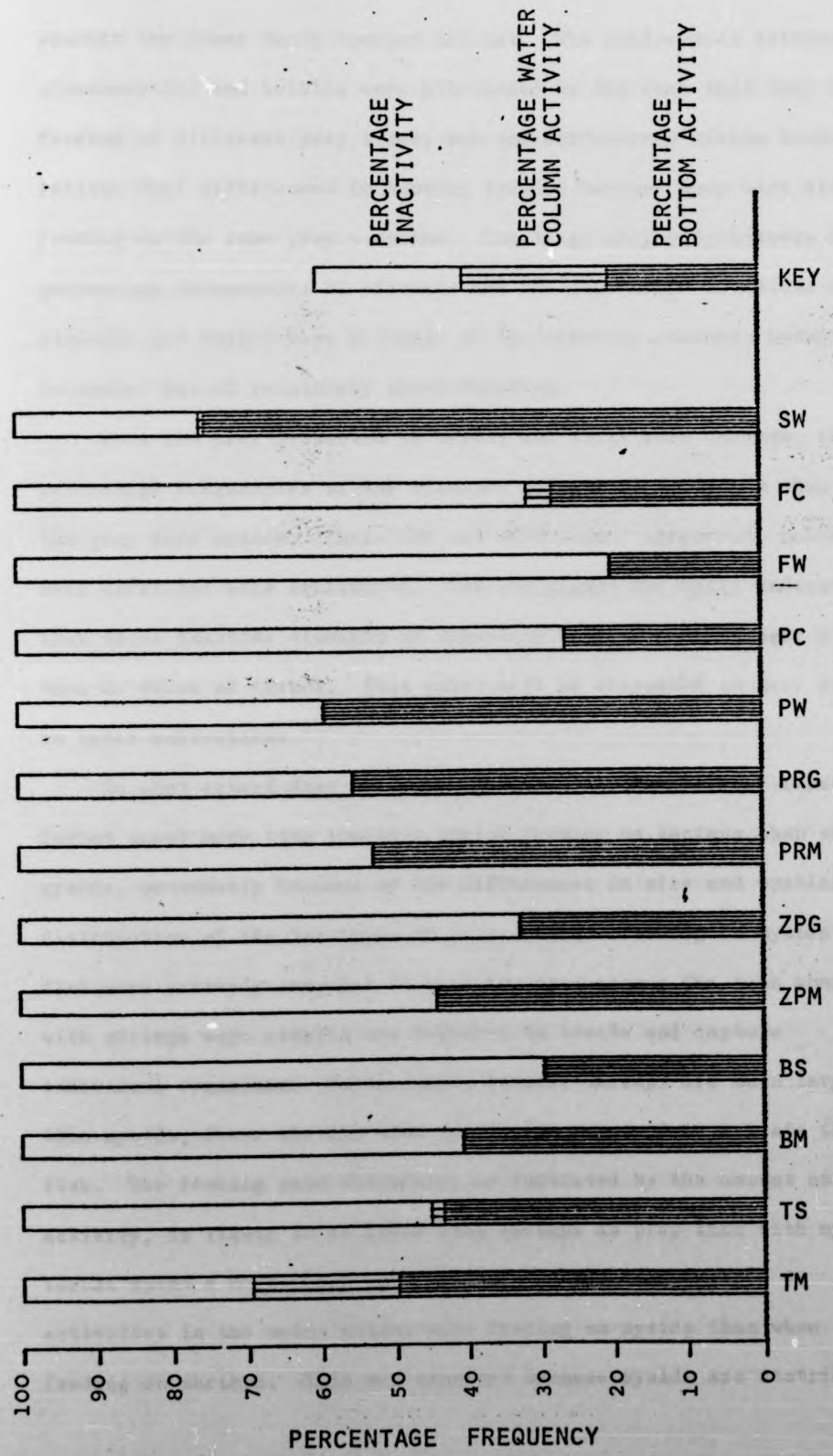

PERCENTAGE INACTIVITY
PERCENTAGE WATER COLUMN ACTIVITY
PERCENTAGE BOTTOM ACTIVITY
KEY
SW
FC
FW
PC
PW
PRG
PRM
ZPG
ZPM
BS
BM
TS
TM
100
90
80
70
60
50
40
30
20
10
0
PERCENTAGE FREQUENCY

FIGURE 12 PERCENTAGE FREQUENCY HISTOGRAMS SHOWING THE PARTITIONING OF BEHAVIOURAL CATEGORIES BASED ON DURATIONS OF ACTIVITY WITHIN AND BETWEEN FEEDING TRIALS.

KEY TO FIGURE

SW - SOLE / ENCHYTRAEID WORMS
FC - FLOUNDER / COROPHIIDS
FW - FLOUNDER / ENCHYTRAEID WORMS
PC - PLAICE / COROPHIIDS
PW - PLAICE / ENCHYTRAEID WORMS
PRG - P. REGIUS / GAMMARIDS
PRM - P. REGIUS / MYSIDS
ZPG - Z. PUNCTATUS / GAMMARIDS
ZPM - Z. PUNCTATUS / MYSIDS
BS - BRILL / SHRIMPS
BM - BRILL / MYSIDS
TS - TURBOT / SHRIMPS
TM - TURBOT / MYSIDS




PERCENTAGE INACTIVITY
PERCENTAGE WATER COLUMN ACTIVITY
PERCENTAGE BOTTOM ACTIVITY
KEY
SW
FC
FW
PC
PW
PRG
PRM
ZPG
ZPM
BS
BM
TS
TM
100
90
80
70
60
50
40
30
20
10
0
PERCENTAGE FREQUENCY

whereas the other three species are not. The differences between pleuronectids and bothids were attributed to the fact that they were feeding on different prey types, but the differences within bothids reflect real differences in feeding tactics because they were all feeding on the same prey - mysids. The large disparity between the percentage frequencies of elements and the percentage durations of elements for turbot were a result of the activity elements being high in number but of relatively short duration.

When the prey presented to turbot and brill were shrimps, the percentage frequencies of the elements matched more closely than when the prey were mysids. There was not such a good agreement, however, when durations were considered. The low figure for brill indicates that their inactive elements of behaviour tend to be of longer duration than do those of turbot. This point will be discussed in more detail in later subsections.

To what extent does the prey species alter the fishes' behaviour? Turbot spent more time inactive whilst feeding on shrimps than on mysids, presumably because of the differences in size and spatial distribution of the two types of prey. Whilst feeding on mysids the fish were actively enagaged in pursuing prey around the tank whereas with shrimps more stealth was required to locate and capture individual organisms. Furthermore, because shrimps are much larger than mysids, fewer shrimps than mysids are required to satiate the fish. The feeding rate therefore, as indicated by the amount of activity, is likely to be lower with shrimps as prey than with mysids. Turbot spent a much higher proportion of their time engaged in activities in the water column when feeding on mysids than when feeding on shrimps. This was expected because mysids are distributed

in the water column whereas shrimps are primarily bottom-dwelling organisms.

Brill, in contrast to turbot, although faced with the same problems of spatial distribution of their prey, showed much greater similarity in their behaviour towards the two prey types. The discrepancy between the element frequencies and element durations for the two prey types is because the inactivity elements have relatively low frequencies but long durations. Brill spent a small proportion of their activity in the water column, irrespective of prey type. Herein lies an important difference between turbot and brill. Brill rarely leave the bottom to feed even for organisms that live above the substratum. Their tactics involve lying in wait or stalking prey which come close to the bottom, whereas turbot leave the substratum and actively pursue their prey in mid-water.

The behaviour of the common topknot, Zeugopterus punctatus and Bloch's topknot, Phrynorhombus regius was very similar. When fed on mysids, most of the behavioural elements were performed on the bottom and about 50% of the time was spent inactive. Water column activity was almost non-existent, which is an important feature and in this respect the topknots are rather similar to brill. Topknots usually lie in wait and attack prey that come within range.

Pleuronectids

Plaice and flounder were each offered enchytraeid worms and corophiids. Their feeding tactics differed much more whilst feeding on worms than on corophiids. Plaice exhibited a very high frequency of bottom activity elements with a high proportion of their time spent in this form of activity. This pattern of behaviour contrasts with

that of flounders, which although exhibiting a high frequency of bottom activity only spent a small proportion of their time engaged in such. The reasons for these differences will be explained in a later subsection.

The major difference between plaice and flounder feeding on corophiids lay in the amount of water column activity exhibited by flounders. They were much more active in their pursuit of these fairly mobile prey organisms, often leaving the substratum to chase a swimming Corophium. Plaice on the other hand always remained on the substratum and did not pursue prey up into the water column.

The different behavioural attributes of the two prey types necessitates different tactics on the part of the two fish species. Both species performed more bottom activity elements when feeding on worms than when feeding on Corophium. Part of the reason for this was that individual worms were smaller than Corophium and more activity was required to obtain sufficient food. At the same time Corophium were more difficult to capture, requiring more complex hunting behaviour, and so they, too, elicited a large number of activity elements. Consideration of the duration of activity elements demonstrates another aspect of the problem. For plaice there was a greater discrepancy between the durations of elements performed in the capture of worms and corophiids than there was between the frequencies. The discrepancy arose because of the almost continuous browsing behaviour employed whilst feeding on worms. The larger biomass of corophiids probably played a part in this discrepancy too, less time being put into feeding activities if the prey was more filling. Flounders spent more time feeding on corophiids than on worms. This seems to invalidate the previous argument, but only if diet

preferences are not taken into consideration. Plaice are more 'worm feeders' than flounders, which usually choose more mobile prey, like crustaceans. It is far more likely, therefore, that the shorter time flounders spent feeding on enchytraeids was a result of diet preferences rather than hunting tactics.

Soles

Sole exhibited a very high frequency of bottom elements and a small amount of water column elements. The durations of the elements of inactivity were quite long, but sole performed a large number of short elements which may be the more pertinent way of viewing the time partitioning. Compared with other feeding trials on enchytraeid worms with plaice and flounder, sole performed higher frequencies of bottom activity elements. In terms of durations, sole spent much more time engaged in bottom activity than plaice or flounders and this was attributed to the mode of prey location. Sole are olfactorial feeders and therefore performed more elements and spent more time in prey location than the more visual feeders such as plaice and flounders.

Summary

In summary, this section has described how the fishes' behaviour may be divided into inactivity, bottom activity and water column activity. The relative proportions of these three types of behaviour were first compared between families and it was found that bothids participated in more water column activity than the other two families. Interspecific comparisons were made next and turbot were found to perform a much larger proportion of their activity in

the water column than all the other species. Other interspecific differences in the behaviour towards the same and different prey were described and partly explained. Disparities were often noted between the behaviour when measured in terms of frequencies and durations. The disparities were attributed to the elements of inactivity being low in relative frequency but long in duration and, conversely, those of activity being high in frequency but of short durations. Finally, it was apparent that the behavioural attributes of the prey species play an important part in modifying the hunting tactics of the predator; this will be emphasised further in later subsections which deal in detail with the separate elements of behaviour of the predators.

4.3. Comparison of the number of elements per feeding session within and between feeding trials.

The number of elements of behaviour within a feeding session was determined from the sum of the frequencies of the separate elements that occurred within the session. It is partly indicative of the activity within a session, because it measures the number of discrete behavioural acts, but it takes no account of durations of acts. A large number of elements within a session indicates an active fish but a low number of elements does not always indicate an inactive fish. For example, the fish may perform a small number of elements of behaviour within a session but the total time spent performing each act may be long, so the time spent engaged in activity may be comparable to a fish that performs a large number of acts each with a short duration.

Table 6 provides a comparison of the number of elements in each session of all feeding trials. For each feeding trial the mean and standard deviations were calculated. The pleuronectids and soleids performed large numbers of elements within their feeding sessions with mean values of 354 and 631 respectively - many more than the bothids with 159. This difference is attributed to the pleuronectids and soleids being more active foragers than the bothids. The bothids are more conventional hunters stalking and capturing prey by elaborate tactics but only performing relatively few behavioural acts. For a complete appreciation of the differences between the hunting tactics the durations of elements must be considered. Sections 4.2 and 4.5 deal with the durations of behavioural elements. The mean number of elements within a session were quite similar within the bothids with the exception of turbot feeding on mysids, where a high frequency

Table 6 A comparison of the number of elements in the sessions of all feeding trials.

Flatfish species	Prey species	Number of elements in each session	Mean	S.D.	Number of sessions
Turbot	Mysids	181, 504, 442, 586, 574, 463, 607, 298, 603, 482	474	140	10
Turbot	Shrimps	242, 172, 212, 195, 152, 69, 104, 128	159	58	8
Brill	Mysids	64, 131, 155, 49, 72, 110, 46, 36, 39, 87, 123, 54, 60 247, 145, 76, 146	96	56	17
Brill	Shrimps	11, 31, 31, 8, 90, 245, 108, 11, 63, 46, 45, 29, 54, 30, 69, 34	57	57	16
Z. punctatus	Mysids	20, 241, 148, 55, 47, 236, 172, 173	136	85	8
P. regius	Mysids	55, 13, 145, 167, 208, 121, 120, 207, 135	130	64	9
Plaice	Worms	224, 100, 492, 867, 808, 43	422	357	6
Plaice	Corophiids	219, 237, 283, 570, 239, 330	313	132	6
Flounder	Worms	297, 157	227	99	2
Flounder	Corophiids	445, 291, 496, 278	377	110	4
Sole	Worms	371, 372, 925, 648, 777, 646, 1153, 757, 94, 811, 584, 808,,264	631	292	13

of behavioural elements occurred in each session. The difference between turbot and the other three species of bothids when feeding on mysids is that turbot actively chase their prey whilst the other bothids stalk their prey. To some extent this pattern is also applicable when shrimps are the prey species; the comparison between turbot and brill shows that turbot performed many more elements per session than brill.

The standard deviations are large which is a result of a small sample size and a large mean. The standard deviations for the bothids are generally much lower than for the pleuronectids or soleids, which shows that the bothids were more consistent between individuals.

In order to test the means a one-way analysis of variance could be used but it makes the assumptions that the variances of the samples are the same and that the mean and variance are independent. A series of F tests were carried out to investigate the homogeneity between variances of the feeding trials. Whilst many of the pairs of comparisons showed variances which did not differ significantly at $p = 0.05$, about one third of the comparisons were significantly different. This finding coupled with the general appearance that the mean and variance were not independent led to the choice of a non-parametric test to compare the samples from the feeding trials. The non-parametric equivalent to the parametric one-way analysis of variance is the Kruskal-Wallis one-way analysis of variance test. In this test the actual values of the samples are replaced by their ranked values which are then used for computation. The number of elements within a session was found to be very different between feeding trials (Kruskal-Wallis one-way analysis of variance statistic $H = 66$, 10 D.F., $p \ll 0.005$). This result, however, was not very

illuminating because there were many variables to consider between feeding trials. More useful information was derived from choosing a specific prey type and assessing the difference between the responses made by particular predators. The number of elements within a session for all the bothids feeding on mysids was very different ($H = 23$, 3 D.F., $p \ll 0.005$). The significance of this result was attributed to the mean value for turbot being very much higher than for the other species because a test comparing brill, Z. punctatus and P. regius, showed that there was no significant difference ($H = 2.3$, 2 D.F., $p > 0.10$).

The number of elements per session was found to be not significantly different between plaice, flounder and sole feeding on enchytraeid worms ($H = 3.16$, 2 D.F., $p > 0.10$).

The number of elements within a session was compared between successive pairs of feeding trials using a Mann-Whitney U test. (The Mann-Whitney U test was preferred to the parametric Student's test for the same reasons that led to the choice of the Kruskal-Wallis test over the parametric analysis of variance.) Table 7 shows the results of Mann-Whitney U tests performed successively on all pairs of feeding trials. The table falls into three distinct regions:

1) Comparisons between bothid-bothid feeding trials
2) Comparisons between bothid-pleuronectid/soleid feeding trials
3) Comparisons between pleuronectid/soleid-pleuronectid/soleid feeding trials.

Comparisons between bothids showed that the number of elements in a session for turbot feeding on mysids was highly significantly different from all other bothid feeding trials. Tests on pairs of feeding trials involving mysids confirmed the foregoing conclusions

Table 7 A comparison of the number of elements in the session between all feeding trials using a Mann-Whitney U test.

Key to abbreviations used in the table

TM - turbot / mysids
TS - turbot / shrimps
BM - brill / mysids
BS - brill / shrimps
ZPM - *Z. punctatus* / mysids
PRM - *P. regius* / mysids
PW - plaice / enchytraeid worms
PC - plaice / corophiids
FW - flounder / enchytraeid worms
FC - flounder / corophiids
SW - sole / enchytraeid worms

ns.....no significant difference at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001

The numbers enclosed in parentheses are the degrees of freedom.

Table 7 A comparison of the number of elements in the session between all feeding trials using a Mann-Whitney U test.

	TS	BM	BS	ZPM	PRM	PW	PC	FW	FC	SW
TM	*** (8,10)	*** (10,17)	*** (10,16)	*** (8,10)	*** (9,10)	ns (6,10)	ns (6,10)	ns (2,10)	ns (4,10)	ns (10,13)

Table 7 A comparison of the number of elements in the session between all feeding trials using a Mann-Whitney U test.

	TS	BM	BS	ZPM	PRM	PW	PC	FW	FC	SW
TM	*** (8,10)	*** (10,17)	*** (10,16)	*** (8,10)	*** (9,10)	ns (6,10)	ns (6,10)	ns (2,10)	ns (4,10)	ns (10,13)
TS		** (8,17)	*** (6,16)	ns (8,8)	ns (8,9)	ns (6,8)	** (6,8)	ns (2,8)	*** (4,8)	*** (8,13)
BM			** (16,17)	ns (8,17)	ns (9,17)	ns (6,17)	*** (6,17)	* (2,17)	*** (4,17)	*** (13,17)
BS				* (8,16)	** (9,16)	** (6,16)	*** (6,16)	* (2,16)	*** (4,16)	*** (13,16)
ZPM					ns (8,9)	ns (6,8)	** (6,8)	ns (2,8)	** (4,8)	*** (8,13)
PRM						ns	*** (6,9)	ns (2,9)	** (4,9)	*** (9,13)
PW							ns (6,6)	ns (2,6)	ns (4,6)	ns (6,13)
PC								ns (2,6)	ns (4,6)	** (6,13)
FW									ns (2,4)	ns (2,13)
FC										ns (4,13)

from the Kruskal-Wallis tests that the number of elements within a session differed significantly between turbot and the other three bothids but that there was no significant difference between brill, Z. punctatus and P. regius. There was also a significant difference between turbot and brill feeding on shrimps.

These comparisons led to the conclusion that turbot perform a large number of behavioural acts whilst feeding, many more than the other bothids examined. This is independent of prey type.

All the bothid trials (excepting turbot/mysids) had significantly less elements per session than the pleuronectid trials on corophiids or the soleid trials on worms, $p<0.02$. Barring three exceptions, there were no differences between the bothid trials and the pleuronectids feeding on worms. There were also no significant differences between the turbot/mysid trial and any of the pleuronectid and soleid trials. Finally, with one exception, there were no differences between the pleuronectid and soleid feeding trials.

In summary there was a spectrum of the number of elements in the session. Brill occupied a position at the lowest extreme, then came the topknots, flounder, turbot, plaice and, at the largest extreme, sole. The number of elements in the session are dependent on feeding tactics of the predator and the behaviour and habits of the prey species.

4.4. Comparison of the percentage frequency of performance of the behavioural elements.

In subsections 4.1 and 4.2 elements of behaviour were grouped into broad categories in order to emphasise the main differences in hunting tactics between the seven species of flatfish. In this subsection, the relative frequency of the elements of behaviour will be studied in greater depth giving further insight into the nature of the differences for all the feeding trials. Frequencies and durations of elements will be considered separately, the latter being covered in section 4.5.

The actual frequencies of the elements can be found in Appendix 1. The number of elements recorded varied between feeding trials so that frequencies have been converted to percentages to facilitate comparison. The results are presented in Table 8.

4.4.1. Goodness of fit statistical tests on the observed element frequency distributions for each feeding trial.

The frequency distributions of the elements of behaviour between the feeding trials seem to differ considerably. This was tested statistically using the raw data given in Appendix 1 by means of a chi-squared goodness of fit test. Pairs of feeding trials were tested successively under the null hypothesis that there was no difference between their frequency distributions. The expected frequencies for each pair of feeding trials taken successively were calculated from the equation:

$$\text{Expected frequency of each cell} = \frac{\text{row total} \times \text{column total}}{\text{grand total}}$$

Table 8 A comparison of the percentage frequencies of behavioural elements between feeding trials

ELEMENT	TURBOT		BRILL		Z.PUNCTATUS		P.REGIUS		PLAICE		FLOUNDER		SOLE
	M	S	M	S	M	G	M	G	W	C	W	C	W
TN	22.72	19.23	13.90	19.12	15.39	22.09	14.09	22.35	22.38	17.73	18.28	20.93	8.81
SV		9.34	0.61	4.64	3.48	8.14	3.76	5.29		1.07	0.22	2.38	0.55
TA	0.11	0.08		0.66	0.55		0.26			0.05			
LV	0.08	0.24	0.98	0.33	2.02		1.54			0.11			0.01
PP													50.95
SW	10.95	2.90	0.06	2.43			0.17		0.32	0.16		0.53	0.20
DN	8.86	3.14	0.67	1.44					0.28	0.16		1.52	0.24
SK	3.14	3.38	0.37	1.88	0.09			0.59	0.12	1.86	2.20	2.91	0.04
SF	11.08	16.88	1.77	9.39	1.47	1.16	0.43	0.59	2.61	12.67	15.42	11.85	17.15
CR	0.61	1.96	14.21	12.38	14.56	10.47	15.97	19.41	0.32			0.07	
FD				0.11					9.98	11.24	12.78	6.82	0.01
RV		0.24	3.54	1.22	7.42	2.33	8.71	4.71	6.39	1.54	2.86	0.40	3.41
PS	8.52	15.07	18.23	18.67	18.50	27.91	15.29	14.71	3.59	30.67	21.15	31.66	1.43
ST							0.17						0.23
FS	1.18	0.86		0.22								0.99	0.24
BY	0.06	0.08	0.12	0.66			0.09		1.22	0.85	0.66	0.73	0.12
FP	0.23	1.33			0.09		0.09					0.07	0.01
UN													0.40
AR	0.08	4.95	5.37	3.76	0.73		0.94		0.99	0.32	0.44	0.33	
RX	0.06	2.04	1.83	1.55	0.92		0.57						
AC			0.67									0.13	
HV	2.76	0.24	0.06									0.07	
LG	2.81	4.32	10.55	4.42	8.70	1.16	9.22	3.53	1.26				
BT	2.55	3.14	9.02	3.20	7.78	1.16	7.94	3.53	24.11	9.27	19.38	6.82	8.69
MS	0.25	1.18	1.52	1.22	0.92		1.28			0.05			
CW	1.62	1.65	6.10	2.54	3.11		5.12	2.35	24.86	10.65	6.39	6.42	6.38
SP	0.06	0.47	0.18		0.18				0.04	0.53		0.27	0.17
HR	2.89	1.96	1.77	3.98	5.50	12.79	7.26	10.00	0.75	0.64	0.22	2.32	0.49
HL	0.25	0.31	0.85	0.33	4.03	11.63	3.67	8.24	0.32	0.37		1.19	0.13
YN	0.19	0.63			0.55	1.16	0.51	3.53				0.53	0.04
JP												0.07	0.12
STN	4.56	1.02		1.33					0.08			0.66	0.18
SLG	6.73	0.47	0.67						0.20				
SBT	5.93	0.31	0.43						0.20	0.05		0.27	
SMS	0.80	0.16	0.24										
STA	0.19											0.07	
SLV	0.34												
SCW	0.34												
RCW					0.46		0.26						
SYN	0.02												
QV					0.09		0.17						
CAR		1.88	4.94	4.20	2.38		2.14	0.59					
TAR		0.47	0.79	0.33	0.18		0.17						
ARV			0.12										
ATA		0.08											
AHL			0.31		0.55								
AHR			0.18		0.37		0.09						
HCR							0.17	0.59					

Key to column heading codes:
C-corophiids; G-gammarids; M-mysids; S-shrimps; W-enchytraeid worms.

If the expected frequency in either of a pair of cells for a particular element was less than 5, the element was omitted from the test. The number of degrees of freedom = (c - 1) (r - 1) where c is the number of columns (the total number of elements with an expected frequency greater than 5) and where r is the number of rows (= 2, because two trials were tested against each other). Table 9 shows the results of this series of tests. The chi-squared values were extremely high for most comparisons. In fact all but three of the comparisons were statistically different ($p \ll 0.01$) leading to a rejection of the null hypothesis in favour of the alternative that there was a difference in the frequency distributions of the elements between pairs of trials. The three comparisons that did not show this level of difference were between the two topknot species feeding on mysids and gammarids (both not significant at $p = 0.05$) and between brill/shrimps and Z. punctatus/gammarids which was significant at $p<0.05$ but which would probably have been more significantly different had there been more elements with expected frequencies greater than 5 upon which to perform the test.

Goodness of fit chi-squared tests were also performed between the three feeding trials involving worms (plaice, flounder and sole), between all feeding trials amalgamated into the categories of family (bothid, pleuronectid and soleid) and between the four feeding trials involving mysids (turbot, brill, Z. punctatus and P. regius). These tests were carried out using a comparable method to that described above. A significant difference was found between all the feeding trials involving worms as the prey (chi-squared = 4667, 14 D.F., $p \ll 0.01$) and between all the feeding trials involving mysids as prey (chi-squared = 4637, D.F. = 72, $p \ll 0.001$) and between the combined

Table 9 Chi-squared 'Goodness of Fit' tests of element frequencies between feeding trials.

	TS	BM	BS	ZPM	ZPG	PRM	PRG	PW	PC	FW	FC	SW
TM	1302	2622	1380	2044	71	2321	117	3880	2421	1228	1610	7746
	(22)	(23)	(19)	(19)	(6)	(20)	(9)	(23)	(21)	(14)	(19)	(25)
TS		780	190	687	21	801	156	1815	940	456	586	3369
		(22)	(19)	(22)	(3)	(22)	(8)	(20)	(21)	(15)	(22)	(13)
BM			293	192	22	232	44	1645	1211	567	1034	4951
			(19)	(16)	(4)	(16)	(8)	(19)	(22)	(13)	(23)	(14)
BS				288	10	360	44	1423	791	385	555	2712
				(20)	(3)	(19)	(6)	(16)	(16)	(14)	(20)	(9)
ZPM					27	24	30	1468	1065	493	837	4125
					(6)	(16)	(9)	(15)	(16)	(13)	(18)	(11)
ZPG						31	10	51	35	39	24	85
						(6)	(5)	(4)	(5)	(4)	(5)	(4)
PRM							32	1493	1218	568	991	4286
							(9)	(15)	(17)	(13)	(20)	(11)
PRG								128	71	163	80	158
								(5)	(5)	(7)	(6)	(5)
PW									1100	401	1319	4065
									(13)	(7)	(16)	(16)
PC										60	135	4141
										(7)	(14)	(11)
FW											116	1007
											(9)	(6)
FC												3890
												(13)

The upper value in each cell represents the chi-squared value of each comparison. The figure in parentheses is the degrees of freedom.

feeding trials for bothids, pleuronectids and soles (chi-squared = 6535, 32 D.F., $p \ll 0.01$).

4.4.2. A summary of the main differences between the frequency of performance of behavioural elements.

The comparison of percentage frequencies of behavioural elements between feeding trials shown in Table 8 is rather difficult and not easy to assimilate. In an attempt to summarise this information two further tables have been constructed. Table 10 shows the commonest elements of behaviour with respect to frequencies for each family and Table 11 shows the commonest elements for each feeding trial. It is apparent from Table 10 that the bothids have a larger repertoire of commonly exhibited elements of feeding behaviour than either the pleuronectids or the soleids. Also the elements that are commonly displayed by the bothids are different from those commonly displayed by the pleuronectids or soleids; the latter two families are much more alike in the commonest elements that they exhibit. Table 11 shows in more detail the differences between feeding trials with respect to the frequencies of the commonest elements exhibited. The remainder of this section will quantify these differences by statistical analysis.

As a point of terminology, 'test group' will refer to separate data sets to be compared whether these be at the family or species level. Tables 12, 14, 16, 18 - 21, and 23 - 26 show the results of chi-squared goodness of fit tests performed on single elements between specified test groups.

The chi-squared analysis for separate elements was part of the calculation necessary to derive the chi-squared values over whole

Table 10 A list of the commonest elements of behaviour with respect to frequency for each family of flatfish.

Description	B	P	S
Elements that occur more frequently than expected *	TN PS CR HR LG SF BT SV HL RV CW	PS TN BT CW SF FD	PP SF TN BT CW
Number of elements that occur more frequently than expected	11	6	5
Cumulative percentage frequency	83	89	92
Additional elements that account for 95% of element frequencies	SW CAR AR DN SK SLG STN RX SBT	RV SK HR	RV
Number of elements that account for 95% of cumulative percentage frequency	20	9	6
Different elements exhibited	43	30	24

Elements are arranged in descending order of frequency.

$$\text{*Expected frequency} = \frac{\text{total number of elements in all feeding trials}}{\text{number of different elements exhibited}}$$

Key: B - Bothids
P - Pleuronectids
S - Soleids

Key to column headings for Table 11

TM - Turbot feeding on Mysids
TS - Turbot feeding on Shrimps
BM - Brill feeding on Mysids
BS - Brill feeding on Shrimps
ZPM - Z. punctatus feeding on Mysids
ZPG - Z. punctatus feeding on Gammarids
PRM - P. regius feeding on Mysids
PRG - P. regius feeding on Gammarids
PW - Plaice feeding on Enchytraeid Worms
PC - Plaice feeding on Corophiids
FW - Flounder feeding on Enchytraeid Worms
FC - Flounder feeding on Corophiids
SW - Sole feeding on Enchytraeid Worms

The elements are arranged in descending order of frequency.

$$\text{Expected frequency} = \frac{\text{Total number of elements in feeding trial}}{\text{Number of different elements exhibited}}$$

Table 11 A list of the commonest elements of behaviour with respect to frequency for each feeding trial.

Description	TM	TS	BM	BS	ZPM	ZPG	PRM	PRG	PW	PC	FW	FC	SW
Elements that occur more frequently than expected	TN	TN	PS	TN	PS	PS	CR	TN	CW	PS	PS	PS	PP
	SF	SF	CR	PS	TN	TN	PS	CR	BT	TN	BT	TN	SF
	SW	PS	TN	CR	CR	HR	TN	PS	TN	SF	TN	SF	TN
	DN	SV	LG	SF	LG	HL	LG	HR	FD	FD	SF	FD	BT
	PS	AR	BT	SV	BT	CR	RV	HL	RV	CW	FD	BT	CW
	SLG	LG	CW	LG	RV	SV	BT			BT		CW	
	SBT	SK	AR	CAR	HR		HR						
	STN	BT	CAR		HL		CW						

Table 11 A list of the commonest elements of behaviour with respect to frequency for each feeding trial.

Description	TM	TS	BM	BS	ZPM	ZPG	PRM	PRG	PW	PC	FW	FC	SW
Elements that occur more frequently than expected	TN	TN	PS	TN	PS	PS	CR	TN	CW	PS	PS	PS	PP
	SF	SF	CR	PS	TN	TN	PS	CR	BT	TN	BT	TN	SF
	SW	PS	TN	CR	CR	HR	TN	PS	TN	SF	TN	SF	TN
	DN	SV	LG	SF	LG	HL	LG	HR	FD	FD	SF	FD	BT
	PS	AR	BT	SV	BT	CR	RV	HL	RV	CW	FD	BT	CW
	SLG	LG	CW	LG	RV	SV	BT			BT		CW	
	SBT	SK	AR	CAR	HR		HR						
	STN	BT	CAR		HL		CW						
		DN	RV				SV						
Number of elements that occur more frequently than expected	8	9	9	7	8	7	9	5	5	6	5	6	5
Cumulative percentage frequency	79	79	86	73	82	93	87	75	88	92	87	85	92
Additional elements to account for 95% of element frequencies	SK	SW	RX	HR	SV	RV	HL	SV	PS	SK	CW	SK	RV
	HR	RX	SF	AR	CW		CAR	RV	SF	RV	RV	SV	
	LG	CR	HR	BT	CAR		LV	LG	LG			HR	
	HV	HR	MS	CW	LV		MS	BT				DN	
	BT	CAR	LV	CW	SF			YN				HL	
	CW	CW	HL	SK	RX							FS	
		FP	TAR	RX	MS								
		MS		DN									
		STN		STN									
				MS									
Number of elements that account for 95% of cumulative percentage frequency	14	18	16	17	15	7	13	10	8	8	7	12	6
Different elements exhibited	31	32	30	25	26	11	27	15	20	20	12	26	24

trials as described in the previous section. The total chi-squared value was calculated as the sum of all the separate chi-squared values for the individual elements, which are the values indicated in Tables 12, 14, 16, 18 - 21 and 23 - 26. The lists of elements in the tables consist of only those elements where the expected frequencies for all test groups were greater than 5 and where the chi-squared results showed a significant difference at $p = 0.05$. In calculating the chi-squared values the direction of the difference between observed frequency minus expected frequency was noted and is indicated in the tables by '+' or '-'. This sign indicates whether an element occurs significantly more or less than expected. It also yields information about the nature of occurrence of elements between test groups.

Tables 12, 14, 16, 18 - 21 and 23 - 26 show:

1) The elements which are significantly different ($p = 0.05$, chi-squared goodness of fit test) in frequency of occurrence between test groups (column 1).

2) The relative magnitude of the significant differences between test groups (column 2). In this case, the chi-squared value can be used as an index of the magnitude of the disparities between test groups for all elements because, within a table, the degrees of freedom for each element are equal.

3) For each test group, the relative abundance of elements compared with an expected theoretical value (columns 4 or 5 or 6). This is because a chi-squared goodness of fit test compares the observed value with an expected value calculated as a proportion of the total element frequency over all test groups.

4) How the differences between observed and expected values for an

element compare between test groups (columns 4, 5 and 6), i.e. which test groups perform a specified element more or less often than expected.

5) Which test group contributes most to the chi-squared value for a specific element, i.e. where the largest disparity between observed and expected values occurs (column 3). If the tables where only two test groups are considered, however, the largest disparity will always be attributed to the test group with the smaller total number of elements. (This is merely a characteristic of the calculations for a chi-squared test.)

The tables convey a large amount of information and to comment on each table in detail would occupy too much space. Instead the first table of the series, Table 12, will be discussed to guide the reader through the important points.

Sixteen elements of behaviour showed a significant difference at $p<0.05$ between bothids, pleuronectids and soleids. Palpation (PP) was the element with the largest disparity between families with a chi-squared value of 1518. Palpation occurred more frequently than expected in the soleids but less frequently than expected in the other two families (see columns 4, 5 & 6). The pleuronectids exhibited the largest disparity between observed and expected values (see column 3). Creep (CR), Forward (FD) and Pause (PS) also displayed very high disparities between families. Creep is an element of behaviour that is particularly associated with bothids, occurring much more often than expected, whilst Forward is particularly associated with the pleuronectids. Pause, on the other hand, occurred much less frequently in soleids than expected. In fact many of the elements listed had negative associations with soleids but positive

Table 12 A summary of the major differences between the bothids, the pleuronectids and soleids with respect to the frequencies of elements.

Elements showing a significant difference between families	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected		
			Bothids	Plueronectids	Soleids
SW	368	B	+	-	-
DN	256	B	+	-	-
CR	677	B	+	-	-
LG	478	B	+	-	-
STN	108	B	+	-	-
SLG	286	B	+	-	-
TN	226	P	+	+	-
SV	50	B	+	+	-
SK	129	B	+	+	-
PS	990	P	+	+	-
HR	121	B	+	+	-
FD	932	P	-	+	-
BT	98	P	-	+	-
CW	179	P	-	+	-
PP	1518	P	-	-	+
SF	115	B	-	-	+

Key: B - bothid
P - pleuronectid

For 2 degrees of freedom the chi-squared value at p = 0.05 is 5.99.

associations with the bothids. Clearly many of these elements occur more often than expected in bothids and this is evidence that this family performs a wide range of behavioural elements. At the other extreme, there are only two elements from this list which soleids performed significantly more than expected, Palpation (PP) and Shuffle (SF). This is evidence that the feeding behaviour of soleids is composed of only a small number of elements, each of which is performed a large number of times.

Differences between the observed and expected values can be compared between families for each element. In many cases there was good agreement between bothids and pleuronectids with soleids showing a dissimilar pattern. For example, Skim occurred more frequently than expected in bothids and pleuronectids but less frequently in soleids. One simple way of assessing the similarity between families with respect to frequencies of elements is to count the number of signs held in common by any two groups. These counts are given in Table 13.

Table 13 The similarity between families as measured by the number of 'like signs' held in common. (Sixteen elements showed significant differences between families.)

	Pleuronectids	Soleids
Bothids	7	3
Pleuronectids		6

Clearly the match between bothids and pleuronectids (7 like signs) was closer than between bothids and soleids (3 like signs). The agreement between plaice and soles was also quite high (6 like signs). This suggests that bothids and soleids, which share common affinity are at the opposite ends of a range whilst pleuronectids lie between and share affinities with both families. Pleuronectids shared affinities with bothids and soleids but only in three elements (FD, BT and CW) was the direction of the difference between observed and expected completely opposite to the other two families. On the other hand, for bothids the direction of the difference between observed and expected frequencies was completely opposite to the other two families in the performance of six elements (SW, DN, CR, LG, STN and SLG) while soleids were alone in seven elements (TN, SV, PS, HR, PP and SF). This was exactly as might be expected assuming bothids and soleids to be at opposite ends of a spectrum.

Creep (CR) was the typical stalking element of the bothids, but was almost never exhibited by pleuronectids and soleids. Because the bothids have elaborate hunting behaviour, they exhibited many elements that were less common in the other families. Bothids performed Shuffle (SF) less often than pleuronectids. Bite probably formed a lower proportion of the behavioural repertoire because the prey items were larger and required more elaborate hunting before capture. The bothids exhibited far less chewing movements than the pleuronectids. This was in accordance with de Groot's observations (1971, p. 144) that bothids swallow their prey intact.

Forward (FD) was the typical approach/attack element of the pleuronectids and was almost totally restricted to this group. This group of fish have relatively simple feeding sequences (see section

4.10) compared to the bothids. Pleuronectid feeding sequences were shorter (see section 4.7) and involved fewer elements (see section 4.6). The elements which did occur, therefore, had higher relative frequencies because there were fewer types. Bite (BT), Chew (CW) and Pause (PS) were common elements in pleuronectid feeding sequences which had a larger relative frequency in this group than in either of the other two.

The soleids exhibited high frequencies of Palpation (PP) and Shuffle (SF) compared with the other two groups. In fact these two accounted for 68% of all elements and constituted most of the feeding sequences of soleids. Their feeding tactics are clearly quite different from those of the bothids and pleuronectids and are attributed to the olfactorial mode of prey location and capture adopted by soleids. It is interesting that Skim (SK), a very rapid pursuit element, had a much lower frequency in soleids, presumably because performance of this element is a response to visual stimuli which soleids do not tend to perceive as readily.

Table 14 is a summary of the major differences in element frequencies for the four bothid species. This table conveys information (described on page 67) of a similar nature to Table 12. The chi-squared values were generally lower in Table 14 (average value 185) than Table 12 (average value 408), indicating that there was a closer fit between test groups (bothid species) than between flatfish families.

Table 15 shows the degree of similarity between bothid species with respect to the frequencies of elements that occur more or less frequently than expected. This table clearly illustrates the extremely high degree of association between Z. punctatus and

Table 14 A summary of the major differences between the bothids feeding on mysids with respect to the frequencies of elements.

Key to the abbreviations used in the table
T - turbot
B - brill
Zp - Z. punctatus
Pr - P. regius

For 3 degrees of freedom the chi-squared value at p=0.05 is 7.8

Table 14 A summary of the major differences between the bothids feeding on mysids with respect to the frequencies of elements.

Elements showing a significant difference between species	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected		
			Turbot	Brill	Z.punctatus	P.regius
TN	79	T B	+	-	-	-

Table 14 A summary of the major differences between the bothids feeding on mysids with respect to the frequencies of elements.

Elements showing a significant difference between species	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected			
			Turbot	Brill	Z.punctatus	P.regius
TN	79	T	+	-	-	-
SW	419	T	+	-	-	-
DN	317	T	+	-	-	-
SK	105	T	+	-	-	-
SF	311	T	+	-	-	-
FS	46	T	+	-	-	-
HV	105	T	+	-	-	-
STN	178	T	+	-	-	-
SLG	234	T	+	-	-	-
SBT	213	T	+	-	-	-
SMS	23	T	+	-	-	-
AR	269	B	-	+	-	-
RX	70	B	-	+	+	-
CR	619	T	-	+	+	+
RV	367	Pr	-	+	+	+
PS	141	T	-	+	+	+
LG	174	T	-	+	+	+
BT	142	T	-	+	+	+
MS	35	B	-	+	+	+
CAR	205	B	-	+	+	+
CW	95	B	-	+	-	+
SV	193	Pr	-	-	+	+
HR	76	Pr	-	-	+	+
HL	155	Zp	-	-	+	+

P. regius. The similarity between brill and both topknots was also high but there was an extremely low similarity between turbot and the other three bothid species.

Table 15 The similarity between bothid species as measured by the number of 'like signs' held in common. (Twenty-five elements showed significant differences between bothid species.)

	Brill	Z. punctatus	P. regius
Turbot	3	2	2
Brill		20	20
Z. punctatus			23

The following conclusions may be drawn from Table 14:

1) Whilst on the substratum, turbot moved by Shuffle (SF) and Skim (SK) much more than the other species. Conversely turbot performed far less Creep (CR), Reverse (RV) and Creep-Arch (CAR) than the other species.

2) Turbot performed many more water column associated elements of behaviour (SW, DN, FS, HV, STN, SLG, SBT and SMS) than expected whilst all the other bothids performed these elements less than expected. Herein lay one of the major differences between these four bothid species - the high proportion of water column activity elements.

In order to examine the differences between brill and the two

Table 16 A summary of the major differences between brill, Z.punctatus and P.regius feeding on mysids with respect to the frequencies of elements.

Elements showing a significant difference between species	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected		
			Brill	Z.punctatus	P.regius
AR	71	B	+	-	-
RX	11	B	+	-	-
CAR	20	B	+	-	-
CW	12	Zp	+	-	+
SF	9	Pr	+	+	-
SV	37	B	-	+	+
RV	33	B	-	+	+
HR	50	B	-	+	+
HL	33	B	-	+	+

Key: B - brill
Zp - Z.punctatus
Pr - P.regius

For 2 degrees of freedom the chi-squared value at p = 0.05 is 5.99.

topknot species, a repeat analysis was carried out omitting turbot. Table 16 represents the results of such an analysis and Table 17 shows the degree of similarity between species.

Table 17 The similarity between brill, Z. punctatus & P. regius as measured by the number of 'like signs' held in common. (Nine elements showed significant differences between species.)

	Z. punctatus	P. regius
Brill	1	1
Z. punctatus		7

With turbot removed from the analysis, the differences between brill and the two species of topknot become more apparent. Z. punctatus and P. regius were remarkably similar, exhibiting the same sign difference between observed and expected frequencies of seven elements. Both topknots infrequently showed associations of the same difference with brill, only once in each case. Therefore it may be inferred that brill share less affinity with the topknots with respect to the frequency of elements than the topknots share with each other. This was substantiated by the chi-squared tests between paired trials (Table 9). The chi-squared values of the individual elements were, however, much lower than with turbot included, indicating that the difference between brill and the topknots is far less substantial than the difference between these three bothids and turbot.

Whilst on the substratum brill performed significantly more Arch (AR), Relax (RX) and Creep-Arch (CAR) than the topknots but less Swivel (SV), Reverse (RV), Head-raise (HR) and Head-lower (HL) than the topknots.

Differences between the topknots with respect to frequencies of elements exhibited, taken over all elements between feeding trials on mysids, were not significantly different ($p = 0.09$). Two individual elements did, however, show significant differences: Shuffle ($p = 0.01$, 1 D.F.), which was performed more often by Z. punctatus and Chew ($p<0.025$, 1 D.F.) which was performed more often by P. regius. Subjectively, Z. punctatus was considered to be on the substratum more than P. regius which hunted more frequently from a vertical tank wall. The significantly greater number of Chew (CW) elements exhibited by P. regius is attributed to this being a smaller species than Z. punctatus and having to perform more ingestion movements on prey of a similar size.

This summary further emphasises the large amount of water column activity exhibited by turbot, the reduced amount of substrate locomotion and high degree of stationary attack tactics in the topknots and the intermediate status of brill which lie between the two extremes of the tactics of turbot and the topknots. Brill most commonly exhibit slow creeping stalking movements on the substratum.

In addition to mysids, feeding trials were also carried out using shrimps as prey for turbot and brill. Table 18 summarises the major differences between the frequencies of elements that showed a significant difference at $p<0.05$. The chi-squared values were much lower (average value 18) than those values for a comparison of turbot and brill feeding on mysids (average value 72; data not included).

Table 18 A summary of the major differences between turbot and brill feeding on shrimps with respect to the frequencies of elements.

Elements showing a significant difference between species	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected	
			Turbot	Brill
SV	16	B	+	-
DN	6	B	+	-
SK	4	B	+	-
SF	21	B	+	-
FP	12	B	+	-
CR	91	B	-	+
RV	8	B	-	+
PS	4	B	-	+
HR	8	B	-	+
CAR	10	B	-	+

Key: B - brill

For 1 degree of Freedom the chi-squared value at p = 0.05 is 3.84.

This result suggests that the behaviour of turbot and brill differs more when they are feeding on mysids than when feeding on shrimps. Table 18 shows that Swivel (SV), Skim (SK) and Shuffle (SF) occur more often than expected in the behavioural repertoire of turbot. These elements are essentially fast pursuit movements. Brill, however, perform more Creep (CR), Reverse (RV), Pause (PS), Head-raise (HR) and Creep-Arch (CAR) elements than expected. These elements typify the hunting tactics of brill, which appear to stalk their prey using stealth and cunning. Turbot, in contrast, rely on speed of pursuit.

Having looked at the differences between species of bothids, the next step was to determine how the feeding behaviour was affected by prey species. Tables 19 and 20 summarise the major differences between the effects of the prey types, mysids and shrimps, on the frequencies of elements of feeding behaviour for turbot and brill respectively. The feeding behaviour of turbot on mysids and shrimps was quite different. Whilst feeding on mysids, which swim in the water column, turbot performed significantly more water column activity elements (SW, DN, HV, STN, SLG, SBT and SMS). Whilst feeding on shrimps, however, the water column activity elements occurred much less frequently than expected. Their place has been taken by substrate activity and attack elements (SV, SF, CR, AR, RX, LG, MS, CAR).

The behaviour of brill feeding on mysids and shrimps was also quite different, although the change in behaviour showed a different trend to that shown by turbot. Whilst feeding on mysids, brill performed more successful elements of attack behaviour than expected (LG, BT, CW) but when the fish were feeding on shrimps these elements occurred less often than expected, showing that shrimps are more

Table 19 A summary of the major differences between turbot feeding on mysids and on shrimps with respect to the frequencies of elements.

Elements showing a significant difference between prey	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected	
			Mysids	Shrimps
TN	6	S	+	-
SW	70	S	+	-
DN	43	S	+	-
HV	29	S	+	-
STN	33	S	+	-
SLG	73	S	+	-
SBT	67	S	+	-
SMS	6	S	+	-
SV	443	S	-	+
SF	27	S	-	+
CR	20	S	-	+
PS	43	S	-	+
FP	26	S	-	+
AR	213	S	-	+
RX	81	S	-	+
LG	7	S	-	+
MS	19	S	-	+
CAR	89	S	-	+

Key: S - shrimps

For 1 degree of freedom the chi-squared value at $p = 0.05$ is 3.84.

Table 20 A summary of the major differences between brill feeding on mysids and shrimps with respect to the frequencies of elements.

Elements showing a significant difference between prey	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected	
			Mysids	Shrimps
RV	12	S	+	-
LG	26	S	+	-
BT	28	S	+	-
CW	15	S	+	-
TN	10	S	-	+
SV	46	S	-	+
SW	36	S	-	+
SK	15	S	-	+
SF	76	S	-	+
HR	11	S	-	+

Key: S - shrimps

For 1 degree of freedom the chi-squared value at p = 0.05 is 3.84.

difficult organisms than mysids to catch, eliciting a correspondingly lower frequency of successful attack elements. (Turbot also showed more Miss (MS) elements than expected when feeding on shrimps.) Brill exhibited more activity elements (TN, SV, SW, SK, SF) than expected whilst feeding on shrimps. These elements of behaviour are associated with searching and pursuit of prey whereas with mysids as prey these elements occurred less often than expected i.e. the proportions of functional types of behaviour had altered. Clearly the behaviour of turbot and brill was considerably modified in response to the stimulation provided by different prey organisms.

Table 21 illustrates the major differences between plaice, flounder and sole feeding on enchytraeid worms. The chi-squared values of the elements showing a significant difference between test groups were high, indicating a poor fit between test groups. Palpation (PP) differed most between test groups but Forward (FD), Pause (PS) and Chew (CW) also showed large disparities.

Table 22 shows the extent of the associations between test groups based on the correspondence of the signs of the difference between observed and expected. Clearly sole and plaice were poorly associated. Flounder lay somewhere between these two extremes, closer to plaice than to sole.

The main differences between the two pleuronectids and the soles were that the pleuronectids exhibited more of the elements Turn (TN), Forward (FD), Pause (PS) and Bite (BT) than expected. These four elements typify pleuronectid feeding behaviour, which could be described as a discontinuous, stop-start type of activity. This is in contrast to the feeding behaviour of sole which is more continuous and flowing in its qualitative appearance. Soles

Table 21 A summary of the major differences between plaice, flounder and sole feeding on enchytraeid worms with respect to the frequencies of elements.

Elements showing a significant difference between species	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected		
			Plaice	Flounder	Sole
RV	44	P	+	-	-
CW	633	P	+	-	-
TN	306	P	+	+	-
FD	861	P	+	+	-
PS	621	F	+	+	-
BT	382	P	+	+	-
SF	298	P	-	+	+
PP	1522	P	-	-	+

Key: P - plaice
F - flounder

For 2 degrees of freedom the chi-squared value for p = 0.05 is 5.99.

performed less Pause (PS) elements than expected but more Shuffle (SF) and Palpation (PP) elements than expected.

Table 22 The similarity between plaice, flounder and sole as measured by the number of 'like signs' held in common. (Eight elements showed significant differences between species.)

	Flounder	Sole
Plaice	5	0
Flounder		3

The differences between plaice and flounder feeding on worms can be examined in more detail if sole are disregarded (Table 23). Most of the difference in behaviour of plaice and flounder occurred in the performance of the elements Shuffle (SF), Pause (PS) and Chew (CW). Plaice performed more CW elements than flounders which is attributed to plaice having a smaller mouth and oesophagus than flounder. Flounder performed significantly more PS and SF elements than expected and plaice performed less than expected. Shuffle (SF) and Forward (FD) are the two main locomotory elements of plaice and flounder on the substratum. FD and SF differ in the amount of ground covered. FD describes a short movement less than half a body length whilst SF takes the fish more than this distance. Plaice and flounder do not differ in the proportion of FD movements but the increased proportion of SF exhibited by flounders shows that they move around

Table 23 A summary of the major differences between plaice and flounder feeding on enchytraeid worms with respect to the frequencies of elements.

Elements showing a significant difference between species	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected	
			Plaice	Flounder
RV	8	F	+	-
CW	59	F	+	-
SF	140	F	-	+
PS	183	F	-	+

Key: F - flounder

For 1 degree of freedom the chi-squared value at p = 0.05 is 3.84.

the tank much more than plaice, and they also make more pauses between activity. In the main, however, the behaviour of plaice and flounder feeding on enchytraeid worms was quite similar.

When the prey organism was changed to corophiids more elements of behaviour showed differences (Table 24). There was no disparities as large as SF and PS (Table 23) but the fact that more elements showed significant differences gave rise to more disparities of feeding tactics between species. Plaice performed FD, RV, BT and CW more often than expected, these being the typical elements of feeding behaviour in plaice. Flounders performed more elements Turn (TN), Swivel (SV), Skim (SK), Head-raise (HR) and Head-lower (HL) than expected and therefore seemed to spend more activity in searching behaviour than plaice.

The final two tables in this subsection summarise the major differences brought about by two different prey types - enchytraeid worms and corophiids - on plaice (Table 25) and flounder (Table 26). The behaviour of plaice differed substantially with prey organisms. When feeding on worms the attack elements Reverse (RV), Arch (AR), Lunge (LG), Bite (BT) and Chew (CW) occurred more often than expected whereas with corophiids, searching and pursuit elements (Swivel (SV), Skim (SK), Shuffle (SF) and Pause (PS)) occurred more often than expected. The largest discrepancy in the performance of a single element occurred with the element Pause (PS) which occurred less often with worms but more often with corophiids. This reflects the fish's ability to browse worms almost continuously, but hunting means that the fish need to stop and search visually for prey.

There is less discrepancy between prey types with flounders, the chi-squared values being much lower. Also fewer elements showed a

Table 24 A summary of the major differences between plaice and flounder feeding on corophiids with respect to the frequencies of elements

Elements showing a significant difference between species	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected	
			Plaice	Flounder
FD	18	F	+	-
RV	11	F	+	-
BT	6	F	+	-
CW	17	F	+	-
TN	4	F	-	+
SV	9	F	-	+
DN	20	F	-	+
SK	4	F	-	+
FS	19	F	-	+
HR	17	F	-	+
HL	8	F	-	+

Key: F - flounder

For 1 degree of freedom the chi-squared value for p = 0.05 is 3.84.

Table 25 A summary of the major differences between plaice feeding on enchytraeid worms and on corophiids with respect to the frequencies of elements.

Elements showing a significant difference between prey	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected	
			Worms	Corophiids
TN	11	C	+	-
RV	58	C	+	-
AR	7	C	+	-
LG	24	C	+	-
BT	133	C	+	-
CW	116	C	+	-
SV	27	C	-	+
SK	38	C	-	+
SF	159	C	-	+
PS	524	C	-	+

Key: C - corophiids

For 1 degree of freedom the chi-squared value for p = 0.05 is 3.84.

Table 26 A summary of the major differences between flounder feeding on enchytraeid worms and on corophiids with respect to the frequencies of elements.

Elements showing a significant difference between prey	Chi^2	Largest disparity attributed to	The direction of the difference between observed and expected	
			Worms	Corophiids
FD	15	W	+	-
BT	57	W	+	-
SV	9	W	-	+
DN	7	W	-	+
PS	14	W	-	+
HR	8	W	-	+

Key: W - enchytraeid worms

For 1 degree of freedom the chi-squared value for p = 0.05 is 3.84.

significant difference. As with plaice, flounder feeding on worms performed more attack elements than expected (Forward (FD) and Bite (BT)), whereas whilst feeding on corophiids these elements occurred less often than expected.

This section has employed an objective statistical approach to quantify dissimilarities between feeding trials with respect to the frequencies of performance of elements. It must be emphasised that the elements listed in each table are those showing significant differences between test groups. The lists therefore do not necessarily include all the important elements performed in the feeding trials. This analysis should consequently be considered in conjunction with Table 8 which shows the percentage frequencies of all the elements exhibited and Table 11 which lists the commonest elements.

4.5. Comparison of the percentage durations of performance of the behavioural elements.

The relative frequencies of behavioural elements for the feeding trials were described in section 4.4. This section deals with the durations of the elements.

The actual total durations of the elements can be found in Appendix 2. The durations of the elements have been converted to percentages to facilitate comparison between feeding trials and appear in Table 27. This table is rather large and not very easy to assimilate so two further tables have been included in an attempt to summarise this information. Table 28 shows the commonest elements of behaviour with respect to durations for each family and Table 29 shows the commonest elements for each feeding trial.

Clearly the feeding behaviour of the bothids is more diverse than that of the pleuronectids or soleids because they exhibit a larger number of different elements. Although the actual number of elements exhibited is large, only approximately a third of each family's repertoire accounts for 95% of the cumulative percentage time and only about a sixth of each family's repertoire occurs more often than expected. Pause and Turn are important elements in the repertoire of all families but other elements are more often associated with one family and not with the others e.g. Creep for bothids, Bury for pleuronectids and Palpation for soleids. The general conclusion to be drawn about the feeding tactics from these lists is that whilst the bothids spend much time performing stalking and approach movements (e.g. Creep, Head-lower, Head-raise, Arch, Creep-Arch) the pleuronectids and soleids spend more time performing elements associated with capture and ingestion of food (e.g. Bite and Chew).

Table 27 A comparison of the percentage durations of behavioural elements between feeding trials.

ELEMENT	TURBOT M	TURBOT S	BRILL M	BRILL S	Z.PUNCTATUS M	Z.PUNCTATUS G	P.REGIUS M	P.REGIUS G	PLAICE W	PLAICE C	FLOUNDER W	FLOUNDER C	SOLE W
TN	17.33	9.19	4.17	3.53	8.90	9.28	6.54	10.89	11.50	4.05	3.31	6.38	6.95
SV		6.25	0.47	0.57	3.94	4.44	3.25	7.86		0.43	0.19	1.56	0.97
TA	0.16	0.06		0.21	0.15		0.14	0.10					
PP													31.62
SW	9.58	0.79	0.00	0.27			0.07		0.24	0.04		0.15	0.22
DN	2.33	0.28	0.04	0.05					0.07	0.03		0.32	0.09
SK	3.53	0.49	0.02	0.08	0.03			0.06	0.12	0.49	0.36	0.90	0.03
SF	19.36	15.95	0.98	2.57	0.49	0.33	0.24	0.08	1.79	3.33	2.83	4.58	20.47
CR	1.23	1.44	15.29	10.53	17.58	5.39	22.08	19.48	0.54			0.03	
FD				0.00					2.34	1.95	1.61	1.43	0.00
RV		0.04	0.58	0.25	2.75	0.39	4.96	1.14	2.23	0.30	0.36	0.10	2.08
PS	29.99	49.14	58.48	67.01	55.79	67.17	46.17	44.61	26.00	59.10	79.83	60.57	19.39
ST							0.46						2.51
FS	3.81	0.77		0.08								3.21	0.38
BY	0.56	5.61	0.72	3.29			0.53		14.57	14.61	0.01	7.86	2.41
FP	0.64	1.62			0.01		0.22					0.01	0.01
UN													1.83
AR	0.03	2.51	7.02	3.43	0.24		0.36		0.24	0.06	0.06	0.70	
RX	0.02	0.40	2.62	0.28	0.74		0.64						
AC			0.03										
HV	1.29	0.04	0.00									0.04	
LG	0.74	0.38	0.57	0.14	0.66	0.06	0.67	0.17	0.30			0.01	
BT	0.67	0.28	0.48	0.10	0.59	0.06	0.57	0.17	5.66	1.61	2.44	1.43	3.05
MS	0.07	0.10	0.08	0.13	0.07		0.09			0.01			
CW	1.74	1.42	3.26	1.21	2.49		4.55	1.19	32.29	12.16	3.83	9.53	7.12
SP	0.02	0.04	0.01		0.01				0.01	0.09		0.06	0.06
HR	1.63	0.60	0.28	0.24	1.27	7.00	1.81	7.58	1.32	0.37	5.06	0.92	0.44
HL	0.08	0.41	1.16	0.03	2.33	5.72	5.47	5.31	0.68	1.27		0.36	0.12
YN	0.14	0.19			0.11	0.17	0.27	0.58				0.28	0.03
JP												0.01	0.13
STN	1.22	0.10		0.04					0.02			0.14	0.10
SLG	1.77	0.04	0.04						0.05				
SBT	1.56	0.03	0.02						0.05	0.01		0.06	
SMS	0.21	0.01	0.01										
STA	0.05												
SCW	0.22												
RCW					0.18		0.27						
SYN	0.02												
QV					0.04		0.06						
CAR		1.63	2.97	4.96	1.39		0.47	0.06					
TAR		0.18	0.42	0.99	0.02		0.02						
ARV			0.08										
ATA		0.03											
AHL			0.16		0.11								
AHR			0.01		0.09		0.01						
HCR							0.07	0.92					

Key to column heading codes:
C - corophiids
G - gammarids
M - mysids
S - shrimps
W - enchytraeid worms

Table 28 A list of the commonest elements of behaviour with respect to duration for each family of flatfish.

Description	B	P	S
Elements that occur for more time than expected*	PS CR TN SF SV HL HR	PS CW BY TN	PP SF PS CW TN
Number of elements that occur for more time than expected	7	4	5
Cumulative percentage time	86	86	86
Additional elements that account for 95% of session time	CW AR CAR SW BY RV	SF BT HR FD	BT ST BY RV
Number of elements that account for 95% of cumulative percentage time	13	8	9
Different elements exhibited	43	30	24

Elements are arranged in descending order of total duration.

*Expected duration = $\frac{\text{total session time}}{\text{number of different elements exhibited}}$

Table 29 A list of the commonest elements of behaviour with respect to duration for each feeding trial.

Description	TM	TS	BM	BS	ZPM	ZPG	PRM	PRG	PW	PC	FW	FC	SW
Elements that occur for more time than expected	PS SF TN SW FS SK	PS SF TN SV BY	PS CR AR TN	PS CR CAR	PS CR TN	PS TN	PS CR TN HL RV CW	PS CR TN SV HR	CW PS BY TN BT	PS BY CW	PS	PS CW BY TN SF	PP SF PS CW TN
Number of elements that occur for more time than expected	6	5	4	3	3	2	6	5	5	3	1	5	5
Cumulative percentage time	84	86	85	83	82	76	90	90	90	86	80	89	86
Additional elements to account for 95% of session time	DN SLG CW HR SBT HV CR	AR CAR FP CR CW SW	CW CAR RX HL SF	TN AR BY SF	SV RV CW HL CAR	HR HL CR SV	SV HR LG	HL	FD RV SF	TN SF FD	HR CW TN SF BT	FS SV BT	BT ST BY RV
Number of elements that account for 95% of cumulative percentage time	13	11	9	7	8	6	9	6	8	6	6	8	9
Different elements exhibited	31	32	30	25	26	11	27	15	20	20	12	26	24

Elements are arranged in descending order of total duration

The distribution of element durations between the feeding trials seemed to differ considerably (Table 29). Differences between selected elements were tested statistically using the Mann-Whitney U and Kruskal-Wallis tests. The durations of those elements which differ widely in occurrence, or those which account for only a very small proportion of the total time between chosen feeding trials have not been tested because such differences have already been made apparent in the previous section on frequency analysis. The elements of very short duration such as LG, BT, MS, SLG, SBT, SMS have also not been tested because the constraints of the recording technique necessitated that they all be ascribed a nominal duration of 1 second. Therefore all the durations will be the same and, again, the frequency analysis will have demonstrated significant differences between these elements. The elements that have been chosen for comparison between test groups are mainly locomotory ones that commonly occur before or after prey attack.

The results of these tests are shown in Table 30. As an example, there is a highly significant difference between the bothids with respect to the duration of Creep ($p<0.001$) and Pause ($p<0.001$). The duration of Creep and Pause are longest for brill and shortest for turbot,with the topknots occupying an intermediate position. The frequency analysis in the previous section, Table 14, showed that Creep and Pause were also less common for turbot but occurred more often than expected for brill, Z. punctatus and P. regius and that this difference was highly significant ($p<0.001$). The comparisons between test groups for duration of elements in Table 30 will not be discussed further in view of considerations of space but to derive maximum appreciation of the interplay between frequencies and

Table 30 Tests of significance to compare the durations of important elements between feeding trials.

*.....significant at p<0.05
**....significant at p<0.01
***...significant at p<0.001
ns....no significant difference at p=0.05

The code letters in parentheses indicate the test group with the longest element durations.
Key to code letters in parentheses:

T - turbot
B - brill
Z - Z.punctatus
Pr - P.regius
P - plaice
F - flounder
S - sole
Sr - shrimp
M - mysid
W - enchytraeid worm
C - corophiid

Test groups are coded in the usual way as indicated in Table 1.

Table 30 Tests of significance to compare the durations of important elements between feeding trials.

Test groups	ELEMENT CODES							
	SW	SF	CR	RV	PS	AR	CW	CAR
TM / BM / ZPM / PRM			***		***			
			(B>Pr>Z>T)		(B>Z>Pr>T)			
BM / ZPM / PRM			ns		***			
					(Pr>Z>B)	(B>Pr>Z)		
BM / ZPM					ns	***		

Table 30 Tests of significance to compare the durations of important elements between feeding trials.

Test groups	ELEMENT CODES							
	SW	SF	CR	RV	PS	AR	CW	CAR
TM / BM / ZPM / PRM			***		***			
		(B>Pr>Z>T)			(B>Z>Pr>T)			
BM / ZPM / PRM			ns	***	***			
				(Pr>Z>B)	(B>Pr>Z)			
BM / ZPM				ns	***			
					(B>Z)			
BM / PRM				***	***			
				(Pr>B)	(B>Pr)			
ZPM / PRM				***	ns			
				(Pr>Z)				
TM / BM	ns	ns	***		***			
			(B>T)		(B>T)			
TS / BS		*	***		**	***		**
		(T>B)	(B>T)		(B>T)	(B>T)		(B>T)
TM / TS	ns	***	*		***	*		
		(Sr>M)	(Sr>M)		(Sr>M)	(Sr>M)		
BM / BS		ns	ns		ns	***		***
						(Sr>M)		(Sr>M)
PW / FW / SW		***			***		***	
		(S>P>F)			(S>P>F)		(P>S>F)	
PW / FW		***			**		ns	
		(P>F)			(P>F)			
PC / FC		ns			ns		ns	
PW / PC		***			***		***	
		(W>C)			(W>C)		(W>C)	
FW / FC		ns			ns		*	
							(C>W)	

durations of elements the elements for test groups shown in Table 30 should be compared with the appropriate table in the frequency analysis section.

The relationship between frequencies and durations of elements tends to be inverse. Clearly an increase in the number of elements that occur in a fixed sample period leads to a decrease in the mean duration of each element. This simple relationship is complicated, however, by two effects. First, about one third of the elements have extremely short durations and with the methods employed could not be measured accurately. They were consequently assigned a nominal duration of 1 second as mentioned above. The frequency-duration relationship for these elements is not inverse because the durations have been fixed at a standard value. Secondly, those elements with extremely long durations (Bury, Pause etc.) provide a considerable buffering effect which masks the simple frequency-duration relationship.

An introduction to the subject of the relationship between durations and frequencies was given in Section 4.1 relating to Fig. 10 and in Section 4.2 relating to Figs. 11 & 12. A consistent difference was discernible from these figures; percentage activity based on frequencies was higher than percentage activity based on durations. This was because the elements of activity tended to be large in number but short in duration, whereas the elements of inactivity showed a reverse trend. This is an important point which should be borne in mind when comparing the frequency and duration of elements.

4.6. Comparison of the number of elements within a sequence.

A sequence is defined as a succession of elements ending with an attack (Bite (BT), Miss (MS), Swim-Bite (SBT), or Swimm-Miss (SMS)). Long sequences indicate either long and complex hunting tactics or a high proportion of searching activity per prey capture. Table 31 is a comparison of some statistics for each feeding trial. A Kruskal-Wallis one-way analysis of variance test showed that there was a highly significant difference between feeding trials ($H = 697$, 10 D.F., $p<<0.005$). A Mann-Whitney U test was therefore performed successively between all possible combinations of pairs of feeding trials to establish in more detail the differences between feeding trials. The results are presented in Table 32.

The frequency distribution of the number of elements within a sequence is skewed so that the mean is not an appropriate estimator of central tendency; the median is preferable with such distributions. The median number of elements within a sequence for bothids was 7.3, for pleuronectids 4.2 and for soleids 6.0. The relatively high value for bothids indicates that their feeding sequences tend to be more complex involving more elements to capture their prey. This is partly due to their hunting tactics and partly because their prey display more elaborate escape mechanisms. The value for soleids is explained by their hunting behaviour being governed by olfactory rather than visual cues, and consequently they performed more elements to locate their prey i.e. they display a higher proportion of searching behaviour than the other groups. The low value for the pleuronectids is because their simpler hunting behaviour requires only a few elements to locate and capture their prey which do not exhibit elaborate escape mechanisms.

Table 31 The number of elements within a sequence for all feeding trials.

Flatfish species	Prey	N	Min.	Max.	Range	Median	Mean
Turbot	M	452	2	78	76	7.6	10.3
Turbot	S	61	3	72	69	8.7	16.9
Brill	M	184	2	29	27	7.0	8.4
Brill	S	40	3	54	51	8.5	11.2
Z.punctatus	M	95	4	51	47	8.2	10.3
Z.punctatus	G	insufficient data					
P.regius	M	108	3	51	48	7.5	9.9
P.regius	G	insufficient data					
Plaice	W	616	2	11	9	3.8	4.1
Plaice	C	176	2	164	162	6.5	10.1
Flounder	W	88	2	42	40	3.9	5.1
Flounder	C	107	2	230	228	5.0	11.7
Sole	W	713	2	120	118	6.0	11.2

Key to prey;
C - corophiids
G - gammarids
M - mysids
S - shrimps
W - enchytraeid worms

N is the total number of sequences.

Table 32 A comparison of the number of elements in each sequence between all feeding trials using a Mann-Whitney U test

	TS	BM	BS	ZPM	PRM	PW	PC	FW	FC	SW
TM	*	*	ns	ns	ns	***	***	***	***	***
TS		**	ns	ns	ns	***	***	***	***	***
BM			*	**	ns	***	ns	***	***	ns
BS				ns	ns	***	**	***	***	*
ZPM					ns	***	***	***	***	***
PRM						***	**	***	***	**
PW							***	ns	***	***
PC								***	**	ns
FW									***	***
FC										**

ns.....not significant at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001
All tests were two-tailed.

A Kruskal-Wallis one-way analysis of variance test showed that there was a significant difference between the four bothid species feeding on mysids ($H = 8.4$, 3 D.F., $p<0.05$). Brill performed fewest elements, then came P. regius and turbot. Z. punctatus performed the most. The value for P. regius, turbot and Z. punctatus were not significantly different at $p = 0.05$ but brill differed at $p<0.05$ from turbot and at $p<0.01$ from Z. punctatus (Table 32). The species therefore form a graded series in which brill, at one extreme, performed less elements per sequence than the other species. Nonetheless, as was seen from Fig. 12, the amount of time brill spent active closely resembled that of Z. punctatus when both species were feeding on mysids and therefore the difference between the two extremes of the series, in terms of the number of elements within a sequence, must be compensated for by brill's longer durations of elements.

When feeding on shrimps, brill exhibited fewer elements than turbot but the difference was not significant at $p = 0.05$ (Table 32). The results nevertheless suggest that brill perform fewer elements when feeding on a given prey than do turbot and that herein lies a basic difference in hunting tactics.

The differences between mysids and shrimps for both turbot and brill were significant ($p<0.05$, Table 32). It is interesting that shrimps elicit more elements per sequence than do mysids, which suggests that shrimps are harder to capture and require more complex hunting than mysids. This suggestion is corroborated by direct observation. The fish appeared to experience more difficulty catching shrimps and this difficulty was attributed to the differences between the ease of capturing enchytraeids and corophiids by plaice and

flounder. Corophiids elicited a higher number of elements within a sequence than enchytraeids ($p \ll 0.001$, Table 32), as they are more mobile and require more elaborate hunting. The figures for the range of elements within a sequence differ markedly between plaice feeding on enchytraeids and corophiids and between flounders feeding on the two types of prey.

Flounder seemed to be able to catch corophiids with less effort than plaice ($p < 0.01$) whereas there was no difference at $p = 0.05$ when the prey was enchytraeid worms. Presumably the immobile worms were easy to catch for both species but corophiids, being more mobile, presented more of a problem for plaice than they did for flounders. This is supported by consideration of their natural diets where plaice tend to feed on immobile prey whereas flounder feed on mobile crustaceans.

A Kruskal-Wallis test showed that there was a highly significant difference between the three feeding trials involving worms as prey ($H = 275$, 2 D.F., $p \ll 0.005$). The soleids performed many more elements to capture their prey than did the pleuronectids. This must be attributed to the different sensory systems used by the two groups, soleids use olfaction and perform more searching behaviour than do the pleuronectids which are predominantly visual feeders, (vision gives more accurate orientation towards prey).

4.7. Comparison of the intervals between attacks.

This subsection complements the previous one by considering sequences with respect to their duration rather than from the number of elements that they contain. The interval between attacks is measured from one second after an attack up to the time of the next attack, Table 33 is a comparison of some statistics for each feeding trial. A Kruskal-Wallis one-way analysis of variance test showed there was a highly significant difference between feeding trials ($H = 785$, 10 D.F., $p \ll 0.005$). A Mann-Whitney U test was therefore performed successively between all possible combinations of pairs of feeding trials to establish in more detail the differences between them. The results are presented in Table 34.

The median value of intervals between attacks was 38 seconds for bothids, 10 seconds for pleuronectids and 12 seconds for soleids. Clearly there was a longer gap between attacks for bothids than for either the pleuronectids or soleids. This difference is attributed to the ratio of the size of prey captured to the size of fish, the distribution of prey, the behaviour of prey and also to the tactics of the predators. The first three considerations will be taken into account in the final discussion but at this stage it is sufficient to emphasise that the bothids, particularly brill, tend to spend long periods of time stalking prey whereas this is not true of the pleuronectids or soleids.

A Kruskal-Wallis one-way analysis of variance test showed that there was a significant difference between the four bothid species feeding on mysids ($H = 234$, 3 D.F., $p \ll 0.002$). The intervals between attacks were shortest for turbot, then came *P. regius*, *Z. punctatus* and finally brill, which exhibited the longest interval.

Table 33 The intervals between attacks for all feeding trials (in seconds).

Flatfish species	Prey	N	Min.	Max.	Range	Median	Mean
Turbot	M	452	2	969	967	18	38
Turbot	S	61	3	960	957	67	162
Brill	M	184	2	1243	1241	95	153
Brill	S	40	3	1212	1209	208	306
Z.punctatus	M	95	7	755	748	63	102
Z.punctatus	G	insufficient data					
P.regius	M	108	6	748	742	60	115
P.regius	G	insufficient data					
Plaice	W	616	2	474	472	8	16
Plaice	C	176	2	515	513	21	56
Flounder	W	88	2	820	818	7	40
Flounder	C	107	2	1194	1192	18	56
Sole	W	713	2	1117	1115	12	30

Key to prey:
C - corophiids
G - gammarids
M - mysids
S - shrimps
W - enchytraeid worms

N is the total number of sequences.

Table 34 A comparison of the intervals between attacks for all feeding trials using a Mann-Whitney U test.

	TS	BM	BS	ZPM	PRM	PW	PC	FW	FC	SW
TM	***	***	***	***	***	***	*	***	ns	***
TS		ns	**	ns	ns	***	***	***	***	***
BM			**	*	*	***	***	***	***	***
BS				***	***	***	***	***	***	***
ZPM					ns	***	***	***	***	***
PRM						***	***	***	***	***
PW							***	ns	***	***
PC								***	*	***
FW									***	***
FC										*

ns.....not significant at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001
All tests were two-tailed.

In all cases, interspecific comparisons using the Mann-Whitney U test revealed that the differences were significant (see Table 34) with the exception of P. regius vs. Z. punctatus. There is clearly a reversal of the pattern which was seen with the number of elements within a sequence where brill performed the fewest number of elements. This demonstrates a very important feature of the hunting tactics of brill. Brill perform a relatively small number of elements to capture their prey but take a long time to carry it out, each element having a long duration. They spend much time stealthily stalking their prey. Turbot, on the other hand, perform relatively more elements per attack but in a much shorter time than brill. When turbot are feeding they are extremely active, especially in the water column, and make a series of rapid actions of short duration. Both species of topknots exhibit similar durations between attacks. The topknots occupy an intermediate position between turbot and brill.

Prey type has an effect on the intervals between attacks. The intervals were longer when shrimps were the prey rather than mysids for both brill, $p<0.01$, and turbot, $p<0.001$. This difference is ascribed to shrimps being harder to catch than mysids. It must be pointed out, however, that the prey density of the two species was different, there being 50 mysids but only 10 shrimps in the feeding enclosures at any one time. This fact no doubt contributes to the longer intervals observed whilst the fish were feeding on shrimps, so that the time taken to locate and capture each individual prey organism was longer.

The plaice took longer to make attacks on both prey types than flounder. The difference was not significant for enchytraeids, but it was for corophiids ($p<0.05$). This was a reversal of the situation

for the number of elements within sequences. The implication from this disparity is that although plaice perform less elements within sequences than flounder, the elements performed by plaice have longer durations.

The rate of feeding for both species on enchytraeid worms was much higher than for corophiids. This was expected since worms required less hunting, being 'browsed', rather than chased, whereas more effort was required to capture corophiids, which accounts for the longer time between attacks with this prey.

There was a significant difference between the three feeding trials involving worms as prey species (Kruskal-Wallis test, $H = 74$, 2 D.F., $p \ll 0.005$). The sole exhibited more time between attacks when feeding on worms than either flounder or plaice, which was attributed to the olfactory mode of prey location in sole.

4.8. Comparison of the prey capture efficiency between feeding trials.

The prey capture efficiency was calculated from the relationship:

$$\text{Efficiency} = \frac{\text{Number of successful captures}}{\text{Total number of attacks}} \times 100$$

Table 35 shows the prey capture efficiencies for each feeding trial.

Clearly the prey capture efficiency was very dependent upon the prey species. It is quite striking that, despite the range of feeding tactics exhibited by the bothids when feeding on mysids, the capture efficiencies were similar between all four species. Shrimps, however, because their escape mechanisms are more elaborate, were not as easily captured by turbot and brill as mysids, but again the figures for turbot and brill were similar.

In all cases where the feeding trials involved worms as prey, capture efficiency was 100%. Both species of pleuronectids also captured corophiids with high efficiences.

The prey of the bothids, being more mobile, require more elaborate hunting tactics and pose more problems in terms of catchability than do the natural prey of the pleuronectids or soleids.

Table 35 A comparison of the prey capture efficiencies between feeding trials.

Flatfish species	Prey species	Prey capture efficiency (%)
Turbot	Mysids	89
Turbot	Shrimps	72
Brill	Mysids	84
Brill	Shrimps	73
Z. punctatus	Mysids	89
P. regius	Mysids	86
Plaice	Worms	100
Plaice	Corophiids	99
Flounder	Worms	100
Flounder	Corophiids	100
Sole	Worms	100

4.9. Organisation of the data into transition matrices.

So far the analysis of feeding behaviour has been concerned with the frequencies and durations of individual elements. These are, however, only the basic units from which the behaviour is organised. The next logical step is to examine how the elements are ordered into feeding sequences.

A transition matrix is a conventional means of representing relationships between behavioural events and has been used by many authors (Nelson, 1964 for glandulo-caudine fishes; Delius, 1969 for skylarks; and Zack, 1975 for opisthobranch molluscs). The simplest transition matrix is concerned with the sequential relationships between pairs of elements.

If there are c behavioural elements then n_i denotes the observed frequency of outcome i, (i = 1 ....., C). Let n_{ij} denote the observed frequency of pairs of events in which outcome i is followed by outcome j. The conventional method of constructing a transition matrix consists of arranging the values n_{ij} as a matrix located in the ith row and the jth column. Tables 36 to 47 show the transition matrices based on pairs of elements for all the feeding trials. Each matrix has been compiled by adding all the separate matrices from each session comprising the feeding trial.

Addition of matrices in this way can lead to complications, but the extent to which addition is undesirable is determined by the purpose of the construction of the matrix. Addition of separate sequences to form a combined matrix is acceptable if the objective is only to create a table summarising the sequential relationships between pairs of elements. If, however, more elaborate numerical/ statistical analysis is to be performed then the validity of such

Table 36 Transition matrix for turbot feeding on mysids

PRECEDING ELEMENT	TN	TA	LV	SW	DN	SK	SF	CR	PS	FS	BY	FP	AR
TN	138	2	1	181		94	369	11	83	34		7	3
TA	1			1			2						
LV	1						1		2				
SW					123					4			
DN	142			5		25	40	1	160	1	1		
SK	74			7			9	4	23				
SF	359			23		4		3	65	3			
CR	8		2	3			1		1				
PS	227			28		20	68	8		5	2	3	1
FS				3	37								
BY				2				1					
FP	8			2						1			
AR													
RX		2							1				
HV				5	5								
LG													
BT	40			1			9	1	33				
MS	5			1			1		3				
CW	39			3		1	10		16				
SP									3				
HR	26	1	1	54		4	13			7		1	
HL	5								3				
YN	4					1	2		1	1			
STN				86	100								
SLG													
SBT				75	131								
SMS				23	7								
STA				9									
SLV				6	5								
SCW				1	11								
SYN					1								
TOTAL	1077	5	4	519	420	149	525	29	394	56	3	11	4

PRECEDING ELEMENT	RX	HV	LG	BT	MS	CW	SP	HR	HL	YN	STN	SLG	SBT	SMS	STA	SLV	SCW	SYN	TOTAL
TN		27	42			9		69	1	1		1							1073
TA								1											5
LV											115	189			4	15	1	1	4
SW		67																	519
DN		2	2			37	1	3											420
SK		6	20			1		5											149
SF		10	18					35		4		1							525
CR		5	9																29
PS		2	8			4		20		3									399
FS											16								56
BY																			3
FP																			11
AR	3		1																4
RX											7	108			5	1			3
HV				121	12														131
LG		2				23	1		11										133
BT		1						1											121
MS		3	2				1	2											12
CW										1									77
SP		1	28			3		1											3
HR											2	17					4		137
HL		6											281	38					12
YN											61	2					11		9
STN		1									7	1							215
SLG											5								319
SBT											3								281
SMS		1																	38
STA																			9
SLV																			16
SCW																			16
SYN																			1
TOTAL	3	131	133	121	12	77	3	137	12	9	216	319	281	38	9	16	16	1	4730

Table 37 Transition matrix for turbot feeding on shrimps

		FOLLOWING													ELEMENT																		
		TN	SV	TA	LV	SW	DN	SK	SF	CR	RV	PS	FS	BY	FP	AR	RX	HV	LG	BT	MS	CW	SP	HR	HL	YN	STN	SLG	SBT	SMS	CAR	TAR	ATA	TOTAL
	TN	30	16			12		29	74	4		47			1	18			4			4	1	3		1						1		245
	SV	9	10			5		3	48	5		25			1	3								10									119
	TA	1															2																1
	LV			1														1								11	5						3
P	SW						19						1									4											37
R	DN	14	6					2	5			6			2	1																		40
E	SK	8				1			9	3		4				12			5					1										43
C	SF	61	49			3		2		8		57				20		1	7					5							13			213
E	CR	3	3			1		1				3				1																		25
E	RV	2	1																															3
D	PS	61	18			4		3	63	2	1			1	11	7			1			2	1	5		7								187
I	FS						9																				2							11
N	BY	1										10																						1
G	FP	6	1																															17
	AR	3	2		3			1		1							12		27												11	3		63
	RX	15	2					2	4			3																						26
E	HV						2																											3
L	LG																			40	15							1						55
E	BT	16	4							1	1	9										9												40
M	MS	4	1						2	1		5										1	1											15
E	CW	2	2					1		1	10					1			1				3											21
N	SP	2										3										1												6
T	HR	1	3			1						1	10		2			1	1					1	4									24
	HL		1						2																									4
	YN	1							7																									8
	STN					9	4																											13
	SLG																										4	2						6
	SBT						4																											4
	SMS						2																									1		2
	CAR	5				1											9		8												2			24
	TAR											1					2		1															6
	ATA																1																	1
TOTAL		245	119	1	3	37	40	43	215	25	3	184	11	1	17	63	26	3	55	40	15	21	6	25	4	8	13	6	4	2	24	6	1	1266

Table 38 Transition matrix for brill feeding on mysids

PRECEDING ELEMENT	FOLLOWING ELEMENT: TN	SV	LV	SW	DN	SK	SF	CR	RV	PS	BY	AR	RX	AC	HV	LG	BT	MS	CW	SP	HR	HL	SLG	SBT	SMS	CAR	TAR	ARV	AHL	AHR	TOTAL
TN	10	1	1			4	17	83	5	48		32				9			5		6	2					3				226
SV	1							2		6		1																			10
LV	1								2	2			6									5									16
SW															1																1
DN	1									9											1										11
SK								2				1				3															6
SF	6							4		3		9				7															29
CR	40		2			2	8		4	75		1				24			2	1	4	1				68					232
RV	22	1						5		12		4				1			11		2										58
PS	101	7					1	106	21			27				9			7		7	1									287
BY		1										1																			2
AR			1						1				12	1		48					4	1				12	4	2	1		87
RX	8							8		5		7									2										30
AC																							10								10
HV																							1								1
LG															148	25															173
BT	9			1			2	5	17	37		1			1			75	1												148
MS	4					1	1	2	13	1					3																25
CW	16							15	5	61	1				1				1												100
SP										3												4									3
HR	1		5						1			1		8	9						1										29
HL	7							2				2		1										7	4						13
SLG																															11
SBT					7																										7
SMS					4																										4
CAR	1		5							5			9			49					1						6		3	2	81
TAR			1							3			2			5					1					1					13
ARV			1										1																1		2
AHL																4														1	5
AHR												1				1															3
TOTAL	228	10	16	1	11	6	29	233	58	282	2	88	30	10	1	173	148	25	100	3	29	14	11	7	4	81	13	2	5	3	1623

Table 39 Transition matrix for brill feeding on shrimps

		FOLLOWING ELEMENT																								
		TN	SV	TA	LV	SW	DN	SK	SF	CR	FD	RV	PS	FS	BY	AR	RX	LG	BT	MS	CW	HR	HL	STN	CAR	TAR	TOTAL
	TN	10	2	1	1	8		4	57	29	1		36	1		7		1			3	8	1		1		171
	SV	4	4			2			4	3						1						24					42
P	TA								3	1			2														6
R	LV	3																									3
E	SW						12																	10			22
C	DN	6							2				5														13
E	SK	1			1				1	7			3			1		3									17
E	SF	45	1		1	1		2		8			21		2						1	3					84
D	CR	25		4				7	3			2	40		1	3		7							19		111
I	FD																				1						1
N	RV	2								1			3					1			4						11
G	PS	55	4			1		2	12	50		2			3	17	1	3			4	1			3		158
	FS																							2			2
	BY	4								1																	5
E	AR	1								1							7	9							14	2	34
L	RX	1		1						5		1	1			4									1		14
E	LG																		29	11							40
M	BT	4						1				5	9								10						29
E	MS	4	1					1		2			3														11
N	CW	3	1						1	3		1	14														23
T	HR	3	29						1									1					2				36
	HL	2								1																	3
	STN					10	1	1																			12
	CAR								1				16			1	4	14								1	37
	TAR																2	1									3
	TOTAL	173	42	6	3	22	13	17	85	112	1	11	153	2	6	34	14	40	29	11	23	36	3	12	38	3	889

Row labels in the left margin read PRECEDING ELEMENT.

Table 40 Transition matrix for Z. punctatus feeding on mysids

PREY		FOLLOWING ELEMENT																										
		TN	SV	TA	LV	SK	SF	CR	RV	PS	FP	AR	RX	LG	BT	MS	CW	SP	HR	HL	YN	RCW	QV	CAR	TAR	AHL	AHR	TOTAL
	TN	9	4	1	3		5	64	5	43		2		12			2		15	1	1			1				168
	SV		1				1	17		16				1					1	1								38
P	TA	2						1		2										1								6
R	LV			1					3	5			4							9								22
E	SK	1																										1
C	SF	3						2		8									2	1								16
E	CR	28	5	1	4	1	2		5	30				22			2		29	7	1		1	20				158
E	RV	21	4	1	1			2		38				1			12				1							81
D	PS	73	13	1			7	51	22		1	3		2			7	1	7	4	3							195
I	FP									1				5										1				1
N	AR																							1	2			8
G	RX			1				1	3										2	2				1				10
	LG														85	10												95
	BT	11	1					3	26	21							9			9		5						85
E	MS								5	4										1								10
L	CW	7	5					3	3	11		1		1				1	2									34
E	SP									2																		2
M	HR	4			10			3		1		1		30			1		8						2			60
E	HL	7	4					11	9	1				3			1		2							6		44
N	YN						1	1		4																		6
T	RCW									5																		5
	QV	1											5	15													2	1
	CAR	1			3					1		1															2	26
	TAR												1	1										2				2
	AHL		1		1									2										1				6
	AHR									1																		4
	TOTAL	168	38	6	22	1	16	159	81	194	1	8	10	95	85	10	34	2	60	44	6	5	1	26	2	6	4	1084

Table 41 Transition matrix for P. regius feeding on mysids

PRECEDING ELEMENT	FOLLOWING ELEMENT: TN	SV	TA	LV	SW	SF	CR	RV	PS	ST	BY	FP	AR	RX	LG	BT	MS	CW	HR	HL	YN	RCW	QV	CAR	TAR	AHR	HCR	TOTAL
TN	14	6	2	2		2	70	7	17			1	6		11			4	20	2				1				165
SV	1	1					16	4	20									1	1									44
TA							1	1	1																			3
LV							2	1	2					4						8							1	18
SW										2																		2
SF	1						2		2																			5
CR	40	3		3				7	31				3		35			2	33	3	2		1	21				184
RV	25	3		1			8		37						1			22	4	1								102
PS	43	28				1	44	20					2		4			11	19		4	1						177
ST	2																											2
BY							1																					1
FP						1																						1
AR				1										1	6									3				11
RX	4						2									93	15											6
LG						1	3	37	21									19		7		2						108
BT	3						2	3	9											1								93
MS							8	10	22		1								1									15
CW	16	2					12	1	3						32					20			1				1	60
HR	4			7	2		13	11	1									1	7									83
HL	6	1	1				2		3						1													41
YN	1						1		1						17													6
RCW	1														1													3
QV	1			2										1	1									1	1			2
CAR	3			1											1									1				25
TAR																				1								2
AHR				1																								1
HCR																												2
TOTAL	165	44	3	18	2	5	187	102	170	2	1	1	11	6	108	93	15	60	85	43	6	3	2	25	2	1	2	1162

Table 42 Transition matrix for P. regius feeding on gammarids

		FOLLOWING ELEMENT															
		TN	SV	SK	SF	CR	RV	PS	LG	BT	CW	HR	HL	YN	CAR	HCR	TOTAL
	TN	6	1	1		17	1	6			1	4	1				38
	SV					5		2				1		1			9
P	SK							1									1
R E	SF								1								1
E L	CR	12	1		1		2	5	4		1	3		2	1		32
C E	RV	5						1			1	1					8
E M	PS	10	4			4	1					3		2			24
E E	LG									6							6
D N	BT	1				1	2	1			1						6
I T	CW					1	1	2									4
N	HR	2				1							12	1		1	17
G	HL	1	2			4	1	1				5					14
	YN	1	1					4									6
	CAR								1								1
	HCR												1				1
	TOTAL	38	9	1	1	33	8	23	6	6	4	17	14	6	1	1	168

Table 43 Transition matrix for plaice feeding on enchytraeid worms

		FOLLOWING ELEMENT																			
		TN	SW	DN	SK	SF	CR	FD	RV	PS	BY	AR	LG	BT	CW	SP	HR	HL	STN	SLG	SBT	TOTAL
P	TN	51	1		2	33	2	150	7	26	1	15	3	249	21		6					567
R	SW			3															1	4		8
E	DN	4								1				1	1							7
C	SK												1	2								3
E	SF	11						3		3	1	1		44	3							66
E	CR							2		2	1			3								8
D	FD	1								6		3		241	2							253
I	RV	34				1		3		3	1			6	114							162
N	PS	39	1			5	2	16	5		2	4	1	5			8	3				91
G	BY	14				1		1							13							29
	AR												25									25
	LG													32								32
E	BT	18				2			104	5	7				474			1				611
L	CW	387			1	24	3	78	44	38	16	2	1	26		1	4	2				627
E	SP	1																				1
M	HR	6	5				1		1				1	2	1			2				19
E	HL	1							1	1	2				1		1					7
N	STN		1																	1		2
T	SLG																				5	5
	SBT			4															1			5
TOTAL		567	8	7	3	66	8	253	162	85	31	25	32	611	630	1	19	8	2	5	5	2528

Table 44 Transition matrix for plaice feeding on corophiids

		FOLLOWING ELEMENT																		
		TN	SV	TA	LV	SW	DN	SK	SF	FD	RV	PS	BY	AR	BT	MS	CW	SP	HR	HL	SBT	TOTAL
P	TN	8			1			13	84	44	4	122	2	1	31	1	22					333
R	SV							1	11	1		6	1									20
E	TA	1																				1
C	LV	1										1										2
E	SW						2														1	3
E	DN											2					1					3
D	SK									1		24	1		9							35
I	SF	8			1					1		181	5		35		6		1			238
N	FD	1										129	2		75		1		3			211
G	RV	5								2		6					14		2			29
	PS	217	18	1		1		20	123	138	7		4	5	15		21		3			573
	BY	6							3	4									1			14
E	AR														6							6
L	BT	13				1			1		11	10					134	2		2		174
E	MS											1										1
M	CW	68	2					1	12	15	5	87	1					8				199
E	SP	1							3	4	1	1										10
N	HR					1			1	1	1				3					5		12
T	HL	4															1		2			7
	SBT						1															1
TOTAL		333	20	1	2	3	3	35	238	211	29	570	16	6	174	1	200	10	12	7	1	1872

Table 45 Transition matrix for flounder feeding on enchytraeid worms

			FOLLOWING ELEMENT										
			TN	SV	SK	SF	FD	RV	PS	BY	AR	BT	CW	HR	TOTAL
		TN			2	29	21	1	19	1		8	2		83
P		SV							1						1
R	E	SK	1				2		4			3			10
E	L	SF	2				14		35		1	18			70
C	E	FD							3			55			58
E	M	RV	5				2		4			1	1		13
E	E	PS	38		5	36	11	1			1	1		1	94
D	N	BY	1						2						3
I	T	AR					1					1			2
N		BT	27	1	2	5	4	9	12	2			26		88
G		CW	9		1		3	1	14			1			29
		HR						1							1
	TOTAL		83	1	10	70	58	13	94	3	2	88	29	1	452

Table 46 Transition matrix for flounder feeding on corophiids

		FOLLOWING												ELEMENT											
		TN	SV	SW	DN	SK	SF	CR	FD	RV	PS	FS	BY	FP	AR	HV	LG	BT	CW	SP	HR	HL	YN	JP	STN	SBT	SLV	TOTAL
PRECEDING ELEMENT	TN	25	3			9	45	1	12		174	4	3		1			22	6		11							316
	SV	3	3	1		3	10		1		11							1			3				1	3		36
	SW				2											2												8
	DN	8	1				2				10								2									23
	SK	1							3		23							10			7							44
	SF	17	3			3			1		127	1						22			4							178
	CR																1											1
	FD	1									67		2		1			32										103
	RV	2									3								1									6
	PS	205	23			25	112		74	1		2	3	1	3			3	8		8		7		7			475
	FS				8														2		1		1					15
	BY	5					1						1															11
	FP					1			1									4								1	1	1
	AR																											5
	HV																	1										2
	LG								2	2	9								73	1		8						1
	BT	8							5	3	43		2							3	1							103
	CW	29	3			3	5		1		2							8				10						97
	SP						1		1			8							5					1				4
	HR	2		6					1		4																	35
	HL	7					1		1		1																	18
	YN	3					2		1																			8
	JP				1																							1
	STN			1	9																			1				10
	SBT				3																			1				4
	SLV																											1
TOTAL		316	36	8	23	44	179	1	103	6	474	15	11	1	5	2	1	103	97	4	35	18	8	1	10	4	1	1506

Table 47 Transition matrix for sole feeding on enchytraeid worms

		FOLLOWING ELEMENT																						
		TN	SV	LV	PP	SW	DN	SK	SF	FD	RV	PS	ST	FS	BY	FP	UN	BT	CW	SP	HR	HL	YN	JP	STN	TOTAL
PRECEDING ELEMENT	TN	31	2		425	3			201		19	7		2	1		5	15		2	6	2		1		722
	SV				24				15		4	2														45
	LV								1																	1
	PP	366	28	1	2154				800	1	176	16					4	617	1	2	10			4		4180
	SW						9						1												6	16
	DN							3	10		1	6														20
	SK				2							1														3
	SF	215	8		1051						30	27						59		2	7		1	2		1402
	FD				1												1	17				1				1
	RV	6			245				1			9					1	1			7		2			280
	PS	15	1		29				39		4			2	4		9	1			7					111
	ST	3				1	2						6				11				2				10	21
	FS						4								3		1				2					20
	BY	2			1									1							2					10
	FP								2		1	11	8								2					1
	UN	3	2		2		2		2		1	5			1			523								33
	BT	13			71				88		11				1					8						712
	CW	57	1		169				241		32	10			1		4									523
	SP	2			5				5		1	1										8		3		14
	HR	9	2			4			3		1	1	1	6		1	1				3					40
	HL		1		3				1			2					1				1					11
	YN				1							1														3
	JP					7	3						6	9												10
	STN					1																				16
TOTAL		722	45	1	4183	16	20	3	1408	1	280	99	22	20	10	1	33	713	524	14	40	11	3	10	16	8195

results may possibly be jeopardised. Ideally the mixing of frequencies obtained from sequences of different lengths in transition matrices should be avoided, although with long sequences the differences are reduced.

Each transition matrix provides information on the transitional frequencies of the behavioural elements which occur during feeding sessions. Table 36, for example, shows the frequency with which Lunge (LG) follows Skim (SK) when turbot feed on mysids or the frequency with which Swim-Lunge (SLG) follows Hover (HV) etc.. Using these data it is possible to reconstruct the 'typical' sequences of elements that a fish displays during a feeding session. Before attempting this, however, following elements must be demonstrated to be truly dependent upon the preceeding element(s) and not independent or random in their sequential relationships.

The row and column totals show that the elements of behaviour are not equally distributed. Table 48 gives the chi-squared goodness of fit values for the observed frequency of occurrences of elements for each feeding trial. All values are highly significant ($p \ll 0.005$) showing that the observed frequency of certain elements differ greatly from the expected frequency within each feeding trial. (Assuming a random distribution of behaviour patterns, the expected frequency is determined by dividing the total number of elements observed by the number of different types of element exhibited for each feeding trial.)

Table 11 gives a list of the elements that occur more often than expected in each feeding trial and the cumulative percentage frequency for which they account. For example, in the feeding trial plaice/enchytraeid worms, 5 elements (CW, BT, TN, FD and RV) occurred

Table 48 The Chi-squared 'Goodness of Fit' test values for the observed frequency of the occurrence of elements.

Flatfish species	Prey species	Chi^2	Degrees of freedom
Turbot	Mysids	10792	30
Turbot	Shrimps	3113	31
Brill	Mysids	3474	29
Brill	Shrimps	1540	24
Z. punctatus	Mysids	1934	25
Z. punctatus	Gammarids	80	10
P. regius	Mysids	2080	26
P. regius	Gammarids	176	14
Plaice	Worms	6920	19
Plaice	Corophiids	4695	19
Flounder	Worms	420	11
Flounder	Corophiids	5326	25
Sole	Worms	52851	23

All tests were significant at $p<0.001$.

more often than expected and they accounted for 87.7% of all behavioural elements observed. From Table 11 it can be seen that in the same feeding trial only 3 additional elements (PS, SF and LG), making 8 (5 + 3) elements in all, were required to account for 95% of all observed elements. By subtraction, the remaining 12 (20 - 8) elements occurred with such low frequencies that they only accounted for 5% of the total.

Clearly each feeding trial contains a large number of elements which occur infrequently (the number of elements that comprise the least frequent 5% of behavioural elements ranges between 5 - 18). Recording occurrences of these infrequent elements yields worthwhile information about the diversity of behavioural elements, which are in many instances characteristic of certain species, such as Reverse-Chew (RCW) and Quiver (QV) for topknots or Omega-Jump (JP) for sole. It does have the disadvantage, however, that a high proportion of elements with low frequencies imposes limitations on the analysis of transition matrices. When testing for independence in a transition matrix, Cochran (1954) has suggested that none of the expected values should be less than one and that less than 20% should be less than 5. If these conditions are not met the chi-squared approximation becomes invalid and the test is not suitable. Chatfield and Lemon (1970) suggest that if the data do not satisfy these conditions, the size of the transition matrix must be reduced by combining the least frequent behaviour patterns with associated patterns. This was not considered to be a suitable approach for this data because complex elements cannot be resolved satisfactorily to simple elements. For example, should Reverse-Chew be combined with Reverse or with Chew?

Lemon and Chatfield (1971) suggest that when the chi-squared

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Lemon and Chatfield (1971) suggest that when the chi-squared

approximation is not valid an alternative approach to the analysis of such data is the application of information theory.

The use of information theory to analyse a sequence of events was pioneered by Miller and Frick (1949) and has since been used fairly widely (see for example Altmann, 1965; Garner, 1962; and Hazlett and Bossert, 1965). A readable introduction to the subject in a psychological context is given by Attneave (1959) and by Garner (1962).

The information theory approach consists of calculating the average conditional uncertainty for strings of elements of different lengths. A 'string' is defined as a sequential series of elements of behaviour consisting of a specified but unlimited number of elements (or events).

The amount of information associated with an event, which has a probability p, can be measured by the quantity $\log_2(1/p)$ which is equal to $-\log_2 p$. With c outcomes, having respective probabilities P(i), the average amount if information is given by:

$$H = E - \log_2 p = - \sum_{i=1}^{i=c} P(i) \log_2 P(i)$$

where E denotes the expected value operator. The quantity H is often called the Shannon measure of information. (NB the logarithmic base 2 is used and H is therefore measured in binary digits or bits.) The maximum value of H is equal to $\log_2 c$ and this occurs when all outcomes are equally probable so that P (i) = 1/c for all i, in which case there is maximum uncertainty. The minimum possible value of H is equal to zero and occurs when one of the outcomes has a probability of one, i.e. there is no uncertainty.

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In order to use information theory as a substitute for a

chi-squared goodness to fit test, H values are calculated for single elements and for pairs of elements. Then if successive events are independent:

$$H \text{ (singles)} < H \text{ (pairs)} = 2 \times H \text{ (singles)}$$

i.e. knowledge of an event does not lead to a reduction in uncertainty of what will be the next event, in other words there is no dependence between an element and that which follows it. If knowledge of an event does not lead to a reduction in uncertainty of what will be the next event, the conditional uncertainty value for pairs of elements H (pairs) will be less than that for twice the value of H (singles) and the relationship:

$$H \text{ (singles)} < H \text{ (pairs)} < 2 \times H \text{ (singles)}$$

demonstrates that successive events are dependent.

Table 49 Values of the Shannon index of information which show that there is at least second order dependence between elements within feeding trials.

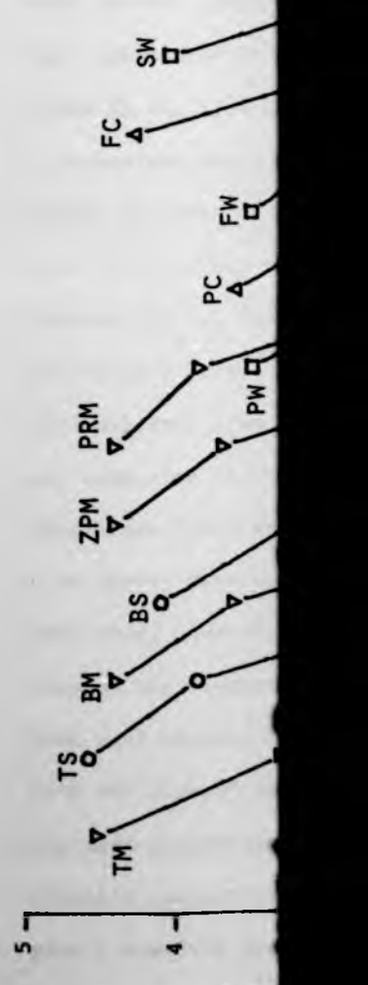
	TM	TS	BM	BS	ZPM	PRM	PW	PC	FW	FC	SW
H (singles)	3.27	3.85	3.59	3.18	3.66	3.82	2.44	2.63	2.69	2.47	2.27
H (pairs)	4.89	5.80	5.21	4.62	5.56	5.91	3.72	4.28	4.43	3.78	3.89
2xH (singles)	6.54	7.70	7.18	6.36	7.32	7.64	4.38	5.26	5.38	4.94	4.54

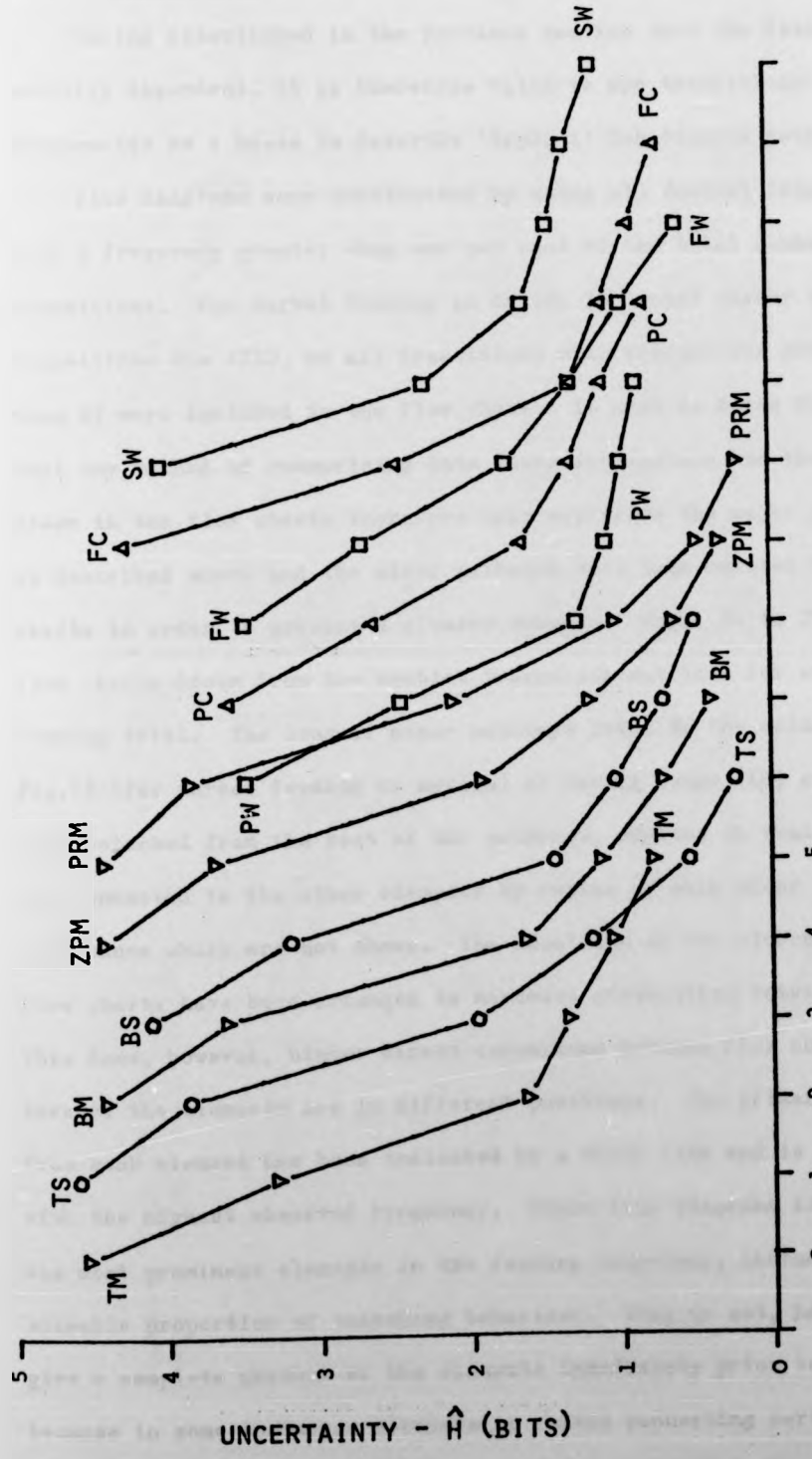
One can discern from Table 49 that pairs of events are not independent and there is clearly a measure of dependence of an event on that which preceeded it. This is entirely in accordance with

expectation since if a predator's hunting was described by a random sequence of behavioural elements it would probably starve to death! It is obvious that the dependency is in this case at least second order (or a first order Markovian model). To determine whether a third order model (knowing the two preceeding behaviour patterns and predicting the third) is appropriate a value of H must be calculated for triplets. To investigate higher order dependencies H values must be calculated for the appropriate number of elements in a string. Chatfield and Lemon (1970) suggest that a graphical procedure is the best means of determining the order of dependency (see Fig. 13) because it is often possible to see the point at which H_i starts to decrease relatively slowly. Such graphs demonstrate the reduction in uncertainty of predicting a behavioural element having the knowledge of the foregoing string of elements. Graphs of all feeding trials show there is at least a second order dependence (or first order Markov chain). In some instances this is very pronounced and is clearly the entire extent of the dependence e.g. Plaice/Worms and Turbot/Mysids, but in other instances e.g. the topknot feeding on mysids there is evidence that the dependence may extend to be third order.

It must be borne in mind, however, that the sequence of events during flatfish feeding behaviour is not merely an innate ordered series of actions but a sensitive interactive system of responses which are modified by their external environments, especially by the stimuli provided by the prey. Therefore although the finding that the data may be described as Markov chains is of considerable interest its significance must not be overemphasised.

FIGURE 13 THE AMOUNT OF UNCERTAINTY ASSOCIATED WITH DIFFERENT ORDERS OF DEPENDENCY FOR ONE FEEDING SESSION FROM EACH FEEDING TRIAL.





(The curve for each feeding trial is moved successively along the abscissa)

4.10. Flow charts.

Having established in the previous section that the data are serially dependent, it is therefore valid to use transitional frequencies as a basis to describe 'typical' behavioural pathways.

Flow diagrams were constructed by using all doublet transitions with a frequency greater than one per cent of the total number of transitions. For turbot feeding on mysids the total number of transitions was 4730, so all transitions with frequencies greater than 47 were included in the flow chart. It must be borne in mind that any method of summarising data loses information and the arrows drawn in the flow charts therefore only represent the major pathways as described above and the minor pathways have been omitted from the charts in order to present a clearer summary. Figs. 14 to 25 are flow charts drawn from the doublet transition matrices for each feeding trial. The loss of minor pathways leads to the situation in Fig.14 (for turbot feeding on mysids) of having Lunge (LG) and Bite (BT) detached from the rest of the pathways, whereas in reality they are connected to the other elements by routes of only minor importance which are not shown. The locations of the elements in the flow charts have been arranged to minimise cross-overs between arrows. This does, however, hinder direct comparison between flow charts because the elements are in different positions. The primary route from each element has been indicated by a thick line and is the route with the highest observed frequency. These flow diagrams illustrate the most prominent elements in the feeding behaviour, including a sizeable proportion of searching behaviour. They do not, however, give a complete picture of the elements immediately prior to attack, because in some instances elements or routes connecting certain

FIGURE 14 FLOW CHART FOR TURBOT FEEDING ON MYSIDS

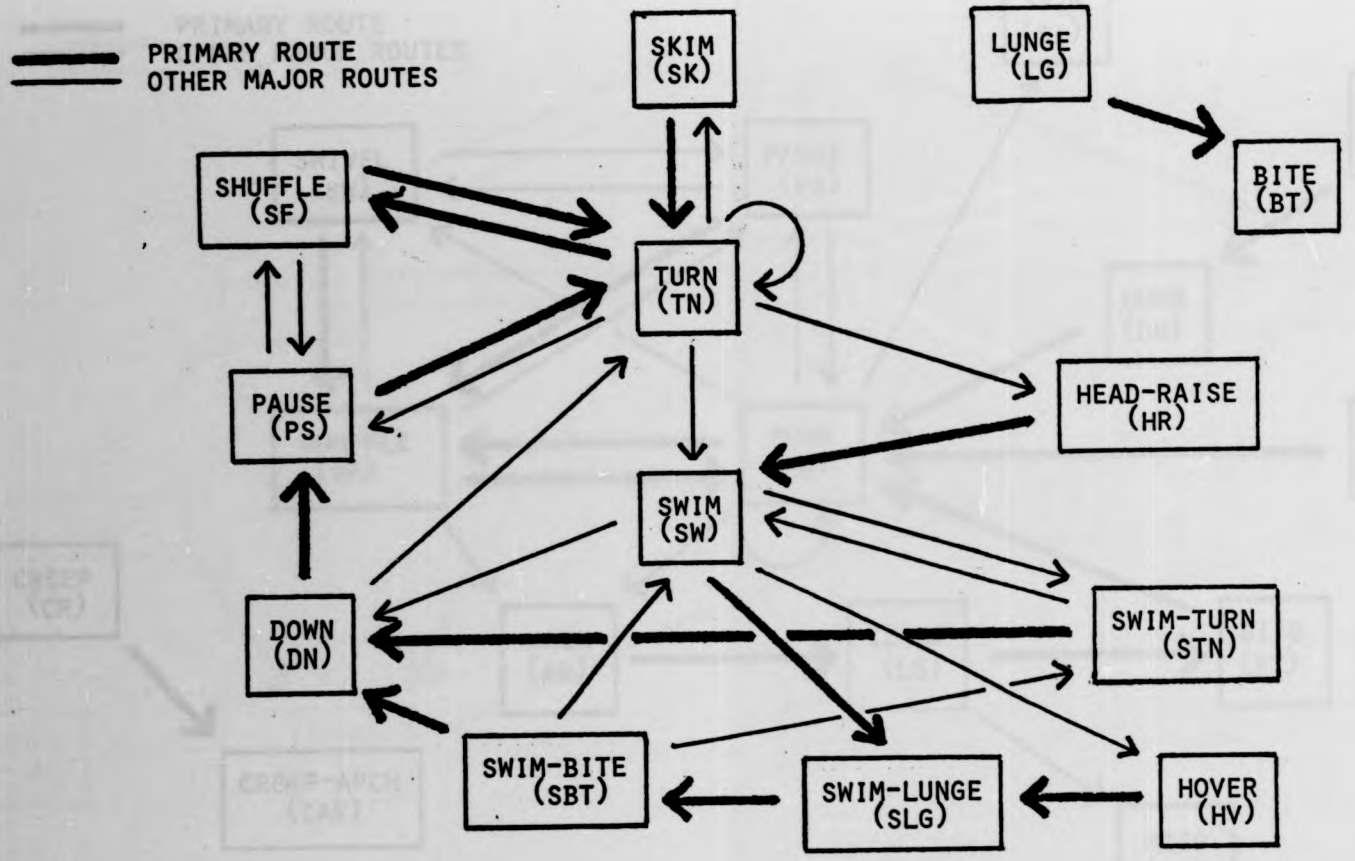


FIGURE 15 FLOW CHART FOR TURBOT FEEDING ON SHRIMPS

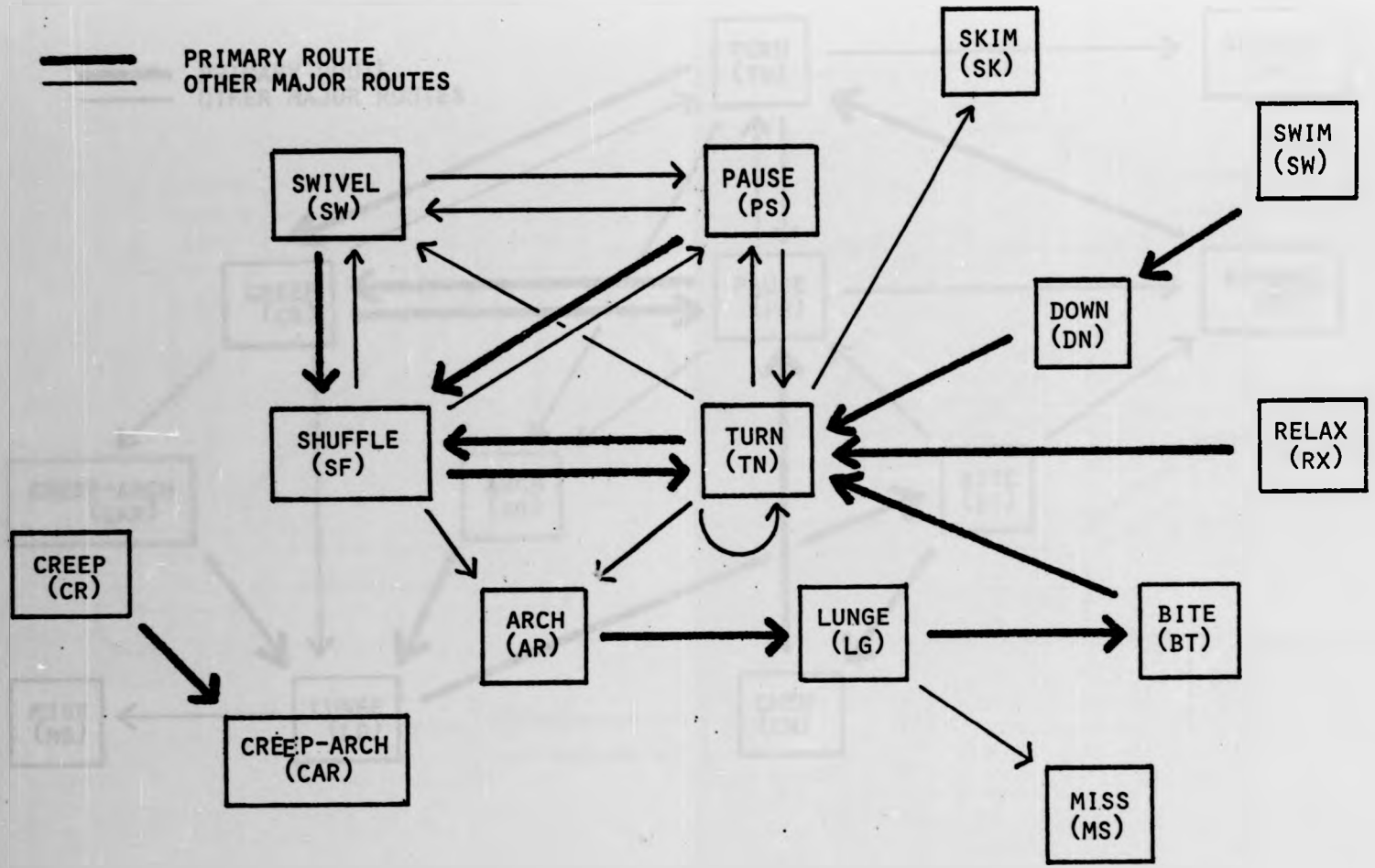


FIGURE 16 . FLOW CHART FOR BRILL FEEDING ON MYSIDS

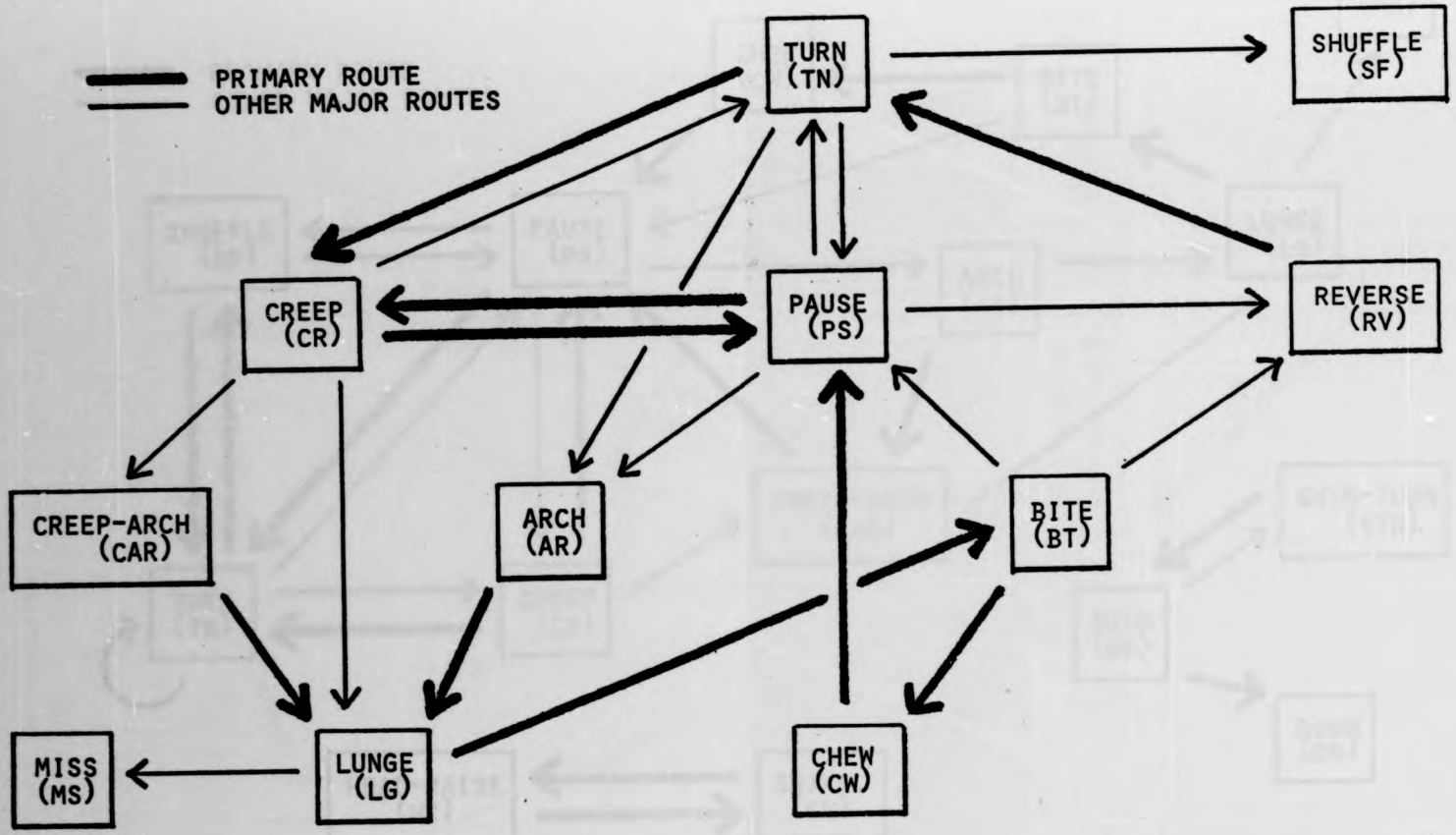


FIGURE 17 FLOW CHART FOR BRILL FEEDING ON SHRIMPS

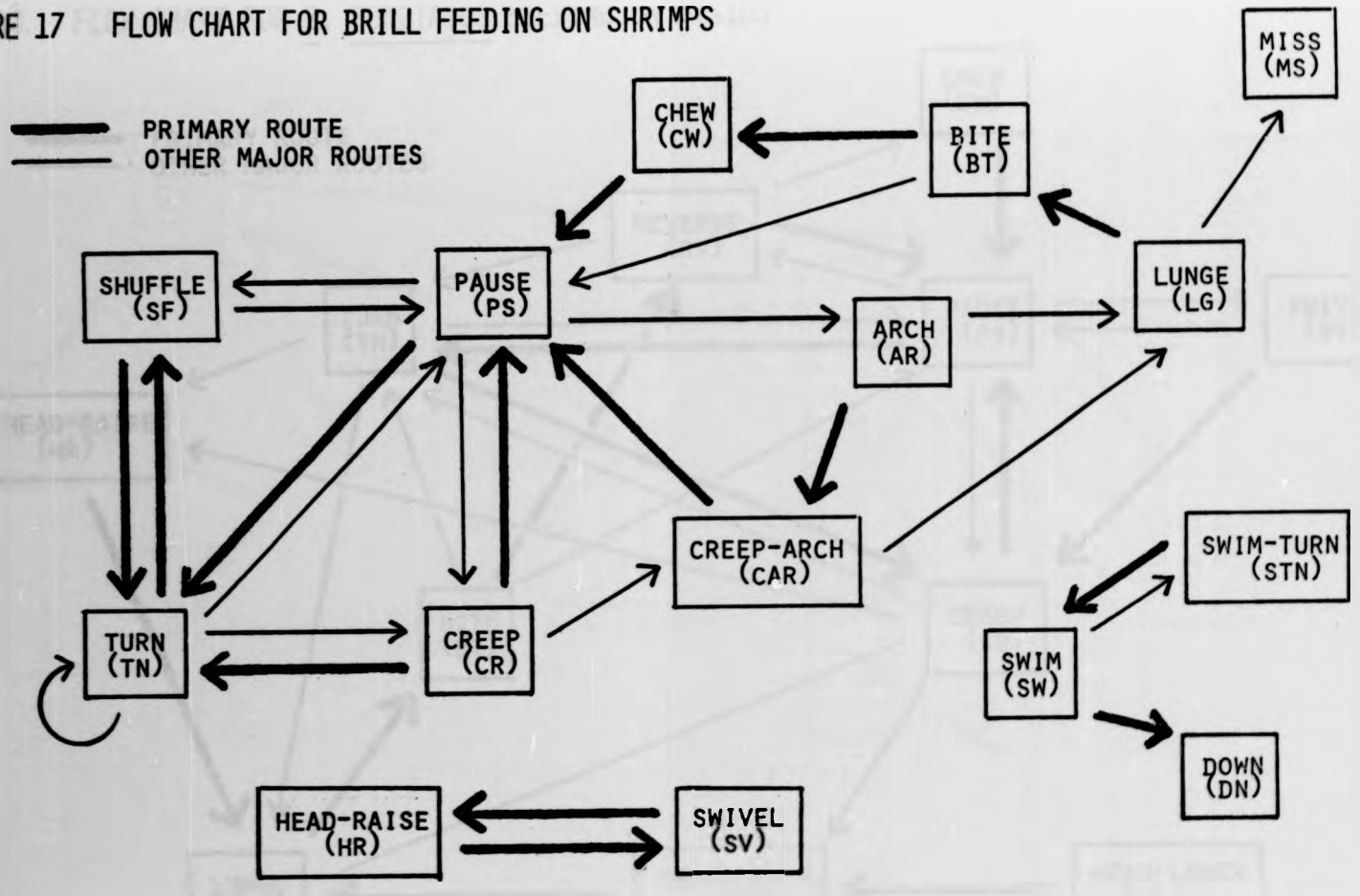


FIGURE 18 FLOW CHART FOR Z. PUNCTATUS FEEDING ON MYSIDS

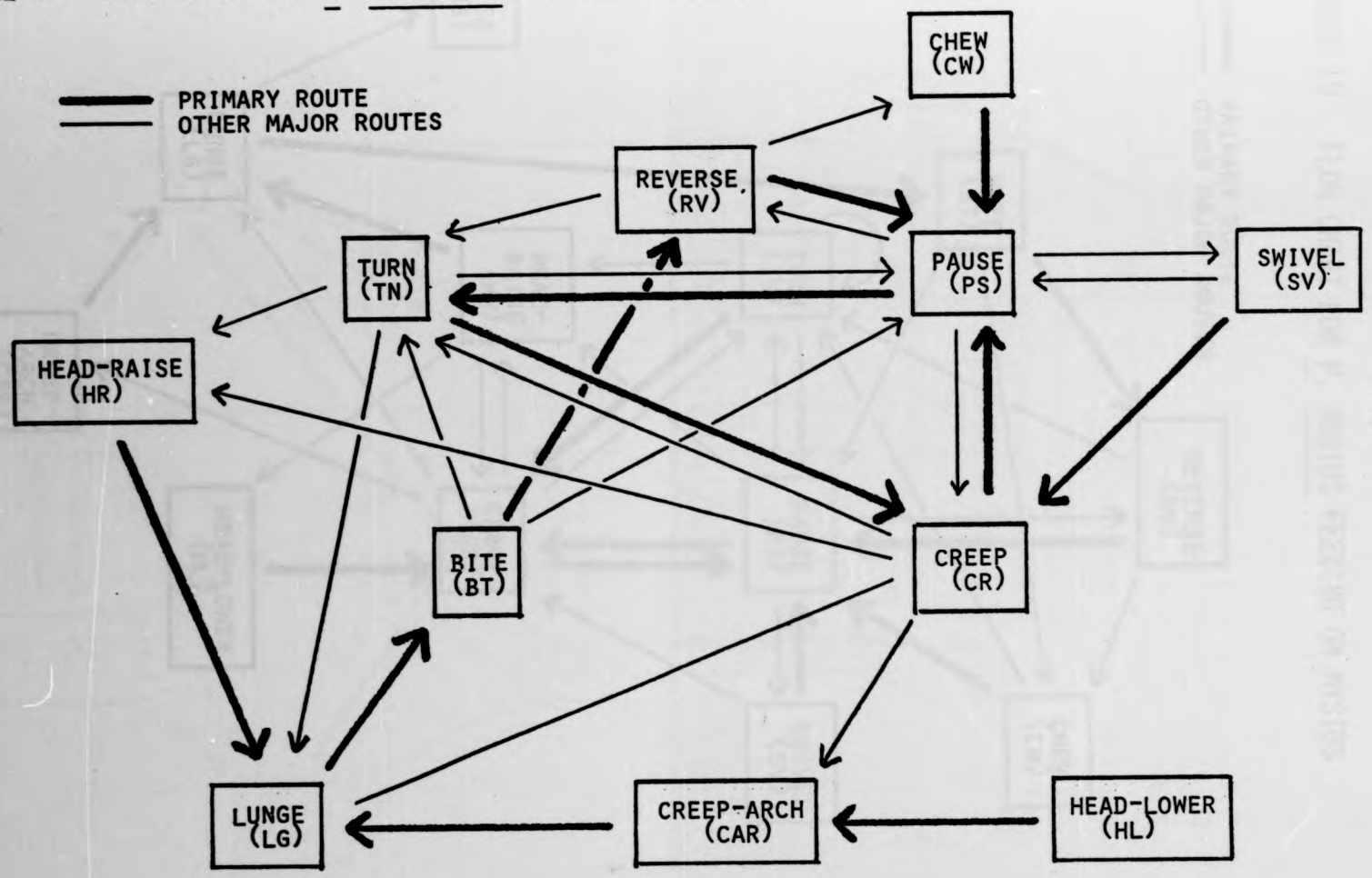


FIGURE 19 FLOW CHART FOR P. REGIUS FEEDING ON MYSIDS

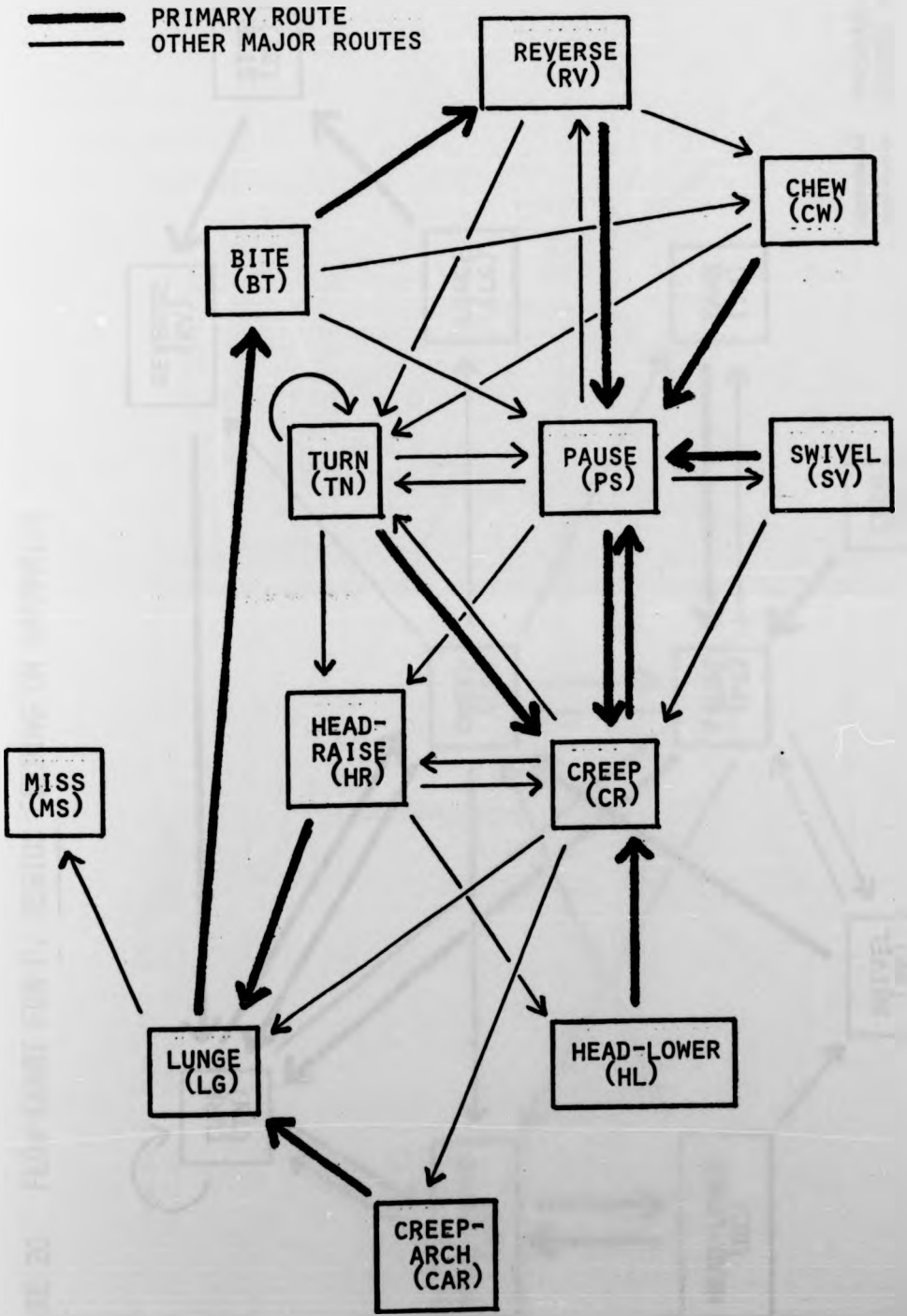


FIGURE 20 FLOW CHART FOR P. REGIUS FEEDING ON GAMMARIDS

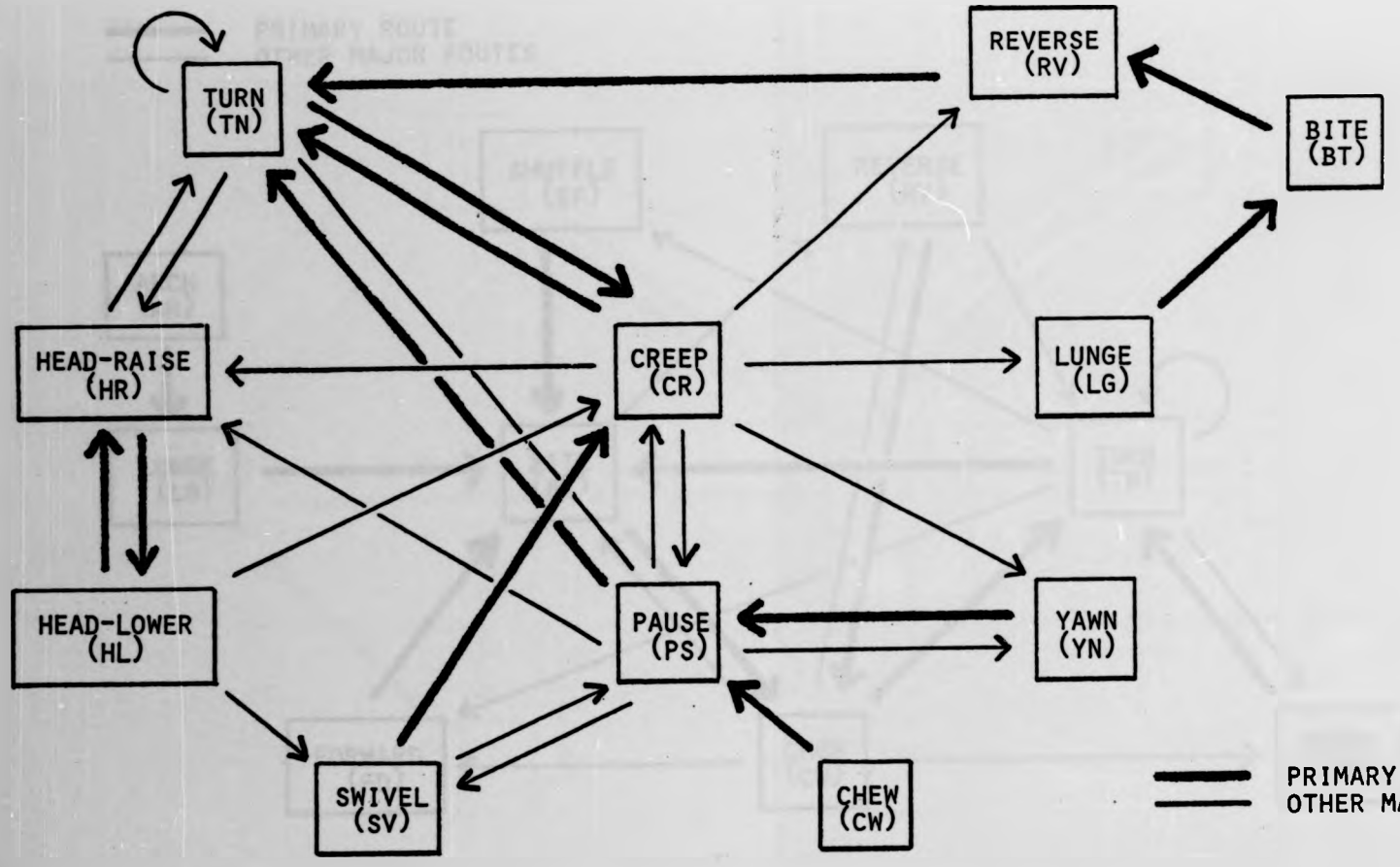


FIGURE 21 FLOW CHART FOR PLAICE FEEDING ON ENCHYTRAEID WORMS

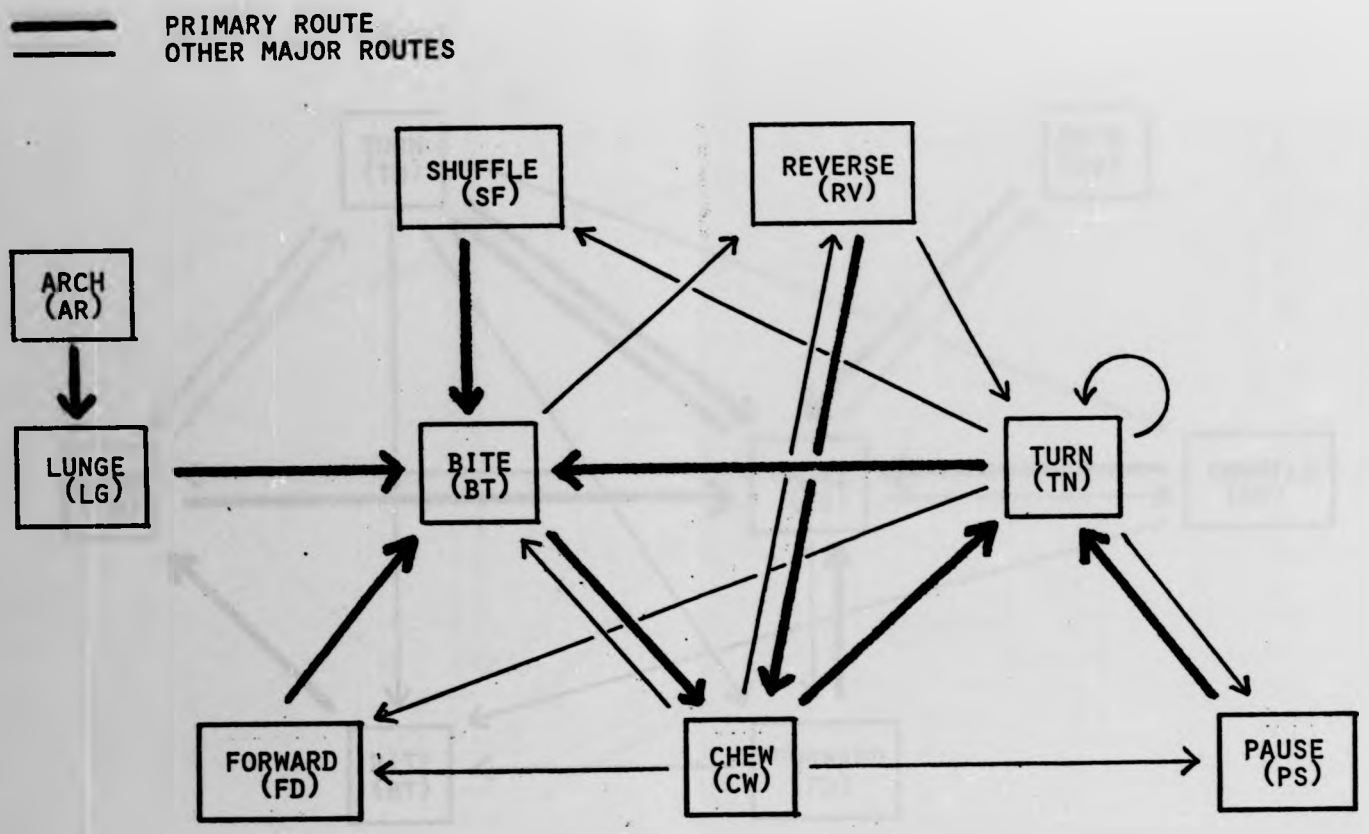


FIGURE 21 FLOW CHART FOR PLAICE FEEDING ON ENCHYTRAEID WORMS

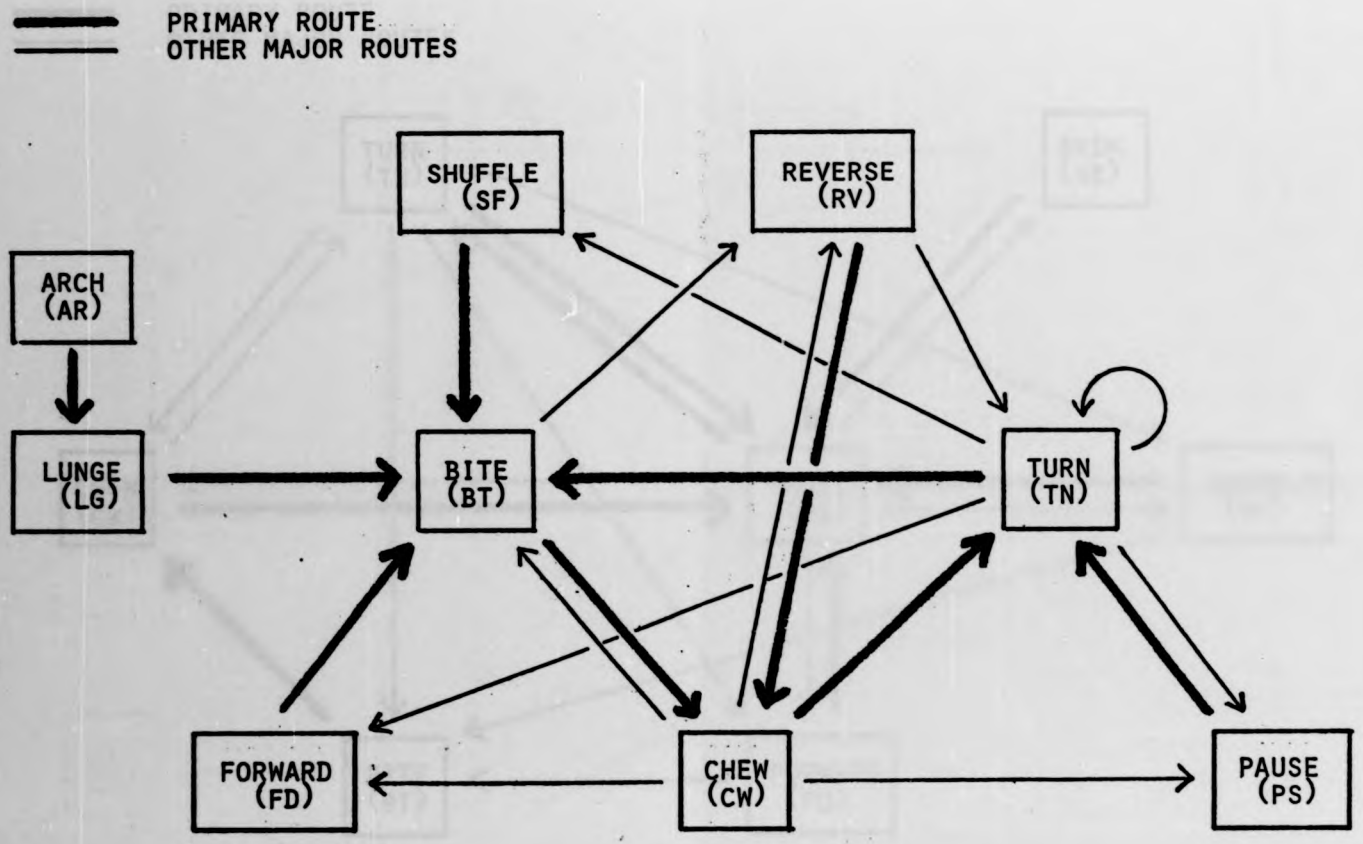


FIGURE 22 FLOW CHART FOR PLAICE FEEDING ON COROPHIIDS

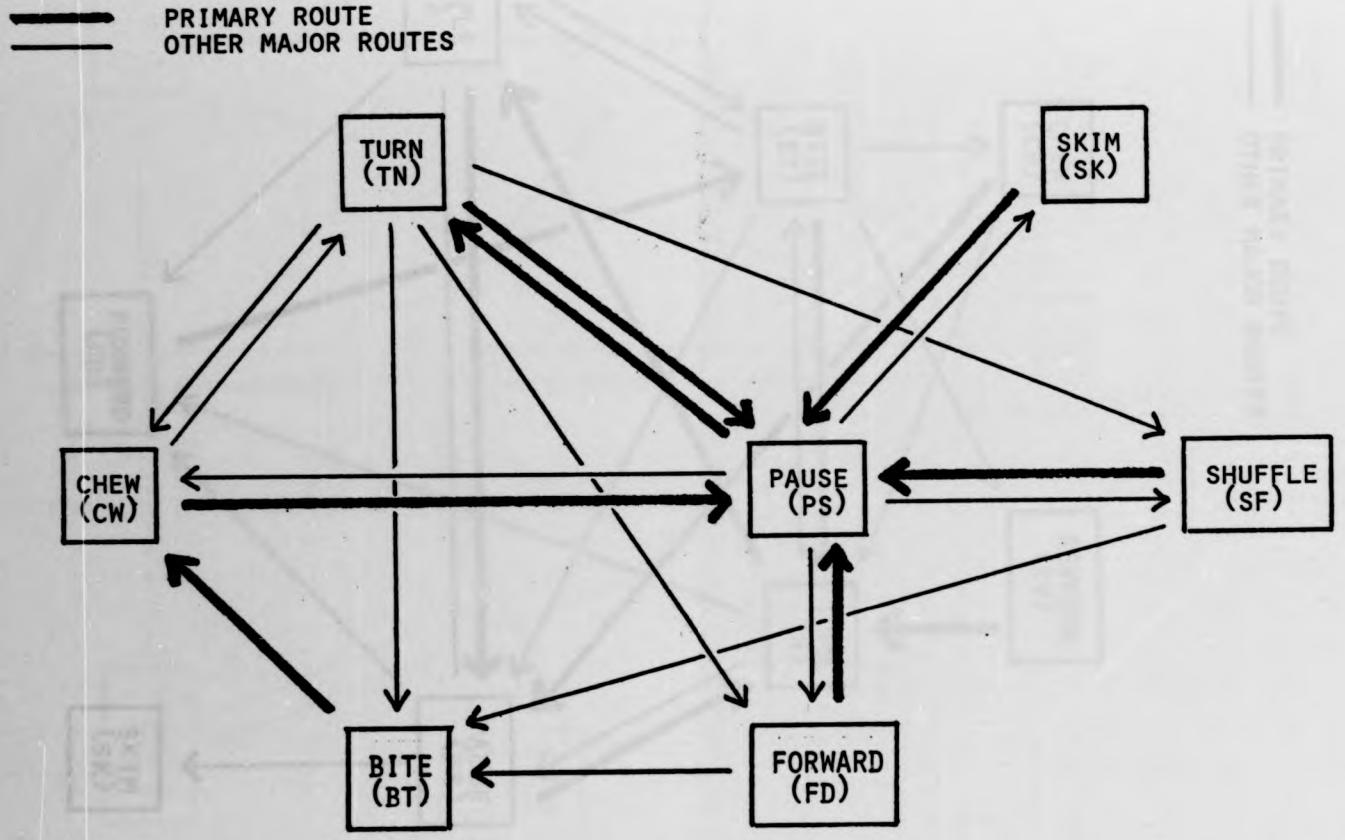


FIGURE 23 FLOW CHART FOR FLOUNDER FEEDING ON ENCHYTRAEID WORMS.

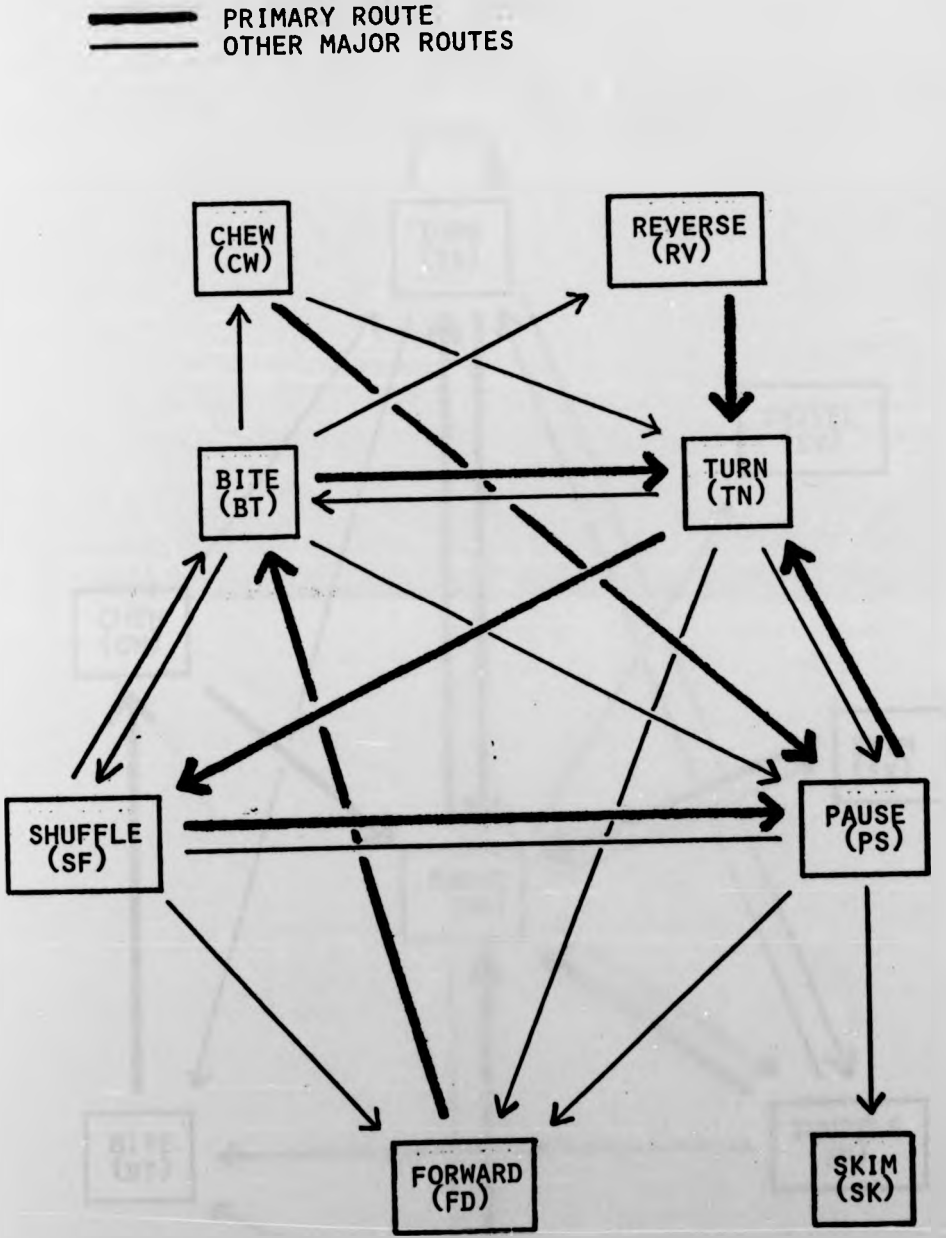


FIGURE 24 FLOW CHART FOR FLOUNDER FEEDING ON COROPHIIDS

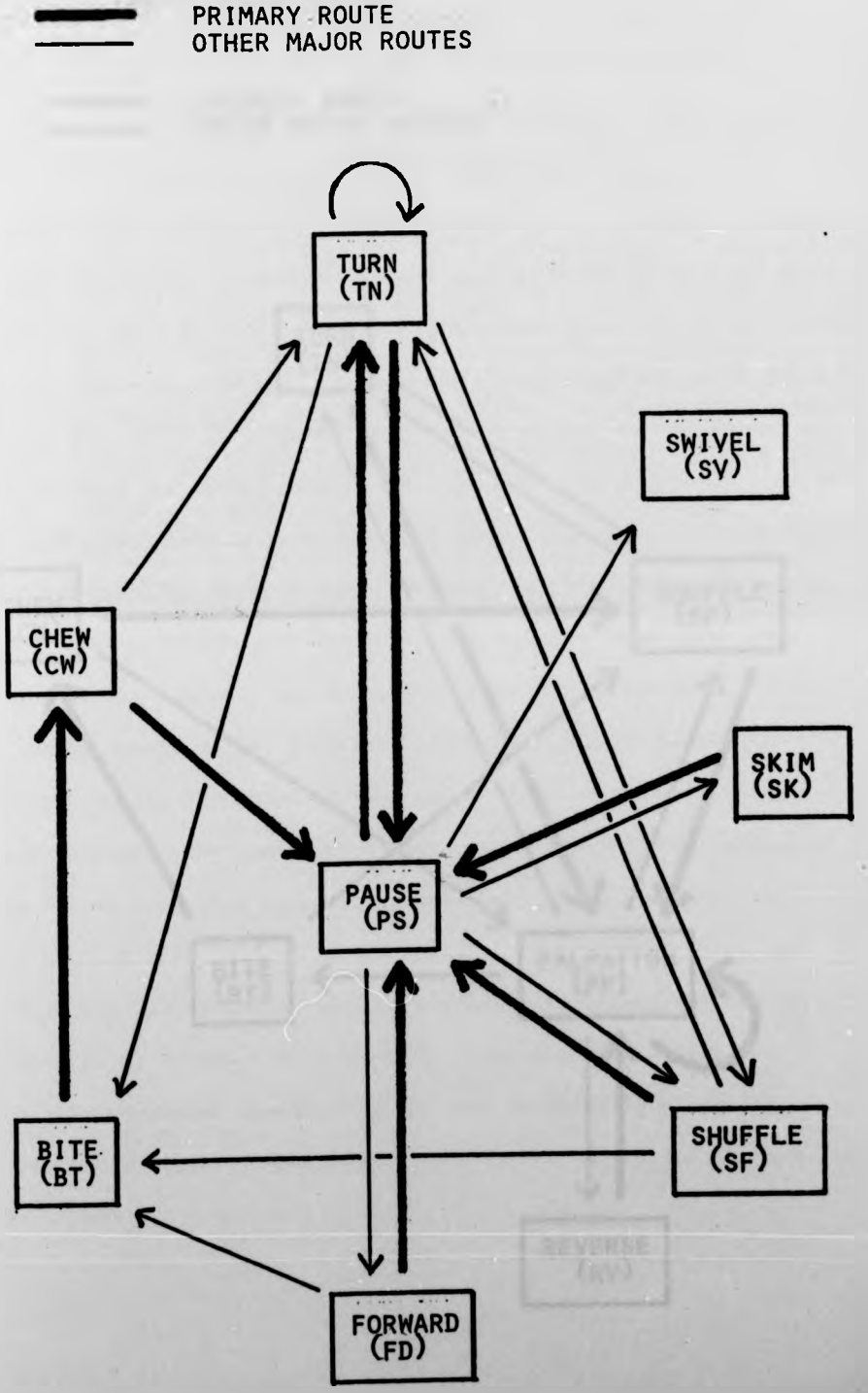
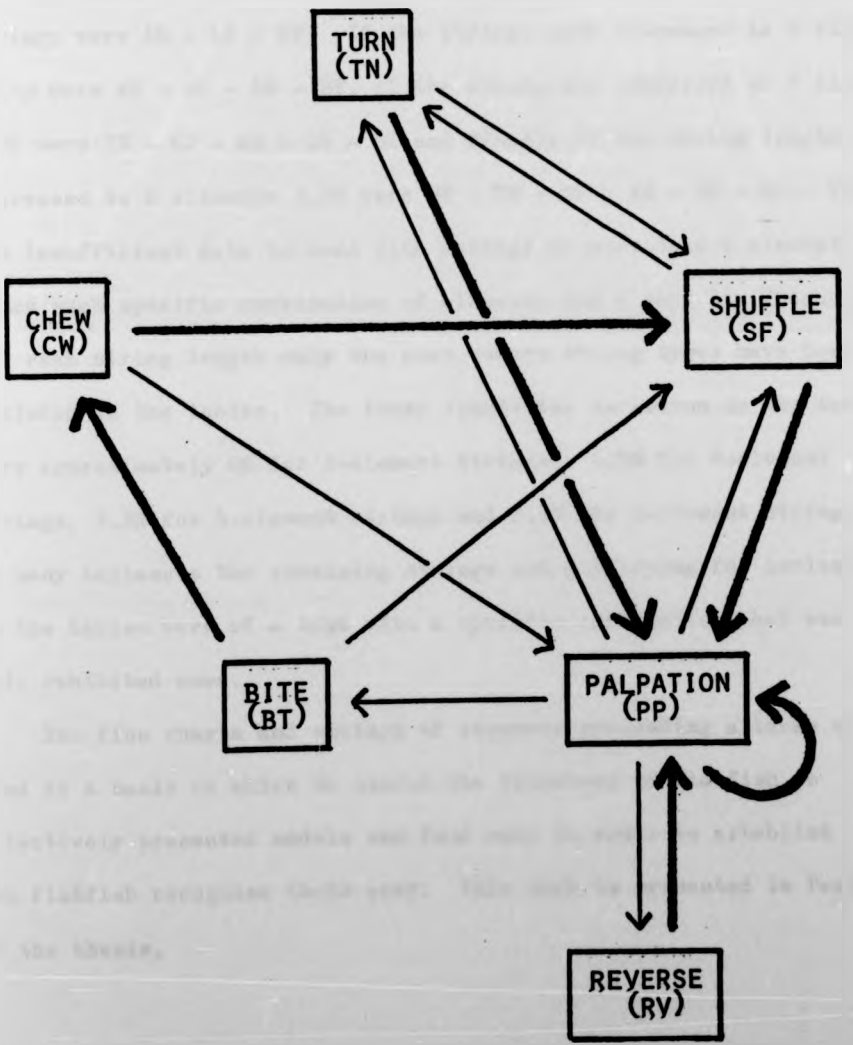


FIGURE 25 FLOW CHART FOR SOLE FEEDING ON ENCHYTRAEID WORMS.



elements have been omitted for the sake of clarity. The most enlightening method of assessing the elements immediately prior to attack is to look at the actual strings of elements themselves. This was carried out for strings of 3, 4, 5 and 6 elements terminated by an attack Bite (BT), Miss (MS), Swim-Bite (SBT) and Swim-Miss (SMS). Tables 50 to 60 show the most common strings of 3, 4, 5 and 6 elements.

In Table 51 for turbot feeding on shrimps 29.5% of all 3 element strings were AR - LG - BT. If the strings were increased to 4 elements 13.1% were SF - AR - LG - BT, if the string was comprised of 5 elements 6.6% were TN - SF - AR - LG - BT and finally if the string length was increased to 6 elements 3.3% were BT - TN - SF - AR - LG - BT. There was insufficient data to deal with strings or more than 6 elements since each specific combination of elements had a very low frequency. For each string length only the most common string types have been included in the tables. The lower limits for inclusion in the tables were approximately 6% for 3-element strings. 4.5% for 4-element strings, 3.3% for 5-element strings and 2.5% for 6-element strings. In many instances the remaining strings not qualifying for inclusion in the tables were of a type with a specific combination that was only exhibited once.

The flow charts and strings of elements preceeding attacks were used as a basis on which to assess the responses of flatfish to selectively presented models and food cues in order to establish how flatfish recognise their prey. This work is presented in Part Three of the thesis.

Table 50 The most commonly observed strings with their percentage frequencies for turbot feeding on mysids.

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				SW	SLG	SBT	36.5
				HV	SLG	SBT	21.7
				TN	LG	BT	8.6
				HR	LG	BT	6.0
4			TN	SW	SLG	SBT	18.4
			SW	HV	SLG	SBT	11.7
			HR	SW	SLG	SBT	6.4
			STN	SW	SLG	SBT	5.8
			TN	HV	SLG	SBT	5.1
5		SF	TN	SW	SLG	SBT	7.3
		TN	SW	HV	SLG	SBT	4.1
		TN	HR	SW	SLG	SBT	4.0
		SW	STN	SW	SLG	SBT	4.0
		PS	TN	SW	SLG	SBT	3.3
6	TN	SF	TN	SW	SLG	SBT	4.2
	PS	TN	SW	HV	SLG	SBT	2.7

Table 51 The most commonly observed strings with their percentage frequencies for turbot feeding on shrimps

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				AR	LG	BT	29.5
				AR	LG	MS	14.7
				CAR	LG	BT	11.5
				SF	LG	BT	9.8
4			SF	AR	LG	BT	13.1
			AR	CAR	LG	BT	6.6
			TN	SF	LG	BT	6.6
			TN	AR	LG	MS	6.6
			TN	AR	LG	BT	4.9
			SK	AR	LG	BT	4.9
			CR	CAR	LG	BT	4.9
5		TN	SF	AR	LG	BT	6.6
		TN	SK	AR	LG	BT	4.9
		SF	SV	AR	LG	BT	3.3
		SF	TN	AR	LG	BT	3.3
		PS	TN	SF	LG	BT	3.3
		SF	TN	AR	LG	MS	3.3
		SW	STN	SW	SLG	SMS	3.3
6	BT	TN	SF	AR	LG	BT	3.3
	TN	SF	TN	AR	LG	MS	3.3

Table 52 The most commonly observed strings with their percentage frequencies for brill feeding on mysids.

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				AR	LG	BT	23.9
				CAR	LG	BT	21.2
				CR	LG	BT	11.4
4			CR	CAR	LG	BT	19.6
			TN	AR	LG	BT	10.9
			CR	CAR	LG	MS	4.9
			TN	CR	LG	BT	4.9
			PS	AR	LG	BT	4.3
5		PS	CR	CAR	LG	BT	7.6
		TN	CR	CAR	LG	BT	6.5
		PS	TN	AR	LG	BT	3.8
		CR	TN	AR	LG	BT	3.3
6	PS	TN	CR	CAR	LG	BT	3.8
	CR	PS	CR	CAR	LG	BT	2.7
	PS	CR	TN	AR	LG	BT	2.2
	PS	TN	SF	AR	LG	BT	2.2
	PS	TN	CR	CAR	LG	MS	2.2

Table 53 The most commonly observed strings with their percentage frequencies for brill feeding on shrimps

Number of elements in string	ELEMENTS COMPRISING STRING					Percentage frequency
3			CAR	LG	BT	30.0
			AR	LG	BT	15.0
			CR	LG	BT	10.0
			SK	LG	BT	7.5
			AR	LG	MS	7.5
			CR	LG	MS	7.5
4		CR	CAR	LG	BT	17.5
		TN	AR	LG	BT	7.5
		AR	CAR	LG	BT	7.5
		CR	SK	LG	BT	5.0
		PS	CAR	LG	BT	5.0
		PS	CR	LG	BT	5.0
		PS	AR	LG	BT	5.0
5	SF	CR	CAR	LG	BT	5.0
	CR	TN	AR	LG	BT	5.0
	CAR	PS	CAR	LG	BT	5.0
	CAR	PS	AR	LG	BT	5.0
	PS	AR	CAR	LG	BT	5.0
6	AR	CAR	PS	AR	LG	BT	5.0
	CAR	PS	AR	CAR	LG	BT	5.0

Table 54 The most commonly observed strings with their percentage frequencies for Z. punctatus feeding on mysids.

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				HR	LG	BT	28.4
				CR	LG	BT	21.1
				CAR	LG	BT	13.7
				TN	LG	BT	11.6
4			CR	CAR	LG	BT	13.7
			CR	HR	LG	BT	12.6
			TN	HR	LG	BT	10.5
			TN	CR	LG	BT	7.4
			CR	TN	LG	BT	5.3
			SV	CR	LG	BT	5.3
5		TN	CR	HR	LG	BT	8.4
		TN	CR	CAR	LG	BT	5.2
		PS	TN	CR	LG	BT	4.2
		PS	CR	CAR	LG	BT	4.2
6	PS	TN	CR	HR	LG	BT	5.3
	PS	TN	CR	CAR	LG	BT	4.2

Table 55 The most commonly observed strings with their percentage frequencies for P. regius feeding on mysids

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				CR	LG	BT	29.6
				HR	LG	BT	25.9
				CAR	LG	BT	13.0
				TN	LG	BT	6.5
4			CR	HR	LG	BT	13.0
			CR	CAR	LG	BT	11.1
			TN	CR	LG	BT	10.2
			PS	CR	LG	BT	5.6
			HR	CR	LG	BT	4.6
5		TN	CR	CAR	LG	BT	5.6
		CW	TN	CR	LG	BT	3.7
		PS	CR	HR	LG	BT	3.7
		CR	TN	AR	LG	BT	3.7
6	CW	TN	CR	CAR	LG	BT	2.8

Table 55 The most commonly observed strings with their percentage frequencies for *P. regius* feeding on mysids

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				CR	LG	BT	29.6
				HR	LG	BT	25.9
				CAR	LG	BT	13.0
				TN	LG	BT	6.5
4			CR	HR	LG	BT	13.0
			CR	CAR	LG	BT	11.1
			TN	CR	LG	BT	10.2
			PS	CR	LG	BT	5.6
			HR	CR	LG	BT	4.6
5		TN	CR	CAR	LG	BT	5.6
		CW	TN	CR	LG	BT	3.7
		PS	CR	HR	LG	BT	3.7
		CR	TN	AR	LG	BT	3.7
6	CW	TN	CR	CAR	LG	BT	2.8

Table 56 The most commonly observed strings with their percentage frequencies for plaice feeding on worms

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				CW	TN	BT	27.4
				TN	FD	BT	24.0
				CW	FD	BT	11.7
4			BT	CW	TN	BT	23.4
			CW	TN	FD	BT	19.0
			BT	CW	FD	BT	7.5
5		TN	BT	CW	TN	BT	14.3
		BT	CW	TN	FD	BT	12.8
		RV	CW	TN	FD	BT	5.5
		FD	BT	CW	TN	BT	5.0
		FD	BT	CW	FD	BT	3.1
6	CW	TN	BT	CW	TN	BT	9.9
	FD	BT	CW	TN	FD	BT	6.3
	TN	BT	CW	TN	FD	BT	5.8
	BT	RV	CW	TN	FD	BT	5.2
	TN	FD	BT	CW	TN	BT	3.2

Table 57 The most commonly observed strings with their percentage frequencies for plaice feeding on corophiids.

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				PS	FD	BT	23.3
				TN	SF	BT	10.8
				TN	FD	BT	10.8
				PS	TN	BT	9.7
4			FD	PS	FD	BT	9.1
			PS	TN	SF	BT	8.0
			SF	PS	FD	BT	6.2
			CW	TN	FD	BT	4.5
			PS	TN	FD	BT	4.5
5		PS	FD	PS	FD	BT	6.8
		PS	SF	PS	FD	BT	4.5
		CW	PS	TN	SF	BT	4.0
		BT	CW	TN	FD	BT	4.0
6	FD	PS	FD	PS	FD	BT	4.0
	BT	CW	PS	TN	SF	BT	3.4
	BT	CW	PS	TN	FD	BT	2.8

Table 58 The most commonly observed strings with their percentage frequencies for flounder feeding on enchytraeid worms.

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				TN	FD	BT	23.9
				SF	FD	BT	15.9
				TN	SF	BT	10.2
				PS	FD	BT	9.1
				PS	SF	BT	6.8
4			TN	SF	FD	BT	11.3
			PS	TN	FD	BT	10.2
			BT	TN	FD	BT	8.0
			PS	TN	SF	BT	5.7
			CW	TN	FD	BT	5.7
			FD	BT	FD	BT	4.5
5		BT	TN	SF	FD	BT	5.7
		FD	BT	TN	FD	BT	5.7
		BT	CW	TN	FD	BT	4.5
		BT	PS	TN	FD	BT	3.4
		FD	BT	CW	FD	BT	3.4
		PS	TN	SF	FD	BT	3.4
		CW	PS	TN	FD	BT	3.4
6	FD	BT	TN	SF	FD	BT	5.7
	TN	FD	BT	CW	FD	BT	3.4
	BT	CW	PS	TN	FD	BT	3.4

Table 59 The most commonly observed strings with their percentage frequencies for flounder feeding on corophiids.

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				PS	FD	BT	14.0
				PS	TN	BT	9.3
				TN	SF	BT	9.3
				PS	SF	BT	8.4
4			BT	CW	TN	BT	4.7
			CW	PS	SF	BT	4.7
			PS	TN	SF	BT	4.7
5		BT	CW	PS	SF	BT	3.7
6	PS	TN	BT	CW	TN	BT	2.8

Table 60 The most commonly observed strings with their percentage frequencies for sole feeding on enchytraeid worms.

Number of elements in string	ELEMENTS COMPRISING STRING						Percentage frequency
3				PP	PP	BT	32.3
				SF	PP	BT	26.1
				RV	PP	BT	11.2
				TN	PP	BT	
4			PP	PP	PP	BT	18.1
			PP	SF	PP	BT	11.6
			CW	SF	PP	BT	7.3
			PP	RV	PP	BT	6.3
			SF	PP	PP	BT	5.9
5		PP	PP	PP	PP	BT	10.4
		BT	CW	SF	PP	BT	7.3
		SF	PP	SF	PP	BT	5.3
		PP	BT	CW	PP	BT	3.9
		PP	SF	PP	PP	BT	3.6
		PP	PP	SF	PP	BT	3.5
		SF	PP	PP	PP	BT	3.4
6	PP	PP	PP	PP	PP	BT	7.3
	PP	BT	CW	SF	PP	BT	7.2
	PP	SF	PP	SF	PP	BT	3.6
	PP	BT	CW	PP	PP	BT	2.4

4.11. A comparison of the ratio between types and lengths of strings of elements preceeding the attack.

If the behaviour of a fish was so rigid that it always performed exactly the same series of elements of behaviour preceeding capturing its prey there would be only one type of string of elements and the behaviour would be completely predictable. Conversely, if every series of elements prior to attack was different there would be as many different string types as there were attacks and the fish's behaviour would be totally unpredictable. The ratio between the number of string types and the total number of attacks can be considered as a measure of the rigidity of predictability of the fish's behaviour. If the ratio is $\frac{\text{Number of string types}}{\text{Total number of attacks}}$ it is apparent that as unpredictability increases i.e. the number of string types becomes larger, the value of the expression approaches one. As the expression was derived to indicate predictability of behaviour it is more logical to have unpredictability tending to zero and predictability tending to one. Thus: $1 - \frac{\text{Number of string types}}{\text{Total number of attacks}}$ is now a useful index of predictability of the fishes' behaviour.

This expression has been evaluated for strings of 2 - 6 elements in length ending with an attack for each feeding trial. The results are illustrated in Figs. 26 and 27. In all feeding trials the index of predictability decreases as the string length increases. This is expected because a longer string length gives more opportunity for variability than a short one.

Comparing the predictability of behaviour with increasing string length for plaice, flounder and soles feeding on worms it is seen that whilst the behaviour of plaice and sole remains highly predictable even

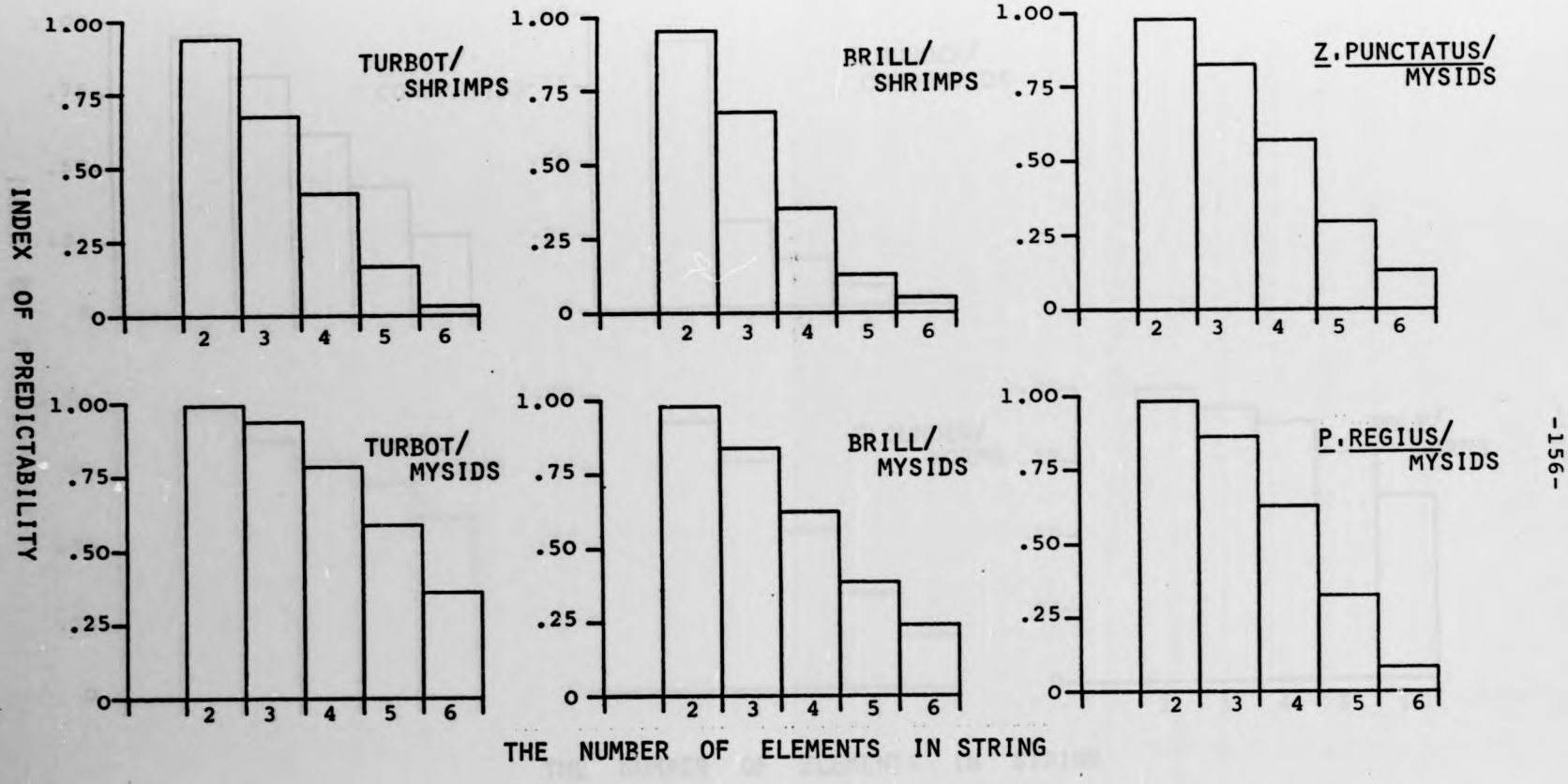


FIGURE 26 BAR DIAGRAMS TO ILLUSTRATE THE DECREASE IN PREDICTABILITY OF ELEMENTS PRIOR TO ATTACK

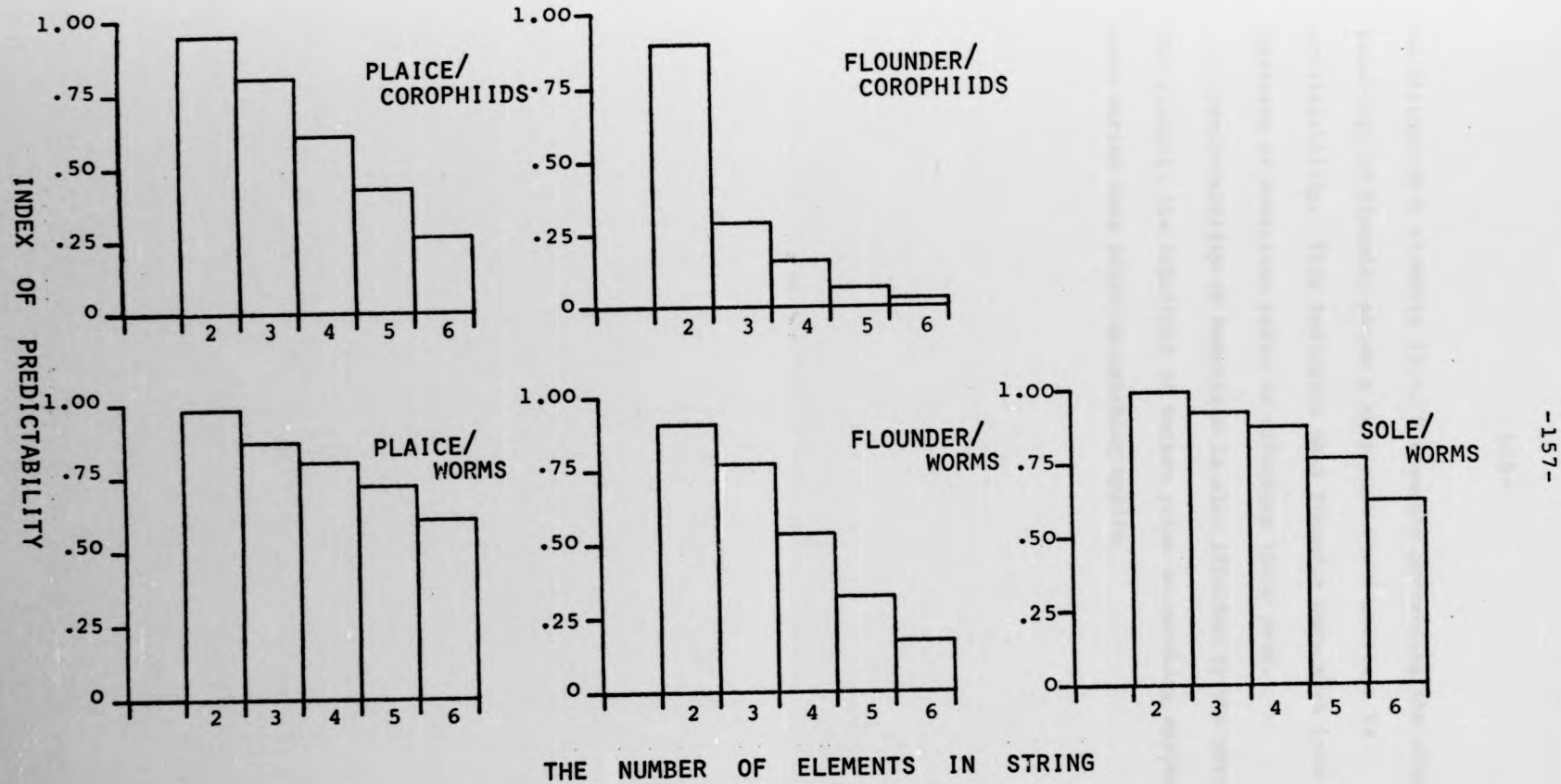


FIGURE 27 BAR DIAGRAMS TO ILLUSTRATE THE DECREASE IN PREDICTABILITY OF ELEMENTS PRIOR TO ATTACK

to strings of 6 elements (i.e. 5 elements preceeding the attack) the behaviour of flounder shows a much more rapid decrease in predictability. This indicates that flounder have much less rigid patterns of behaviour prior to attacking their prey.

Predictability of behaviour is also affected by the prey species. For example, the behaviour of turbot prior to catching shrimps is far more varied than prior to catching mysids.

4.12. Summary of the differences between the tactics of feeding behaviour presented in Part Two.

The most concise and convenient means of summarising the difference between the tactics is that of a table because it facilitates comparison. Table 61 summarises the results of the analysis of major variables that have been compared between families of flatfish and feeding trials in Part Two of this study.

Table 61 A summary of the most important variables presented in Part Two.

Key to abbreviations used in the table

BTH - combined bothid trials
TM - turbot / mysids
TS - turbot / shrimps
BM - brill / mysids
BS - brill / shrimps
ZPM - *Z. punctatus* / mysids
ZPG - *Z. punctatus* / gammarids
PRM - *P. regius* / mysids
PRG - *P. regius* / gammarids
PLN - combined pleuronectid trials
PW - plaice / enchytraeid worms
PC - plaice / corophiids
FW - flounder / enchytraeid worms
FC - flounder / corophiids
SW - sole / enchytraeid worms

DESCRIPTION OF VARIABLE	BTH	TM	TS	BM	BS	ZPM	ZPG	PRM	PRG	PLN	PW	PC	FW	FC	SW
FREQUENCY:															
WATER COLUMN ACTIVITY	6	34	6	2	4	-	-	-	-	1	1	-	-	3	1
BOTTOM ACTIVITY	77	58	79	80	77	82	72	84	85	76	94	68	78	65	97
INACTIVITY	17	8	15	18	19	18	28	16	15	23	5	32	22	32	2
DURATION:															
WATER COLUMN ACTIVITY	3	20	2	-	-	-	-	-	-	1	-	-	-	4	1
BOTTOM ACTIVITY	43	50	43	41	29	44	33	53	55	33	59	26	20	28	75
INACTIVITY	54	30	55	59	71	56	67	47	45	66	41	74	80	68	24

DESCRIPTION OF VARIABLE	BTH	TM	TS	BM	BS	ZPM	ZPG	PRM	PRG	PLN	PW	PC	FW	FC	SW
FREQUENCY:															
WATER COLUMN ACTIVITY	6	34	6	2	4	-	-	-	-	1	1	-	-	3	1
BOTTOM ACTIVITY	77	58	79	80	77	82	72	84	85	76	94	68	78	65	97
INACTIVITY	17	8	15	18	19	18	28	16	15	23	5	32	22	32	2
DURATION:															
WATER COLUMN ACTIVITY	3	20	2	-	-	-	-	-	-	1	-	-	-	4	1
BOTTOM ACTIVITY	43	50	43	41	29	44	33	53	55	33	59	26	20	28	75
INACTIVITY	54	30	55	59	71	56	67	47	45	66	41	74	80	68	24
No. DIFFERENT ELEMENTS EXHIBITED	43	31	32	30	25	26	11	27	15	30	20	20	12	26	24
No. OF ELEMENTS MORE FREQUENT THAN EXPECTED	11	8	9	9	7	8	6	9	5	6	5	6	5	6	5
No. OF ELEMENTS THAT OCCUR FOR MORE TIME THAN EXPECTED	7	6	5	4	3	3	2	6	5	4	5	3	1	5	5
No. OF ELEMENTS THAT ACCOUNT FOR:															
95% OF CUMULATIVE % FREQUENCY	20	14	18	16	17	15	7	13	10	9	8	8	7	12	6
95% OF CUMULATIVE % TIME	13	13	11	9	7	8	6	9	6	8	8	6	6	8	9
THREE COMMONEST ELEMENTS:															
FREQUENCIES	TN	TN	TN	PS	TN	PS	PS	CR	TN	PS	CW	PS	PS	PS	PP
	PS	SF	SF	CR	PS	TN	TN	PS	CR	TN	BT	TN	BT	TN	SF
	CR	SW	PS	TN	CR	CR	HR	TN	PS	BT	TN	SF	TN	SF	TN
DURATIONS	PS	PS	PS	PS	PS	PS	PS	PS	PS	PS	CW	PS	PS	PS	PP
	CR	SF	SF	CR	CR	CR	TN	CR	CR	CW	PS	BY	HR	CW	SF
	TN	TN	TN	AR	CAR	TN	HR	TN	TN	BY	BY	CW	CW	BY	PS
COMMONEST FORM OF LOCOMOTION	CR	SF/ SW	SF	CR	CR	CR	CR	CR	CR	SF	FD	SF	SF	SF	SF
MEAN No. OF ELEMENTS / SESSION	159	474	159	96	57	136	86	130	85	354	422	313	227	377	631
MEAN No. OF ELEMENTS / SEQUENCE	7.3	7.6	8.7	7.0	8.5	8.2	-	7.5	-	4.2	3.8	6.5	3.9	5.0	6.0
MEAN INTERVAL BETWEEN ATTACKS (SECS)	38	18	67	95	208	63	-	60	-	10	8	21	7	18	12
MEAN PREY CAPTURE EFFICIENCY (%)	85	91	73	86	73	89	-	86	-	100	100	99	100	100	100

PART THREE

VISUAL RECOGNITION OF PREY BY TURBOT

1. INTRODUCTION

The previous section described the different feeding tactics of representatives from the three most important taxonomic groups of flatfish. Their tactics were found to be very different. To some extent the feeding tactics must be adapted to cope with the range of different prey types that are eaten by the different species. This section of the work sets out to describe how flatfish recognise their prey and what are the important prey stimuli that elicit the feeding response.

Little work has been done in this field. The major contribution has been by de Groot (1971). He presented 1, 2, 4 and 8 cm black wooden balls to six species of flatfish, with and without chemical stimuli. He found that turbot and brill did not respond to any of these sizes of spherical models and that the addition of a chemical stimulus did not improve the response. The fish did, however, respond to shrimp and fish models.

This work attempts to determine the nature of the important stimuli provided by a shrimp model that are not provided by de Groot's spherical models; that is, to determine why turbot and brill respond to shrimp models but not to spherical ones. In solving this problem the critical prey stimuli important to turbot and brill in recognising their food should be discovered. To carry out this investigation the feeding behaviour described in the previous section will be used as a means of assessing the effectiveness of selectively presented models and food cues to initiate the feeding response.

2. METHODS

Thirty eight 0-group turbot and twenty nine 0-group brill, all between 2.0 - 3.5 cm, were captured at two local beaches: Camais Nathais (O.S. Grid Reference - NM 875382) and Ardmucknish Bay (O.S. Grid Reference - NM 897387) during August and September 1976 by a push net method.

In the laboratory these fish were maintained in tanks 120 x 54 x 18 cm with constant air and water flows. They were fed on two species of mysids, Praunus flexuosus (Müller) and Neomysis integer (Leach). The amount of food provided was a little above maintenance requirements of the species to achieve a slow growth rate.

In order to standardise the hunger levels of the fish prior to experimentation, they were passed through a 64 hour cycle involving 3 different tanks. Four individuals were tested each day. From 0 - 24 hours four fish were maintained in a the stock tank to a tank of 120 x 54 x 18 cm provided with an ad libitum diet of mysids so that each fish could become completely satiated. From 24 - 48 hours the fish were kept in a holding tank of similar dimensions to allow digestion of food in their guts. At 48 hours (approximately 17:00 hours B.S.T. each day) the fish were transferred from the holding tanks to the experimental tanks, and were allowed a further 16 hours, without food, to settle down in the experimental environment before being tested at 09:00 hours the following morning.

The experiments were conducted in two clear perspex tanks 175 x 30 cm filled to a depth of 24 cm with constantly replenished sea water maintained at 15 $\pm$ 1^{o}C (see Fig. 28). Each was divided in half by an opaque darvic panel to provide a total of four separate experimental enclosures, each 86 cm in length and containing one fish. A vertical

FIGURE 28 THE EXPERIMENTAL ENCLOSURE

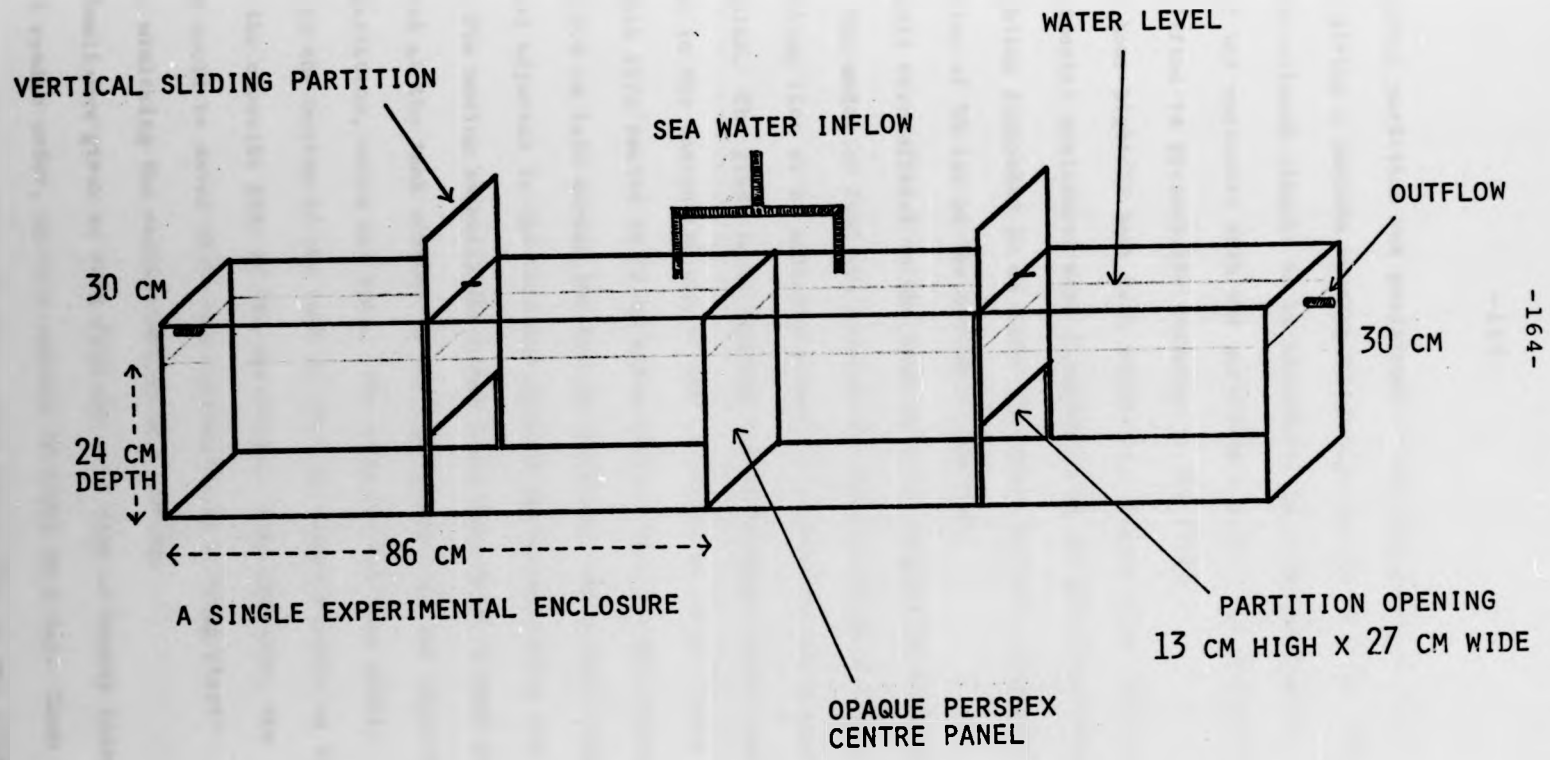
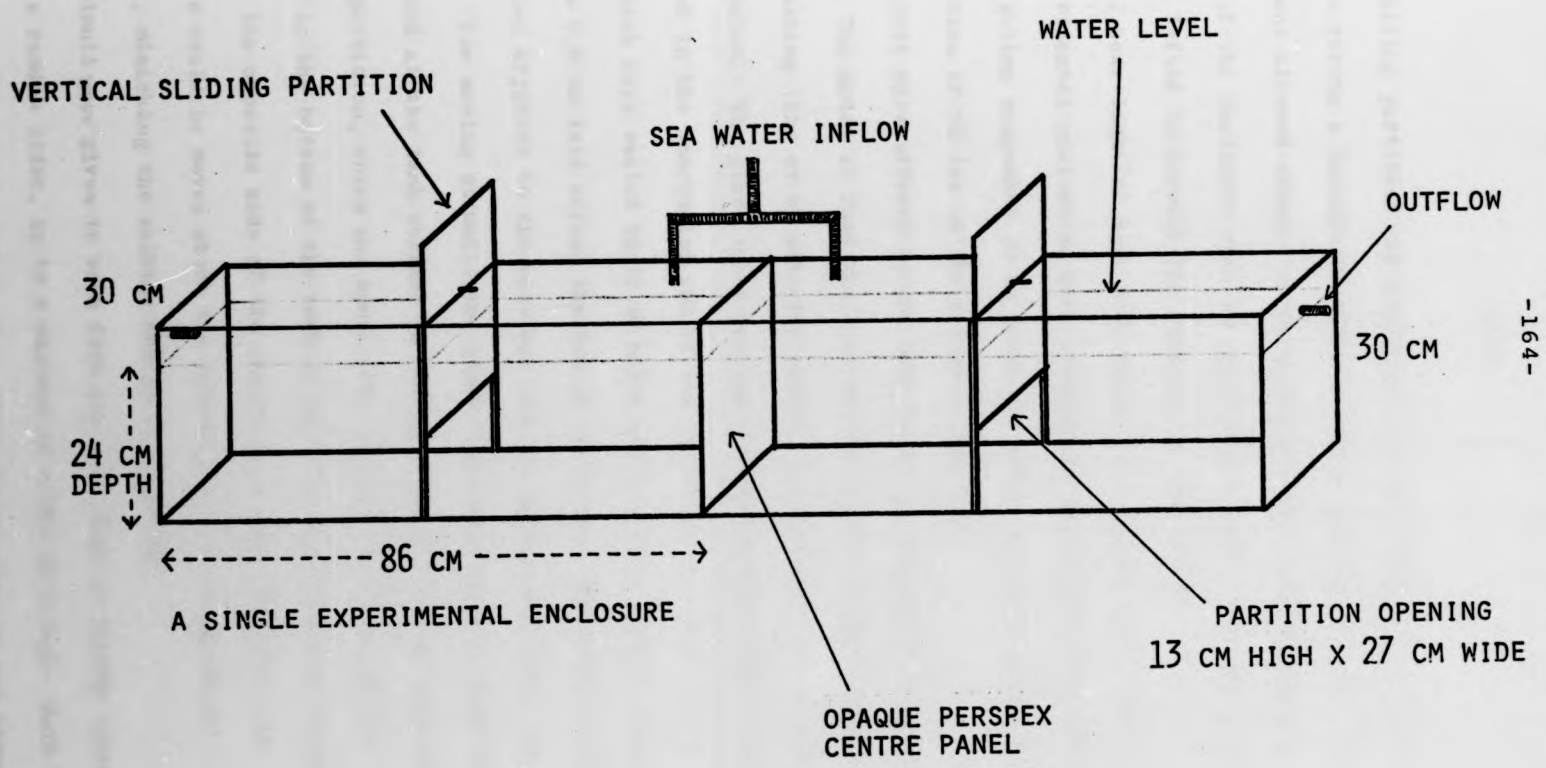


FIGURE 28 THE EXPERIMENTAL ENCLOSURE



opaque sliding partition was positioned at the mid-point of each enclosure giving a maximum opening 13 cm high and 27 cm wide. This arrangement allowed stimuli to be introduced into the unoccupied portion of the enclosure with the partition closed. The partition was then lifted to present the stimulus to the fish.

A 12 hour light/12 hour dark regime was imposed upon the fish. The experimental enclosures were illuminated by 60 watt fluorescent strip lighting suspended 30 cm above the water surface, giving an illumination of 50 lux on the bottom of the tank.

Stimuli were offered to the fish on 35 cm lengths of 4 mm glass tubing. The model or food was held at the tip by either a loop of nylon fishing line or by adhesive cement, depending on the nature of the stimulus. The glass tubes bearing the stationary stimuli were suspended in the unoccupied end of the enclosure by bored rubber bungs which were seated in 12 mm holes drilled in a perspex strip 36 x 5 a 0.6 cm laid across the top of the tank. The stimuli were positioned adjacent to the vertical sliding partition, which was closed. For moving stimuli, the glass tubes were held by hand and introduced at the tank surface in the unoccupied side and adjacent to the partition, which was open. The stimulus was then gently lowered to the bottom of the tank so that it became visible to the fish on the opposite side of the partition. With practice, the stimulus could be moved about the substratum in a 'stop/start' fashion, mimicking the walking motion of a shrimp.

Stimuli were given to each fish one at a time at hourly intervals and in a random order, up to a maximum of eight in a day. Each stimulus was offered for 3 minutes, after which time it was removed. A dictating machine was used to record the fishes' behaviour during

the 3 minute period of stimulus presentation. The response of each fish was scored in the following manner:-

4 points (maximum response) for orientate-approach attack; Type 4 response.

3 points for orientate-complete approach (but no attack); Type 3 response.

2 points for orientate-incomplete approach (but no attack); Type 2 response.

1 point for orientate only; Type 1 response.

0 points for no visible response; Type 0 response.

A "complete approach" was defined as that amount of movement required by the fish to put itself in a position close enough to the stimulus for it to make an attack. All other approach movements were classed as "incomplete". In practice, a "complete approach" usually resulted in the fish stopping one body length away from the stimulus and was often followed by an Arch-Relax-Turn Away sequence of behaviour (see Part Two - Flatfish feeding tactics). When the stimulus was inedible and the fish gave a type 4 response a small (25 - 30 mm) dead shrimp was dropped into the tank as a reward. At the end of the day, the four fish were removed from the experimental enclosures, their length measured, and they were replaced by four new fish which had passed through a similar 64 hour pre-trial cycle as described above.

Screens were not used to isolate the observer from the fish. As described in the methods section of Part Two, with screens in place the fish seemed very much less responsive to stimuli and were easily alarmed by any slight disturbance, burying themselves in the sand and becoming completely inactive. When accustomed to seeing continuous movements of the observer, the fish spent much more time active and

were generally more responsive.

A series of six experiments on I-group turbot and one experiment on I-group brill were performed to investigate the important visual cues that enable the fish to recognise their prey.

3. EXPERIMENT 1. TO INVESTIGATE THE EFFECTS OF PREY LOCOMOTION AND ORIENTATION FOR TURBOT AND BRILL.

EXPERIMENT 1A : TURBOT

The objectives of the experiment

Both 0-group and I-group turbot and brill have very similar diets, and the dietary "succession" from metamorphosis is as follows: copepods, small amphipods, mysids, shrimps, sand eels (see Part One).

Both these species are very active predators. Although their feeding strategies differ somewhat (see Part Two), it was expected that they would be stimulated by similar prey attributes because they are closely related and have similar diets.

The two most striking features shown by all their prey organisms are rapid movement and the horizontal dimension of the body being five to ten times greater than the vertical dimension. In order to test the importance of these two attributes, a series of stimuli were presented to turbot in part A of experiment 1 and to brill in part B of experiment 1.

The experimental design

Initially only six stimuli were offered to the fish, but this trial was abandoned and repeated with the inclusion of stimulus 7 (see explanation in the text below). The stimuli were as follows:-

Stimulus 1 - control: a moving blank glass tube

Stimulus 2 - a stationary vertical dead shrimp

Stimulus 3 - a stationary horizontal dead shrimp

Stimulus 4 - a moving vertical dead shrimp

Stimulus 5 - a moving horizontal dead shrimp

Stimulus 6 - a free live shrimp

Stimulus 7 - a moving blank glass tube drawn through the sand

This selection of stimuli allowed the interaction between the orientation and movement of the prey to be compared. At this point it is necessary to differentiate between two types of prey movement. The first is small rapid movements of the appendages necessary for locomotion, respiration and other body functions. The second is total body displacement to a new location. This experiment was designed to investigate the latter type of movement. In order to eliminate all appendage movements, all the shrimps used for stimuli 2, 3, 4 and 5 were killed by asphyxiation in screw-topped bottles filled with water. Shrimps were chosen with body lengths between 30 - 34 mm, which was well within the prey handling capabilities of the fish which ranged from 9.0 - 13.0 cm with a median of 10.6 cm.

During the first three days of the experiment something quite unexpected was discovered. Whilst offering stimulus 1 (a moving blank glass tube), it was noticed that if the tip of the glass tube was accidently dipped into the sand and sand grains were agitated, a very rapid type 3 response of Turn-Skim was observed in four of the twelve fish. They showed very little response if the tube did not agitate the sand grains. The immediacy of this response suggested that movement of the sand was an important stimulus which could invalidate the control experiments. This experiment was therefore abandoned.

A second run was set up using stimuli 1 - 6 as above but also including a seventh stimulus, a moving glass tube drawn through the sand. Great care was also taken to ensure that the moving stimuli 1, 4 and 5 were not allowed to disturb the substratum but simply to glide across the surface.

The raw data from this experiment can be found in Appendix 3. It shows the scores of each individual fish to each stimulus in a 38 x 7 table, the length and total score of each fish to all stimuli (row totals), the group stimulus response total (column totals) and the average (arithmetic mean) response score of the fish to each stimulus. Table 62 provides a condensed summary of the raw data. This table casts the seven stimuli (columns) against five response types (rows), each cell containing a frequency value. It must be emphasised strongly that all the statistics employed in the analysis of this experiment were performed on the raw data. Both the Friedman Two Way Analysis of Variance and the Wilcoxon Matched-Pairs Signed-Ranks test (Siegel, 1956) are applicable to data from related samples i.e. all treatments being common to each individual, and the data about the individual have been lost by summarising in Table 62. Nevertheless, the table demonstrates the distribution of response types against stimuli. For example, there were 32 no responses (type 0) to the control blank tube (stimulus 1) compared with only 4 type 0 responses to stimulus 6 (the free live shrimp). In contrast there were no type 4 responses to the control blank tube compared with 27 type 4 responses to stimulus 6. The group stimulus response total was derived from the product of the frequency and the number of points awarded for each type of response. For example, the group stimulus response total for stimulus 3 was:

$(33 \times 0) + (3 \times 1) + (1 \times 2) + (0 \times 3) + (1 \times 4) = 9$ points

From this value an average was calculated which can be used to compare the strengths of the responses to the seven stimuli. Again, it must be strongly emphasised that these arithmetic mean values are derived from ordinal, not arithmetic, measurements and they should not be assessed

Table 62 A frequency table of the response types to stimuli offered in Experiment 1A.

Response Type	STIMULUS NUMBER 1	2	3	4	5	6	7
0	32	36	33	27	19	4	16
1	2	1	3	2	3	2	1
2	4	1	1	2	4	4	7
3	0	0	0	0	1	1	0
4	0	0	1	7	11	27	14
Total	10	3	9	34	58	121	73
N	38	38	38	38	38	38	38
Mean	0.3	0.1	0.2	0.9	1.5	3.2	1.9
Ranked Order	5	7	6	4	3	1	2

Key to stimuli
1 - control: a moving blank glass tube
2 - a stationary vertical dead shrimp
3 - a stationary horizontal dead shrimp
4 - a moving vertical dead shrimp
5 - a moving horizontal dead shrimp
6 - a free live shrimp
7 - a moving blank glass tube drawn through the sand

'Total' is the group stimulus response total and is derived by adding all the response type scores for each stimulus in turn.

'N' is the total number of fish in the sample.

by the laws of arithmetic. These means can be assessed only by their ranks. There are no grounds to suppose that a stimulus which gives a mean value of 3.0 is twice as effective as a stimulus which gives a mean value of 1.5, because the final mean values are only a reflection of the original response scoring system.

It was expected that the stimulation given by the free live shrimps (stimulus 6) would be closest to that provided by wild shrimps being hunted by turbot in the sea. The group response score to the free live shrimp can be considered therefore as a standard by which to compare the other test stimuli. It follows that the closer a group stimulus response total for any of the test stimuli is to the group stimulus response total for the free live shrimp (the standard value), the more attractive the test stimulus was considered to be.

Results and discussion

Although the figures stand on their own and show differences, statistical methods must be employed to make substantiated inferences about the importance of the various stimuli. The Friedman Two-Way Analysis of Variance test was used to determine whether there were any statistical differences between the stimuli. Under the null hypothesis that there was no difference in responsiveness to the seven stimuli, a value of 71.35 for χr^2, the Friedman Statistic, with six degrees of freedom has a probability of $<<0.001$. This led to a rejection of the null hypothesis in favour of the alternative that the seven visual stimuli differ in their effect upon the behavioural response of the fish. In order to determine where the differences occurred, a Wilcoxon Matched-Pairs Signed-Ranks test was performed successively between all possible pairs of stimuli. Table 63 shows

Table 63 The probability values of the Wilcoxon Matched-Pairs Signed-Ranks test performed successively between all possible pairs of stimuli offered in Experiment 1A.

STIMULUS NUMBER	1	2	3	4	5	6	7
1		ns	ns	(4) *	(5) **	(6) ***	(7) **
2			ns	(4) **	(5) **	(6) ***	(7) **
3				(4) *	(5) **	(6) ***	(7) **
4					(5) *	(6) ***	(7) **
5						(6) **	ns
6							(6) **

Key to stimuli
1 - control: a moving blank glass tube
2 - a stationary vertical dead shrimp
3 - a stationary horizontal dead shrimp
4 - a moving vertical dead shrimp
5 - a moving horizontal dead shrimp
6 - a free live shrimp
7 - a moving blank glass tube drawn through the sand

The stimulus of a pair producing the greater response is indicated by the number in parentheses.
ns.....not significant at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001
All tests were two-tailed.

the probability values of two-tailed tests for all such comparisons. The figure given in parentheses is the code number of the stimulus eliciting the greater response. To discover the effect of movement the following comparisons were made and the results were:

i) Stimulus 4 (moving-vertical) was greater than stimulus 2 (stationary-vertical), $p<0.01$.

ii) Stimulus 5 (moving-horizontal) was greater than stimulus 3 (stationary-horizontal), $p\ll 0.01$.

iii) The combined effect of stimuli 4 and 5 was greater than the combined effect of stimuli 2 and 3, $p\ll 0.01$.

This evidence shows clearly the importance of movement in eliciting a feeding response in turbot.

To investigate the effect of body orientation, the following comparisons were made and the results were:

i) Stimulus 5 (horizontal-moving) was greater than stimulus 4 (vertical-moving), $p<0.05$.

ii) Stimulus 3 (horizontal-stationary) was not significantly different at the 5 per cent level from stimulus 2 (vertical-stationary).

iii) The combined effect of stimuli 3 and 5 was greater than the combined effect of stimuli 2 and 4, $p<0.01$.

These comparisons show that horizontal body orientation is a stronger prey attribute for eliciting a feeding response than a vertical body orientation.

Further information on the relative importance of motion and prey orientation can be gained from adding the group stimulus responses for shared traits.

Table 64 The group stimulus response scores for the shared traits movement and prey orientation for turbot.

	Moving	Stationary	Total	Difference
Horizontal	58	9	67	30
Vertical	34	3	37	
Total	92	12		
Difference	80			

In Table 64 a range of 80 points between moving and stationary stimuli compared with the much narrower range of 30 points between horizontal and vertical stimuli implies that movement is a stronger stimulus than orientation of the body. The preference order for stimuli with respect to these two attributes is:

moving horizontal > moving vertical > stationary horizontal > stationary vertical.

These results therefore confirm the predictions of prey motion and body axis orientation made before the experiment was performed and based on the most obvious attributes of the natural prey of turbot.

The orientation of shrimps in both vertical presentations (stimuli 2 and 4) was arranged so that in half of them the head was uppermost and in the remainder the tail was uppermost. Analysis of this data shows that the direction of vertical body orientation was not important (Table 65). A Mann-Whitney U test was performed on the data for stimulus 4 (moving-vertical) and the results were as

follows:

Table 65 Distribution of response types for stimulus 4 with respect to the position of the head of the shrimp stimulus for turbot.

Response Type	0	1	2	3	4	Number of fish
Head uppermost	16	1	1	0	1	19
Tail uppermost	11	1	1	0	6	19
					Total	38

For $N_1 = 19$ and $N_2 = 19$, U = +128. Applying a correction for tied observations Z = -1.92, p = 0.055. This result suggests that the the position of the head (or tail) has no effect upon the responsiveness of the fish to a vertically orientated shrimp.

Comparison of the group stimulus response totals and the arithmetic means show that stimulus 7 is ranked second highest, even bettering the response to a moving horizontal shrimp (stimulus 5). This is quite outstanding especially when compared with stimulus 1 (the control) which is not drawn through the sand and is ranked fifth. From Table 63 the Wilcoxon comparisons show stimulus 7 to elicit a significantly stronger effect than stimuli 1, 2 or 3 at $p \ll 0.01$ and than stimulus 4 at $p < 0.05$. That is, stimulus 7 is stronger than a moving or stationary vertical shrimp and a stationary horizontal shrimp. There is no difference between stimulus 7 and a moving

horizontal shrimp (stimulus 5).

The response to stimulus 6 was clearly much higher than the response to the best of the artificial models, stimulus 7 ($p<0.02$), the mean group response score being greater than one whole point higher than that to stimulus 7. This implies that a live shrimp has other attributes which are important for recognition of prey in turbot that have not been investigated in this experiment. Although it is conceivable that this is not the case and that had the attributes of stimulus 5 and 7 been combined, then the response to such a stimulus might have more closely approached the response to a live shrimp.

The importance of movement as an initiator of the feeding response is further emphasised by considering the statistical comparisons between the control (stimulus 1) and the other stimuli in Table 63. There is no significant difference between a moving blank glass tube and a stationary stimulus whether it bears a horizontal or a vertical shrimp. This demonstrates the low level of responsiveness to a stationary shrimp. However, the additive effects of movement plus the shrimp stimulus combine to elicit a significantly stronger response to stimuli 4, 5 and 6 than to a blank control tube.

When the moving control tube was drawn through the sand the response was very much stronger than when it was not (stimulus 7 > stimulus 1, $p \ll 0.01$), suggesting that the response to agitation of the sand grains is important in the latter stages of prey capture when pursued shrimps, if not caught, immediately quickly bury themselves in the sand. The method of burying agitates the sand particles in a similar way to stimulus 7 and turbot stalking shrimps were often observed to lunge at this burying movement in the sand, even when no part of the shrimp was visible, and successfully capture the prey.

This response would also be useful when feeding on sand eels which bury themselves in the sand in a similar manner.

Summary of conclusions

1) A moving stimulus elicited a very much stronger response than a stationary stimulus.

2) A horizontally orientated stimulus was preferable to a vertically orientated stimulus.

3) Motion was a stronger attribute than orientation.

4) The direction of vertical orientation (head or tail uppermost) was not important.

5) Turbot respond very well to the stimulus of sand grain agitation, such as the disturbance caused by drawing the tip of a glass tube through the sand.

6) There was a large discrepancy between the responsiveness of turbot to a free live shrimp and the responsiveness to the best of the artificial stimuli (the agitation of sand grains).

EXPERIMENT 1 B : BRILL

The objectives of the experiment

Brill are closely related to turbot. They share very similar diets although their feeding strategies differ markedly (see Part Two). It would seem reasonable to expect, however, that many of the prey attributes and behaviours eliciting a response in turbot would be equally effective food cues for brill. This experiment compares and contrasts the responses of brill to the prey attributes of locomotion and orientation with the responses of turbot to the same.

The experimental design

The seven stimuli offered to turbot in experiment 1.A were repeated using 29 I-group brill ranging between 8.9 - 13.6 cm with a median length of 11.7 cm. All the other aspects of the experimental regime were as described in section 1.A of this experiment.

Results and discussion

Appendix 4 contains the raw data for brill and Table 66 shows a summary of this information. As in the previous part of experiment 1, the raw data was first tested with the Friedman Two-Way Analysis of Variance test under the null hypothesis that there was no difference between the stimuli. The Friedman statistic was $\chi_r^2 = 27.25$ with 6 degrees of freedom. The probability of this result occurring by chance alone is <0.001 which leads to a rejection of the null hypothesis in favour of the alternative that the different stimuli cause different behavioural responses. Table 67 shows the results of the Wilcoxon analysis on successive pairs of stimuli.

To investigate the effect of movement the following comparisons

Table 66 A frequency table of the response types to stimuli offered in Experiment 1B.

Response Type	STIMULUS NUMBER 1	2	3	4	5	6	7
0	26	27	27	23	14	13	16
1	1	2	1	2	4	0	0
2	0	0	1	0	1	0	2
3	2	0	0	1	0	1	5
4	0	0	0	3	10	15	6
Total	7	2	3	17	46	63	43
N	29	29	29	29	29	29	29
Mean	0.2	0.1	0.1	0.6	1.6	2.2	1.5
Ranked Order	5	7	6	4	2	1	3

Key to stimuli
1 - control: a moving blank glass tube
2 - a stationary vertical dead shrimp
3 - a stationary horizontal dead shrimp
4 - a moving vertical dead shrimp
5 - a moving horizontal dead shrimp
6 - a free live shrimp
7 - a moving blank glass tube drawn through the sand

'Total' is the group stimulus response total and is derived by adding all the response type scores for each stimulus in turn.

'N' is the total number of fish in the sample.

Table 67 The probability values of the Wilcoxon Matched-Pairs Signed-Ranks test performed successively between all possible pairs of stimuli offered to Brill in Experiment 1B.

STIMULUS NUMBER	1	2	3	4	5	6	7
1		ns	ns	ns	(5) **	(6) **	(7) **
2			ns	(4) *	(5) **	(6) **	(7) **
3				(4) *	(5) **	(6) **	(7) **
4					(5) *	(6) **	ns
5						ns	ns
6							ns

Key to stimuli
1 - control: a moving blank glass tube
2 - a stationary vertical dead shrimp
3 - a stationary horizontal dead shrimp
4 - a moving vertical dead shrimp
5 - a moving horizontal dead shrimp
6 - a free live shrimp
7 - a moving blank glass tube drawn through the sand

The stimulus of a pair producing the greater response is indicated by the number in parentheses.
ns.....not significant at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001
All tests were two-tailed.

were made and the results were:

i) Stimulus 4 (moving-vertical) was greater than stimulus 2 (stationary-vertical), $p = 0.05$.

ii) Stimulus 5 (moving-horizontal) was greater than stimulus 3 (stationary-horizontal), $p \ll 0.01$.

iii) The combined effect of stimuli 4 and 5 was greater than the combined effect of stimuli 2 and 3, $p \ll 0.01$.

These results show clearly the importance of movement for eliciting a feeding response in brill.

To investigate the effect of body orientation the following comparisons were made and the results were:

i) Stimulus 5 (horizontal-moving) was greater than stimulus 4 (vertical-moving), $p < 0.02$.

ii) Stimulus 3 (horizontal-stationary) was not significantly different to stimulus 2 (vertical-stationary) at the 5 per cent level.

iii) The combined effect of stimuli 3 and 5 was greater than that of stimuli 2 and 4, $p < 0.01$.

These comparisons show that horizontal body orientation is a stronger prey attribute for eliciting a feeding response than vertical body orientation.

Further information on the relative importance of motion and prey orientation can be gained from adding the group stimulus response scores for shared traits (see Table 68).

As with turbot in the previous experiment, there was a wider range between moving/non-moving stimuli (58 points) than between horizontal/vertical stimuli (30 points), implying that in brill the movement stimulus has a stronger effect than the orientation of the body of the prey. The separation between the two traits, however, is

not as great in brill as it was in turbot; but this may be due to a smaller sample size. The preference order for stimuli with respect to these two attributes was :

moving horizontal > moving vertical > stationary horizontal > stationary vertical.

Table 68 The group stimulus response scores for the shared traits movement and prey orientation for brill.

	Moving	Stationary	Total	Difference
Horizontal	46	3	49	30
Vertical	17	2	19	
Total	63	5		
Difference	58			

These results confirm the predictions about prey motion and body axis orientation made before the experiment was performed. The hypothesis that turbot and brill would respond to similar stimuli because they feed on similar prey types is also supported.

The orientation of shrimps in both vertical presentations (stimuli 2 and 4) was arranged so that in half the presentations the head was uppermost and in the remainder the tail was uppermost. Table 69 shows the distribution of the frequency of response types for both conditions on the data from stimulus 4 (moving/vertical).

Table 69 Distribution of response types for stimulus 4 with respect to the position of the head of the shrimp stimulus for brill.

Response Type	0	1	2	3	4	Number of fish
Head uppermost	12	1	0	1	1	15
Tail uppermost	11	1	0	0	2	14
					Total	29

For N_1 = 14 and N_2 = 15, U = +102.5. Applying a correction for tied observations Z = -0.15, p = 0.44. Therefore the direction of the head (or tail) of a vertically orientated shrimp does not make any contribution to the responsiveness of brill to stimulus 4.

Comparison of the group stimulus response totals and the arithmetic means shows that stimulus 7 (the blank tube drawn through the sand) is ranked third highest. Clearly the stimulus was as important to brill as it was to turbot, and presumably for the same reasons. The group response to stimulus 7 (43 points) was almost as good as that to stimulus 5 (the moving horizontal shrimp, 46 points). Stimulus 7 was significantly stronger than stimuli 1, 2 and 3 but showed no significant difference over stimuli 4, 5 or 6 (see Table 67).

The importance of movement in initiating the feeding response of brill is further emphasised by considering the statistical comparisons between the control stimulus 1 and the other stimuli in Table 67. There was no significant difference between a moving blank glass tube and a stationary stimulus whether it bore a horizontal or a vertical shrimp. This demonstrates the low level of responsiveness to a

Table 69 Distribution of response types for stimulus 4 with respect to the position of the head of the shrimp stimulus for brill.

Response Type	0	1	2	3	4	Number of fish
Head uppermost	12	1	0	1	1	15
Tail uppermost	11	1	0	0	2	14
					Total	29

For $N_1 = 14$ and $N_2 = 15$, U = +102.5. Applying a correction for tied observations Z = -0.15, p = 0.44. Therefore the direction of the head (or tail) of a vertically orientated shrimp does not make any contribution to the responsiveness of brill to stimulus 4.

Comparison of the group stimulus response totals and the arithmetic means shows that stimulus 7 (the blank tube drawn through the sand) is ranked third highest. Clearly the stimulus was as important to brill as it was to turbot, and presumably for the same reasons. The group response to stimulus 7 (43 points) was almost as good as that to stimulus 5 (the moving horizontal shrimp, 46 points). Stimulus 7 was significantly stronger than stimuli 1, 2 and 3 but showed no significant difference over stimuli 4, 5 or 6 (see Table 67).

The importance of movement in initiating the feeding response of brill is further emphasised by considering the statistical comparisons between the control stimulus 1 and the other stimuli in Table 67. There was no significant difference between a moving blank glass tube and a stationary stimulus whether it bore a horizontal or a vertical shrimp. This demonstrates the low level of responsiveness to a

stationary shrimp stimulus. Even a moving vertical shrimp was not significantly better than a moving blank rod, which demonstrates the low level of importance of a vertically orientated stimulus. The response to a blank tube when drawn through the substratum was much greater than that to the blank tube not drawn through the substratum.

The order of responsiveness of brill to the stimuli can be summarised as follows:

free live shrimp > moving horizontal shrimp > blank rod drawn through the sand > moving vertical shrimp > moving blank rod not drawn through the sand > stationary horizontal shrimp > stationary vertical shrimp.

The results of these two experiments confirm the expectations about the relative importance of the prey attributes of motion and body orientation based on the prominent attributes of the prey organisms of turbot and brill. The responses of both species to each stimulus were compared statistically using a Mann-Whitney U test, and the results of these comparisons are shown in Table 70. Tests were performed under the null hypothesis that there was no difference in the responsiveness between turbot and brill to each stimulus.

The responses of turbot and brill to stiumuli 1-5 and stimulus 7 showed no significant difference at $p = 0.05$. This demonstrates that the two species responded in very similar ways to the artificial stimuli. A difference was observed at $p = 0.03$ in the responses to the free live shrimp, however, brill showed a weaker response than turbot. These comparisons imply that while brill are as equally stimulated as turbot by prey movement, horizontal orientation and sand grain agitation, they are less inclined to respond to the stimulus provided by a live shrimp. This apparent anomaly could be explained by the fact that whilst the traits of movement, orientation and sand

grain disturbance are generalised non-specific stimuli, a shrimp is a specific stimulus and recognition culminates in the formation of a "search image" which may take longer to develop in brill than in turbot. None of the turbot or brill had experienced shrimps while in captivity before the onset of this experiment. Comparison of the mean group response totals shows that for stimuli 1-5 and 7, the brill and turbot are very close. For stimulus 6, whereas brill respond by only about 0.5 of a point on the scoring scale better than stimulus 5 or 7, it is the very pronounced increase in responsiveness of turbot to a live shrimp (greater than 1 point) which accounts for the difference between turbot and brill. There may be other attributes of a live shrimp not tested in this experiment that are more important for recognition of a prey stimulus in turbot than they are in brill. Possibly movement, orientation and sand grain agitation account for more of the essential criteria for recognition of prey for brill than they do for turbot.

Table 70 The results of Mann-Whitney U tests performed between turbot and brill for each stimulus.

Stimulus	Probability value (two-tailed tests)
1	0.56
2	0.81
3	0.41
4	0.41
5	0.86
6	0.03
7	0.30

Summary of conclusions

1) A moving stimulus elicited a very much greater response than a stationary stimulus.

2) A horizontally orientated stimulus was preferable to a vertically orientated stimulus.

3) Motion was a stronger attribute than orientation.

4) The direction of vertical orientation (head uppermost or tail uppermost) was not important.

5) Brill respond very well to the stimulus of sand grain agitation, such as the disturbance caused by drawing the tip of a glass tube through the sand.

6) The stimulus of a free live shrimp is stonger than any of the artificial stimuli.

A comparative analysis of the similarities and differences between turbot and brill

1) Both species were strongly responsive to a moving stimulus.

2) Both species preferred horizontally orientated to vertically orientated prey.

3) The results suggest that the relative difference between locomotion and orientation is greater for turbot than for brill.

4) The direction of the head of vertically orientated stimuli was not important to either species.

5) Sand grain agitation elicited a strong response in both species.

6) Brill were less responsive to free live shrimps than were turbot.

7) Possibly prey movement, orientation and sand grain agitation account for more of the essential criteria for recognition of prey for brill than they do for turbot.

4. EXPERIMENT 2. TO INVESTIGATE THE EFFECTS OF APPENDAGE MOVEMENT AND SIZE OF PREY.

The experimental design

The seven stimuli presented were as follows:-

Stimulus 1 - a moving blank glass tube.

Stimulus 2 - a stationary immobilised live shrimp 2/7 of fish length.

Stimulus 3 - a stationary dead shrimp 2/7 of fish length.

Stimulus 4 - a moving immobilised live shrimp 2/7 of fish length.

Stimulus 5 - a moving dead shrimp 2/7 of fish length.

Stimulus 6 - a free live shrimp 2/7 of fish length.

Stimulus 7 - a free live shrimp greater than half fish length.

In order to control their locomotion, the live shrimps for stimuli 2 and 4 were immobilised by securing them to glass tubes. Live shrimps for stimuli 6 and 7 were not immobilised but were free to move about the tank at will. Dead shrimps used for stimuli 3 and 5 were killed by asphyxiation as in the previous experiment. The effect of appendage movements were observed by comparing the behavioural responses of the fish to live shrimps and to dead shrimps with locomotion present (stimuli 4 and 5) and with locomotion absent (stimuli 2 and 3). Thirty-eight I-group turbot were used in this experiment, between 9.8 - 13.7 cm in length with a median length of 11.2 cm. Shrimps between 2.8 - 3.9 cm were judged by experience to be of a suitable size to feed to turbot of this size without them becoming satiated too quickly. Shrimps within these size limits made up the bulk of the population in Dunstaffnage Bay during the summer months and were therefore readily available in large numbers. To set a rigid relationship between prey and predator size an arbitrary ratio of 2:7 therefore was chosen so that whatever the size

of the predator, the size of the prey offered was always in proportion (i.e. for stimuli 2, 3, 4, 5 and 6). A large shrimp 7.2 cm in length was used for stimulus 7. This was the largest shrimp which could be found in the Dunstaffnage Bay population.

Results and discussion

The raw data for this experiment can be found in Appendix 5, and Table 71 provides a summary of this information. The Friedman statistic χ_r^2 for the seven stimuli was 40.46 with 6 degrees of freedom. This result was highly significant ($p<0.001$) and led to a rejection of the null hypothesis that the seven visual stimuli were equal in their effect upon the behavioural response of the fish. Table 72 shows the probability values of two-tailed tests between all possible pairs of stimuli.

In order to discover the effect of appendage movements on the behavioural response, the following comparisons were made and the results were:

i) Stimulus 2 (stationary-live) was greater than stimulus 3 (stationary-dead) $p<0.01$.

ii) Stimulus 4 (moving-live) was greater than stimulus 5 (moving-dead), $p<0.05$.

iii) The combined effect of stimuli 2 and 4 was greater than the combined effect of stimuli 3 and 5, $p<<0.01$.

These results show clearly that immobilised live shrimps were more attractive to turbot than immobilised dead shrimps. This effect is attributed to the appendage movements which are present in live shrimps but absent from dead ones. When the responses to stimuli 4 and 5 were added together, their combined effect was greater than the

Table 71 A frequency table of the response types to stimuli offered in Experiment 2.

Response Type	STIMULUS NUMBER 1	2	3	4	5	6	7
0	21	18	25	7	10	6	6
1	0	0	0	0	1	1	0
2	2	0	4	1	2	0	3
3	1	5	3	0	1	1	14
4	14	15	6	30	24	30	15
Total	63	75	41	122	104	124	108
N	38	38	38	38	38	38	38
Mean	1.7	2.0	1.1	3.2	2.7	3.3	2.8
Ranked Order	6	5	7	2	4	1	3

Key to stimuli
1 - a moving blank glass tube
2 - a stationary immobilised live shrimp 2/7 of fish length
3 - a stationary dead shrimp 2/7 of fish length
4 - a moving immobilised live shrimp 2/7 of fish length
5 - a moving dead shrimp 2/7 of fish length
6 - a free live shrimp 2/7 of fish length
7 - a free live shrimp greater than half fish length

'Total' is the group stimulus response total and is derived by adding all the response type scores for each stimulus in turn.

'N' is the total number of fish in the sample.

Table 72 The probability values of the Wilcoxon Matched-Pairs Signed-Ranks test performed successively between all possible pairs of stimuli offered in Experiment 2.

STIMULUS NUMBER	1	2	3	4	5	6	7
1		ns	ns	(4) **	(5) **	(6) **	(7) **
2			(2) **	(4) **	(5) **	(6) **	(7) **
3				(4) ***	(5) **	(6) ***	(7) ***
4					(4) *	ns	ns
5						(6) *	ns
6							ns

Key to stimuli
1 - a moving blank glass tube
2 - a stationary immobilised live shrimp 2/7 of fish length
3 - a stationary dead shrimp 2/7 of fish length
4 - a moving immobilised live shrimp 2/7 of fish length
5 - a moving dead shrimp 2/7 of fish length
6 - a free live shrimp 2/7 of fish length
7 - a free live shrimp greater than half fish length

The stimulus of a pair producing the greater response is indicated by the number in parentheses.
ns.....not significant at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001
All tests were two-tailed.

combined effect from stimuli 2 and 3, $p<0.001$. This result confirms the findings of experiment 1 and emphasises the importance of movement.

Further information on the relative importance of prey motion and appendage movements can be gained from the results of combining the group stimulus response scores for shared traits (see Table 73). There is a wider range between moving/non-moving shared traits than between appendage movements/no appendage movements for shared traits, implying that the movement (locomotory) stimulus has a stronger effect than the appendage movement stimulus.

Table 73 The group stimulus response scores for the shared traits prey locomotion and prey appendage movements for turbot

	Moving	Stationary	Total	Difference
Appendage movements (live)	122	75	197	
				52
No appendage movements (dead)	104	41	145	
Total	226	116		
Difference		110		

The difference in the response produced by stimuli 6 and 7 demonstrates the effect of prey size on the responsiveness of turbot. The nature of the behavioural response to shrimps 2/7 of the fish's

length (shrimp lengths were between 2.8 - 3.9 cm for stimulus 6) was not significantly different from that to shrimps greater then half the fish length (7.2 cm for stimulus 7), $p<0.05$. However, the proportion of type 4 responses that terminated in successful prey capture (Bite) compared with the proportion of unsuccessful attempts (Miss) was very different (see Table 74).

Table 74 The results of all type 4 responses to stimuli 6 and 7 for turbot. The result of an attack was either success (Bite) or failure (Miss) to capture the prey shrimp.

	STIMULUS		
	No. 6	No. 7	Total
Bite	22	0	22
Miss	8	15	23
Total	30	15	45

The value of the chi-square statistic was 18.7 with 1 degree of freedom. This result was highly significant ($p \ll 0.001$) and shows that although the behavioural response was no different between a large shrimp 7.2 cm in length and the shrimps between 2.8 - 3.9 cm, shrimps of this large size provided feeding stimuli but could not be caught. The largest size shrimp available was 7.2 cm and consequently it was not possible to determine whether shrimps larger than this eventually inhibit rather than stimulate the feeding response.

Kislalioglu and Gibson (1976a) state that the optimum prey

thickness is approximately half the maximum aperture of the mouth in Spinachia spinachia (L.) and give a prey thickness to mouth size ratio of about 0.53. This value compares well with a value of 0.59 for Lepomis given by Werner (1974). Stimulus 7 had a prey thickness of 12 mm and the predicted range of mouth size of the experimental turbot was 14.4 - 18.6 mm. (This information was calculated from a regression of mouth aperture on total fish length; the regression equation was $y = 1.0697x + 3.9189$.) The ratio of prey thickness to median mouth aperture (15.9 mm) was 0.75 for stimulus 7, considerably higher than either of the above-mentioned values. Stimulus 7 was well above the optimum prey size but still small enough to fit into the mouth of even the smallest fish (14.4 mm). Therefore it seems physically possible for stimulus 7 to have been consumed by any of the fish had it been caught.

The importance of movement was once again emphasised by the difference in response to the moving blank tube (stimulus 1) and to the two stationary stimuli (2 and 3). Although the response to the stationary live shrimp (stimulus 2) was ranked higher than stimulus 1, there was no significant difference between stimulus 1 and stimulus 2 or stimulus 1 and 3 at $p = 0.05$.

The group response score for stimuli 4 and 6 (moving immobilised live shrimp and free live shrimp respectively) differed by only 2 points and the responses showed no significant difference at $p = 0.05$. This was encouraging and indicated that mounting a shrimp on a glass tube did not detectibly alter the attractiveness when compared with a free live shrimp. This result in itself could be considered as a validation of the method of stimulus presentation.

The rank order for strength of behavioural response to these

seven stimuli was as follows: free live shrimp > moving immobilised live shrimp (appendage movements present) > large free live shrimp 7.2 cm in length > moving immobilised dead shrimp (appendage movements absent) > stationary immobilised live shrimp (appendage movements present) > moving control blank tube > stationary immobilised dead shrimp (appendage movements absent).

Four of the stimuli (1, 3, 5 and 6) were common to experiments 1 and 2. In all cases these stimuli elicited higher group response scores the second time of presentation (i.e. in experiment 2). Table 75 shows a comparison of the two sets of group response totals to the four stimuli. It appeared that the fish were responding better to the stimuli at the second time of presentation. This was tested statistically using a one-tailed Mann-Whitney U test. Stimuli 1, 3 and 5 were found to have elicited a significantly better response at the second time of presentation ($p = 0.0005$, $p = 0.008$ and $p = 0.0026$ respectively). Stimulus 6 was found not to be significantly different between experiment 1 and 2 ($p = 0.2912$). These results might be explained by instrumental conditioning.

Table 75 A comparison of the group response totals for four stimuli common to experiments 1 and 2.

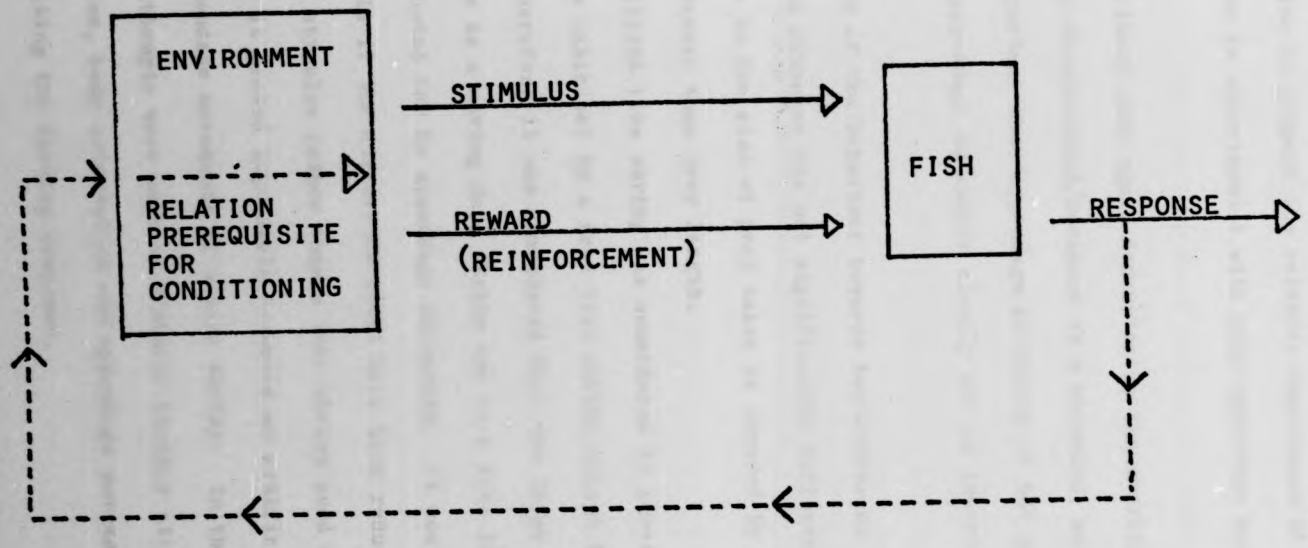
	Stimulus 1	Stimulus 3	Stimulus 5	Stimulus 6
Experiment 1	10	9	58	121
Experiment 2	63	41	104	124

Figure 29 (Adapted from Rachlin 1970) depicts the mechanism of instrumental conditioning. Instrumental conditioning occurs when there is a feedback loop so that the response either directly or indirectly results in a reward which is in turn reinforcement for the behavioural response. In these experiments, the stimulus, an artificial model which may or may not be convincing as food in its own right, initiates a response from the fish. If the response is 'correct' (i.e. type 4, a complete attack) the fish gets a reward which reinforces the response for the next stimulus presentation. In these experiments the reward may be either an edible stimulus or a reward dropped into the tank if the stimulus was inedible.

This mechanism could therefore account for the increase in responsiveness of the fish to the stimuli in experiment 2 compared with the the responsiveness to the same stimuli in experiment 1. The dilemma of whether to opt for a reward system or a non-reward system was given careful consideration before finalising the details of the method of this series of experiments. On one hand lies the possibility of conditioning the fish to respond to any stimuli offered but the alternative of not offering a reward would have been likely to cause a diminution in the strength of the behavioural responses to the stimuli. It was considered at the onset of the experiments to accept the likelihood of conditoning occurring and to keep this in mind whilst comparing stimuli in different experiments. Attempts have been made in the design of the experiments to minimise as much as possible the need to compare stimuli from different experiments; hence the repetition of certain stimuli.

The response to stimulus 6 showed little improvement in the third experiment compared with the first. This was probably because the

FIGURE 29 THE MECHANISM FOR INSTRUMENTAL CONDITIONING (ADAPTED FROM RACHLIN, 1970)



response in experiment 1 was high and there was little room for improvement in experiment 2.

Taking the possibility of conditioning into account, it was considered unwise to compare the relative importance of the effect of prey orientation in experiment 1 with prey appendage movements in experiment 2.

This experiment once again demonstrates the overriding importance of overall body displacement/movement as a stimulus, an attribute which is far more important than appendage movements of the prey. Nevertheless, appendage movements clearly are an important stimulus to turbot.

Comparison of the behaviour towards two different sizes of shrimps showed that the response was not significantly different, but that the eventual limit to the size of prey taken is imposed by prey catchability rather than prey length.

An immobilised live shrimp was considered to provide all the essential cues exhibited by a free live shrimp except for appendage movements. Therefore it was considered that the large difference in responsiveness to a moving dead shrimp and to a free live shrimp could be accounted for by appendage movements. It would however have been preferable if the difference could have been reduced by means of an artificial stimulus rather than a live shrimp used as stimulus 4. Unfortunately it proved impossible to build an artificial model to mimic the appendage movements of a live shrimp. In the remaining experiments attempts were made to discover whether stimuli other than locomotion, body orientation and appendage movements play any role in eliciting the feeding response.

Summary of conclusions

1) Shrimps with appendage movements were more attractive to turbot than shrimps without appendage movements.

2) Appendage movements alone were not as important as locomotion of the stimulus.

3) Within the limits of the experiment size of the prey stimulus did not affect the strength of the behavioural response.

4) Size of the prey affected the prey capture rate. Large prey were more difficult to catch than small prey.

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5. EXPERIMENT 3. TO INVESTIGATE THE EFFECTS OF THE RATIO OF VERTICAL AND HORIZONTAL COMPONENTS OF STIMULUS ORIENTATION.

The objectives of the experiment

In this experiment a series of cylindrical wooden models was constructed to investigate further the ability of the turbot to discriminate between horizontal and vertical components of the prey.

The experimental design

The stimuli were presented as follows:-

Stimulus 1 - cylindrical wooden model, 30 x 6 mm, length:height = 1:5

Stimulus 2 - cylindrical wooden model, 60 x 6 mm, length:height = 1:10

Stimulus 3 - cylindrical wooden model, 90 x 6 mm, length:height = 1:15

Stimulus 4 - cylindrical wooden model, 120 x 6 mm, length:height = 1:20

Stimulus 5 - cylindrical wooden model, 30 x 12 mm, length:height = 1:2.5

Stimulus 6 - cylindrical wooden model, 30 x 18 mm, length:height = 1:1.6

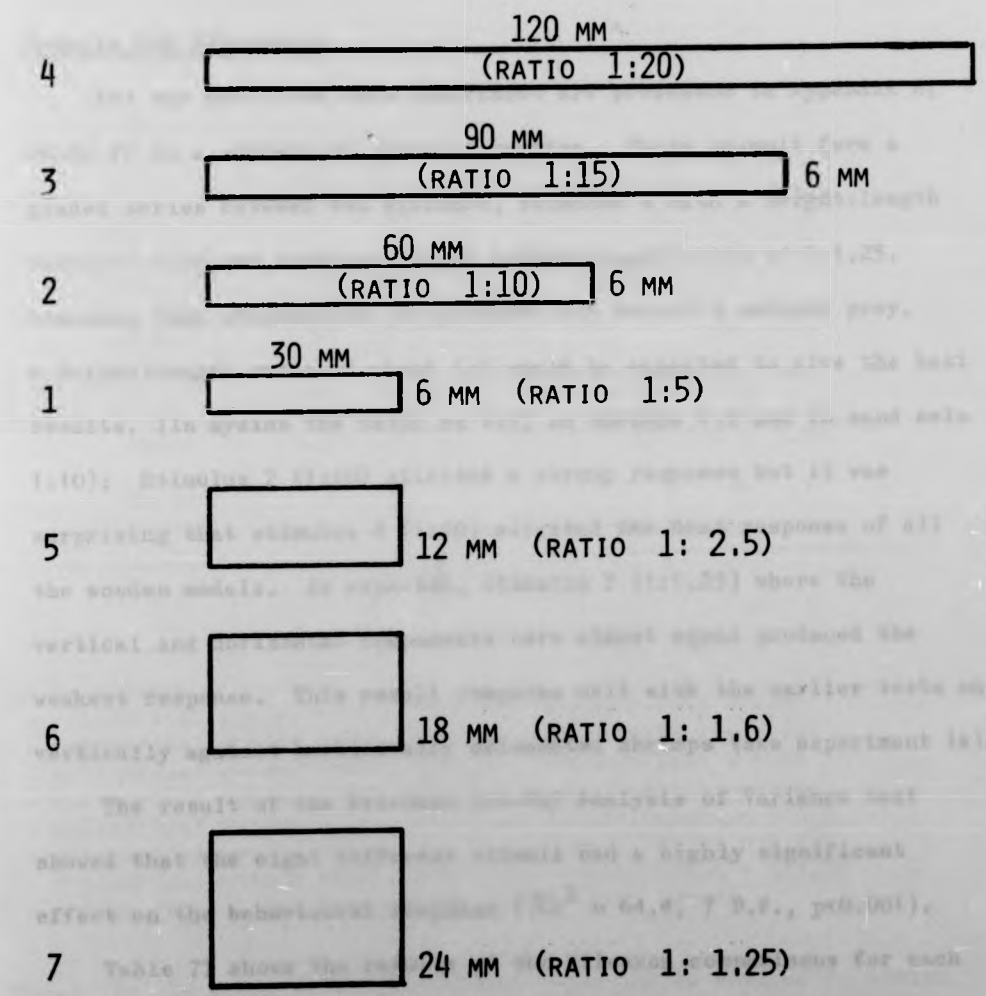
Stimulus 7 - cylindrical wooden model, 30 x 24 mm, length:height = 1:1.25

Stimulus 8 - moving immobilised live shrimp, 2/7 of fish length.

Figure 30 gives a visual representation of these stimuli. The models were made from wood which was light in colour and close to both the natural colour of shrimps and sand. As before, the models were presented by attaching them to the end of glass tubes. All models were presented with the additional stimulus of movement which mimicked the motion of a live shrimp in an attempt to maximise responses to these artificial models.

Throughout the course of these experiments the 38 turbot continued to increase in size. At this point the median length was 11.4 cm and the range was 10.2 - 14.0 cm. Shrimps between 2.9 - 4.0 cm

FIGURE 30 THE DETAILS OF THE STIMULI PRESENTED TO INVESTIGATE THE EFFECTS OF THE RATIO OF VERTICAL AND HORIZONTAL COMPONENTS OF STIMULUS ORIENTATION (EXPERIMENT 3).



ALL STIMULI WERE MOVING.
STIMULI 1 TO 7 WERE CONSTRUCTED FROM WOODEN DOWELLING.

were used in this experiment for stimulus 8 and as rewards where necessary and these conformed to the arbitrary ratio of 2:7 for prey: fish length as described in the previous experiment to maintain a fixed relationship between size of prey and size of predator.

Results and discussion

The raw data from this experiment are presented in Appendix 6; Table 76 is a summary of this information. These stimuli form a graded series between two extremes, stimulus 4 with a height:length ratio of 1:20 and stimulus 7 with height:length ratio of 1:1.25. Assuming that stimulation is optimised for turbot's natural prey, a height:length ratio of about 1:8 would be expected to give the best results. (In mysids the ratio is 1:7, in shrimps 1:7 and in sand eels 1:10). Stimulus 2 (1:10) elicited a strong response but it was surprising that stimulus 4 (1:20) elicited the best response of all the wooden models. As expected, stimulus 7 (1:1.25) where the vertical and horizontal components were almost equal produced the weakest response. This result compares well with the earlier tests on vertically against horizontally orientated shrimps (see experiment 1A).

The result of the Friedman One-Way Analysis of Variance test showed that the eight different stimuli had a highly significant effect on the behavioural response ($\chi_r^2 = 64.4$, 7 D.F., $p<0.001$).

Table 77 shows the results of the Wilcoxon comparisons for each stimulus successively tested against all other stimuli. There were no significant differences at $p = 0.05$ between all possible pairs involving stimuli 1-5 except for stimulus 4 with 5, where stimulus 4 was significantly stronger than stimulus 5, ($p<0.02$). However, stimuli 1, 2, 3 and 4 were all significantly greater than stimuli 6 and

Table 76 A frequency table of the response types to stimuli offered in Experiment 3.

Response Type	STIMULUS NUMBER 4	3	2	1	5	6	7	8
	increase in V/H ratio							
0	16	20	17	18	24	28	28	9
1	2	1	4	3	1	3	4	0
2	5	8	3	4	6	4	5	0
3	14	7	13	12	7	3	1	0
4	1	2	1	1	0	0	0	29
Total	58	46	53	51	34	20	17	116
N	38	38	38	38	38	38	38	38
Mean	1.5	1.2	1.4	1.3	0.9	0.5	0.4	3.0
Ranked Order	2	5	3	4	6	7	8	1

Key to stimuli
1 - cylindrical wooden model, 30x6 mm, length:height = 1:5
2 - cylindrical wooden model, 60x6 mm, length:height = 1:10
3 - cylindrical wooden model, 90x6 mm, length:height = 1:15
4 - cylindrical wooden model, 120x6 mm, length:height = 1:20
5 - cylindrical wooden model, 30x12 mm, length:height = 1:2.5
6 - cylindrical wooden model, 30x18 mm, length:height = 1:1.6
7 - cylindrical wooden model, 30x24 mm, length:height = 1:1.25
8 - moving immobilised live shrimp, 2/7 of fish length

'Total' is the group stimulus response total and is derived by adding all the response type scores for each stimulus in turn.

'N' is the total number of fish in the sample.

'V/H ratio' is the ratio of vertical component to horizontal component.

Table 77 The probability values of the Wilcoxon Matched-Pairs Signed-Ranks test performed successively between all possible pairs of stimuli offered in Experiment 3.

		STIMULUS NUMBER							
		1	2	3	4	5	6	7	8
STIMULUS NUMBER	1		ns	ns	ns	ns	(1) **	(1) **	(8) ***
	2			ns	ns	ns	(2) **	(2) **	(8) ***
	3				ns	ns	(3) **	(3) **	(8) ***
	4					(4) *	(4) **	(4) **	(8) ***
	5						ns	(5) *	(8) ***
	6							ns	(8) ***
	7								(8) ***

Key to stimuli
1 - cylindrical wooden model, 30x6 mm, length:height = 1:5
2 - cylindrical wooden model, 60x6 mm, length:height = 1:10
3 - cylindrical wooden model, 90x6 mm, length:height = 1:15
4 - cylindrical wooden model, 120x6 mm, length:height = 1:20
5 - cylindrical wooden model, 30x12 mm, length:height = 1:2.5
6 - cylindrical wooden model, 30x18 mm, length:height = 1:1.6
7 - cylindrical wooden model, 30x24 mm, length:height = 1:1.25
8 - moving immobilised live shrimp, 2/7 of fish length

The stimulus of a pair producing the greater response is indicated by the number in parentheses.
ns.....not significant at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001
All tests were two-tailed.

7 ($p<0.01$). These results show the effect of the graded series of stimuli. In many cases the difference between adjacent stimuli in the series was not significant but the trend through the series clearly was significant, with the largest differences occurring between the two extremes of the series (stimulus 4 and stimulus 7). Inspection of the change in group response totals shows that stimulus 5 (1:2.5) was the point in the scale at which the greatest disparity occurred. In the pictorial representation of the stimuli (Fig. 30) stimulus 5 is, at least to the human eye, the point at which the stimuli change from being predominantly horizontal to being appreciably vertical or squat. This apparent change in stimulus also seemed to affect turbot, being the point in the scale at which the horizontal component was not prominent enough to register as the configuration of a prey organism. The group response to stimulus 8, a moving immobilised live shrimp (116 points) was very close to the group response to a free live shrimp given in experiment 3 (124 points) and was not significantly different from it ($p = 0.6892$, Mann-Whitney U test, two-tailed test).

If the height:length ratio of a wooden model approximating to that of a shrimp (stimulus 1, 1:5) and its locomotion were the only important stimuli enabling turbot to recognise a model as potential prey, then one would expect the responses to stimulus 1 and stimulus 5 (a moving horizontal dead shrimp) in experiment 2 to be similar. However, this was not the case; the moving horizontal dead shrimp in experiment 2 elicited a significantly greater behavioural response than a moving wooden model with a height:length ratio of 1:5, ($p<0.001$, Mann-Whitney U test, two-tailed test). The implication from this result is that attributes other than locomotion and horizontal

orientation were lacking from the wooden model (stimulus 1) so that it was not as attractive to turbot as a moving horizontal dead shrimp. The most obvious attributes lacking from stimulus 1 were certain characteristics of shape of a shrimp. It was also conceivable that the conspicuousness of the model was not appropriate. The wooden models were not counter-shaded and they appeared lighter dorsally and darker ventrally, the reverse of the natural condition. The lack of counter-shading made the models more conspicuous. Most prey organisms exhibit some form of cryptic camouflage to conceal their presence and it is conceivable that turbot have a 'search image' which at least takes account of cryptic colouration. In experiment 4 a series of models was constructed to test aspects of the attributes of shape and inconspicuousness.

Summary of conclusions

1) Turbot prefer long thin horizontal stimuli to short squat ones.
2) The group response total shows the largest decrease between stimuli with height:length ratios of 1:5 and 1:2.5 (stimuli 1 and 5).
3) All the four stimuli with height:length ratios greater than 1:5 elicit responses that are not significantly different, suggesting that once the height:length ratio reaches a critical value no further attractiveness is provided by increasing the ratio.
4) The group response to even the best models was poor compared with the response to the immobilised live shrimp.

6. EXPERIMENT 4. TO INVESTIGATE THE EFFECTS OF SHAPE AND COUNTER-SHADING OF A PREY STIMULUS.

The objectives of the experiment

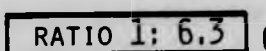
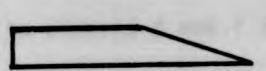
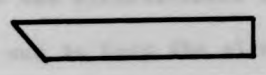
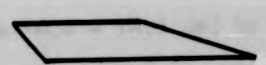
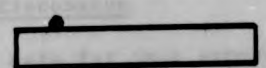
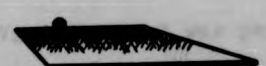
In this experiment cylindrical wooden models were used to test whether the shape of the stimulus was important for eliciting a feeding response. Two of the models were also counter-shaded to determine whether the degree of conspicuousness was important.

The experimental design

The shape of the head and tail and the presence of eyes were the traits chosen as the most likely features of shrimp appearance that turbot might recognise. The stimuli are shown in Figure 31. The responses to these stimuli were compared with the responses to an unshaped cylindrical wooden model to investigate the importance of each trait. The effect of conspicuousness was tested by comparing two unshaped models, one of which had been counter-shaded. The combined effect of shape and conspicuousness in an artificial model was determined by using a model possessing the three traits of shape, referred to above, and counter-shading. The response elicited by such a model was compared with the response to an unshaped model to discover if the attributes of shape and conspicuousness, when taken together, improved the response to a moving horizontally orientated model lacking these attributes. A moving immobilised live shrimp was also included as a reference standard linking back to stimulus 8 in experiment 2.

Models 2 and 7 were counter-shaded by several applications of a light oak wood stain to the dorsal surface. The eyes were made from the heads of insect pins coated with black paint. Head and body

FIGURE 31 THE DETAILS OF THE STIMULI PRESENTED TO INVESTIGATE THE EFFECT OF SHAPE AND COUNTER-SHADING (EXPERIMENT 4).

STIMULUS	CONFIGURATION AND DESCRIPTION OF MODELS
1	 6 MM UNSHAPED
2	 UNSHAPED WITH COUNTER-SHADING
3	 TAIL SHAPING
4	 HEAD SHAPING
5	 HEAD & TAIL SHAPING
6	 UNSHAPED WITH EYES
7	 HEAD & TAIL SHAPING, WITH EYES & COUNTER-SHADING
8	MOVING IMMOBILISED LIVE SHRIMP, 38 MM IN LENGTH

STIMULI 1 TO 7 WERE CONSTRUCTED FROM 6 MM WOODEN DOWELLING, 38 MM IN LENGTH.
ALL STIMULI WERE MOVING.

shaping was designed to mimic the body contours of a shrimp when viewed from the side. Appendages were not given to these models.

The series of stimuli in experiment 3 were 30 mm in length. In the present experiment the length of the models was increased to 38 mm. There were two reasons for this increase; first, dowelling was available at 6, not 5 mm diameter and in order to maintain a height : length ratio of 1:6.5 for the stimuli (the natural height:length in shrimps) it was simpler to increase the length than to decrease the diameter. The increase in stimulus length to 38 mm was not considered to invalidate comparisons between stimuli of 30 mm and 38 mm because the response to stimuli 6 and 7 in experiment 3 showed that if the ratio remained constant, absolute size (up to at least 72 mm) did not contribute to the effectiveness of the stimulus. The second reason for the increase was to keep the size of the stimulus in proportion to the size of the fish which had reached a median length of 11.5 cm (with a range between 10.2 - 14.3 cm) by the time this experiment was performed.

Results and discussion

The raw data for this experiment are presented in Appendix 7 and Table 78 shows a summary of this information. A Friedman Two-Way Analysis of Variance test was performed on these data to test the null hypothesis that there was no difference in the behavioural response to the eight stimuli. The result of this analysis was highly significant ($\chi r^2 = 76.15$, 7 d.f., $p<0.001$) and led to a rejection of the null hypothesis in favour of the alternative that there was a difference in the behavioural response to the eight stimuli.

The group stimulus response totals suggest that stimulus 8 (the immobilised live shrimp) made a very large contribution to the result

Table 78 A frequency table of the response types to stimuli offered in Experiment 4.

Response Type	STIMULUS NUMBER 1	2	3	4	5	6	7	8
0	26	20	17	22	25	21	15	3
1	3	7	5	3	2	2	3	0
2	7	5	12	10	8	12	11	0
3	2	4	3	2	2	2	7	0
4	0	2	1	1	1	1	2	35
Total	23	37	42	33	28	36	54	140
N	38	38	38	38	38	38	38	38
Mean	0.6	1.0	1.1	0.9	0.7	0.9	1.4	3.7
Ranked Order	8	4	3	6	7	5	2	1

Key to stimuli
1 - cylindrical wooden model, 38x6 mm, unshaped
2 - cylindrical wooden model, 38x6 mm, unshaped with counter-shading
3 - cylindrical wooden model, 38x6 mm, with tail shaping
4 - cylindrical wooden model, 38x6 mm, with head shaping
5 - cylindrical wooden model, 38x6 mm, with head & tail shaping
6 - cylindrical wooden model, 38x6 mm, unshaped with eyes
7 - cylindrical wooden model, 38x6 mm, with head & tail shaping, eyes & counter-shading
8 - moving immobilised live shrimp, 38 mm in length

'Total' is the group stimulus response total and is derived by adding all the response type scores for each stimulus in turn.

'N' is the total number of fish in the sample.

being significant. With stimulus 8 removed (χ_r^2 = 8.58, 6 d.f., p = 0.20) there was no significant difference in the behavioural responses elicited by the seven cylindrical wooden models. This demonstrates the strong effect of a live shrimp compared with any of the cylindrical wooden models.

The Wilcoxon test was applied to all possible pairs of stimuli and the results are presented in Table 79. The Friedman test on stimuli 1 to 7 implies (because there is no significant difference) that Wilcoxon analysis is not necessary, but this is not so. Firstly, the two tests differ in their operation. Whereas the Friedman test uses many stimuli simultaneously and is less sensitive to differences between pairs of stimuli, the Wilcoxon test is designed specifically for pairs of treatments. Secondly, the Wilcoxon test makes more efficient use of data. Thus the Wilcoxon test may show differences that are not apparent in the Friedman analysis.

The ranked order of group response totals show stimuli 7>3>2>6>4>5>1. The differences between totals were small and were not significant between stimuli 2, 6, 4, 5 and 1 at p = 0.05. Stimulus 3 only showed a significant difference to stimulus 1. Stimulus 7, the strongest of all the artificial models, was significantly different in its effect to stimuli 2, 4, 5 and 1 at $p < 0.05$. Stimulus 7 was expected to be the strongest since it combined all the attributes of shape. The inference from all these comparisons was that the characteristics of shape tested made only minor contributions to the effectiveness of models compared with the effectiveness of an unshaped model (stimulus 1). Of all the traits tested, the two models with counter-shading (2 and 7) seemed to elicit better responses. Also,

Table 79 The probability values of the Wilcoxon Matched-Pairs Signed-Ranks test performed successively between all possible pairs of stimuli offered in Experiment 4.

STIMULUS NUMBER	1	2	3	4	5	6	7	8
1		ns	(3) *	ns	ns	ns	(7) **	(8) ***
2			ns	ns	ns	ns	(7) *	(8) ***
3				ns	ns	ns	ns	(8) ***
4					ns	ns	(7) *	(8) ***
5						ns	(7) *	(8) ***
6							ns	(8) ***
7								(8) ***

Key to stimuli
1 - cylindrical wooden model, 38x6 mm, unshaped
2 - cylindrical wooden model, 38x6 mm, unshaped with counter-shading
3 - cylindrical wooden model, 38x6 mm, with tail shaping
4 - cylindrical wooden model, 38x6 mm, with head shaping
5 - cylindrical wooden model, 38x6 mm, with head and tail shaping
6 - cylindrical wooden model, 38x6 mm, unshaped with eyes
7 - cylindrical wooden model, 38x6 mm, with head and tail shaping, eyes and counter-shading
8 - moving immobilised live shrimp, 38 mm in length

The stimulus of a pair producing the greater response is indicated by the number in parentheses.
ns.....not significant at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001
All tests were two-tailed.

tail shaping seemed the most important of all the traits of shape.

As was expected, stimulus 8 (the moving immobilised live shrimp) was a significantly stronger stimulus than any of the other 7 models ($p<0.001$). The group response total of even the best model (7) was very much less than the group response total for stimulus 8, indicating that stimulus 7 was lacking certain important characteristics.

Apart from stimulus 7 lacking appendage movements, which were found to be important in experiment 3, it was to the human eye, even with counter-shading, more conspicuous than the cryptic colouration of a shrimp. In the next experiment the models were designed to be less conspicuous in order to test for discrimination between cryptic and non-cryptic colouration of models.

Summary of conclusions

1) The shape of the model was not found to be an important stimulus to initiate a feeding response. Most of the shaped models were found to be no more effective than an unshaped model.

2) Tail shape alone was the most important of all the traits of shape that were tested.

3) When all the traits of shape were added together, the response was improved somewhat, although it remained greatly inferior to the response to an immobilised live shrimp.

4) Counter-shading alone was not an effective means of camouflaging a model to increase its attractiveness.

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Summary of conclusions

1) The shape of the model was not found to be an important stimulus to initiate a feeding response. Most of the shaped models were found to be no more effective than an unshaped model.

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3) When all the traits of shape were added together, the response was improved somewhat, although it remained greatly inferior to the response to an immobilised live shrimp.

4) Counter-shading alone was not an effective means of camouflaging a model to increase its attractiveness.

7. EXPERIMENT 5. TO INVESTIGATE THE EFFECTS OF SHAPE, ODOUR AND INCONSPICUOUSNESS OF A PREY STIMULUS.

The objectives of the experiment

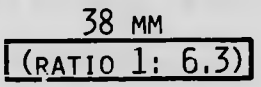
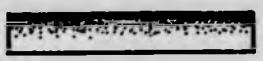
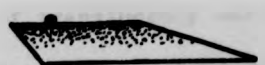
The cylindrical wooden models used in experiments 2 and 4 elicited low scores (58 being the highest) compared with the scores elicited by immobilised live shrimps (140 points). Therefore these models, even at their best for the traits that they test, were inferior to the stimulus of a real shrimp. To the human eye the wooden models looked very conspicuous and unlike the appearance of a shrimp. Shrimps have a translucent appearance and are also well camouflaged against the colour of sand. Some of the stimuli used in experiment 4 were repeated in this experiment but were made to mimic more closely the colouration of shrimps; that is, they were made less conspicuous in order to test whether turbot show a greater response to a cryptically coloured food cue.

Although it is generally accepted by authors who have studied the feeding behaviour of flatfish (Bateson, 1890; Scheuring, 1921; Pipping, 1927a, 1927b; and de Groot, 1971) that the odour is not an important food cue for turbot in prey location it was felt necessary to include an olfactory cue to verify the findings of earlier work and to eliminate odour from considerations of stimuli attractiveness.

The experimental design

Figure 32 shows the models used in this experiment. Six models were constructed from 6 mm diameter clear plastic tubing. To investigate colouration and translucency, dorsal black stippling and sand grain covering were used. These two colour forms could be compared with a clear uncoloured model. It was expected that the model

FIGURE 32 THE DETAILS OF THE STIMULI PRESENTED TO INVESTIGATE THE EFFECT OF ODOUR, SHAPE AND INCONSPICUOUSNESS (EXPERIMENT 5).

STIMULUS	CONFIGURATION AND DESCRIPTION OF MODELS
1	 38 MM (RATIO 1: 6.3) 6 MM CLEAR, UNSHAPED
2	 BLACK STIPPLE COUNTER-SHADING, UNSHAPED
3	 SAND GRAIN COUNTER-SHADING, UNSHAPED
4	 SAND GRAIN COVERED, CONTAINING A DUMMY PLASTICENE SHRIMP
5	 SAND GRAIN COVERED, CONTAINING A FRESHLY KILLED SHRIMP
6	 BLACK STIPPLE COUNTER-SHADING WITH EYES, HEAD & TAIL SHAPING
7	 WOOD STAIN COUNTER-SHADING WITH EYES, HEAD & TAIL SHAPING
8	MOVING IMMOBILISED LIVE SHRIMP, 38 MM IN LENGTH

ALL STIMULI WERE MOVING.

STIMULI 1 TO 6 WERE CONSTRUCTED FROM 6 MM CLEAR PLASTIC TUBING, 38 MM IN LENGTH.

STIMULUS 7 WAS CONSTRUCTED FROM WOODEN DOWELLING OF SIMILAR DIMENSIONS.

counter-shaded with sand grains would be the most effective of the three, since it most closely resembled the natural appearance of a shrimp. Sand grain counter-shading was achieved by applying a thin film of all-purpose adhesive to the dorsal surface of the model and rolling it in dry sand. Black stipple counter-shading was obtained by use of a Rotring pen.

Stimuli 4 and 5 tested for any effect of odour. A freshly killed shrimp was inserted inside a sand grain covered plastic tube. Both ends were left completely open. As a control, a second sand grain covered plastic tube contained a plasticine model shrimp. This control was necessary in case the dark silhouette of the shrimp was visible through the walls of the tube of stimulus 5 and made it more visually attractive to the fish. Both stimuli were kept broadside to the fish so that all that was visible was a sand grain covered tube 38 mm in length.

Stimulus 7 from experiment 4 was repeated here (cylindrical wooden model with counter-shading, eyes, head and tail shaping). The importance of translucency was tested by comparing the wooden stimulus 7 with a model bearing similar traits of shape but made from clear plastic tube with black stipple counter-shading.

The experimental fish ranged in length between 10.3 - 14.5 cm with a median length of 11.7 cm.

Results and discussion

The raw data for this experiment are presented in Appendix 8 and Table 80 shows a summary of this information. A Friedman Two-Way Analysis of Variance test was performed on this data to test the null hypothesis that there was no difference in behavioural response to the

Table 80 A frequency table of the response types to stimuli offered in Experiment 5.

Response Type	STIMULUS NUMBER 1	2	3	4	5	6	7	8
0	16	19	15	15	19	17	19	7
1	1	3	1	2	0	2	0	0
2	9	4	2	8	2	2	5	0
3	12	10	12	10	8	11	12	0
4	0	2	8	3	9	6	2	31
Total	55	49	73	60	64	63	54	124
N	38	38	38	38	38	38	38	38
Mean	1.4	1.3	1.9	1.6	1.7	1.7	1.4	3.3
Ranked Order	6	8	2	5	3	4	7	1

Key to stimuli
1 - clear plastic tubing, unshaped
2 - clear plastic tubing, with black stipple counter-shading, unshaped
3 - clear plastic tubing, with sand-grain counter-shading, unshaped
4 - sand-grain covered plastic tubing, unshaped, containing a dummy plasticene shrimp
5 - sand-grain covered plastic tubing, unshaped, containing a freshly killed shrimp
6 - clear plastic tubing, with black stipple counter-shading, head and tail shaping and 'eyes'
7 - cylindrical wooden model, with wood stain counter-shading, head and tail shaping and 'eyes'
8 - immobilised live shrimp, 38 mm in length

Stimuli 1-7 were all 38x6 mm.
All stimuli were presented with the additional stimulus of movement.

'Total' is the group stimulus response total and is derived by adding all the response type scores for each stimulus in turn.

'N' is the total number of fish in the sample.

eight stimuli. The result of this analysis was highly significant (χ_r^2 = 47.3, 7 D.F., p<0.001) and led to a rejection of the null hypothesis in favour of the alternative that there was a difference in the behavioural response to the eight stimuli. As in the Friedman analysis in the previous experiment, the group response totals suggested that most of the effect could be attributed to the high response score to stimulus 8 (the immobilised live shrimp). With stimulus 8 removed from the analysis there was no significant difference between the behavioural responses elicited by stimuli 1 - 7 (χ_r^2 = 7.3, 6 D.F., p = 0.3). This demonstrates the strong effect of a live shrimp compared to any of the artificial models.

A sand grain coloured translucent unshaped model (stimulus 3) was ranked higher in group response total than a clear unshaped tube (stimulus 1) which in turn was ranked higher than a black stipple counter-shaded translucent unshaped model (stimulus 2). The difference between stimulus 3 and stimulus 2 was significant p<0.05 (see Table 81 for the significance levels of Wilcoxon comparisons for all stimuli). This result demonstrates that an inconspicuous, well camouflaged model is more attractive to turbot than one with prominent colouration such as black stippling.

Similarly, a translucent body with eyes, counter-shading, head and tail shaping (stimulus 6) elicited a greater group response total than a more conspicuous model with similar attributes (stimulus 7). The difference was not large enough to be significant but in view of the poorer response to stimulus 2 compared with stimulus 3 the attractiveness of the translucency of stimulus 6 was probably lessened by the black stipple counter-shading. This gave the model a more prominent colour contrast than that preferred by turbot.

Table 81 The probability values of the Wilcoxon Matched-Pairs Signed-Ranks test performed successively between all possible pairs of stimuli offered in Experiment 5.

STIMULUS NUMBER	1	2	3	4	5	6	7	8
1		ns	ns	ns	ns	ns	ns	(8) ***
2			(3) *	ns	ns	ns	ns	(8) ***
3				ns	ns	ns	ns	(8) ***
4					ns	ns	ns	(8) ***
5						ns	ns	(8) ***
6							ns	(8) ***
7								(8) ***

Key to stimuli
1 - clear plastic tubing, unshaped
2 - clear plastic tubing, with black stipple counter-shading, unshaped
3 - clear plastic tubing, with sand-grain counter-shading, unshaped
4 - sand-grain covered plastic tubing, unshaped, containing a dummy plasticene shrimp
5 - sand-grain covered plastic tubing, unshaped, containing a freshly killed shrimp
6 - clear plastic tubing, with black stipple counter-shading, head and tail shaping and 'eyes'
7 - cylindrical wooden model, with wood stain counter-shading, head and tail shaping and 'eyes'
8 - immobilised live shrimp, 38 mm in length

The stimulus of a pair producing the greater response is indicated by the number in parentheses.
ns.....not significant at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001
All tests were two-tailed.

The two models 4 and 5 elicited lower responses than stimulus 3. Although this result was not significant, it does give further support to the idea of translucency being important to turbot. Stimuli 4 and 5 were completely covered with sand grains and although the natural sand colour was a point in their favour, the models were not translucent.

Five of the stimuli were compared with stimuli in the preceeding experiment and the results confirm the findings of the present experiment. A two-tailed Mann-Whitney U test was used to make these comparisons. The clear unshaped stimulus 1 was significantly stronger than the unshaped wooden model (stimulus 1 in the previous experiment), $p = 0.004$. This supports the conclusion that an inconspicuous translucent stimulus was more effective than an opaque wooden one. A black stipple counter-shaded unshaped clear plastic model (stimulus 2) showed no significant difference from a counter-shaded wooden model (stimulus 2 in the previous experiment) ($p = 0.43$) and the black stipple counter-shaded unshaped model with head, tail and eyes (stimulus 6) showed no significant difference to a similar model (stimulus 7 in the previous experiment) made from counter-shaded wooden dowelling ($p = 0.478$). These two results support the finding in this experiment that black stipple counter-shading offsets the attractiveness of a translucent model because the dark colour makes it more conspicuous. When the black stippling was replaced by sand grain counter-shading (stimulus 3), however, the counter-shaded translucent model elicited a significantly stronger response than did the counter-shaded wooden model (stimulus 2 in the preceeding experiment) ($p = 0.018$). This result may be taken as further proof of the attractiveness of sand grain colouration on a translucent tube base, presumably because it makes the model less conspicuous. Finally, no

The two models 4 and 5 elicited lower responses than stimulus 3. Although this result was not significant, it does give further support to the idea of translucency being important to turbot. Stimuli 4 and 5 were completely covered with sand grains and although the natural sand colour was a point in their favour, the models were not translucent.

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significant difference was found between stimulus 7 which was the same model in both experiments ($p = 0.98$). In fact the group response total in both cases was exactly the same, 54 points, which indicates very good repeatability.

Turning now to the effect of odour, there was no significant difference between the responses elicited by stimuli 4 and 5. In fact, the group response totals were very close (60 and 64). Clearly the odour of a shrimp in stimulus 5 made it no more attractive than stimulus 4. Thus odour was concluded not to be an important stimulus enabling turbot to locate a shrimp. This was to be expected and supports the evidence of all past work on the importance of olfactory stimuli for turbot. The inference from this result is that whatever the differences were between models and real shrimps in this series of experiments, they certainly were not due to shrimp odour.

Of all the artificial models presented to turbot in experiments 2, 4 and 5, the best stimulus has been 3 in the current experiment, a moving sand grain counter-shaded translucent unshaped tube with a height:length ratio of 1:6.3. The score for this stimulus was 73 compared with an average score for an immobilised live shrimp of 126 over the three experiments. Thus the gap between the response score of the best of the artificial stimuli and a free live shrimp remains large. In experiment 3 a better score than 73 was obtained by using a dead shrimp, stimulus 5 (104 points, significant at $p = 0.008$), Mann-Whitney U test, one-tailed test). At this point, with most of the practical attributes already incorporated into models, it was felt that a change of approach was necessary in order to close the

gap between the best artificial model and a real live shrimp. Instead of trying to improve the models further, it was decided to try and make real shrimps less attractive and approach the problem from an analytic rather than a synthetic viewpoint.

Summary of conclusions

1) Translucent models were more effective than opaque ones.

2) Cryptic colouration closely resembling the natural colour of sand, on which shrimps disguise themselves, was preferable to more conspicuous colouration such as black stippling.

3) The odour of a shrimp was not an important stimulus for turbot when locating their prey.

4) The best shrimp model was a moving, sand grain counter-shaded, translucent, unshaped tube with a height:length ratio of 1:6.3.

8. EXPERIMENT 6. TO INVESTIGATE THE EFFECT OF ARTIFICIAL LEGS ON A MODEL AND THE EFFECT OF DISGUISING THE APPEARANCE OF A REAL SHRIMP.

The objectives of the experiment

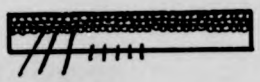
In this experiment an attempt was made to narrow the gap in group total response scores between the best model so far (a moving, sand grain counter-shaded translucent unshaped tube with a height:length ratio of 1:6.3, stimulus 3 in experiment 5) and the moving immobilised live shrimp. This was carried out in two ways. Firstly, by adding legs to the model and secondly by attempting to make a live shrimp less attractive by colouring it, removing its legs and inhibiting leg movements by anaesthetisation.

The experimental design

Figure 33 shows the stimuli presented in this experiment. Legs made from translucent fishing line were inserted into holes drilled into the side of a sand grain counter-shaded clear plastic tube 38 mm in length (stimulus 2). Three pairs of long legs 7 mm in length anteriorly represented the pereiopods (walking legs) and five pairs of short legs 4 mm in length posteriorly represented the pleopods (used for walking and swimming in shrimps). The effect of the presence of artificial legs was investigated by comparing the responses to stimulus 2 with the responses to stimulus 1, which did not possess legs.

Stimulus 6 was a moving immobilised live shrimp which could be compared with stimuli 3, 4 and 5 to test for any reduction in attractiveness if shrimps were coloured, were without legs or were without leg movements respectively. Stimulus 3 consisted of shrimps coloured bright pink by immersion in a 1% solution of Rosé Bengal in

FIGURE 33 THE DETAILS OF THE STIMULI PRESENTED TO INVESTIGATE THE EFFECT OF ARTIFICIAL LEGS ON A MODEL AND THE EFFECT OF DISGUISING THE APPEARANCE OF A REAL SHRIMP (EXPERIMENT 6).

STIMULUS	CONFIGURATION AND DESCRIPTION OF MODELS
1	 SAND GRAIN COUNTER-SHADING, NO LEGS
2	 SAND GRAIN COUNTER-SHADING, WITH LEGS
3	LIVE SHRIMP + ROSE BENGAL STAINING
4	LIVE SHRIMP: LEGS REMOVED
5	LIVE SHRIMP: NO LEG MOVEMENTS
6	LIVE SHRIMP

STIMULI 1 & 2 WERE CONSTRUCTED FROM 6 MM PLASTIC TUBING, 38 MM IN LENGTH.
STIMULI 3 TO 6 WERE IMMOBILISED SHRIMPS, 38 MM IN LENGTH.
ALL STIMULI WERE MOVING.

sea water for 5 minutes. All the pereiopods and pleopods were removed from shrimps used for stimulus 4. For stimulus 5 shrimps were anaesthetised by immersion in a 30% solution of magnesium chloride in sea water. The recommended dosage of magnesium chloride, 7.5% (Pantin, 1946) was found to take too long to inhibit the appendage movements so the dosage was increased to reduce the time taken for anaesthetisation.

The median length of the fish by the time of this experiment had increased to 11.8 cm ranging from 10.3 - 14.6 cm.

Results and discussion

Appendix 9 contains the raw data for this experiment and Table 82 shows the results in a summarised form. The group stimulus response totals clearly fall into two groups; those of the artificial models (stimuli 1 and 2) and the shrimp stimuli (stimuli 3, 4, 5 and 6). The artificial models elicited lower response scores than the shrimp stimuli.

Friedman analysis showed that there was a significant effect of the six stimuli on the behavioural response (χr^2 = 33.2, 5 D.F., $p<0.001$). This was most likely to be attributed to the difference in responsiveness of the fish to the artificial models compared with the four shrimp stimuli.

Table 83 shows the Wilcoxon analysis of pairs of stimuli. There was no significant difference between stimuli 1 and 2. It might be inferred from this result that legs are not important features for turbot to recognise their prey. This may be true if the legs are not moving, but moving appendages were found to make a contribution to stimulus attractiveness in experiment 3. It is quite probable that

Table 82 A ferquency table of the response types to stimuli offered in Experiment 6.

Response Type	STIMULUS NUMBER 1	2	3	4	5	6
0	8	6	4	4	2	3
1	0	0	0	0	0	0
2	4	3	0	1	0	0
3	12	16	1	0	2	3
4	14	13	33	33	34	32
Total	100	106	135	134	142	137
N	38	38	38	38	38	38
Mean	2.6	2.8	3.5	3.5	3.7	3.6
Ranked Order	6	5	3	4	1	2

Key to stimuli
1 - clear plastic tubing, 38x6 mm, with sand-grain counter shading and no 'legs'
2 - clear plastic tubing, 38x6 mm, with sand-grain counter-shading and with 'legs'
3 - immobilised live shrimp, 38 mm in length, dyed with Rose Bengal
4 - immobilised live shrimp, 38 mm in length, with legs removed
5 - immobilised live shrimp, 38 mm in length, with legs immobile
6 - immobilised live shrimp, 38 mm in length, with legs free

'Total' is the group stimulus response total and is derived by adding all the response type scores for each stimulus in turn.

'N' is the total number of fish in the sample.

Table 83 The probabilty values of the Wilcoxon Matched-Pairs Signed-Ranks test performed successively between all possible pairs of stimuli offered in Experiment 6.

		STIMULUS NUMBER 1	2	3	4	5	6
STIMULUS NUMBER				(3)	(4)	(5)	(6)
	1		ns	**	**	**	**
	2			(3) **	(4) **	(5) **	(6) **
	3				ns	ns	ns
	4					ns	ns
	5						ns

Key to stimuli
1 - clear plastic tubing, 38x6 mm, with sand-grain counter-shading and no 'legs'
2 - clear plastic tubing, 38x6 mm, with sand-grain counter-shading and with 'legs'
3 - immobilised live shrimp, 38 mm in length, dyed with Rose Bengal
4 - immobilised live shrimp, 38 mm in length, with legs removed
5 - immobilised live shrimp, 38 mm in length, with legs immobile
6 - immobilised live shrimp, 38 mm in length, with legs free

The stimulus of a pair producing the greater response is indicated by the number in parentheses.
ns.....not significant at p=0.05
*.....significant at p<0.05
**.....significant at p<0.01
***.....significant at p<0.001
All tests were two-tailed.

the legs were not realistic enough, being straight lengths of fishing nylon which did not look much like jointed shrimp appendages.

There was no significant difference between any of the live shrimps (stimuli 3, 4, 5 and 6). It was therefore concluded that none of the three treatments designed to reduce the attractiveness of a live shrimp was effective. This was surprising and is to some extent inconsistent with the earlier results. A possible explanation lies in the fact that the high proportion of real shrimp stimuli caused the fish to be less selective in their choices and more likely to go after any stimuli that were presented. This explanation would certainly account for the increased responsiveness to a moving sand grain counter-shaded clear unshaped stimulus (stimulus 1) compared with the responses to an identical stimulus given in the previous experiment (stimulus 3). The group response scores for this stimulus were 73 points in experiment 5 compared with 100 points in the present experiment. These responses were tested using the Mann-Whitney U test and although not significant at $p = 0.05$ ($Z = 1.84$, $p = 0.06$) the probability value was not far from $p = 0.05$.

There still remains quite a large gap between the best score elicited by an artificial model (106 points) and the worst score due to a real shrimp stimulus (134 points). The difference between the responses to these two stimuli was significant at $p<0.01$. In fact the responses to all four shrimp stimuli were significantly different from the responses to both the artificial stimuli ($p<0.01$). Therefore the gap itself is real and significant.

The arithmetic means (Table 82) show that for the two artificial stimuli the value of about 2.7 was one response type lower than for the shrimp stimuli (value about 3.6). This means that whereas the

average response to an artificial model was a type 3 (complete approach) the average response to a shrimp model was a type 4 (an attack). Thus the artificial models seemed convincing enough to draw the fish to a position close enough to make an attack but failed to be strong enough at close range to stimulate an attack. The artificial models, therefore, were still lacking some attribute(s) of real shrimps.

In order to verify that the responsiveness to the immobilised live shrimp stimulus had not changed over the course of the experiments a Kruskal-Wallis One-Way Analysis of Variance test was performed. There was found to be no change in responsiveness to immobilised live shrimps over the last four experiments ($H = 1.62$, 3 D.F., $p = 0.7$).

This was the last experiment performed in this series of investigations on how turbot recognise their prey.

Summary of conclusions

1) Artificial legs were either not sufficiently realistic to influence the strength of the feeding response, or the presence or absence of legs (without appendage movements) made no difference to the attractiveness of the model.

2) The responsiveness of the fish to live shrimps could not be reduced by disguising the shrimps. The ability to recognise a shrimp was not impaired by reducing the camouflage, removing the appendages or preventing appendage movements.

3) It has not been possible to account for all the attributes of shrimp recognition used by turbot.

GENERAL DISCUSSION.

The Relevance of the Laboratory Findings to the Natural Behaviour in the Sea.

In order to relate the laboratory results to the behaviour of fish in the sea some degree of speculation is required because there are no well-documented reports of natural behaviour patterns in the sea. A study has, however, been carried out by Gibson (Pers. comm.) which describes the activity and feeding behaviour of plaice in the sea. Gibson's work complements some aspects of the present study and supports some of the observations. There is a large body of literature concerned with the theory of feeding strategies and factors which modify behaviour and this information will also be used to assess the relevance of the laboratory findings.

The natural feeding behaviour of flatfish in the sea is likely to be modified somewhat by the artificial environment. In the absence of all other oonsiderations, the feeding area allocated to each individual fish has considerably restricted the space available for feeding. The effects of such confinement will undoubtedly have altered the proportions of the locomotory elements of behaviour. The elements Swim, Skim, Creep and Shuffle would no doubt have longer durations in the sea since the fish have more ground to cover and more space in which to move.

The presence of tank walls has the effect of increasing the number of Turns required in order to avoid collision so the elements Turn and Swivel probably have elevated frequencies. In addition, two or possibly three elements are artefacts of the unnatural environment. These are Flap-Swim, Flap and Settle. The first and second of these are performed with the snout of the fish pressed against the tank

walls, in the water column and on the substratum respectively. These elements seem to be an attempt by the fish to pass through the tank walls, which they can presumably see through; but such obstacles would not usually be encountered in the sea. Settle describes the fish coming to rest on a vertical tank wall. All species seem to be able to adhere to flat vertical surfaces very well and remain in such a position for long periods with little effort. Arnold (1969) described the reactions of plaice to water currents and commented on their 'clamped-down posture' in varying water velocities in an attempt to avoid being swept away by currents. In addition the ability to adhere to surfaces might possibly be an adaptation against predation; by adhering to the substratum flatfish would be difficult to capture. The body form and colouration of turbot, brill, plaice, flounder and sole is well suited for a life on sandy or muddy bottoms where they are well camouflaged and can bury themselves in the substratum. Topknots, however, are different. The colouration and habitat of topknots is completely different from these other species and they do not often bury themselves. Wheeler (1969) reports that topknots cling to the sides of rocks deriving shelter from crevices and plant material. My observations of their behaviour and colouration suggest that they are well adapted for this mode of life. Invariably they were to be found on a vertical surface, venturing onto the horizontal bottom only occasionally. Thus for the topknots Settle seems an important element.

The laboratory feeding regime has probably increased the feeding intensity and decreased the feeding duration compared with the pattern expected in the natural habitat. Vertebrate predation generally increases as a function of prey density in a characteristic way,

described by Holling (1965) as a type-3 functional response curve. Descriptions of the feeding behaviour in Part Two of this study have been carried out at fixed prey densities but density is an important parameter in the feeding of predators. The prey density was set so that it did not limit the feeding rate of the fish. The high prey density was also desirable in order to record sufficient feeding activity during a conveniently short sampling period. This has compressed feeding, which may last for several hours during a 24 hour cycle in the natural habitat, into a short period of time. Clearly the effect on the behaviour would be to alter the balance of feeding/non-feeding activities and in consequence the proportions of feeding elements would appear artificially higher than they would in the natural habitat.

Searching for prey is "any hunger-dependent behaviour of a predator likely to bring a prey within range of its exteroceptors" (de Ruiter, 1967). At high prey densities the need for food searching activities is reduced because the chances of a fish encountering a prey item are high. In the sea, food searching probably forms a large part of the feeding behaviour cycle. According to the literature, the time spent searching for prey varies considerably, e.g. 15% in oyster catchers Haematopus ostralegus (Drinnan, 1957), 17% and 20% in two protozoa respectively (Salt, 1967) and 37% in the predatory whelk Thais lapillus (Connell, 1961). Observations in the wild indicate that the percentage of total time, when food is scarce, devoted to feeding behaviour varies inversely with the abundance of food. During scarcity this time may increase to almost 80% (Gibb's data in Lack, 1954) in goldcrests and tits. In the laboratory tank, however, with the method employed, it has not

been possible to quantify food searching. Nevertheless certain elements of behaviour do seem likely to represent searching e.g. Shuffle, Turn and Palpation.

The effect of hunger on the feeding behaviour cycle has been well documented and appears to have two effects. A decrease in hunger increases selectivity. Many authors report increased selectivity with respect to prey size: Ivlev (1961) for pike, perch, carp, bream, Bleak and Macrodytes circumflexus, Nakamura (1962) for skipjack tuna, Blaxter (1963) for herring larvae, Galbraith (1967) for rainbow trout and yellow perch, Ware (1972) for rainbow trout and Kislalioglu and Gibson (1975, 1976a) for fifteen-spined sticklebacks. Data provided by Beukema (1968) indicate that, with increasing satiation, three-spined sticklebacks became more selective feeders. At the start of a feeding sesssion fish ate foods differing in palatability (Tubifex worms, Drosophila larvae and Enchytraeus) with equal frequency. With increasing satiation, the more palatable foods were selected with progressively greater frequency than less palatable foods. A similar increase in selectivity with increasing satiety was reported for carp feeding on Chironomid larvae, amphipods, isopods and molluscs (Ivlev, 1961).

The second effect of decreased hunger (or increased satiation) is to increase the complexity of predatory behaviour, e.g. Tugendhat (1960) for three-spined sticklebacks and Chiszar and Windell (1973) for bluegill sunfish. The work of Brett (1971) on sockeye salmon also showed that the rate of feeding declined as hunger decreased. Similarly, satiation in rats has been shown to increase such measures of instrumental behaviour as latency to eat (Zimbardo and Montgomery, 1957; Bolles, 1962, 1965) and latency to resume eating after

interruption by a sudden distracting stimulus (Siegel and Correia, 1963). A comparable finding was reported for rabbits and chickens by Bousfield and Sherif (1932). Chiszar and Windell (1973) suggest that the two effects are related. The increased complexity of sunfish predatory behaviour with increased satiety reflects an increase in selectivity during the feeding session. The increase in stopping, turning, orientating and approach behaviour may represent an increased tendency to inspect and perhaps to reject the prey organisms.

Prey density and hunger interact in the natural environment; both play an important role in modifying predatory behaviour. If prey density is low, predator hunger will be high. Observations in the wild indicate that the percentage of total time devoted to feeding behaviour varies inversely with the abundance of food in the predator's habitat, and during food scarcity this may amount to as much as 90% (Kluyver, 1950; Gibb, 1960). The scarcer the food, the greater is the fraction of this percentage spent on food searching.

In the three-spined stickleback, the distance transversed per unit of time increases with deprivation and decreases with satiation. This decrease is less marked than the drop in responsiveness to encountered prey induced by satiation. Even when the responsiveness approaches zero, the fish will continue to perform some exploratory swimming (Beukema, 1967). In the three-spined stickleback, the frequency and degree of completeness of approaches to encountered prey wax and wane with hunger and satiation (Beukema, 1967; Tugendhat, 1960). Degree of completeness is more strongly influenced than frequency; slight intention movements of approach are still common even when satiation is considerably advanced. At high satiety levels, however, the fish

may ignore prey at close range. The less palatable the prey, the more rapid is the decrease of the approach tendency with growing satiation. The maximum distance from which prey are detected does not appear to change with hunger over the range studied (Beukema, 1967).

The foregoing account of the findings of other workers gives an indication of the way in which the laboratory feeding behaviour of flatfish may be modified in the sea. In the present study the experimental fish were obviously very hungry and were provided with a high density of prey - two factors that have made the feeding responses very intense. It is unlikely that fish would encounter prey densities as high as those of the experimental regime (with the possible exception of mysids which migrate in dense shoals with the changing of the tides in estuaries (Mauchline, 1971). It is also unlikely that, under normal conditions, the fish would become as hungry as they were under the experimental regime because they would have free access to food when hunger demanded. The difference between the behaviour observed in the laboratory and that in the sea are probably due mainly to differences in the intensity of activity. Gibson (1975 & pers. comm.) has estimated that plaice spend between 6 - 17% of their time during the daylight hours moving about on the bottom. Even allowing a generous 5% extra for non-locomotory activities such as chewing. They are probably inactive for about 80% of their time. A distinction must be made here between daytime and night-time activities. The feeding of plaice is largely restricted to the daylight period (Franz, 1910; Petersen, 1911; Steven, 1930; Jones, 1952; Hempel, 1956, 1964; de Groot, 1964). It is generally agreed, however, that in plaice pelagic swimming

activity is largely confined to the night. This is based on the reported aquarium observations of Blegvad (1916), Boulenger (1929), Harder and Hempel (1954), Woodhead (1960) and de Groot (1964, 1971). Supporting evidence from daytime and night-time trawl catches is not conclusive (see de Groot, 1971, pages 160 - 184). Because plaice are supposed to feed mainly during the daylight hours, comparisons will only be drawn with my observations and their daytime bottom activity in the sea. The nocturnal pelagic swimming behaviour will not be considered.

Gibson's observations suggest that in the sea the feeding activity of plaice (and probably all the other species too) is punctuated by much more inactivity than has been recorded in the laboratory feeding where the proportion of time spent inactive ranged between 31% for turbot feeding on mysids to 80% for flounder feeding on worms (see Summary, Table 61, page 160). The other most important difference between laboratory and natural feeding behaviour lies in the quantity of searching behaviour exhibited. There would also probably be many more incomplete feeding cycles in the sea with fish testing out potential prey items, some of which would prove unfruitful.

Learning is another factor that plays an important part in modifying predatory behaviour, Of the range of prey attributes perceived by a predator, some will elicit a stronger feeding response than others. A limited set of features termed 'sign stimuli' predominate in the recognition of an object as potential prey. Learning to recognise a set of sign stimuli leads to the formation of 'search images'. Search image formation raises the responsiveness of a predator to a level determined by the frequency of encounters with

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the prey and by its relative palatability (de Ruiter, 1967). Much has been written on the theory of search images (Tinbergen, 1960; Holling, 1965; Krebs, 1973; Curio, 1976) and further discussion is not required here. It is certainly feasible that by providing the fish with only a single prey species at a time that search images aided the fish in detecting and recognising additional prey individuals in the laboratory tanks. Whether this is true or not the formation of search images would be less likely to occur in the sea because the greater prey diversity would allow the fish access to a more diverse diet. Evidence for the formation of search images by fish in the same way as birds (Tinbergen, 1960) has not proved conclusive. Beukema (1968) reports that the maximum distance from which the three-spined stickleback can detect a new prey species increases with its experience with that prey; in encounters at closer range the more experienced fish is more likely to detect the prey. An improvement in prey detection has also been found in rainbow trout (Ware, 1971) with experience. Curio (1976) points out, however, that the difference between "learning to see" and forming a preference for familiar food depends on how learning to see is defined in operational terms.

Whatever the processes that are manifested in fish learning it is clear that experience influences prey detection and recognition. Learning could account for the high level of responsiveness of turbot to shrimps in Part Three of this investigation. Repetitive encounters coupled with a high palatability (assumed because shrimps form a large part of the diet of similar sized fish in the sea during late summer (Jones, 1973))are the two essential requisites for more efficient prey detection by experience.

Learning can greatly assist the predator in its search for food either by providing information on the most likely locations to find prey or by making concealment of the prey more recognisable to the predator. In the laboratory tank, learning gives rise to conditioning so that the fish may sometimes recognise stimuli as cues by which it can procure food, cues which otherwise would not normally elicit a feeding response.

Conditioning is brought about by the natural process of learning. In the laboratory, conditioning may become an unwanted accompaniment to the manipulations necessary to perform particular behavioural experiments, as was found during the experiments in Part Three. There was evidence that the fish were more responsive to specific models on the second time of presentation (see experiment 2). This may, however, have been part of a more general learning process by which the fish became conditioned to respond to artificial models presented attached to glass tubes because they were rewarded for doing so by receiving a shrimp if they made a type 4 response. The dilemma of whether to opt for a reward/non-reward presentation regime has been discussed in experiment 2. Flatfish have been observed to learn quickly (de Groot, 1971) but doubt exists as to whether sufficient presentations have been made to the fish to account for this sort of conditioning. To some extent this increase in responsiveness to artificial models may be partly attributable to the fish becoming more at ease in the experimental enclosures.

No doubt another criticism of the method could be raised that naive fish should have been used in each separate experiment to overcome the problem of conditioning. This would have been impractical for several reasons. The complete series of experiments

took many months to perform but wild turbot were available on the beaches for only 2 - 3 months each year (Gibson, pers. comm.). Wild fish available in the surf zone of the beaches were also too small for experimentation, being only 2 - 3 cm in length. A stock of fish had therefore to be maintained in captivity throughout the winter months so that they could be grown on to a large enough size to be used in the following spring/summer to coincide with the increase in shrimp populations. It was felt to be crucial that during this time the fish be maintained on natural live food to avoid changing the natural criteria of prey recognition, which might occur if they were fed on an artificial diet. Burghardt (1969) provides evidence that artificially induced prey preferences can modify the behaviour of newly hatched snakes of the genus Thamnophis to horse meat extracts. Sufficient mysids were available during the winter months for 40 fish but not for the 300 fish which would have been required if different fish were used for each experiment. The method chosen was therefore considered to be the most realistic means of conducting the experiments despite the objections of using the same fish for all the experiments. This problem, although a limitation of the method, does not invalidate the findings because the provision of suitable control stimuli coupled with convincing statistical differences does substantiate the conclusions.

Although the effect of conditioning does seem to have played a role in modifying the behaviour of turbot to the artificial stimuli provided in the laboratory, conditioning does seem to have a place in the natural environment as demonstrated by the responses of dabs to the noise of divers' aqualung and demand valves (Chapman, Johnstone, Dunn and Creasey, 1974). This suggests that although conditioning

and associations formed in the laboratory are to some extent disadvantageous to the experimenter, they are illustrations of true adaptive behaviour which permits the fish to utilise every opportunity to benefit itself.

Social feeding was found to play a role in the feeding behaviour of flatfish. Perception by individuals not only of the food itself but also of the feeding behaviour of other of the same and other species influences approach tendencies. Whether social interactions influence motivation to feed or dispel any uncertainties about food recognition is unclear, but this phenomenon was observed on many occasions in the preliminary experiments when several fish were maintained together, particularly when artificial diets were offered. Conversely, the diminished feeding responses of some fish when held in isolation also seemed to be partly attributable to the lack of social interactions. All experiments were performed with isolated individuals to remove any complications to the feeding behaviour brought about by interaction between individuals.

These observations are corroborated by those of Keenleyside (1955), who observed that if one member of a school of hungry three-spined sticklebacks begins to feed, others will quickly swim towards it. This results in a rapid increase in the density of the school. The new arrivals may try to take prey from the first fish or they may search for food in the same area.

Olla and Samet (1974) observed the role of visual stimuli in the social facilitation of feeding behaviour in the striped mullet. When isolated fish viewed a feeding group, the initiation of feeding was greatly aided, with the total number of feedings remaining high until the latter part of a test. The latency to feed was longer for fish

that could not see a feeding group.

Welty (1934) obtained evidence for social facilitation of feeding in several species of fish. The more usual finding is that the initiation of feeding within groups of fish somehow activates intragroup agonistic behaviour (Albrecht, 1966; Newman, 1956). Brawn (1961, 1969) has presented evidence that with cod (Gadus morhua) social facilitation or "co-operation" functions during prey location but is followed by increased,more intense aggression shortly after feeding. Although Baird (1968) has concluded that "feeding lowers the threshold of aggressive behaviour", the only comprehensive attempt at explaining the apparent interaction of these behaviours has been that of Albrecht (1966). He has proposed that, due to a postulated homonomous relationship between predatory and aggressive patterns, these two functionally distinct behaviours are motivationally linked such that motivational summation occurs. Poulsen and Chiszar (1975) conclude that whether or not such harmony exists, until the possible effects of social interactions on feeding are determined, it cannot be certain that data obtained with isolated subjects represents the 'normal' feeding behaviour of the species.

The experimental work has shown that the behaviour of flatfish is well adapted to their different modes of feeding. In addition to behavioural adaptations, the flatfish also show morphological and physiological adaptations which complement the behavioural ones. In order to appreciate fully the context of the behavioural differences these other adaptations, which have not themselves formed part of the experimental work, will be discussed briefly before the ecological significance of the findings of this work is discussed.

The Role of Sensory Systems in Prey Detection

Vision and olfaction are the two most important sensory systems used by flatfish in the detection of prey.

One of the earliest studies on prey detection by flatfish was that of Bateson (1890) who divided several species into "fishes which seek their food by scent" and "fishes which seek their food by sight". The common sole belonged to the first group, turbot, brill, common topknot (Bothidae), plaice, flounder (Pleuronectidae) to the second group. He observed that, at some interval after the food had been thrown into the aquarium, sole perceived it with a writhing jump from the bottom. This writhing jump is identical to the omega jump described by Kruuk (1963). When searching for food the sole shambles along the bottom in an undulating walking movement on the fin rays of its dorsal and anal fins. The head is raised upwards and sideways and gently pats the ground at intervals; the element of behaviour called palpation in the present study refers to this gentle patting of the ground at intervals. With its villiform papillae, which cover the lower side of the head region, it investigates the bottom in search of food. When the head is right above the food the sole seizes it at once. The sole appears to be unable to find food that does not lie on the bottom and will not succeed in finding food suspended in the water unless it be lowered so that the sole is able to cover part of it with the lower side of its head, when it seizes it at once. Of plaice and turbot Bateson remarked that the importance of the olfactory organs is obscure.

Scheuring (1921) studied the relation between the eyes and the feeding behaviour of several fishes, including seven flatfish species. The turbot depends only on its eyes for catching prey; it catches prey only in front of it. The plaice catches prey only on the bottom in

front of it; soles rely mainly on their tactile sense, the eyes playing an unimportant role.

Pipping (1927a, 1927b) made observations on the relationship between smell and the feeding behaviour of turbot, flounder and sole. She observed that turbot cannot find their food by smell, flounder being similar. Although a certain alertness of the fish was noticed when buried food was offered, the flounder was not capable of localising prey by means of its smell. Soles are very well adapted to finding their prey olfactorially, without the use of vision.

Steven (1930) described the feeding habits and behaviour of four species of flatfish. He states that sole, in foraging for prey, depend entirely on tactile sense, the eyes being very small and scarcely moveable. The fish is provided with a dense mass of tactile villi on its lower cheek, which is thus equipped to function as a very sensitive tactile organ. Steven's other observations on the feeding behaviour of soles also corroborate those of Bateson.

Field studies on the hearing of two species of flatfish, Pleuronectes platessa and Limanda limanda, the common dab, show that they are sensitive to sounds in the frequency range from 30 - 250 Hz with greatest sensitivity around 110 - 160 Hz (Chapman and Sand, 1974). Maier (1909) was the first to investigate the sense of hearing in flatfish. He tried unsuccessfully to condition sole and turbot to sounds using food as a reward. Similarly Bull (1928) was unable to condition plaice and flounder using electric shock as punishment. There is, however, evidence that dabs do learn to use sound as a means of detecting prey. Chapman, Johnstone, Dunn and Creasey (1974) found that dabs were attracted to the recorded sound of divers' aqualung and demand valves in Loch Torridon. They suggest that the fish associate

the noise with the presence of food organisms disturbed from the sea bed by the diver and that they had become conditoned to the noise over a period of time.

Sharks have been reported to use hearing to find prey (Banner, 1972; Nelson & Gruber, 1963). Sharks follow unusual or escape movements of prey animals from up to 200 metres away by virtue of their lateral line organ; when close to a potential victim, they may use a number of senses in combination before actually attacking. It is still open to question whether the lateral line organ can also be used alone to localise a prey accurately.

Another possible method of prey detection which would be particularly suitable for use by plaice is sensitivity to water movements, specifically the water currents emitted from the siphon tubes of molluscs. Plaice are known to feed on these siphons (Edwards and Steele, 1968) and it has been suggested by de Groot (1971) that they may be able to detect exhalent water currents from such structures. Of course such currents would be likely to contain odour traces of the molluscs and to prove that detection and recognition were due to rheotaxis rather than olfaction would not be easy.

Evidence Supporting the Relative Importance of Sensory Systems by a Comparative Study of the Brains of the Pleuronectiformes.

Table 84 is a summary of the findings of work performed by Evans (1937) in a comparative study of the brains of the pleuronectiformes. This correlates very well with the conclusions based on the observations and experiments to be found in the literature and from my own experience of the relative importance of the various sensory

systems in prey detection by flatfish.

Table 84 A summary of the conclusions of Evans (1937) on a comparison of the brains of the Pleuronectiformes.

Species	Olfactory lobes	Optic lobes	Facial lobes	Central acoustic lobes	Somatic sensory lobes
Sole night feeder diet - worms	large	small	v.small	large	large
Plaice ground feeder diet -worms & molluscs	medium	large	large	nil	medium
Turbot diet - mostly fish	small	large	small	nil	large

Looking first at the sole, Bateson (1890) wrote of the well known papillary area on the lower surface of the head that "contrary to expectation these villi do not bear sense organs", of the nature of taste buds and Evan's (1937) observations confirm this fact, although it has been denied by Cunningham (1896), that the facial lobe is very small. If taste buds were present it would be expected to be well developed. The observation also explains the great size of the somatic-sensory lobe. The olfactory system is highly developed in the sole but the eyes and optic lobes are small. The presence of a well-marked central acoustic lobe is usually associated with considerable

power of hearing. Evans suggests, therefore, that the large acoustic lobe is associated with an auditory function or at least with the perception of vibrations. The tapping of the sand, so characteristic of the sole's method of hunting, is reminiscent of the tapping and listening for hidden worms exhibited by a thrush feeding on a lawn or seabirds such as the sheldrake and certain gulls which tap for worms in a similar way on the sea shores. If this conclusion is accepted, sole feed by smell, touch and hearing represented centrally in the olfactory somatic-sensory and central acoustic lobes, all of which are markedly developed.

Steven (1930) describes the feeding behaviour of the lemon sole Microstomus kitt (= Pleuronectes microcephalus). It is always on the move and comes to rest in a characteristic attitude with the head and forepart of the body raised well off the bottom. Remaining perfectly still in this position, it scans the ground with its very prominent and moveable eyes. Should it then spy a worm cautiously emerging from its burrow, it pounces upon it with a kind of forward leap, bringing its mouth down almost vertically upon its victim by a strong arching of the anterior part of the body. The plaice and dab behave in a similar manner when searching for food but they do not raise their heads quite so high before they pounce.

Plaice, being a bottom feeder, has a type of brain that characterises its mode of hunting. The olfactory organs are moderately developed, while the optic lobes and eyes are very large. The facial lobes are also well marked. Indicating the provision of taste buds, but the somatic sensory lobes are less prominent and neither is there any sign of an acoustic lobe or central acoustic area. Feeding, therefore, seems to be by sight, smell and gustatory sensations,

according to Evans.

The eyes of the plaice are lifted up from the head, presumably to give a better view of the substratum. This contrasts with the situation found in turbot, the eyes of which are only raised slightly. These differences are attributed to the types of prey on which these fish feed. Whereas plaice need to look down onto the substratum to see prey that are partially buried, turbot only need to be able to spot prey moving across the substratum or swimming in the water column. The low profile of the eyes of turbot would also presumably aid in concealment of the predator from its prey, but this is less important for plaice.

The diet of mature turbot is almost exclusively fish (Cunningham, 1896; Fulton, 1905; Redeke, 1906; Franz, 1910; Steven, 1930; Hartley, 1940; de Groot, 1971). The brain of turbot is just what would be expected from a fish-eating predator. The optic lobes are well defined, the somatic-sensory lobes are large (as in other purely fish-eating gadoids e.g. pollack, Evans, 1937), there is no central acoustic lobe and the facial lobes are small.

Clearly there is a good correlation between the prominence of the relative parts of the sensory systems of the flatfish and their observed diets and feeding habits.

The Adaptation in the Jaws of Flatfish to their Feeding Habits

Turbot (Cunningham, 1896; Fulton, 1905; Redeke, 1906; Franz, 1910; Steven, 1930; Hartley, 1940; Rae, 1957; de Groot, 1971) and brill (Holt, 1895; Redeke, 1906; Franz, 1910; Hertling, 1928; Williams, Perkins and Hinde, 1963, de Groot, 1971) feed mainly on fish such as

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sand-eels, clupeoids, gadoids and gobies. Cunningham (1896) described how turbot lie in wait on the bottom, where they are well camouflaged, until a fish comes near enough for them to swim up suddenly and catch it. He presumably saw this in aquaria but Hiatt and Strasburg (1960) have observed Bothus mancus, a rather similar flatfish, feeding in this way in nature. Norman (1934) claimed that Psettodes also feeds in this way.

Yazdani (1969) has studied the adaptation in the jaws of flatfish in relation to food and feeding behaviour. The turbot has a fairly large mouth with small teeth and a fairly big buccal cavity. This arrangement seems to be more suited to seizing and sucking in large prey, such as fish, than biting or cutting between the jaws. The inwardly curved teeth are probably used to prevent the prey from escaping whilst it is being sucked into the mouth. This is verified by my observations where captured prey which were only half inside the fish's mouth could often be seen making struggles to escape and presumably the teeth were of use in preventing prey escape. The relatively low percentage frequency and duration of element Chew exhibited by the bothids suggests that prey are swallowed whole rather than being fragmented by the jaws. It is suggested that Chew might be used by the bothids as an aid to swallowing prey. Certainly shrimps were swallowed whole by turbot and brill, although not always with apparent ease. Chew did not always occur; presumably it was not necessary if the prey was sufficiently small compared with the size of the fish's anterior alimentary tract.

Mackie and Adron (1978) provided evidence that inosine 5-monophosphate aids in promoting ingestion of prey by turbot by stimulating the gustatory receptors. A study of serial sections of the

turbot head revealed that taste buds were present on the oesophagus, gill rakers, palate and lips and they were generally associated with large numbers of teeth. Sufficient inosine 5-monophosphate could be released by penetration of the teeth, during Chewing, into the muscle of the prey animal to stimulate the taste receptors.

Turbot take a large proportion of their prey in mid-water (a high percentage of Swim-Bite elements) although they lie in wait for it on the bottom. The symmetrical mouth opening of this species seems to correlate with the fact that its feeding posture in the water would be essentially similar to that of a symmetrical fish. The advantages of protrusion of the jaw (well developed in turbot and brill) would also seem to be similar to those of the symmetrical fish taking prey in mid-water. The correlation between the jaws and feeding habits of the brill, Z. punctatus and P. regius, is similar to that of the turbot.

The plaice-type species are visual feeders but mainly take bottom living and slow moving food such as molluscs, polychaete worms and echinoderms. The two main foods of plaice are bivalve molluscs and polychaetes (Leeuwenhoek, 1687; Cunningham, 1896, 1897; Redeke, 1906, 1909; Franz, 1910; Todd, 1914; Blegvad, 1916; Hertling, 1928; Blegvad, 1930; Steven, 1930, Ritchie, 1939; Hartley, 1940; Jones, 1952; Williams et al, 1963; de Groot, 1964; Lande, 1973). Flounders, on the other hand, eat crustaceans and bivalve molluscs in the sea and chironomid larvae in rivers (Redeke, 1906; Hertling, 1928; Stadel, 1936; Hartley, 1940; Radforth, 1940; Mulicki, 1947; Williams et al, 1963; Moore and Moore, 1976).

The plaice has a fairly small mouth-opening with cutting edges on the jaws of the blind side. This seems well suited to bite off parts of bivalve molluscs which are the main food of this species.

The molariform teeth of the pharyngeal tooth-plates also seem well suited for crushing small bivalves. In the present study, plaice performed a high frequency and long duration of Chew elements. Chew in plaice, although outwardly similar in appearance to the Chew of the bothids probably has a different function. It appears that prey may be partially fragmented if too large to be passed intact down the oesophagus, which is smaller than that of the bothids. Sometimes Chew was followed by Spit. In such instances the food particle appeared to be fragmented in the buccal cavity and then ejected, either to be discarded if unsuitable for swallowing or for the separate fragments to be subsequently taken into the mough again and swallowed singly. This pattern was noticed particularly with pleuronectids and soleids feeding on worms where several worms had clumped together into a ball. This sequence of behavioural elements appeared to separate the worms so that individual worms could be consumed and any particles of debris which had become incorporated into the ball could be discarded. Although balls of enchytraeid worms are not typical prey for plaice, this description illustrates the manner in which plaice probably deal with large prey items.

The plaice takes its prey in a nearly horizontal position, with the head raised off the bottom (Steven, 1930 and my own observations). The arching of the head seems necessary during feeding, for otherwise the head would be automatically lifted up when the suspensorium of the blind side was abducted, as the mouth opened, and this might be expected to hinder the catching of the prey (Yazdani, 1969). Strong arching would be necessary to get the mouth near enough to feed on the bottom, were it not that the open mouth is directed downwards towards the blind side. The absence of most of the teeth on the jaws

of the occular side is probably correlated with the fact that seizing or biting on the prey is mainly done by the jaws of the blind side.

The open mouth of the flounder is similar to that of the plaice but the teeth of the jaws do not seem to be suitable for biting off the food. The obtusely conical teeth of the pharyngeal tooth-plates also seem unsuitable for crushing molluscan shells. These differences seem correlated with the fact that the main food of the flounder, unlike that of plaice, is crustaceans and, in fresh water, chironomid larvae; bivalve molluscs only occasionally form the bulk of the food (Yazdani, 1969).

The sole is a nocturnal feeder and takes strictly bottom living food such as polychaete worms (Cunningham, 1890; Cunningham, 1896; Redeke, 1906; Todd, 1907; Redeke and Tesch, 1911; Mohr, 1918; Steven, 1930; Hartley, 1940; Reys, 1960). When feeding, the sole remains on the bottom and takes its food from the blind side of the mouth. The jaws are very asymetrical (Yazdani, 1969). It is only able to take food that lies on the bottom and that can be covered with the lower surface of the head (Cunningham, 1896; Steven, 1930). The jaw mechanism of the blind side suggests that it is ideally suited to take bottom food without arching the head (in the present study sole were never observed to arch the head). The downwardly directed tube-like open mouth of the blind side seems as much suited to suck in the worm as the fully open mouth of the plaice, achieved by deflecting the upper jaw to the blind side. The inwardly curved teeth on the jaws of the blind side seem well suited to seize the worm and prevent it from escaping. The jaw mechanism of the common sole, therefore, seems more specialised for taking bottom food than that of the plaice-type species (Yazdani, 1969).

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Earlier work done by van Dobben (1937), de Blok (1955, 1956, 1957) and Fluchter (1963) on the functional morphology of the jaw apparatus in several species of flatfish also supports the adaptive importance of the jaw apparatus in relation to the main types of food discussed by (Yazdani (1969). They observed that the mouth of turbot is very well adapted to feed on larger quick moving prey. The mouth of plaice is very well adapted to feed on bottom living prey. The mouth of sole is specialised to feed on a muddy bottom.

The jaws of flatfish show clear adaptations to different modes of feeding. The jaw of turbot-type species are less specialised and have some characteristics which are found in a few of the most generalised acanthoptenygian families. The jaws of plaice-type species are more specialised than those of turbot-type species and their mechanisms show that they are better suited to take bottom food. The jaws of sole-type species are highly specialised for taking bottom food.

The Morphology of the Digestive System in Relation to Food

Various authors have discussed and studied the morphology of the alimentary tract of flatfish (Rathke, 1824; Kyle, 1900; Wu, 1932; Norman, 1934), but until quite recently comparatively little attention was paid to the morphological features in relation to the food of flatfishes (Suyehiro, 1934; 1941; Mikawa, 1953; Moiseev, 1953; Hatanaka, Kosaka, Sato, Yamati and Fukui, 1954; Koltzer, 1956; Matsubara and Ochiai, 1963; Amoaka, 1964; Ochiai, 1966; de Groot, 1969). Most of these accounts deal with Pacific species of flatfish. De Groot (1971) illustrates the shape of the alimentary tract and the structure of the gillrakers in many flatfish species and quantifies the relative

lengths of different parts of the alimentary tract in some of the more common species found in European waters. The bothid fishes have a large oesophagus and stomach, with a simple intestinal loop. The gillrakers, however, are large and in the larger species each raker has a series of small teeth. Turbot and brill have two pyloric appendices, Z. punctatus has none. The plaice-type pleuronectids have a smaller oesophagus and stomach, a more complicated intestinal loop, gillarches with fewer and smaller teeth than the former type. There are 1 - 2 pyloric appendices in plaice and flounder. The soles have a very small oesophagus and stomach and an intestinal loop which is more complicated than in the pleuronectids or bothids. They have simple gillrakers but pyloric appendices are absent.

De Groot (1971) suggest that the flatfish can be divided into three groups on the basis of the type of food eaten:

I. Fish feeders, e.g. Bothidae

II. Crustacean feeders, e.g. Pleuronectidae

III. Polychaete-mollusc feeders e.g. Soleidae.

This subdivision is supported by the relative dimensions of the different sections of the alimentary tract. The buccal and pharyngeal cavities together with the oesophagus and the stomach form about 50% of the whole tract in the Bothidae, 30 - 32% in the Pleuronectidae and about 20% in the Soleidae. The significance of these differences will be understood if the food taken by these fish is considered. The bothids are fish-feeders which grasp their relatively large prey at once and swallow it intact. The food is almost entirely digested in the stomach. The soleids and the plaice, on the other hand, are polychaete feeders taking small prey, often contaminated with

indigestible items, at a higher frequency. They do not need a storage capacity for large prey as the fish-feeders do and a long intestine is much better suited to digest small but frequent quantities of well fragmented food. The crustacean feeders such as flounder take up an intermediate position.

These findings and conclusions of de Groot fit very well with the observations and conclusions on the differences in behaviour and feeding tactics of the present study. In particular, consider the differences in frequencies of elements prior to attack between turbot feeding on mysids and plaice feeding on worms, the flow charts for the same comparisons, the prominence of elements of ingestion such as Chew in plaice, and the difference in tactics of plaice feeding on worms compared with crustaceans e.g. corophiids.

The structure of the gillrakers also gives an indication of the type of food consumed. Gillrakers are indispensable to fish-feeders becaue they prevent the prey, grasped alive, from struggling out of the mouth. They therefore have to be large and on each raker is a series of small teeth. Polychaete feeders do not need such large gillrakers, for once the prey has been sucked in it easily passes on to the stomach.

It was observed by Wu (1932) and corroborated by de Groot (1971) that the pyloric appendices are well developed in the bothids but are lacking in the soleids. Svetovidov (1934) stated that the pyloric appendices increase in size with the sizes of the prey. The physiological function of the pyloric appendices in the digestion of fishes is not clear. They may form an absorbent organ only or they may have a secretory function as well. In either function an increased surface or volume might intensify the effectiveness of the

organ (de Groot, 1969).

Conclusions of Prey Recognition and Comparison with Other Findings.

The evidence from the series of models presented to turbot in the experiments of Part Three of this work suggest that the important stimuli for prey recognition are: prey locomotion, prey appendage movements, a predominantly horizontal orientation with a height: length ratio of not less than 1:5, cryptic colouration and a general inconspicuous appearance.

These criteria are not very specific. Nevertheless all the organisms that form the natural diet of turbot in the sea conform to this description e.g. amphipods, mysids, shrimps, sand eels and small fish. In fact a euryphagic predator would be at a disadvantage if the stimuli by which it recognised its prey were too specific.

These conclusions support and explain de Groot's (1971) observations. Clearly the ratio of the horizontal and vertical components of his spherical models was not appropriate to trigger a response from turbot. The situation was made worse by these balls being coloured black and so being neither cryptically coloured nor conspicuous. The lack of any improvement by the use of a chemical stimulus combined with spherical balls is quite consistent with the findings of this study.

The surprisingly strong response to sand grain agitation might be due to conditioning. On the other hand, the fish had been maintained in laboratory tanks without sand; they had been collected from the sea at a young age and if conditioning had occurred in the early stages of life it would seem unlikely that the fish would have

retained such a response without reinforcement for 8 months. It seems more probable that the response to sand grain agitation was innate. This then poses the obvious question of whether the additional stimulus of sand grain agitation combined with the best artificial model might have produced a response closer to that obtained to an immobilised live shrimp. Unfortunately this test was not performed. The high response of the fish to the immobilised live shrimp, however, was not brought about by sand grain agitation because care was taken to avoid such an additional stimulus.

The response to sand grain agitation would clearly be useful for the fish, certainly whilst feeding on benthic invertebrates, which would no doubt disturb the substratum in the course of their movement across it.

Earlier in the study it had been hoped to investigate the nature of prey movement more precisely than was in fact accomplished. Several motorised means of stimulus presentation using variable speed motors were constructed but for a variety of reasons these ideas were abandoned. It has not been possible to evaluate the effects of quality (continuous/periodic) or quantity (speed) of prey movement. This feature of the prey's behaviour might be of importance to the fish. Ivlev's (1961) work showed that the speed of the prey made a contribution to the selectivity of pike, perch and larvae of Macrodytes circumflexus; in all cases the fish preferred slower moving prey. Kislalioglu and Gibson (1976b) also demonstrated the importance of movement as a stimulus for prey selection by Spinachia spinachia. The optimum speed of prey movement for Spinachia was approximately 3 cm/sec, similar to that given by Meesters (1940) for the related Gasterosteus. Speed of prey, however, is only likely to be

of importance to the bothids because they feed on very mobile prey whereas the pleuronectids and soles do not.

A Discussion of Flatfish Feeding Strategies and Tactics

Interfamily differences in behaviour and morphology can be related to the prey types comprising the diets. The bothids are basically daylight fish feeders. Their prey is always mobile and their feeding behaviour reflects the problem of capturing mobile prey. The behaviour of the bothids shows considerable adaptations to catching prey which possess means of escape. The behaviour is complex displaying many different elements giving versatility as tactics and counter-tactics are employed to capture elusive prey. The commonest form of approaching prey is by slowly creeping towards it, interspersed by short pauses. The flattened body shape and colouration give the predators concealment so that they can take their prey unaware. They also keep their heads well down on the substratum. While observing these fish stalking their prey one cannot fail to notice the restraint and co-ordination required to avoid alerting the prey to the predators presence. Because prey often leave the bottom the bothids also frequently perform feeding activities in the water-column in pursuit of prey (see Table 61). Bothids have a rather large repertoire of common elements of behaviour and there are many different activities in a typical sequence of prey capture.

The pleuronectids are also visual feeders and take mainly slow-moving bottom-living food but active crustaceans are also taken. The pleuronectids are well adapted to their prey and, in the main, do not have to contend with the problems of catching fast moving prey as do

the bothids. This is not to say, however, that their prey do not possess defence mechanisms. Worms for example retreat into their burrows and the siphon tubes of molluscs can also be retracted. Whereas bothids can lie in wait for suitable prey to pass by the pleuronectids have to search for their food. Most commonly the pleuronectids move about the bottom by Shuffling but they pause frequently to scan around them to locate prey. This resting posture is very different to that of turbot and involves lifting the anterior of the body and head, on the dorsal and anal fins, clear of the substratum (also described by Steven, 1930). The fish obviously benefits in this way by increasing its field of vision. When suitable prey has been located the fish moves forward cautiously but determinedly to bring its head down upon its prey.

While feeding the pleuronectids rarely leave the bottom - there is obviously no need for them to. They exhibit a small repertoire of common behavioural elements and the simple sequences that they display by comparison with the bothids, are adaptations to feeding on prey with less elaborate escape tactics. Similarly their total behavioural repertoire is considerably smaller than that of the bothids. They are the least active in the laboratory because their prey is less demanding to capture. In the sea, however, the reverse may be the case. The fact that their prey is composed of smaller items necessitates more frequent feeding. In contrast the bothids which take larger items probably spend long periods inactive whilst digesting a large meal. This point was made clear in studies on the rate of passage of food through the alimentary canal of flatfish. De Groot (1971) determined that evacuation of food from the stomach was completed by 24-48 hrs. in plaice, 72-96 hrs. in turbot and about

24 hrs. in sole at 10°C. Edwards (1971) determined that evacuation from plaice stomachs took 15 hrs. De Groot also recorded the length of time required for complete clearing of the food from the alimentary tract; 96 hrs. for turbot, 72 hrs. in plaice and 72 hrs. in sole. Using a barium sulphate meal Edwards calculated the time for a meal to reach the rectum in plaice at 10°C was 35 hrs. De Groot mentioned that the long periods needed to digest food in turbot limits the period to search for the next meal. He states that this is in agreement with the fact that turbot is not a very active fish as compared with plaice and sole. It may be assumed that once food has been digested that fish feeders will become very active. In contrast the strategies of plaice and sole are based on 'little and often'.

The soles show many affinities with pleuronectids but there are some major differences. Soles prey on sedentary annelids and molluscs. They are in no way suited to feed on mobile prey. They are night feeders with a poorly developed sense of vision. During feeding their small eyes are not seen to move at all, in contrast to the very rapid movements of the eyes in bothids and pleuronectids. Owing to the fact that they feed by smell, touch and hearing they are only able to capture immobile prey because by performing the element of behaviour called Palpation, which they exhibit most commonly, they actually cover prey with their villiform papillae and test prey by touch, by which time mobile prey would have escaped. Much of the small behavioural repertoire accounts for the fish moving about on the bottom by Shuffling performing Palpation searching for food. This method of locating prey is not as efficient as vision for a given prey density (compare the interval between attacks for sole and plaice feeding on enchytraeid worms Table 33) and necessitates that the fish keep on

the move, this is shown by the low inactivity figure for sole (Table 61). Sole are probably not at a disadvantage, however, in the sea because the prey densities of worms are likely to be higher, than those of more mobile organisms, where the substratum is suitable for worms to live. Sole do not often leave the bottom when feeding because there is no need for them to do so.

The foregoing discussion of interfamily differences has given an account of how the behavioural adaptations relate to the typical food organisms in the diets. There are, however, finer interspecific differences as well as differences in the behaviour of an individual species depending on the nature of its prey.

With the pleuronectids and soles the major problem is to locate prey, with the bothids, however, not only do they have to locate prey but also they may have to actively pursue it. This fact largely contributes to the complexity of bothid feeding behaviour. Two approaches are utilised. Turbot and brill adopt the method of going after prey with more speed and many attempts end in an outright chase. They make many attempts but expend much energy in doing so. They exhibit feeding sequences in which the interval between attacks is much shorter than for brill. Shuffle and Swim are the two most important elements of locomotion, Creep is unimportant in the repertoire of turbot feeding on mysids and presumably other water borne organisms too. Brill, in contrast to turbot, approach prey very slowly and make relatively fewer attempts. The capture efficiences are comparable for the two tactics but turbot no doubt capture more prey per unit time. There again brill, in expending less energy to capture prey presumably do not require as much food as turbot. Creeping is the chief approach

behaviour for brill, they also perform many Arch elements when poised to Lunge. Turbot do not. The differences between turbot and brill, which must be due to internal factors derived either from genetic and/or learning processes, permit these two species to co-exist and feed on the same sized prey, with the same spatial distribution in the same habitat but not compete for niche space.

The second feeding strategy seen in the bothids is that of "sit and wait" predation. This method is adopted by the topknots. Topknots spend much time on vertical surfaces where they wait for passing prey. Their most common forms of locomotion are Creep and Reverse, they also perform Head-Raise in which the anterior of the body is elevated at angles up to 80^{o} from the surface on which they rest. Employing these three elements topknots can manoeuvre themselves into suitable capture positions and often reach upwards to Lunge at prey. Their camouflage is such that they would blend in very well with rocks covered with red and brown algae enabling them to capture prey by surprise. After prey capture they Reverse back into their original location. This method of prey capture probably uses even less energy than that of brill but at the same time may be rather restrictive if prey density is low and this may partly account for the topknots being much smaller species than turbot or brill. Also large fish would be less able to conceal themselves in such situations. No doubt they maximise their chances of prey capture by residing in places where suitable prey are likely to be encountered, such as in amongst clumps of weed. They perform no water-column activity and their degree of inactivity is comparable to that of brill. The interval between attacks is midway between that of turbot and brill (see Table 33).

The turbot seems to be a very versatile hunter and its behaviour is very much determined by the behaviour of its prey. The behaviour of turbot is very different when feeding on water borne prey such as mysids compared with bottom living prey such as shrimps. Its strategy of "many attempts" still holds true but it exhibits a range of behavioural elements by which it is adapted to catch water borne prey. In contrast the behaviour of brill is more similar for the two prey types.

Plaice and flounder exhibit different behaviour when feeding on worms and corophiids. Water column activity is not common in the pleuronectids but the proportion of bottom activity and inactivity varies with prey type. When the prey is worms bottom activity is high and involves short locomotory movements and a high proportion of Bites. The number of elements in a sequence is small and the interval between attacks is short. Corophiids, however, being more mobile necessitate that the fish perform more searching and approach behaviour and consequently move about more. The interval between attacks is longer and there are more elements required to capture the prey. The proportion of Bites is much lower. These differences are attributed to prey size, prey distribution and prey behaviour.

Behavioural differences that may account for the different prey types found in the stomachs between plaice and flounder are much less pronounced than between the bothid species. Nevertheless the evidence does suggest that flounders are better adapted to feed on crustaceans than plaice but less well adapted to feed on worms. Flounders are more mobile than plaice (performing more Skim and Shuffle elements) making them better suited to pursue more mobile prey. This is also suggested by the larger number of Shuffles that preceed Bite in

flounder. In contrast, plaice exhibit Forward-Bite much more often by which means they are better suited to taking less mobile organisms because they have to get closer to the prey before a capture. The Shuffle-Bite situation corresponds to prey capture following pursuit. Flounders perform much less Chewing than plaice which is attributed to their anterior alimentary tracts being slightly larger than that of plaice and the teeth of their jaws do not form a continuous cutting edge so seem less suitable for biting off the food. Flounders also capture corophiids at shorter intervals employing less elements than plaice.

Probably the most important feature that reduces niche competition between these two species is the greater ability of flounders to tolerate low salinities which allows them to penetrate into estuaries and other hyposaline environments. This does, however, provide a further problem for flounders because in estuaries they meet with competition from soles which are extremely well adapted for feeding on muddy substrata. The flounder's inability to compete with soles for worms has no doubt led to the flounder becoming better suited to take the more mobile organisms of the estuarine environment such as crustacea, and insect larvae. In this respect the niche of the flounder is probably closer to that of the dab. The dab feeds on mobile organisms in higher salinities and therefore avoids competition with the plaice.

The flatfish are a very successful group of ubiquitous predators. They are well adapted to a demersal mode of existence. Their flattened shape gives them a measure of protection against their own predators by enabling them easily to bury themselves with a fine layer of sand to avoid detection or if detected they provide an awkward mouthful for any predator which is not considerably larger than themselves or at

least possess an exceptionally large mouth for its size e.g. a monk-fish. Their cryptic colouration provides them with a good camouflage making them difficult to see when resting on a sandy substratum.

They show considerable adaptations in behaviour and morphology between families and between species within families. From the point of view of feeding strategies these various adaptations enable them to make use of a wide range of prey types which reduces competition for niche space between species. The behaviour, brain, sensory systems, structure and functioning of the jaws, modifications to the alimentary tract of flatfish all seem to have undergone adaptive radiation. It is therefore apparent that the differences in diet of the flatfish studied are accounted for by the behavioural tactics employed but that such differences are only fully realised when combined with the adaptive morphological differences. Such is the way that adaptive radiation has reduced competition between species and thereby permitted the flatfish to make full use of the resources of niche space available in the inshore seas.

ADDI[illegible]

The ta[illegible]nomy of flatfishes adopted in this study follows that set out [illegible]y Norman (1934, 1966). It has been suggested, however, by Greenwood, Rosen, Weitzman and Myers (1966) that the sub-families Bothinae and Scophthalminae should be elevated to the status of family, which places turbot and brill into a different family to the topknots. This revision has not been wholly agreed by systematists but the findings of the present study, based on the differences of behaviour, do partly substantiate this division.

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APPENDICES

APPENDIX 1 A COMPARISON OF THE FREQUENCIES OF BEHAVIOURAL ELEMENTS BETWEEN FEEDING TRIALS

	TURBOT		BRILL		Z. PUNCTATUS		P. REGIUS		PLAICE		FLOUNDER		SOLE
ELEMENT	M	S	M	S	M	G	M	G	W	C	W	C	W
TN	1077	245	228	173	168	19	165	38	567	333	83	316	722
SV		119	10	42	38	7	44	9		20	1	36	45
TA	5	1		6	6		3			1			
LV	4	3	16	3	22		18			2			1
PP													4183
SW	519	37	1	22			2		8	3		8	16
DN	420	40	11	13					7	3		23	20
SK	149	43	6	17	1			1	3	35	10	44	3
SF	525	215	29	85	16	1	5	1	66	238	70	179	1408
CR	29	25	233	112	159	9	187	33	8			1	
FD				1					253	211	58	103	1
RV		3	58	11	81	2	102	8	162	29	13	6	280
PS	404	192	299	169	202	24	179	25	91	576	96	478	117
ST							2						19
FS	56	11		2								15	20
BY	3	1	2	6			1		31	16	3	11	10
FP	11	17			1		1					1	1
UN													33
AR	4	63	88	34	8		11		25	6	2	5	
RX	3	26	30	14	10		6						
AC			10										
HV	131	3	1									2	
LG	133	55	173	40	95	1	108	6	32			1	
BT	121	40	148	29	85	1	93	6	611	174	88	103	713
MS	12	15	25	11	10		15			1			
CW	77	21	100	23	34		60	4	630	200	29	97	524
SP	3	6	3		2				1	10		4	14
HR	137	25	29	36	60	11	85	17	19	12	1	35	40
HL	12	4	14	3	44	10	43	14	8	7		18	11
YN	9	8			6	1	6	6				8	3
JP												1	10
STN	216	13		12					2			10	16
SLG	319	6	11						5				
SBT	281	4	7						5	1		4	
SMS	38	2	4										
STA	9											1	
SLV	16												
SCW	16												
RCW					5		3						
SYN	1												
QV					1		2						
CAR		24	81	38	26		25	1					
TAR		6	13	3	2		2						
ARV			2										
ATA		1											
AHL			5		6								
AHR			3		4		1						
HCR							2	1					
TOTAL	4740	1274	1640	905	1092	86	1171	170	2534	1878	454	1510	8210

APPENDIX 2 A COMPARISON OF THE DURATIONS OF BEHAVIOURAL ELEMENTS BETWEEN FEEDING TRIALS

	TURBOT		BRILL		Z.PUNCTATUS		P.REGIUS		PLAICE		FLOUNDER		SOLE
ELEMENT	M	S	M	S	M	G	M	G	W	C	W	C	W
TN	3120	1323	1275	1018	1282	167	1060	392	1242	437	119	459	1626
SV		898	145	164	567	80	526	283		46	7	112	228
TA	28	9		60	22		22			11			
LV	6	3	39	3	22		18			2			1
PP													7398
SW	1725	113	1	79			11		26	4		11	52
DN	420	40	11	14					7	3		23	20
SK	636	71	6	22	4			2	13	53	13	65	7
SF	3484	2297	300	740	71	6	38	3	193	360	102	330	4789
CR	221	207	4680	3032	2532	97	3577	698	58			2	
FD				1					253	211	58	103	1
RV		5	178	72	396	7	804	41	241	32	13	7	486
PS	5399	7076	17894	19299	8034	1209	7480	1606	2808	6383	2874	4361	4538
ST							75						588
FS	686	111		24								231	89
BY	100	808	219	948			85		1574	1578	4	566	563
FP	116	233			1		36					1	2
UN													428
AR	5	361	2147	987	35		58		26	6	2	5	
RX	3	57	803	82	107		104						
AC			10									3	
HV	232	6	1									1	
LG	133	55	173	40	95	1	108	6	32				
BT	121	40	148	29	85	1	93	6	611	174	88	103	713
MS	12	15	26	39	10		15			1			
CW	314	204	999	348	358		737	43	3487	1313	138	686	1667
SP	3	6	3		2				1	10		4	14
HR	294	86	87	69	183	126	293	273	143	40	182	66	102
HL	14	59	354	8	336	103	886	191	73	137		26	27
YN	25	28			16	3	44	21				20	8
JP												1	31
STN	220	15		12					2			10	23
SLG	319	6	11						5				
SBT	281	4	7						5	1		4	
SMS	38	2	4										
STA	9												
SLV	16											1	
SCW	39				26		44						
RCW													
SYN	3				6		9						
QV													
CAR		235	908	1428	200		77	2					
TAR		26	130	285	3		4						
ARV			26										
ATA		4											
AHL			50		16								
AHR			4		13		2						
HCR							12	33					
TOTAL	18000	14400	30600	28800	14400	1800	16200	3600	10800	10800	3600	7200	23400

Appendix 3 Response scores of individual fish (turbot) to each stimulus presented in Experiment 1A.

Fish's Length (cm)	STIMULUS NUMBER 1	2	3	4	5	6	7	Row Total
11.4	0	0	1	0	0	2	0	3
13.0	0	0	0	4	4	2	4	14
10.5	0	0	0	0	1	4	0	5
10.4	0	0	0	0	0	4	0	4
10.6	0	0	0	0	0	4	0	4
9.9	0	0	0	0	3	3	2	8
11.3	0	0	0	0	4	4	4	12
10.4	2	0	0	0	4	4	4	14
10.1	0	0	4	4	0	4	4	16
9.0	2	2	0	0	2	4	2	12
11.2	0	0	0	2	0	2	2	6
10.7	0	0	1	1	1	4	2	9
9.2	0	0	0	0	0	4	4	8
10.9	2	0	0	0	0	4	0	6
9.7	0	0	0	0	0	1	0	1
9.1	0	0	0	0	0	4	2	6
10.3	0	0	2	0	4	4	0	10
10.7	0	0	0	0	0	4	2	6
10.6	0	0	0	0	0	4	4	8
11.2	2	0	0	4	4	4	4	18
9.8	0	0	0	0	0	4	1	5
10.6	0	0	0	2	4	4	0	10
11.1	0	0	0	0	0	0	0	0
11.2	0	0	0	0	0	1	0	1
9.9	0	0	0	0	0	0	4	4
9.6	0	0	0	0	1	4	2	7
10.9	0	0	0	0	0	0	0	0
11.0	0	0	0	0	2	4	2	8
10.9	0	0	0	0	4	4	4	12
10.3	0	0	0	4	4	4	4	16
11.5	0	1	0	4	4	4	4	17
11.7	0	0	0	0	2	4	4	10
11.7	1	0	0	1	4	4	0	10
10.8	1	0	1	0	0	4	0	6
11.4	0	0	0	0	0	2	4	6
10.0	0	0	0	4	4	4	0	12
9.5	0	0	0	4	2	4	4	14
10.6	0	0	0	0	0	0	0	0
Column Total	10	3	9	34	58	121	73	308
Mean	0.26	0.08	0.24	0.89	1.53	3.18	1.92	

The column total is the 'group stimulus response score'

Appendix 4 Response scores of individual fish (brill) to each stimulus presented in Experiment 1B.

Fish's Length (cm)	STIMULUS NUMBER 1	2	3	4	5	6	7	Row Total
12.5	0	0	0	1	1	4	2	8
12.0	0	0	0	0	4	4	4	12
11.0	1	0	0	0	4	4	4	13
9.2	0	0	0	0	4	4	0	8
9.1	0	0	0	0	0	0	0	0
12.7	0	0	0	0	0	0	0	0
12.1	3	1	0	0	0	4	4	12
8.9	0	0	0	0	0	4	4	8
13.6	0	0	0	0	1	4	0	5
9.8	0	0	0	4	1	4	3	12
10.3	0	0	0	0	4	4	3	11
12.5	0	0	0	0	1	4	0	5
11.0	0	0	0	0	4	0	4	8
12.0	0	0	0	3	4	0	3	10
9.3	0	0	0	0	4	4	2	10
13.5	0	0	1	0	0	3	4	8
13.5	0	0	0	0	0	4	0	4
9.9	0	0	0	4	0	0	0	4
11.7	0	0	0	0	4	4	0	8
11.7	3	1	2	4	4	0	0	14
9.8	0	0	0	0	0	0	0	0
11.5	0	0	0	1	2	0	0	3
13.3	0	0	0	0	0	0	0	0
11.9	0	0	0	0	0	0	0	0
12.6	0	0	0	0	0	0	0	0
10.9	0	0	0	0	0	0	0	0
10.6	0	0	0	0	0	4	0	4
12.9	0	0	0	0	4	4	3	11
12.2	0	0	0	0	0	0	3	3
Column Total	7	2	3	17	46	63	47	181
Mean	0.24	0.07	0.10	0.59	1.59	2.17	1.48	

The column total is the 'group stimulus response score'

Appendix 5 Response scores of individual fish to each stimulus presented in Experiment 2.

Fish's Length (cm)	STIMULUS NUMBER 1	2	3	4	5	6	7	Row Total
12.2	0	4	0	4	1	4	4	17
13.7	0	4	0	4	4	4	3	19
12.1	4	4	4	4	4	4	4	28
11.8	4	0	0	4	4	4	4	20
11.8	0	0	0	0	0	0	0	0
11.9	3	3	4	4	4	4	3	25
11.7	2	0	0	4	4	4	3	17
11.2	4	0	0	4	4	4	2	18
11.7	4	4	4	4	4	4	3	27
10.8	4	3	4	4	4	4	4	27
10.6	4	4	3	4	4	4	2	25
11.2	0	3	0	4	2	4	3	16
11.9	0	4	4	4	4	3	4	23
11.8	2	4	0	4	4	4	3	21
11.0	0	4	0	2	4	4	4	18
11.7	0	0	0	0	0	1	3	4
11.0	4	4	4	4	4	4	4	28
11.2	4	0	0	4	4	4	4	20
10.7	0	3	2	4	4	4	3	20
11.3	0	0	0	4	4	4	4	12
10.2	4	4	0	4	3	4	4	23
10.1	4	0	0	4	4	4	3	19
9.8	0	3	2	4	4	4	3	20
10.5	0	0	0	0	0	4	4	8
10.6	4	4	2	4	4	4	4	26
11.6	4	4	3	4	4	4	4	27
10.9	4	0	0	4	4	4	0	16
11.7	0	0	2	0	0	0	3	5
9.8	0	0	0	0	0	0	4	4
10.7	0	4	3	4	4	4	3	22
11.0	0	4	0	4	4	0	3	15
11.5	0	0	0	0	0	0	0	0
10.9	0	0	0	4	2	4	0	10
10.3	0	0	0	4	0	4	4	12
11.0	0	0	0	4	0	4	0	8
11.4	0	0	0	0	0	0	0	0
11.8	4	0	0	4	4	4	3	19
11.7	0	4	0	4	4	4	2	18
Column Total	63	75	41	122	104	124	108	637
Mean	1.66	1.97	1.08	3.21	2.74	3.26	2.84	

The column total is the 'group stimulus response score'

Appendix 6 Response scores of individual fish to each stimulus presented in Experiment 3.

Fish's Length (cm)	STIMULUS NUMBER 1	2	3	4	5	6	7	8	Row Total
10.7	0	3	2	3	0	0	0	4	12
10.5	0	0	0	2	0	0	0	4	6
11.1	0	3	0	0	0	0	0	4	7
11.5	0	0	0	0	0	0	0	0	0
11.3	3	0	0	0	0	0	0	4	7
11.3	3	0	0	2	0	0	0	4	9
11.4	0	0	0	2	0	0	0	4	6
10.9	0	0	0	0	0	0	0	4	4
12.0	1	0	0	3	3	0	1	4	12
11.4	1	3	0	3	0	0	0	4	11
10.2	0	0	0	0	0	0	0	4	4
12.1	2	3	3	1	3	1	2	4	19
12.0	0	0	0	0	0	0	0	0	0
11.9	3	3	0	3	3	3	0	4	19
12.0	0	0	0	0	0	0	0	0	0
12.0	0	3	3	2	3	0	0	4	15
10.3	3	3	3	4	2	3	3	4	25
11.1	4	4	3	3	2	2	2	4	24
11.0	3	3	0	3	3	0	0	4	16
10.5	0	0	0	0	0	0	0	0	0
11.6	2	2	2	0	0	0	0	4	10
11.8	0	0	0	0	0	0	0	0	0
11.9	1	0	2	0	0	0	0	0	3
11.0	3	0	2	2	2	0	2	4	15
11.5	0	0	0	0	0	0	0	0	0
12.1	0	3	3	0	0	0	0	0	6
12.0	0	0	3	0	3	0	0	4	10
11.0	0	0	2	0	0	0	0	0	2
11.2	2	3	2	3	3	3	1	4	21
11.4	0	1	0	0	0	2	1	4	8
11.0	3	3	4	3	2	2	2	4	24
12.5	2	2	4	1	2	0	0	4	15
12.0	3	3	3	3	0	1	0	4	17
12.3	3	1	2	3	2	0	0	4	15
14.0	3	2	2	3	0	2	0	4	16
12.5	3	1	0	3	0	1	0	4	12
11.3	3	3	1	3	1	0	1	4	16
10.8	0	1	0	3	0	0	2	4	10
Column Total	51	53	46	58	34	20	17	116	395
Mean	1.34	1.39	1.21	1.53	0.89	0.53	0.45	3.05	

The column total is the 'group stimulus response score'

Appendix 7 Response scores of individual fish to each stimulus presented in Experiment 6.

Fish's Length (cm)	STIMULUS NUMBER 1	2	3	4	5	6	7	8	Row Total
12.0	0	0	0	0	0	0	0	4	4
12.2	2	1	2	2	2	2	2	4	17
11.7	0	1	1	2	2	2	1	4	13
12.0	0	1	2	0	0	0	0	0	3
11.9	0	1	0	0	3	0	0	4	8
11.5	0	0	0	0	0	2	3	4	9
11.0	0	2	2	0	2	2	0	4	12
10.4	2	3	2	1	3	2	3	4	20
12.0	0	0	2	0	0	0	3	4	9
12.5	0	0	0	0	0	0	1	4	5
12.0	0	1	0	3	0	0	2	4	10
11.2	2	2	2	2	1	0	3	4	16
11.3	0	4	0	3	0	0	2	4	13
12.1	0	0	3	0	0	0	3	4	10
11.0	3	3	2	2	2	2	2	4	20
11.1	0	3	2	0	0	0	4	4	13
10.7	0	2	0	0	0	0	0	4	6
12.2	1	0	3	0	0	0	1	4	9
12.4	1	2	2	1	0	2	0	4	12
12.1	2	0	1	2	0	2	0	4	11
11.6	0	0	0	0	0	0	2	4	6
10.9	0	0	0	0	0	0	0	4	4
12.0	0	0	0	0	0	0	0	4	4
10.2	0	0	0	0	0	0	2	4	6
10.7	0	1	0	0	1	1	2	4	9
11.3	0	3	3	0	0	0	2	4	12
12.3	1	1	1	2	0	3	0	4	12
12.2	0	0	1	1	0	2	2	4	10
11.5	0	0	1	0	0	1	3	4	9
10.9	2	0	0	2	2	2	2	4	14
11.4	0	2	0	0	0	2	0	4	8
11.3	3	4	4	4	4	4	4	4	31
10.5	0	0	0	0	0	0	0	0	0
11.9	0	0	0	0	0	0	0	0	0
11.5	2	0	0	0	2	0	0	4	8
14.3	2	0	2	2	2	0	0	4	12
11.2	0	0	2	2	2	2	2	4	14
11.7	0	0	2	2	0	3	3	4	14
Column Total	23	37	42	33	28	36	54	140	393
Mean	0.61	0.97	1.11	0.87	0.74	0.95	1.42	3.68	

The column total is the 'group stimulus response score'

Appendix 8 Response scores of individual fish to each stimulus presented in Experiment 5.

Fish's Length (cm)	STIMULUS NUMBER 1	2	3	4	5	6	7	8	Row Total
11.4	2	3	3	2	0	2	3	4	19
12.0	2	0	0	0	0	0	0	0	2
12.1	3	3	3	2	3	3	3	4	24
11.8	3	3	1	1	2	0	0	4	14
11.4	2	3	3	3	4	3	2	4	24
12.0	0	0	0	0	0	0	0	0	0
11.7	0	0	3	0	3	0	0	4	10
10.6	3	0	0	3	4	3	0	4	17
14.5	3	3	4	4	3	4	3	4	28
11.8	2	2	3	3	4	1	3	4	22
12.1	2	0	0	0	0	0	0	0	2
12.2	0	0	3	0	0	3	0	0	6
12.6	3	3	3	2	4	4	3	4	26
11.4	3	3	4	4	3	4	4	4	29
11.1	3	0	0	0	0	0	3	4	10
12.0	0	0	0	0	0	0	0	4	4
10.5	1	2	0	3	3	3	3	4	19
10.7	3	0	3	1	4	0	0	4	15
11.7	2	1	4	3	0	0	2	4	16
12.5	0	0	0	0	0	0	3	4	7
12.2	3	1	3	3	3	2	2	4	21
11.5	2	2	0	2	0	3	3	4	16
11.2	3	3	4	3	4	4	2	4	27
12.1	3	4	4	3	4	3	4	4	29
12.4	0	1	0	4	0	1	0	4	10
11.0	0	0	3	2	2	3	0	4	14
10.8	2	3	4	2	0	4	0	4	19
10.4	0	0	2	0	0	0	0	0	2
10.9	3	3	4	3	4	3	3	4	27
11.8	0	0	0	0	0	3	3	4	10
11.7	0	0	0	0	0	0	0	0	0
12.6	0	0	0	2	0	0	0	4	6
11.3	2	4	0	0	3	4	0	4	17
12.3	0	0	3	3	4	0	3	0	13
11.2	0	0	4	2	3	0	0	4	13
11.4	0	2	2	0	0	3	2	4	13
12.1	0	0	0	0	0	0	0	4	4
12.5	0	0	3	0	0	0	0	4	7
Column Total	55	49	73	60	64	63	54	124	542
Mean	1.45	1.29	1.92	1.58	1.68	1.66	1.42	3.26	

The column total is the 'group stimulus response score'

Appendix 9 Response scores of individual fish to each stimulus presented in Experiment 6.

Fish's Length (cm)	STIMULUS NUMBER 1	2	3	4	5	6	Row Total
11.9	3	2	3	4	4	4	20
11.4	4	3	4	4	3	3	21
12.0	3	3	4	4	4	4	22
12.5	4	4	4	4	4	4	24
11.4	3	3	0	4	4	4	18
10.3	0	0	4	4	4	0	12
10.7	4	0	4	4	4	0	16
12.5	2	3	4	4	4	4	21
12.3	4	3	4	4	4	4	23
11.0	0	4	4	4	4	4	20
11.9	3	0	0	4	3	4	14
12.4	3	3	4	4	4	4	22
11.4	0	3	4	4	4	4	19
11.8	0	4	4	0	4	4	16
11.6	3	3	4	4	4	4	22
11.5	3	0	4	4	4	4	19
11.1	3	2	4	2	4	4	19
12.2	2	2	4	4	4	4	20
10.9	3	4	4	4	4	4	23
12.1	4	4	4	4	4	4	24
11.0	4	3	4	4	4	4	23
12.1	3	3	4	4	4	4	22
12.1	2	3	4	4	4	4	21
11.7	4	4	4	4	4	4	24
12.7	4	4	4	4	4	4	24
12.1	3	3	4	4	4	3	21
12.0	0	0	4	0	0	4	8
12.2	0	0	0	0	0	0	0
11.4	4	4	4	4	4	4	24
11.8	4	3	4	4	4	4	23
12.5	4	4	4	4	4	4	24
12.1	0	3	0	4	4	4	15
11.1	0	3	4	0	4	3	14
11.7	4	4	4	4	4	4	24
14.6	3	4	4	4	4	4	23
10.6	4	4	4	4	4	4	24
10.7	2	3	4	4	4	4	21
11.5	4	4	4	4	4	4	24
Column Total	100	106	135	134	142	137	754
Mean	2.63	2.79	3.55	3.53	3.74	3.61	

The column total is the 'group stimulus response score'

APPENDIX 10

COMPUTER PROGRAM TO ANALYSE FEEDING BEHAVIOUR OF FLATFISH - PART ONE

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C*************************************************************

C          PROGRAM ANALYSES SEQUENCES OF BEHAVIOUR

C     USES SUBROUTINES: STAT, RYTMAT, FQFEED, FQTAB, NB2CHR

C*************************************************************

      SUBROUTINE STAT (NORYTE,AN,AMAX,AMIN,RANGE,SUMY,SUMYSQ,
     ,AMEDN,AVE,VAR,STDEV,STERR,CFDISP,CFVAR)
C.....PROGRAM ORDERS N NUMBERS AND CALCULATES THE SIMPLE
C     STATISTICS: MAXIMUM AND MINIMUM VALUES, RANGE, SUM OF
C     VALUES, SUM OF VALUES SQUARED, MEDIAN, MEAN, VARIANCE,
C     STANDARD DEVIATION, STANDARD ERROR, COEFFICIENT OF
C     DISPERSION AND COEFFICIENT OF VARIATION
      REAL  ROWSUM(48), COLSUM(48), ELCODE(48), B(48)
      INTEGER  W, ISTORE(4200)
      COMMON  /C1/ELCODE, NUMEL, B, ROWSUM, COLSUM, TOTALR,
     ,TOTALC
      COMMON  /C3/W      /C4/ISTORE
      SUMY=0.0
      SUMYSQ=0.0
      N=AN
      NN=N-1
C SORT NUMBERS, SMALLEST IN ISTORE(1) - LARGEST IN ISTORE(N)
      DO 10 I=1,NN
      I1=I+1
      DO 20 J=I1,N
      IF(ISTORE(I)-ISTORE(J)) 20, 20, 1
    1 ITEMP=ISTORE(I)
      ISTORE(I)=ISTORE(J)
      ISTORE(J)=ITEMP
   20 CONTINUE
   10 CONTINUE
C CALCULATE SIMPLE STATISTICS
      DO 30 J=1,N
   30 SUMY=SUMY+ISTORE(J)
      AVE=SUMY/AN
      DO 40 K=1,N
      SUMYSQ=SUMYSQ+((FLOAT(ISTORE(K)))**2)
   40 CONTINUE
      SUMSQY=SUMYSQ-((SUMY**2)/AN)
      VAR=SUMSQY/(AN-1.)
      STDEV=SQRT(VAR)
      STERR=STDEV/(SQRT(AN))
      CFVAR=(STDEV*100.)/AVE
      CFDISP=VAR/AVE
      AMIN=ISTORE(1)
      AMAX=ISTORE(N)
      RANGE=ISTORE(N)-ISTORE(1)
```

```
      I1=(N+1)/2
      I2=(N+2)/2
      AMEDN=(FLOAT(ISTORE(I1))+FLOAT(ISTORE(I2)))/2.0
C WRITE ORDERED ARRAY OF NUMBERS WITH HEADING INFORMATION
      IF(NORYTE) 5, 15, 25
   25 WRITE(W,29)
   29 FORMAT('0',15X,'INPUT NUMBERS'/)
      WRITE(W,39) (ISTORE(K), K=1,N)
   39 FORMAT(' ',20I6)
C WRITE SIMPLE STATISTICS
    5 WRITE(W,49) N, AVE, AMEDN, VAR, RANGE, STDEV, AMIN,
     ,STERR, AMAX, CFDISP, CFVAR
   49 FORMAT('0',12X,'NUMBER OF VALUES',I6/22X,'MEAN =',
     ,E12.4,20X,'MEDIAN =',E12.4/18X,'VARIANCE =',E12.4,21X,
     ,'RANGE =',E12.4/8X,'STANDARD DEVIATION =',E12.4,13X,
     ,'MINIMUM VALUE =',E12.4/12X,'STANDARD ERROR =',E12.4,
     ,13X,'MAXIMUM VALUE =',E12.4/'COEFFICIENT OF DISPERSION',
     ,' =',E12.4/ 2X,'COEFFICIENT OF VARIATION =',E12.4)
      WRITE(W,59) SUMY, SUMYSQ
   59 FORMAT('SUMY =',E18.6,15X,'SUMYSQ =',E18.10)
   15 RETURN
      END



      SUBROUTINE FQFEED(MXCLAS,IDIST,NCOUNT,LLN,LGVALS)
C.....PROGRAM DECODES A FREQUENCY DISTRIBUTION AND FEEDS
C     THE NUMBERS INTO A LINEAR ARRAY
      DIMENSION  IDIST(250), ISTORE(4200), LGVALS(120,2)
      COMMON  /C2/LG     /C4/ISTORE
      NCOUNT=0
      DO 10 I=1,MXCLAS
      IF(IDIST(I)) 10, 10, 5
    5 ICLASS=IDIST(I)
      DO 20 J=1,ICLASS
      NCOUNT=NCOUNT+1
      ISTORE(NCOUNT)=I
   20 CONTINUE
   10 CONTINUE
      IF(LLN.EQ.0) RETURN
C OPTIONAL EXTRA CONVERSION FOR ISOLATED LARGE VALUES STORED
C  OUTSIDE THE MAIN FREQUENCY DISTRIBUTION IN A LINEAR ARRAY,
C  THE ARRAY STORES PAIRED VALUES - THE BEHAVIOUR CODE AND
C  ITS DURATION.
      DO 30 K=1,LLN
      IF(LGVALS(K,1).NE.LG) GOTO 30
      NCOUNT=NCOUNT+1
      ISTORE(NCOUNT)=LGVALS(K,2)
   30 CONTINUE
      RETURN
      END

      SEGMENT
```

```
      SUBROUTINE FQTAB(LA,LB,BOUTMX,STORE,JSTORE,LSTORE)
C.....PROGRAM WRITES A FREQUENCY TABLE
      INTEGER  BOUTMX, W, JSTORE(60,35), LSTORE(35)
      REAL  STORE(35)
      COMMON  /C3/W
      WRITE(W,225)
  225 FORMAT('1','FREQUENCY TABLE FOR BOUT LENGTH VALUES')
      WRITE(W,206) (STORE(JJL), JJL=LA,LB)
  206 FORMAT(/'BOUT',7X,24A5/)
      DO 211 JJJ=1,BOUTMX
      WRITE(W,212) JJJ, (JSTORE(JJJ,KKJ), KKJ=LA,LB)
  212 FORMAT(I5,5X,24I5)
  211 CONTINUE
      WRITE(W,232) (LSTORE(KKM), KKM=LA,LB)
  232 FORMAT('0','TOTALS',3X,24I5)
      RETURN
      END


      SUBROUTINE RYTMAT(TMAT,COUNT)
C.....PROGRAM CONDENSES A 48*48 TRANSITION MATRIX BY REMOVING
C     THOSE ELEMENTS THAT DO NOT OCCUR IN THE SESSION
C     IT CALCULATES ROWSUMS, COLUMN SUMS AND TOTALS AND
C     WRITES THEM TOGETHER WITH HEADING INFORMATION HELD IN
C     'COMMON' ARRAYS WITH THE CALLING PROGRAM
      REAL  TMAT(48,48), ROWSUM(48), COLSUM(48), ELCODE(48)
      REAL  B(48), FQCODE(35), TEMP(35,35)
      INTEGER  W, IFMT(9), COUNT(48), IFRM(9)
      COMMON  /C1/ELCODE, NUMEL, B, ROWSUM, COLSUM, TOTALR,
     ,TOTALC
      COMMON  /C3/W
      DATA  IFMT(1), IFMT(2), IFMT(3), IFMT(5), IFMT(6),
     ,IFMT(7), IFMT(8), IFMT(9) /0, 4H(11X, 1H,,
     ,4H(A3,, 4H3X),, 4H6HRO, 4HWSUM, 1H) /
      DATA  IFRM(1), IFRM(2), IFRM(3), IFRM(4), IFRM(5),
     ,IFRM(7), IFRM(8), IFRM(9) /0, 4H(1X,, 4HA1,1, 4HX,A3,
     ,4H,2X,,4HF6,1, 4H,F9,, 2H1) /
      IR=0
      DO 54 IJ=1,NUMEL
      IF(COUNT(IJ),EQ,0) GOTO 54
      IR=IR+1
      FQCODE(IR)=ELCODE(IJ)
      IC=0
      DO 55 IK=1,NUMEL
      IF(COUNT(IK),EQ,0) GOTO 55
      IC=IC+1
      TEMP(IR,IC)=TMAT(IJ,IK)
   55 CONTINUE
   54 CONTINUE
C.....CALCULATE ROW AND COLUMN SUMS
      DO 88 IJ=1,IR
      ROWSUM(IJ)=0,0
      COLSUM(IJ)=0,0
      DO 86 IK=1,IR
      ROWSUM(IJ)=ROWSUM(IJ)+TEMP(IJ,IK)
      COLSUM(IJ)=COLSUM(IJ)+TEMP(IK,IJ)
   86 CONTINUE
   88 CONTINUE
```

```
C.....CALCULATE MATRIX TOTALS BY ROWS AND COLUMNS
      TOTALR=0.0
      TOTALC=0.0
      DO 84 IJ=1,IR
      TOTALR=TOTALR+ROWSUM(IJ)
      TOTALC=TOTALC+COLSUM(IJ)
   84 CONTINUE
C.....WRITE PAGE OF TRANSITION MATRIX
      I=0
      CALL NB2CHR (IFMT(4),IR)
      CALL NB2CHR (IFRM(6),IR)
      LS=1
      IF(IR.LE.19) GOTO 99
      WRITE(W,30) I
   30 FORMAT(I1,40X,'FOLLOWING BEHAVIOUR')
      WRITE(W,31) (FQCODE(JN), JN=1,19)
   31 FORMAT(11X,20(A3,3X))
      DO 36 JM=1,IR
      WRITE(W,32) B(JM), FQCODE(JM), (TEMP(JM,JN), JN=1,19)
   32 FORMAT(' ',A1,1X,A3,2X,20F6.1)
   36 CONTINUE
      WRITE(W,33) (COLSUM(JN), JN=1,19)
   33 FORMAT('COLSUM ',20F6.1)
      IR2=IR=19
      CALL NB2CHR (IFMT(4),IR2)
      CALL NB2CHR (IFRM(6),IR2)
      LS=20
      IF(IR.GT.25) I=1
C.....WRITE PAGE OF TRANSITION MATRIX
   99 WRITE(W,30) I
      WRITE(W,IFMT) (FQCODE(JN), JN=LS,IR)
      DO 10 JM=1,IR
      WRITE(W,IFRM) B(JM), FQCODE(JM), (TEMP(JM,JN),
     ,JN=LS,IR), ROWSUM(JM)
   10 CONTINUE
      WRITE(W,33) (COLSUM(JN), JN=LS,IR)
      WRITE(W,34) IR, TOTALR, IC, TOTALC
   34 FORMAT(/I3,' ROWS OF MATRIX - TOTAL    =',
     ,F8.1/I3,' COLUMNS OF MATRIX - TOTAL =',F8.1)
      RETURN
      END


      SUBROUTINE NB2CHR (IFORM,NUM)
C.....VARIALBLE FORMAT NEEDS CHARACTER INFORMATION NOT
C     NUMERIC, SO NUMERIC HAS TO BE CONVERTED TO CHARACTER
      ITENS=NUM/10
      IUNITS=NUM-(ITENS*10)
      IFORM=(64*(ITENS+16))+(IUNITS+16)
      RETURN
      END


      SEGMENT
```

```
C.....MAIN PROGRAM.....
C KEY TO VARIABLES AND DESCRIPTION

C....REAL SESSION VARIABLES
C  ELCODE  1-D ARRAY, ELEMENT ALPHA CODE CHARACTERS
C  SESCOD  1-D ARRAY, SESSION CODE
C  TELSES  NUMBER OF ELEMENTS IN SESSION (REAL 'NELSES' VALUE)
C  TBEHAV  TOTAL NUMBER OF ELEMENTS EXHIBITED
C  EXPTED  EXPECTED NUMBER OF ELEMENTS EXHIBITED
C  SEQ     NUMBER OF SEQUENCES IN A SESSION (REAL 'ISEQ' VALUE)
C  ANELSQ  MEAN NUMBER OF ELEMENTS IN SEQUENCE
C  RKELEM  2-D ARRAY OF FREQUENCIES OF ELEMENTS PRECEEDING AN
C                                                      ATTACK
C
C  TKELEM  1-D ARRAY, COLUMN TOTALS OF ARRAY RKELEM
C  PKELEM  2-D ARRAY, PROBABILITY VALUES OF 'RKELEM' ARRAY
C  NOATAK  TOTAL NUMBER OF ATTACKS
C  CAPEFF  PREY CAPTURE EFFICIENCY
C  RELFRQ  1-D ARRAY, RELATIVE FREQUENCY OF EACH ELEMENT
C  RUTTOT  SUM OF ALL THE DIFFERENT ELEMENT DURATIONS
C  STATS   2-D ARRAY, STORAGE OF SIMPLE STATISTICS
C  ROWSUM  1-D ARRAY, ROW TOTALS OF TRANSITION MATRIX
C  COLSUM  1-D ARRAY, COLUMN TOTALS OF TRANSITION MATRIX
C  TOTALR  TRANSITION MATRIX TOTAL (BY ROWS)
C  TOTALC  TRANSITION MATRIX TOTAL (BY COLUMNS)
C  FQCODE  1-D ARRAY, ELCODE STORE FOR ELEMENT FREQUENCY
C                                  TABLE COLUMN HEADINGS
C

C....REAL MULTI-SESSION VARIABLES
C  EIJ     2-D ARRAY, EXPECTED VALUE OF TRANSITION MATRIX
C                                                      CELLS
C
C  PRCENT  2-D ARRAY, PERCENTAGE OF TRANSITION OCCURRENCES
C  SCODES  2-D ARRAY, STORES ALL SESSIONS COMPRISING THE
C                                  MULTI-SESSION ANALYSIS
C
C  GCOUNT  1-D ARRAY, FREQUENCY OF EACH ELEMENT
C  GELFRQ  1-D ARRAY, RELATIVE FREQUENCY OF EACH ELEMENT
C  GELSES  TOTAL NUMBER OF ELEMENTS
C  GRELEM  2-D ARRAY, FREQUENCIES OF ELEMENTS PRECEEDING AN
C                                                      ATTACK
C
C  GTELEM  1-D ARRAY, COLUMN TOTALS OF 'GRELEM' ARRAY
C  GPELEM  2-D ARRAY, PROBABILITY VALUES OF 'GRELEM' ARRAY
C  STORE   1-D ARRAY, STORAGE ARRAY - OUTPUT FACILITY

C....INTEGER SESSION VARIABLES
C  R       DEVICE NUMBER CODE - READ
C  W       DEVICE NUMBER CODE - WRITE
C  N       COUNTER - NUMBER OF ELEMENTS ON DATA CARD
C  I       COMMON VARIABLE SUBSCRIPT 1-20
C  J       'ITIME' SECONDS SUBSCRIPT
C  K       'ITIME' MINUTES SUBSCRIPT
C  L       'TIMSEC' SUBSCRIPT
C  M       DO-LOOP INTEGER SUBSCRIPT
C  IELEM   ALPHA  CODE FOR ELEMENTS
C  INUM    NUMERICAL CODE FOR ELEMENTS
C  ITIME   RAW TIME DATA
C  MINTOS  MINUTES EXPRESSED IN SECONDS
C  TIMSEC  TIME EXPRESSED IN SECONDS
C  DETECT  DETECT END OF SESSION
C  OPTOUT  DATA INPUT ERROR, GOTO NEXT SESSION
C  MINS    VARIABLE FOR UNWRITTEN MINUTE VALUES
```

```
C  LAST     LAST 'TIMSEC' VALUE ON A DATA CARD
C  NOTIME   VARIABLE TO DETECT NO TIME DATA
C  COUNT    1-D ARRAY, TO TOTAL FREQUENCY OF EACH ELEMENT
C  FQNEWS   1-D ARRAY, FOR FREQUENCY OF 'RNEWS' VALUES
C  NOSESS   NUMBER OF SESSIONS
C  J        COUNTER FOR BLOCKS OF 40 DATA VALUES
C  NELSES   NUMBER OF ELEMENTS IN SESSION
C  ISEQ     NUMBER OF SEQUENCES WITHIN SESSION
C  IB       1-D ARRAY, BEGINNING OF EACH NEW SEQUENCE
C  IE       1-D ARRAY, END OF EACH SEQUENCE
C  NEWS     1-D ARRAY, NUMBER OF ELEMENTS WITHIN A SEQUENCE
C  NNELSQ   = INTEGER(ANELSQ)
C  INC      INCREMENT
C  PRECEL   PRECEEDING ELEMENT COLUMN FOR 'RKELEM' ARRAY
C  LQNEWS   LARGEST 'NEWS' VALUE
C  TMAT     2-D ARRAY, TRANSITION MATRIX FOR PRECEEDING/
C                      FOLLOWING ELEMENT FREQUENCIES
C
C  R        1-D ARRAY, MATRIX MARGIN LABEL VARIABLE
C  NUMBT    1-D ARRAY, NUMBER OF EACH TYPE OF ELEMENT
C  BOUT     1-D ARRAY, STORAGE  OF SEQUENTIAL ELEMENT
C                                          DURATIONS
C
C  BOUTMX   THE MAXIMUM ELEMENT DURATION OF THE SESSION
C  RR       THE NUMBER OF 'NUMBT' GREATER THAN 60 SECONDS
C  FQBOUT   2-D ARRAY, STORAGE OF FREQUENCY TABLES FOR
C                                 ELEMENT DURATION
C
C  FQBTTT   1-D ARRAY,  FREQUENCY TOTAL PER ELEMENT DURATION
C  OVER60   2-D ARRAY, STORAGE OF ELEMENT DURATIONS > 60 SECS
C  BEHAV    1-D ARRAY, STORAGE OF THE NUMERICAL CODES OF THE
C                      SEQUENCES OF BEHAVIOUR
C
C  TIMVAL   1-D ARRAY, STORAGE OF TIME VALUES IN SECONDS
C                CORRESPONDING TO ORDINAL NUMERICAL CODE OF
C                BEHAVIOURAL SEQUENCES, IE, IN 'BEHAV' ARRAY
C
C  BTCYCL   DURATIONS BETWEEN ATTACKS
C  ZEQ      = ISEQ
C  BLK      COUNTER VARIABLE FOR BLOCK INPUT OF 20
C  COLNR    ROW NUMBER OF 'NEWS' FREQUENCY TABLE, IN TENS
C  ISTORE   1-D ARRAY, MULTI-PURPOSE STORE

C....;INTEGER MULTI-SESSION VARIABLES
C  JFQNWS   1-D ARRAY, FREQUENCY OF 'NEWS' VALUES
C  JLQNWS   LARGEST 'NEWS' VALUE
C  JTMAT    2-D ARRAY, TRANSITION MATRIX
C  JBTFRQ   2-D ARRAY, ELEMENT DURATION FREQUENCY
C  JBTFQT   1-D ARRAY, 'JBTFRQ' COLUMN TOTALS
C  FQBTCY   1-D ARRAY, FREQUENCY OF DURATIONS BETWEEN ATTACKS
C  MXBOUT   THE MAXIMUM ELEMENT DURATION OF ALL THE SESSIONS
C  BTCYMX   MAXIMUM DURATION BETWEEN ATTACKS
C  LSTORE   1-D ARRAY, STORAGE ARRAY = OUTPUT FACILITY
C  JSTORE   1-D ARRAY, STORAGE ARRAY = OUTPUT FACILITY
C  NUMEL    THE NUMBER OF DIFFERENT BEHAVIOURAL ELEMENTS
C  LONGST   2-D ARRAY, STORAGE OF ELEMENT DURATIONS > 60 SEC
C  OVR200   2-D ARRAY, STORAGE OF DURATIONS BETWEEN ATTACKS
C                                        > 200 SECONDS
C

C INTEGER VARIABLES USED IN DO-LOOPS AND SUBSCRIPTS
C      I, J, K, L, M, N, NN
C      I, II, IJ, IK, IL, IM, IN,
C      J, JI, JJ, JK, JL, JM, JN,
C      K, KI, KJ, KK, KL, KM, KN,
```

```
C      L, LI, LJ, LK, LL, LM, LN,
C      M, MI, MJ, MK, ML, MM, MN,
C      N, NI, NJ, NK, NL, NM, NN,
C      JJI, JJJ, JJK, JJL, JJM, JJN
C      KKI, KKJ, KKK, KKL, KKM, KKN
C      LLI, LLJ, LLK, LLL, LLM, LLN
C      LA, LB, LC, LD, LE, LF, LG, LH, LO, LP, LR, LS, LT, LU,
C      LV

C STATEMENT LABELS
C      1-58, 60-98
C      100-175
C      200-225, 233-249
C      400-439, 445-457, 460-467

C ELEMENTS OF FEEDING BEHAVIOUR
C  TURN                 TN      01
C  SWIVEL TURN          SV      02
C  TURN AWAY            TA      03
C  LEAVE                LV      04
C  PALPATION            PP      05
C  SWIM                 SW      06
C  DOWN                 DN      07
C  SKIM                 SK      08
C  SHUFFLE              SF      09
C  CREEP                CR      10
C  FORWARD              FD      11
C  REVERSE              RV      12
C  PAUSE                PS      13
C  SETTLE               ST      14
C  FLAP SWIM            FS      15
C  BURY                 BY      16
C  FLAP                 FP      17
C  UNDULATE             UN      18
C  BODY ARCH            AR      19
C  BODY RELAX           RX      20
C  ARC                  AC      21
C  HOVER                HV      22
C  LUNGE                LG      23
C  BITE                 BT      24
C  MISS                 MS      25
C  CHEW                 CW      26
C  SPIT                 SP      27
C  HEAD RAISE           HR      28
C  HEAD LOWER           HL      29
C  YAWN                 YN      30
C  OMEGA JUMP           JP      31
C  SWIM-TURN           STN      32
C  SWIM-LUNGE          SLG      33
C  SWIM-BITE           SBT      34
C  SWIM-MISS           SMS      35
C  SWIM-TURN AWAY       STA      36
C  SWIM-LEAVE          SLV      37
C  SWIM-CHEW           SCW      38
C  REVERSE-CHEW        RCW      39
C  SWIM-YAWN           SYN      40
C  QUIVER               QV      41
C  CREEP-BODY ARCH     CAR      42
C  TURN-BODY ARCH      TAR      43
```

```
C  ARCH-REVERSE      ARV       44
C  ARCH-TURN AWAY    ATA       45
C  ARCH-HEAD LOWER   AHL       46
C  ARCH-HEAD RAISE   AHR       47
C  HEAD LIFT-CREEP   HCR       48
C  END OF SESSION    END       99
C  GAP IN DATA       GAP

C TYPE STATEMENTS

      BLOCK DATA
      REAL  ROWSUM(48), COLSUM(48), ELCODE(48), B(48)
      COMMON  /C1/ELCODE, NUMEL, B, ROWSUM, COLSUM, TOTALP,
     ,TOTALC
      DATA B(11), B(21), B(22), B(23), B(24), B(25), B(26),
     ,B(27), B(28), B(29), B(30), B(31), B(32), B(33), B(34),
     ,B(35), B(36), B(37), B(38), B(39), B(40), B(41), B(42),
     ,B(43), B(44), B(45), B(46), B(47), B(48)/29*5H     /
      DATA B(1)/5HP     /, B(2), B(20)/2*5HR     /, B(4)/
     ,5HC     /, B(3), B(5), B(6), B(13)/4*5HE     /, B(8),
     ,B(17)/2*5HI     /, B(7), B(9), B(10), B(12), B(14),
     ,B(15), B(16), B(18), B(19)/5HD     , 5HN     , 5HG     ,
     ,5HB     , 5HH     , 5HA     , 5HV     , 5HO     , 5HU     /
      DATA   ELCODE(1),  ELCODE(2) / 5H TN   , 5H SV   /
      DATA   ELCODE(3),  ELCODE(4) / 5H TA   , 5H LV   /
      DATA   ELCODE(5),  ELCODE(6) / 5H PP   , 5H SW   /
      DATA   ELCODE(7),  ELCODE(8) / 5H DN   , 5H SK   /
      DATA   ELCODE(9),  ELCODE(10)/ 5H SF   , 5H CR   /
      DATA   ELCODE(11), ELCODE(12)/ 5H FD   , 5H RV   /
      DATA   ELCODE(13), ELCODE(14)/ 5H PS   , 5H ST   /
      DATA   ELCODE(15), ELCODE(16)/ 5H FS   , 5H BY   /
      DATA   ELCODE(17), ELCODE(18)/ 5H FP   , 5H UN   /
      DATA   ELCODE(19), ELCODE(20)/ 5H AR   , 5H RX   /
      DATA   ELCODE(21), ELCODE(22)/ 5H AC   , 5H HV   /
      DATA   ELCODE(23), ELCODE(24)/ 5H LG   , 5H BT   /
      DATA   ELCODE(25), ELCODE(26)/ 5H MS   , 5H CW   /
      DATA   ELCODE(27), ELCODE(28)/ 5H SP   , 5H HR   /
      DATA   ELCODE(29), ELCODE(30)/ 5H HL   , 5H YN   /
      DATA   ELCODE(31), ELCODE(32)/ 5H JP   , 5HSTN   /
      DATA   ELCODE(33), ELCODE(34)/ 5HSLG   , 5HSBT   /
      DATA   ELCODE(35), ELCODE(36)/ 5HSMS   , 5HSTA   /
      DATA   ELCODE(37), ELCODE(38)/ 5HSLV   , 5HSCW   /
      DATA   ELCODE(39), ELCODE(40)/ 5HRCW   , 5HSYN   /
      DATA   ELCODE(41), ELCODE(42)/ 5H QV   , 5HCAR   /
      DATA   ELCODE(43), ELCODE(44)/ 5HTAR   , 5HARV   /
      DATA   ELCODE(45), ELCODE(46)/ 5HATA   , 5HAHL   /
      DATA   ELCODE(47), ELCODE(48)/ 5HAHR   , 5HHCR   /
      END


      REAL  ELCODE(48), FQCODE(35), B(48), SESCOD(3)
      REAL  NOATAK, RELFRQ(48), ROWSUM(48), COLSUM(48)
      REAL  RKELEM(48,15), TKELEM(15), PKELEM(48,15)
      REAL  EIJ(48,48), PRCENT(48,48), STATS(35,14)
      REAL  GELSES, QCOUNT(48), GELFRQ(48), SCODES(30,3)
      REAL  GRELEM(48,15), QTELEM(15), QPELEM(48,15)

      INTEGER  R, W, TMAT(48,48), JTMAT(48,48), ISTORE(4200)
      INTEGER  ZEQ, OPTOUT, DETECT, BLK, COLNB, LAST, P, RR
```

```
      INTEGER  INUM(20), ITIME(40), MINTOS(20), TIMSEC(20)
      INTEGER  COUNT(48), IELEM(20), PRECEL, IB(250), IE(250)
      INTEGER  NEWS(250), FQNEWS(250), BTCYCL(250), BOUT(550)
      INTEGER  NUMBT(48), BOUTMX, BEHAV(1200), TIMVAL(1200)
      INTEGER  FQBOUT(60,35), FQBTTT(35), OVER60(20,2)
      INTEGER  JBTFRQ(60,48), JBTFQT(48), JFQNWS(250), JLGNWS
      INTEGER  FQBTCY(250), BTCYMX, OVR200(120,2), ELEM
      INTEGER  LONGST(120,2)

      COMMON   /C1/ELCODE, NUMEL, B, ROWSUM, COLSUM, TOTALR,
     ,TOTALC
      COMMON   /C2/LG      /C3/W      /C4/ISTORE

      EQUIVALENCE  (RKELEM(1,1), PKELEM(1,1))
      EQUIVALENCE  (GRELEM(1,1), GPELEM(1,1))
      EQUIVALENCE  (RELFRQ(1), GELFRQ(1))
      EQUIVALENCE  (EIJ(1,1), STATS(1,1))

      NUMEL=48
      R=37
      W=2
C.....(W REFERS TO ALL CALCULATED OUTPUT DATA)
      IZ=2
C.....(IZ REFERS TO INPUT BEHAVIOURS AND TIMES, NUMERICAL
C     CODES AND TIMES IN SECONDS, AND THE ARRAYS 'BEHAV'
C     AND 'TIMVAL', THEY MAY BE INCLUDED, IF IZ=2, OR
C     EXCLUDED, AS DESIRED)
      ID=32
C.....(ID WILL CREATE A DISK FILE CONTAINING THE ARRAYS
C     'BEHAV' AND 'TIMVAL', IF AN '&ASSIGN;32;' CARD
C     BEARING A FILENAME IS INCLUDED AS A CONTROL CARD)

C.....INITIALISE MULTI-SESSION VARIABLES BEFORE BEGINNING
  450 GELSES=0.0
      MXBOUT=0
      DO 403 LB=1,250
      JFQNWS(LB)=0
  403 CONTINUE
      DO 404 LC=1,15
      GTELEM(LC)=0.0
      DO 405 LA=1,NUMEL
      GRELEM(LA,LC)=0.0
  405 CONTINUE
  404 CONTINUE
      DO 408 LA=1,NUMEL
      DO 409 LD=1,NUMEL
      ROWSUM(LA)=0.0
      COLSUM(LA)=0.0
      JTMAT(LA,LD)=0
  409 CONTINUE
  408 CONTINUE
      DO 412 LA=1,NUMEL
      GCOUNT(LA)=0.0
  412 CONTINUE
      DO 414 LA=1,NUMEL
      JBTFQT(LA)=0
      DO 415 LE=1,60
      JBTFRQ(LE,LA)=0
  415 CONTINUE
```

```
 414 CONTINUE
     DO 418 LF=1,200
     FOBTCY(LF)=0
 418 CONTINUE
     DO 68 LA=1,2
     DO 70 LB=1,120
     OVR200(LB,LA)=0
     LONGST(LB,LA)=0
  70 CONTINUE
  68 CONTINUE
     IM1=0
     IM2=0
     NOSESS=0
     NORESP=0
     NOBITE=0



C SESSION ANALYSIS


C.....FIRST PART OF PROGRAM CONVERTS ALPHA ELEMENT
C      BEHAVIOURAL CODE TO A NUMERICAL ONE AND TIME FROM
C      MINS AND SECS TO SECS
C READ & WRITE SESSION CODE
  132 READ(R,1)SESCOD(1),SESCOD(2),SESCOD(3)
      NOSESS=NOSESS+1
    1 FORMAT(/3A8)
      SCODES(NOSESS,1)=SESCOD(1)
      SCODES(NOSESS,2)=SESCOD(2)
      SCODES(NOSESS,3)=SESCOD(3)
C LOOK FOR 'ANALYSE' TO INITIATE MULTI-SESSION ANALYSIS
      IF(SESCOD(1).EQ.8H ANALYSE) GOTO 400
      WRITE(W,2)SESCOD(1),SESCOD(2),SESCOD(3)
    2 FORMAT(5H1    ,3A8,//)
C INITIALISE STORAGE ARRAYS
      DO 157 KKI=1,1200
      BEHAV(KKI)=0
      TIMVAL(KKI)=0
  157 CONTINUE
      BEHAV(1)=13
      BLK=0
      J=0
      OPTOUT=0
      LLN=1
      TOBEHAV=FLOAT(NUMEL)
      MINS=00
      NOTIME=0
  128 DETECT=0
      LAST=00

C READ 20 BEHAVIOURAL ELEMENTS AND WRITE
  100 READ(R,3)(IELEM(I),I=1,20)
    3 FORMAT(20A4)
      IF(IELEM(1).NE.4H  NO) GOTO 155
      NORESP=NORESP+1
      WRITE(W,154)
  154 FORMAT(36HOFISH GAVE NO RESPONSE IN 30 MINUTES)
```

```
      GOTO 132
  155 WRITE(IZ,4)(IELEM(I),I=1,20)
    4 FORMAT(/10A6,5X,10A6)

C CONVERT ALPHA ELEMENT CODE TO A NUMERICAL CODE
      N=0
      DO 101 I=1,20
      N=N+1
      IF(IELEM(I).NE.4H  TN) GOTO 102
      INUM(I)=01
      GOTO 101
  102 IF(IELEM(I).NE.4H  HR) GOTO 103
      INUM(I)=28
      GOTO 101
  103 IF(IELEM(I).NE.4H  SW) GOTO 104
      INUM(I)=06
      GOTO 101
  104 IF(IELEM(I).NE.4H  SK) GOTO 105
      INUM(I)=08
      GOTO 101
  105 IF(IELEM(I).NE.4H  SF) GOTO 106
      INUM(I)=09
      GOTO 101
  106 IF(IELEM(I).NE.4H  CR) GOTO 107
      INUM(I)=10
      GOTO 101
  107 IF(IELEM(I).NE.4H  FD) GOTO 108
      INUM(I)=11
      GOTO 101
  108 IF(IELEM(I).NE.4H  RV) GOTO 109
      INUM(I)=12
      GOTO 101
  109 IF(IELEM(I).NE.4H  AR) GOTO 110
      INUM(I)=19
      GOTO 101
  110 IF(IELEM(I).NE.4H  HV) GOTO 111
      INUM(I)=22
      GOTO 101
  111 IF(IELEM(I).NE.4H  LG) GOTO 112
      INUM(I)=23
      GOTO 101
  112 IF(IELEM(I).NE.4H  BT) GOTO 113
      INUM(I)=24
      GOTO 101
  113 IF(IELEM(I).NE.4H  MS) GOTO 114
      INUM(I)=25
      GOTO 101
  114 IF(IELEM(I).NE.4H  CW) GOTO 115
      INUM(I)=26
      GOTO 101
  115 IF(IELEM(I).NE.4H  SP) GOTO 116
      INUM(I)=27
      GOTO 101
  116 IF(IELEM(I).NE.4H  PS) GOTO 117
      INUM(I)=13
      GOTO 101
  117 IF(IELEM(I).NE.4H  BY) GOTO 118
      INUM(I)=16
      GOTO 101
```

```
118 IF(IELEM(I),NE,4H  DN) GOTO 119
    INUM(I)=07
    GOTO 101
119 IF(IELEM(I),NE,4H  HL) GOTO 120
    INUM(I)=29
    GOTO 101
120 IF(IELEM(I),NE,4H  TA) GOTO 121
    INUM(I)=03
    GOTO 101
121 IF(IELEM(I),NE,4H  LV) GOTO 122
    INUM(I)=04
    GOTO 101
122 IF(IELEM(I),NE,4H  FS) GOTO 123
    INUM(I)=15
    GOTO 101
123 IF(IELEM(I),NE,4H  FP) GOTO 124
    INUM(I)=17
    GOTO 101
124 IF(IELEM(I),NE,4H  YN) GOTO 125
    INUM(I)=30
    GOTO 101
125 IF(IELEM(I),NE,4H  SV) GOTO 133
    INUM(I)=02
    GOTO 101
133 IF(IELEM(I),NE,4H  RX) GOTO 126
    INUM(I)=20
    GOTO 101
126 IF(IELEM(I),NE,4H  PP) GOTO 140
    INUM(I)=05
    GOTO 101
140 IF(IELEM(I),NE,4H  ST) GOTO 141
    INUM(I)=14
    GOTO 101
141 IF(IELEM(I),NE,4H  UN) GOTO 142
    INUM(I)=18
    GOTO 101
142 IF(IELEM(I),NE,4H  AC) GOTO 143
    INUM(I)=21
    GOTO 101
143 IF(IELEM(I),NE,4H HCR) GOTO 145
    INUM(I)=48
    GOTO 101
145 IF(IELEM(I),NE,4H  JP) GOTO 146
    INUM(I)=31
    GOTO 101
146 IF(IELEM(I),NE,4H STN) GOTO 158
    INUM(I)=32
    GOTO 101
158 IF(IELEM(I),NE,4H SLG) GOTO 159
    INUM(I)=33
    GOTO 101
159 IF(IELEM(I),NE,4H SBT) GOTO 160
    INUM(I)=34
    GOTO 101
160 IF(IELEM(I),NE,4H SMS) GOTO 161
    INUM(I)=35
    GOTO 101
161 IF(IELEM(I),NE,4H STA) GOTO 162
    INUM(I)=36
```

```
      GOTO 101
  162 IF(IELEM(I),NE,4H SLV) GOTO 163
      INUM(I)=37
      GOTO 101
  163 IF(IELEM(I),NE,4H SCW) GOTO 164
      INUM(I)=38
      GOTO 101
  164 IF(IELEM(I),NE,4H RCW) GOTO 165
      INUM(I)=39
      GOTO 101
  165 IF(IELEM(I),NE,4H SYN) GOTO 166
      INUM(I)=40
      GOTO 101
  166 IF(IELEM(I),NE,4H  QV) GOTO 167
      INUM(I)=41
      GOTO 101
  167 IF(IELEM(I),NE,4H CAR) GOTO 168
      INUM(I)=42
      GOTO 101
  168 IF(IELEM(I),NE,4H TAR) GOTO 169
      INUM(I)=43
      GOTO 101
  169 IF(IELEM(I),NE,4H ARV) GOTO 170
      INUM(I)=44
      GOTO 101
  170 IF(IELEM(I),NE,4H ATA) GOTO 171
      INUM(I)=45
      GOTO 101
  171 IF(IELEM(I),NE,4H AHL) GOTO 172
      INUM(I)=46
      GOTO 101
  172 IF(IELEM(I),NE,4H AHR) GOTO 173
      INUM(I)=47
      GOTO 101
  173 IF(IELEM(I),NE,4H GAP) GOTO 147
      N=N-1
      GOTO 129
  147 IF(IELEM(I),NE,4H END) GOTO 134
      INUM(I)=99
      DETECT=1
      GOTO 129
  134 IF(IELEM(N),NE,4H    ) GOTO 127
      INUM(I)=0
      GOTO 101
C WRITE NATURE OF ERROR (IF ANY)
  127 WRITE(W,12)IELEM(I)
      OPTOUT=1
   12 FORMAT(5X,8HERROR = ,A4)
  101 CONTINUE
C WRITE NUMERICAL CODES OF N BEHAVIOURAL ELEMENTS
  129 WRITE(IZ,6)(INUM(I),I=1,N)
    6 FORMAT(10I6,5X,10I6)

      IF(NOTIME,EQ,1) GOTO 177


C  READ TIME DATA FOR N BEHAVIOURAL ELEMENTS
      READ(R,7)(ITIME(K),K=1,40)
```

```
      GOTO 101
  162 IF(IELEM(I),NE,4H SLV) GOTO 163
      INUM(I)=37
      GOTO 101
  163 IF(IELEM(I),NE,4H SCW) GOTO 164
      INUM(I)=38
      GOTO 101
  164 IF(IELEM(I),NE,4H RCW) GOTO 165
      INUM(I)=39
      GOTO 101
  165 IF(IELEM(I),NE,4H SYN) GOTO 166
      INUM(I)=40
      GOTO 101
  166 IF(IELEM(I),NE,4H  QV) GOTO 167
      INUM(I)=41
      GOTO 101
  167 IF(IELEM(I),NE,4H CAR) GOTO 168
      INUM(I)=42
      GOTO 101
  168 IF(IELEM(I),NE,4H TAR) GOTO 169
      INUM(I)=43
      GOTO 101
  169 IF(IELEM(I),NE,4H ARV) GOTO 170
      INUM(I)=44
      GOTO 101
  170 IF(IELEM(I),NE,4H ATA) GOTO 171
      INUM(I)=45
      GOTO 101
  171 IF(IELEM(I),NE,4H AHL) GOTO 172
      INUM(I)=46
      GOTO 101
  172 IF(IELEM(I),NE,4H AHR) GOTO 173
      INUM(I)=47
      GOTO 101
  173 IF(IELEM(I),NE,4H GAP) GOTO 147
      N=N-1
      GOTO 129
  147 IF(IELEM(I),NE,4H END) GOTO 134
      INUM(I)=99
      DETECT=1
      GOTO 129
  134 IF(IELEM(N),NE,4H    ) GOTO 127
      INUM(I)=0
      GOTO 101
C WRITE NATURE OF ERROR (IF ANY)
  127 WRITE(W,12)IELEM(I)
      OPTOUT=1
   12 FORMAT(5X,8HERROR = ,A4)
  101 CONTINUE
C WRITE NUMERICAL CODES OF N BEHAVIOURAL ELEMENTS
  129 WRITE(IZ,6)(INUM(I),I=1,N)
    6 FORMAT(10I6,5X,10I6)

      IF(NOTIME,EQ,1) GOTO 177


C  READ TIME DATA FOR N BEHAVIOURAL ELEMENTS
      READ(R,7)(ITIME(K),K=1,40)
```

```
    7 FORMAT(40I2)
      IF(ITIME(1),EQ,77,AND,ITIME(2),EQ,77) NOTIME=1
      IF(NOTIME,EQ,1) GOTO 177
C CONVERT TIMES TO SECONDS AND WRITE
  176 DO 131 M=1,20
      MINTOS(M)=0
      TIMSEC(M)=0
  131 CONTINUE
      N=N*2
      L=0
      DO 130 K=1,N,2
      L=L+1
C IF A VALUE FOR MINS HAS NOT BEEN WRITTEN IN 'ITIME' ASSUME
C     THE PRECEEDING VALUE
      IF(ITIME(K),EQ,2H  )ITIME(K)=MINS
      MINTOS(L)=ITIME(K)*60
      J=K+1
      IF(IELEM(L),NE,2H  ) GOTO 39
      ITIME(K)=0
      GOTO 130
   39 TIMSEC(L)=MINTOS(L)+ITIME(J)
      MINS=ITIME(K)
  130 CONTINUE
C WRITE  RAW TIME DATA FOR N BEHAVIOURAL ELEMENTS
      WRITE(IZ,8)(ITIME(K),K=1,N)
    8 FORMAT(10(1X,I2,1H:,I2),5X,10(1X,I2,1H:,I2))
      N=N/2
C CHECK CALCULATED TIMES FOR A PROGRESSIVE NUMERICAL INCREASE
C     AND WRITE ERROR IF THIS IS NOT THE CASE
      IF(TIMSEC(1),GT,LAST) GOTO 139
      WRITE(W,11) TIMSEC(1)
      OPTOUT=1
  139 NN=N-1
  137 IF(N,EQ,1) GOTO 138
      DO 136 L=1,NN
      IF(TIMSEC(L+1),NE,0) GOTO 174
      IF(TIMSEC(L)-TIMSEC(L+2)) 136, 135, 135
  174 IF(TIMSEC(L),LT,TIMSEC(L+1)) GOTO 136
      IF(TIMSEC(L),EQ,1800,OR,IELEM(L+1),EQ,4H GAP) GOTO 138
  135 WRITE(W,11)TIMSEC(L)
      OPTOUT=1
   11 FORMAT(5X,8HERROR = ,I4)
  136 CONTINUE
C WRITE TIME DATA IN SECONDS FOR N BEHAVIOURAL ELEMENTS
  138 WRITE(IZ,9)(TIMSEC(L),L=1,N)
    9 FORMAT(10I6,5X,10I6)
C STORE NUMERICAL CODES & TIME DATA IN ARRAYS BEHAV & TIMVAL
  177 JI=BLK+1
      JL = JI+(N-1)
      DO 148 I = JI , JL
      LLM=I-BLK
      LLN=LLN+1
      IF(INUM(LLM),NE,0) GOTO 175
      LLN=LLN-1
      GOTO 148
  175 BEHAV(LLN)=INUM(LLM)
      IF(NOTIME,EQ,1) GOTO 148
      TIMVAL(LLN)=TIMSEC(LLM)
  148 CONTINUE
```

```
      BLK=BLK+N
C DETECT END OF SESSION
      IF(DETECT.EQ.1) GOTO 200
      LAST=TIMSEC(N)
C PROCEED TO NEXT PAIR OF DATA CARDS
      GOTO 100


C.....ANALYSIS OF SEQUENCES OF BEHAVIOUR

C.....CONSTRUCT A FREQUENCY TABLE & RELATIVE FREQUENCY TABLE
C     FOR THE OCCURRENCE OF ELEMENTS IN THE SESSION
  200 DO 72 KL=1,NUMEL
      COUNT(KL)=0
   72 CONTINUE
      WRITE(IZ,1000) LLN
 1000 FORMAT(//3HLLN,5X,I4//)
      WRITE(IZ,1001) (BEHAV(LX), LX=1,LLN)
 1001 FORMAT(5HBEHAV,5X,(20I6),/(11X,(20I6)))
      IF(NOTIME.EQ.1) GOTO 58
      WRITE(IZ,1002) (TIMVAL(LX), LX=1,LLN)
 1002 FORMAT(7HOTIMVAL,4X,(20I6),/(11X,(20I6)))

C.....WRITE LLN, 'BEHAV', AND 'TIMVAL' TO DISK FILE
      WRITE(ID,1000) LLN
      WRITE(ID,1001) (BEHAV(LX), LX=1,LLN)
      WRITE(ID,1002) (TIMVAL(LX), LX=1,LLN)

   58 IF(OPTOUT.EQ.1) GOTO 132
C DOES DATA VALUE DENOTE END OF SESSION (CODE 99), IF NOT ADD
C  VALUE TO ELEMENT FREQUENCY ARRAY AND PROCEED TO NEXT VALUE
      DO 60 I=1,1200
      IF(BEHAV(I).EQ.99)GOTO 61
      COUNT(BEHAV(I))=COUNT(BEHAV(I))+1
   60 CONTINUE
   61 NELSES=0
      NELSES=I-1
      TELSES=FLOAT(NELSES)

C    CALCULATE RELATIVE FREQUENCY
      DO 24 KM=1,NUMEL
      RELFRQ(KM)=0.0
      IF(COUNT(KM).EQ.0) GOTO 38
      RELFRQ(KM)=(COUNT(KM))*100./(FLOAT(NELSES))
      GOTO 24
   38 TBEHAV=TBEHAV-1.
   24 CONTINUE
      EXPTED=NELSES/TBEHAV

C    WRITE NUMBER OF ELEMENTS IN SESSION (TELSES)
      WRITE(W,13)
   13 FORMAT('1ANALYSIS OF OCCURRENCE OF ELEMENTS IN THE ',
     ,'SESSION')
      WRITE(W,21) NELSES, TBEHAV, EXPTED
   21 FORMAT('0NUMBER OF ELEMENTS IN THE SESSION.....',F4.0,
     ,I4/'NUMBER OF BEHAVIOURAL TYPES EXHIBITED.....',F4.0,
     ,//'FREQUENCY OF BEHAVIOURAL TYPES EXPECTED.....',F4.0/)
C WRITE FREQUENCY TABLE & RELATIVE FREQUENCY TABLE
```

```
      WRITE(W,424)
      DO 69 KM=1,NUMEL
      IF(COUNT(KM).EQ.0) GOTO 69
      WRITE(W,23) ELCODE(KM), COUNT(KM), RELFRQ(KM)
   23 FORMAT(5X,A4,5H =    ,I4,8X,F7.3)
   69 CONTINUE

      IF(COUNT(24).NE.0.OR.COUNT(34).NE.0) GOTO 90
      IF(COUNT(25).NE.0.OR.COUNT(35).NE.0) GOTO 90
      NOBITE=NOBITE+1
      WRITE(W,42)
   42 FORMAT('0THE FISH DID NOT MAKE AN ATTACK IN THIS',
     ,' SESSION')
      GOTO 132

C  ADD IN TO MULTI-SESSION STORAGE
   90 GELSES=GELSES+TELSES
      DO 402 LA=1,NUMEL
      GCOUNT(LA)=GCOUNT(LA)+COUNT(LA)
  402 CONTINUE

C.....DIVIDE THE SESSION INTO SEQUENCES WHICH END WITH AN
C     ATTACK AND DETERMINE THE NUMBER OF ELEMENTS WITHIN
C     EACH SEQUENCE
      ISEQ=1
      IB(ISEQ)=1
      DO 81 KN=1,250
      NEWS(KN)=0
   81 CONTINUE
C   BEGIN TO SCAN THE DATA VALUES
      DO 63 LK=1,NELSES
C   IF DATA VALUE IS NOT AN ATTACK (CODES: 24, 25, 34 OR 35)
C     PROCEED UNTIL AN ATTACK OCCURS
      IF(BEHAV(LK).EQ.24.OR.BEHAV(LK).EQ.34) GOTO 98
      IF(BEHAV(LK).NE.25.AND.BEHAV(LK).NE.35) GOTO 63
C   IF DATA VALUE IS AN ATTACK RECOGNISE BEGINNING AND
C     END OF I TH SEQUENCE AND HOW MANY ELEMENTS
C     ('NEWS' VALUE) IT CONTAINS
   98 IE(ISEQ)=LK
      NEWS(ISEQ)=IE(ISEQ)-IB(ISEQ)+1
C   DETERMINE THE BEGINNING OF THE NEXT SEQUENCE AND REPEAT
      ISEQ=ISEQ+1
      IB(ISEQ)=LK+1
   63 CONTINUE
      ISEQ=ISEQ-1
      SEQ=FLOAT(ISEQ)

C CALCULATE STATISTICS FOR NUMBER OF ELEMENTS WITHIN A
C     SEQUENCE
      WRITE(W,25)
   25 FORMAT('1','ANALYSIS OF NUMBER OF ELEMENTS WITHIN A',
     ,' SEQUENCE'//)
      WRITE(W,27) (NEWS(LL), LL=1,ISEQ)
   27 FORMAT(18H0NEWS VALUES ARE :,5X,(25(I3,1X)),/(23X,
     ,(25(I3,1X))))
      DO 91 LL=1,ISEQ
      ISTORE(LL)=NEWS(LL)
   91 CONTINUE
      IF(SEQ.LT.2.) GOTO 94
```

```
      CALL STAT(1,SEQ,D1,D2,D3,D4,D5,D6,D7,D8,D9,D10,D11,D12)
      LGNEWS=IFIX(D1)
      MNELSQ=IFIX(D7)
      GOTO 96
   94 LGNEWS=NEWS(1)
      MNELSQ=NEWS(1)

C CONSTRUCT A FREQUENCY TABLE FOR 'NEWS' VALUES
   96 DO 78 MK=1,250
      FQNEWS(MK)=0
   78 CONTINUE
      DO 79 ML=1,ISEQ
      FQNEWS(NEWS(ML))=FQNEWS(NEWS(ML))+1
      JFQNWS(NEWS(ML))=JFQNWS(NEWS(ML))+1
   79 CONTINUE
      WRITE(W,14)
   14 FORMAT(34HOFREQUENCY TABLE FOR NEWS VALUES: ,7X,1H1,4X,
     ,1H2,4X,1H3,4X,1H4,4X,1H5,7X,1H6,4X,1H7,4X,1H8,4X,1H9,
     ,3X,2H10)
      COLNB=-10
      IM=-9
      IN=0
      LGNEWS=LGNEWS+10
      DO 80 IL=1,LGNEWS,10
      COLNB=COLNB+10
      IM=IM+10
      IN=IN+10
      WRITE(W,26) COLNB, (FQNEWS(L),L=IM,IN)
   26 FORMAT(1H0,32X,I3,1X,5(I5),3X,5(I5))
   80 CONTINUE

C CALCULATE AND WRITE PREY CAPTURE EFFICIENCY
      NOATAK=0.
      NOATAK=FLOAT(COUNT(24)+COUNT(25)+COUNT(34)+COUNT(35))
      CAPEFF=0.
      CAPEFF=((COUNT(24)+COUNT(34))/NOATAK)*100.
      WRITE(W,16) CAPEFF
   16 FORMAT(//////'PREY CAPTURE EFFICIENCY.....',F6.2)

C.....MODE OF BEHAVIOUR PRECEEDING AN ATTACK
      DO 82 NK=1,15
      TKELEM(NK)=0.0
      DO 83 MN=1,NUMEL
      RKELEM(MN,NK)=0.
   83 CONTINUE
   82 CONTINUE
C    FOR EVERY SEQUENCE
      DO 64 NL=1,ISEQ
      INC=2
      PRECEL=0
      JB=IB(NL)
      JE=IE(NL)-1
C WORKING WITHIN A SEQUENCE WHAT IS THE OCCURRENCE OF
C     ELEMENTS PRECEEDING AN ATTACK
      DO 65 NN=JB,JE
      PRECEL=PRECEL+1
      IF(PRECEL.GT.MNELSQ)GOTO 64
      IF(PRECEL.GT.15) GOTO 64
      ELEM=BEHAV(IB(NL)+NEWS(NL)-INC)
```

```
C BUILD UP THE ARRAY RKELEM TO SHOW THE DISTRIBUTION OF
C ELEMENTS PRECEEDING AN ATTACK, PROCESS CONTINUES UNTIL
C EITHER ALL ELEMENTS WITHIN SEQUENCE ARE EXHAUSTED OR THE
C MEAN 'NEWS' VALUE IS REACHED OR 15 PRECEEDING LOCATIONS
C HAVE BEEN SCANNED.
      RKELEM(ELEM,PRECEL)=RKELEM(ELEM,PRECEL)+1.
   71 INC=INC+1
   65 CONTINUE
   64 CONTINUE
      LLN=MNELSQ
      IF(LLN.GT.15) LLN=15
C    FIND COLUMN TOTALS,TKELEM OF ARRAY RKELEM
      DO 77 NN=1, LLN
      DO 73 KK=1,NUMEL
      TKELEM(NN)=TKELEM(NN)+RKELEM(KK,NN)
   73 CONTINUE
   77 CONTINUE

C  ADD IN TO MULTI-SESSION STORAGE
      DO 406 LC=1,15
      GTELEM(LC)=GTELEM(LC)+TKELEM(LC)
      DO 407 LA=1,NUMEL
      GRELEM(LA,LC)=GRELEM(LA,LC)+RKELEM(LA,LC)
  407 CONTINUE
  406 CONTINUE

C TABULATE FREQUENCY OF ELEMENT OCCURRENCE AGAINST ITS CODE
C     IN ELEMENT LOCATIONS PRECEEDING AN ATTACK
      WRITE(W,28)
   28 FORMAT('1BEHAVIOUR PRECEEDING AN ATTACK')
      WRITE(W,17)
   17 FORMAT(/4X,'ELEMENT',4X,'COLUMNS CORRESPOND TO',
     ,'SUCCESSIVE ELEMENT LOCATIONS PRECEEDING AN ATTACK !',
     ,/16X,'IE(SEQ)=1, IE(SEQ)=2, ..... IE(SEQ)=MNELSQ'/)
      DO 95 NI =1, NUMEL
      IF(COUNT(NI),EQ,0) GOTO 95
      WRITE(W,18) ELCODE(NI), (RKELEM(NI,MI),MI=1,LLN)
   95 CONTINUE
   18 FORMAT(7X,A4,7X,15(F6,0,1X))
      WRITE(W,19) (TKELEM(KJ),KJ=1,LLN)
   19 FORMAT(11H0    TOTALS,7X,15(F6,0,1X))

C  CONVERT ARRAY TO PROBABILITIES
      DO 74 LJ=1, LLN
      DO 76 MJ =1, NUMEL
      IF(TKELEM(LJ),EQ,0) GOTO 74
      PKELEM(MJ,LJ)=RKELEM(MJ,LJ)/TKELEM(LJ)
   76 CONTINUE
   74 CONTINUE

C  TABULATE THE ARRAY OF PROBABILITIES, PKELEM
      I=0
      IF(TBEHAV.GT.25.) I=1
      WRITE(W,20) I
   20 FORMAT(I1,9X,'TABLE EXPRESSES THE ABOVE AS',
     ,'PROBABILITIES'/)
      DO 97 KI=1,NUMEL
      IF(COUNT(KI),EQ,0) GOTO 97
      WRITE(W,22) ELCODE(KI), (PKELEM(KI,NJ),NJ=1,LLN)
```

```
   22 FORMAT( 7X,A4,7X,15(F6.3,1X))
   97 CONTINUE

C.....CONSTRUCT A TRANSITION MATRIX
      DO 66 IJ=1,NUMEL
      DO 67 IK=1,NUMEL
      TMAT(IJ,IK)=0
   67 CONTINUE
   66 CONTINUE
      NEL=NELSES-1
      DO 62 LK=1,NEL
      KKI=LK+1
      TMAT(BEHAV(LK),BEHAV(KKI))=TMAT(BEHAV(LK),BEHAV(KKI))+1
   62 CONTINUE

C  ADD IN TO MULTI-SESSION STORAGE
      DO 410 LA=1,NUMEL
      DO 411 LD=1,NUMEL
      JTMAT(LA,LD)=JTMAT(LA,LD)+TMAT(LA,LD)
      EIJ(LA,LD)=FLOAT(TMAT(LA,LD))
  411 CONTINUE
  410 CONTINUE

C    WRITE TRANSITION MATRIX
      WRITE(W,29)
   29 FORMAT(18H1TRANSITION MATRIX)
      CALL RYTMAT(EIJ,COUNT)

      IF(NOTIME.EQ.1) GOTO 132


C.....ELEMENT DURATION ANALYSIS
      WRITE(W,214)
  214 FORMAT('1ELEMENT DURATION ANALYSIS')
      WRITE(W,241)
  241 FORMAT('0WRITE ELEMENT DURATION ARRAYS'/)

C    INITIALISE VARIABLES
      BUTTOT=0.
      LLN=0
      RR=0
      BOUTMX=0
      INC=0
      DO 208 JJJ=1,35
      DO 215 JJM=1,14
      STATS(JJJ,JJM)=0.0
  215 CONTINUE
  208 CONTINUE
      DO 210 I=1,20
      OVER60(I,1)=0
      OVER60(I,2)=0
  210 CONTINUE

      DO 201 P=1,NUMEL
      NUMBT(P)=0
      DO 202 JJI=1,550
      BOUT(JJI)=0
  202 CONTINUE
```

```
C PROCEED THROUGH DATA TO CALCULATE ELEMENT DURATIONS
  209 DO 203 I=1,NELSES
      IF(BEHAV(I),NE,P) GOTO 203
      JJN=I+1
      IF(BEHAV(JJN),EQ,4,OR,BEHAV(JJN),EQ,37) JJN=JJN+1
      NUMBT(P)=NUMBT(P)+1
      JJI=NUMBT(P)
      BOUT(JJI)  =TIMVAL(JJN)-TIMVAL(I)
  203 CONTINUE

      IF(NUMBT(P),EQ,0) GOTO 201
      JJM=NUMBT(P)
      WRITE(W,221) ELCODE(P),  (BOUT(JJI), JJI=1,JJM)
  221 FORMAT(1H0,A4,12X,2015,/(17X,2015))

C CALCULATE SIMPLE STATISTICS FOR ELEMENT DURATION ANALYSIS
      IF(NUMBT(P)-1) 201, 240, 220
  220 INC=INC+1
      DO 248 J=1,JJM
      ISTORE(J)=BOUT(J)
  248 CONTINUE
      AN=FLOAT(JJM)
      CALL STAT(0,AN,STATS(INC,1),STATS(INC,2),STATS(INC,3),
     ,STATS(INC,4),STATS(INC,14),STATS(INC,6),STATS(INC,7),
     ,STATS(INC,8), STATS(INC,9),STATS(INC,10),STATS(INC,11),
     ,STATS(INC,12))
      STATS(INC,5)=AN
      GOTO 219
  240 INC=INC+1
      STATS(INC,1)=BOUT(1)
      STATS(INC,2)=BOUT(1)
      STATS(INC,4)=BOUT(1)
      STATS(INC,5)=1,
      STATS(INC,6)=BOUT(1)
      STATS(INC,7)=BOUT(1)
      STATS(INC,14)=BOUT(1)*BOUT(1)
  219 IF(P,EQ,4,OR,P,EQ,37) GOTO 247
      BUTTOT=BUTTOT+STATS(INC,4)
      STATS(INC,13)=STATS(INC,4)*100,/1800,

C CALCULATE FREQUENCY TABLES FOR ELEMENT DURATIONS
  247 DO 243 JJI=1,JJM
      IF(BOUT(JJI),GT,BOUTMX,AND,,NOT,BOUT(JJI),GT,60)BOUTMX=
     ,BOUT(JJI)
  243 CONTINUE
      IF(BOUTMX,GT,MXBOUT) MXBOUT=BOUTMX
      RR=RR+1
      FQCODE(RR)=ELCODE(P)
      DO 223 JJJ=1,60
      FQBOUT(JJJ,RR)=0
  223 CONTINUE
      DO 224 JJI=1,JJM
      IF(BOUT(JJI),LE, 60) GOTO 238
      LLN=LLN+1
      JBTFQT(P)=JBTFQT(P)+1
      OVER60(LLN,1)=P
      OVER60(LLN,2)=BOUT(JJI)
      GOTO 224
  238 FQBOUT(BOUT(JJI),RR)=FQBOUT(BOUT(JJI),RR)+1
```

```
C CONSTRUCT AN ELEMENT DURATION FREQUENCY ARRAY
      JBTFRQ(BOUT(JJI),P)=JBTFRQ(BOUT(JJI),P)+1
  224 CONTINUE
  201 CONTINUE

C WRITE FREQUENCY TABLES FOR ELEMENT DURATIONS
      DO 204 JJL=1,RR
      FQBTTT(JJL)=0
      DO 205 KKL=1,BOUTMX
      FQBTTT(JJL)=FQBTTT(JJL)+FQBOUT(KKL,JJL)
  205 CONTINUE
  204 CONTINUE
      IF(RR-24) 244, 244, 245
  244 CALL FQTAB(1,RR,BOUTMX,FQCODE,FQBOUT,FQBTTT)
      GOTO 236
  245 CALL FQTAB(1,24,BOUTMX,FQCODE,FQBOUT,FQBTTT)
      CALL FQTAB(25,RR,BOUTMX,FQCODE,FQBOUT,FQBTTT)

  236 IF(LLN.EQ.0) GOTO 249
      DO 242 I=1,LLN
      LLM=OVER60(I,1)
      IM1=IM1+1
      LONGST(IM1,1)=OVER60(I,1)
      LONGST(IM1,2)=OVER60(I,2)
      WRITE(W,237) ELCODE(LLM), OVER60(I,2)
  237 FORMAT(//'LENGTH OF ELEMENT....',A3,' LASTED FOR....',
     ,I4,' SECONDS')
  242 CONTINUE

C WRITE STATISTICS FOR ELEMENT DURATION ANALYSIS
  249 WRITE(W,239)
  239 FORMAT('1STATISTICS FOR ELEMENT DURATION ANALYSIS'//)
      WRITE(W,216)
  216 FORMAT('0ELCODE', 4X,'AMAX',4X,'AMIN',3X,'RANGE',4X,
     ,'SUMY',7X,'N',4X,'AMEDN',5X,'MEAN',' VARIANCE',
     ,'  ST.DEV,',' S',',T.ERR,',' CF.DISP',3X,'CF.VAR',
     ,' TIM PART',3X,'SUMYSQ'//)
      DO 218 I=1,INC
      WRITE(W,217) FQCODE(I), (STATS(I,II), II=1,14)
  217 FORMAT(3X,A4,5F8.0,2F9.3,F10.2,5F9.3,F9.0)
  218 CONTINUE
      WRITE(W,246) BUTTOT
  246 FORMAT(24X,9HBUTTOT = ,F6.0/////)

C....TO CALCULATE THE TIMES BETWEEN ATTACKS
      WRITE(W,156)
  156 FORMAT('1ANALYSIS OF TIMES BETWEEN ATTACKS'//)
      ZEQ=1
      DO 151 KKK=1,ISEQ
      BTCYCL(KKK)=0
  151 CONTINUE
      LLK=ISEQ-1
      BTCYCL(1)=TIMVAL(IE(1))
      DO 152 LLJ=1,LLK
      ZEQ=ZEQ+1
      BTCYCL(ZEQ)=TIMVAL(IE(ZEQ))-TIMVAL(IE(LLJ))
  152 CONTINUE
      WRITE(W,153) (BTCYCL(LLI),LLI=1,ISEQ)
```

```
153 FORMAT('0','BITE CYCLE DURATIONS',4X,2015,/(25X,2015))

C CONSTRUCT A FREQUENCY TABLE FOR DURATIONS BETWEEN ATTACKS
      DO 150 LLI=1,ISEQ
      ISTORE(LLI)=BTCYCL(LLI)
      IF(BTCYCL(LLI).LE.200) GOTO 149
      IM2=IM2+1
      OVR200(IM2,1)=1
      OVR200,IM2,2)=BTCYCL(LLI)
      GOTO 150
149   FQBTCY(BTCYCL(LLI))=FQBTCY(BTCYCL(LLI))+1
150   CONTINUE
      IF(SEQ.LT.2,) GOTO 132
      CALL STAT(1,SEQ,D1,D2,D3,D4,D5,D6,D7,D8,D9,D10,D11,D12)

      GOTO 132


C PERFORM MULTI-SESSION ANALYSIS AND OUTPUT VARIABLES
400   WRITE(W,448)
448   FORMAT(22H1SPECIES ANALYSIS FOR!)
      NOSESS=NOSESS-1
      WRITE(W,449) NOSESS
449   FORMAT(///31HNUMBER OF SESSIONS IN ANALYSIS!,18X,I2)
      WRITE(W,452)
452   FORMAT(////26HINDIVIDUAL IDENTIFICATION!)
      DO 464 I=1,NOSESS
      WRITE(W,463) (SCODES(I,J), J=1,3)
463   FORMAT(50X,3A8)
464   CONTINUE
      WRITE(W,451) NORESP, NOBITE
451   FORMAT(//////18HREPLICATE DETAILS!,31X,12HNO RESPONSE!,
     ,I6,20X,8HNO BITES,I6)
      WRITE(W,420) GELSES
420   FORMAT('1TOTAL NUMBER OF BEHAVIOURAL ELEMENTS.:.:.:.:',
     ,F5.0//)
      WRITE(W,424)
424   FORMAT(8HOELEMENT,5X,9HFREQUENCY,3X,'REL. FREQUENCY'//)

      TBEHAV=FLOAT(NUMEL)
      DO 421 LA=1,NUMEL
      GELFRQ(LA)=0.0
      IF(GCOUNT(LA).EQ.0.0) GOTO 465
      GELFRQ(LA)=GCOUNT(LA)*100./GELSES
      WRITE(W,423)ELCODE(LA), GCOUNT(LA), GELFRQ(LA)
423   FORMAT(1X,A4,8X,F6.0,6X,F7.3)
      GOTO 421
465   TBEHAV=TBEHAV-1.
421   CONTINUE
      EXPTED=GELSES/TBEHAV
      WRITE(W,466) TBEHAV, EXPTED
466   FORMAT(///'NUMBER OF BEHAVIOURAL TYPES EXHIBITED:.:.:.:',
     ,F4.0/'FREQUENCY OF BEHAVIOURAL TYPES EXPECTED.:.:.',F4.0)

C CALCULATE SIMPLE STATISTICS FOR ALL SESSION 'NEWS' VALUES
      WRITE(W,25)
      CALL FQFEED(250,JFQNWS,IN,0,0)
      AN=FLOAT(IN)
```

```
      CALL STAT(1,AN,D1,D2,D3,D4,D5,D6,D7,D8,D9,D10,D11,D12)
      JLGNWS=IFIX(D1)

C PRINT FREQUENCY TABLE OF 'NEWS' VALUES FOR ALL SESSIONS
      WRITE(W,14)
      COLNB=-10
      IM=-9
      IN=0
      LGNEWS=JLGNWS+10
      DO 426 IL=1,LGNEWS,10
      COLNB=COLNB+10
      IM=IM+10
      IN=IN+10
      WRITE(W,25) COLNB, (JFQNWS(L), L=IM,IN)
  426 CONTINUE
      WRITE(W,427) JLGNWS
  427 FORMAT(11H0JLGNWS =  ,I4)

C CALCULATE SPECIES PREY CAPTURE EFFICIENCY
      NOATAK=0.
      NOATAK=GCOUNT(24)+GCOUNT(25)+GCOUNT(34)+GCOUNT(35)
      CAPEFF=0.0
      CAPEFF=((GCOUNT(24)+GCOUNT(34))/NOATAK)*100.
      WRITE(W,16) CAPEFF

C PRINT RELEM & PELEM ARRAYS FOR ALL SESSIONS ADDED TOGETHER
      WRITE(W,28)
      WRITE(W,17)
      DO 428 NI=1,NUMEL
      IF(GCOUNT(NI).EQ.0) GOTO 428
      WRITE(W,18) ELCODE(NI), (GRELEM(NI,MI), MI=1,15)
  428 CONTINUE
      WRITE(W,19)(GTELEM(KJ), KJ=1,15)
      DO 429 LJ=1,15
      DO 430 MJ=1,NUMEL
      IF(GTELEM(LJ).EQ.0.0) GOTO 429
      GPELEM (MJ,LJ)=GRELEM(MJ,LJ)/GTELEM(LJ)
  430 CONTINUE
  429 CONTINUE
      I=0
      IF(TBEHAV.GT.25.) I=1
      WRITE(W,20) I
      DO 431 KI=1,NUMEL
      IF(GCOUNT(KI).EQ.0) GOTO 431
      WRITE(W,22) ELCODE(KI), (GPELEM(KI,NJ), NJ=1,15)
  431 CONTINUE

C WRITE SPECIES TRANSITION MATRIX
      WRITE(W,29)
      DO 92 LA=1,NUMEL
      DO 93 LD=1,NUMEL
      EIJ(LA,LD)=FLOAT(JTMAT(LA,LD))
   93 CONTINUE
   92 CONTINUE
      CALL RYTMAT(EIJ,GCOUNT)

C CALCULATE EXPECTED TRANSITION MATRIX AND PERCENTAGE OF
C       TRANSITION OCCURRENCES
      DO 56 IJ=1,NUMEL
```

```
      ROWSUM(IJ)=0.0
      COLSUM(IJ)=0.0
      DO 57 IK=1,NUMEL
      ROWSUM(IJ)=ROWSUM(IJ)+EIJ(IJ,IK)
      COLSUM(IJ)=COLSUM(IJ)+EIJ(IK,IJ)
   57 CONTINUE
   56 CONTINUE
      TOTALR=0.0
      DO 54 IJ=1,NUMEL
      DO 55 IK=1,NUMEL
      EIJ(IJ,IK)=0.0
      PRCENT(IJ,IK)=0.0
   55 CONTINUE
      TOTALR=TOTALR+ROWSUM(IJ)
   54 CONTINUE
      DO 40 LA=1,NUMEL
      DO 41 LB=1,NUMEL
      IF(ROWSUM(LA).EQ.0.0) GOTO 40
      EIJ(LA,LB)=ROWSUM(LA)*COLSUM(LB)/(TOTALR)
      PRCENT(LA,LB)=JTMAT(LA,LB)*100./ROWSUM(LA)
   41 CONTINUE
   40 CONTINUE

C WRITE EXPECTED TRANSITION MATRIX
      WRITE(W,45)
   45 FORMAT(27H1EXPECTED TRANSITION MATRIX)
      CALL RYTMAT(EIJ,GCOUNT)

C WRITE PERCENTAGE TRANSITION MATRIX
      WRITE(W,48)
   48 FORMAT(29H1PERCENTAGE TRANSITION MATRIX)
      CALL RYTMAT(PRCENT,GCOUNT)

C CALCULATE ELEMENT DURATION FREQUENCY TABLE TOTALS
      DO 436 KKL=1,NUMEL
      DO 437 JJI=1,MXBOUT
      JBTFQT(KKL)=JBTFQT(KKL)+JBTFRQ(JJI,KKL)
  437 CONTINUE
  436 CONTINUE

C PRINT ELEMENT DURATION FREQUENCY TABLE
      RR=0
      DO 416 LO=1,NUMEL
      IF(JBTFQT(LO).EQ.0) GOTO 416
      RR=RR+1
      FQBTTT(RR)=0
      FQCODE(RR)=ELCODE(LO)
      DO 417 JJJ=1,MXBOUT
      FQBOUT(JJJ,RR)=JBTFRQ(JJJ,LO)
      FQBTTT(RR)=FQBTTT(RR)+JBTFRQ(JJJ,LO)
  417 CONTINUE
  416 CONTINUE
      IF(RR-24) 458, 458, 459
  458 CALL FQTAB(1,RR,MXBOUT,FQCODE,FQBOUT,FQBTTT)
      GOTO 401
  459 CALL FQTAB( 1,24,MXBOUT,FQCODE,FQBOUT,FQBTTT)
      CALL FQTAB(25,RR,MXBOUT,FQCODE,FQBOUT,FQBTTT)

  401 BUTTOT=0.0
```

```
      DO 435 JJJ=1,35
      DO 434 JJM=1,14
      STATS(JJJ,JJM)=0.0
  434 CONTINUE
  435 CONTINUE

      WRITE(W,85)
   85 FORMAT('1')
      WRITE(W,413) (LONGST(LC,1), LC=1,IM1)
  413 FORMAT(/'ELCODE',31I4)
      WRITE(W,419) (LONGST(LC,2), LC=1,IM1)
  419 FORMAT(/'VALUES',31I4)

C CALCULATE STATISTICS OF ELEMENT DURATIONS FOR ALL SESSIONS
      WRITE(W,239)
      INC=0
      DO 468 LG=1,NUMEL
      IF(JBTFQT(LG).EQ.0) GOTO 468
      DO 438 LA=1,MXBOUT
      BOUT(LA)=JBTFRQ(LA,LG)
  438 CONTINUE
      CALL FQFEED(MXBOUT,BOUT,IN,IM1,LONGST)
      IF(IN-1) 468, 432, 433
  433 INC=INC+1
      AN=FLOAT(IN)
      CALL STAT(0,AN,STATS(INC,1),STATS(INC,2),STATS(INC,3),
     ,STATS(INC,4),STATS(INC,14),STATS(INC,6),STATS(INC,7),
     ,STATS(INC,8),STATS(INC,9),STATS(INC,10),STATS(INC,11),
     ,STATS(INC,12))
      STATS(INC,5)=AN
      GOTO 455
  432 INC=INC+1
      DO 425 LH=1,MXBOUT
      DO 439 K=1,7
      STATS(INC,K)=ISTORE(1)
  439 CONTINUE
      STATS(INC,3)=0.
      STATS(INC,5)=1.
      STATS(INC,13)=ISTORE(1)*100./(1800.*(NOSESS*(NOBITE+
     ,NORESP)))
      STATS(INC,14)=ISTORE(1)*ISTORE(1)
  425 CONTINUE
  455 IF(LG.EQ.4.OR.LG.EQ.37) GOTO 468
      BUTTOT=BUTTOT+STATS(INC,4)
      STATS(INC,13)=STATS(INC,4)*100./(1800.*(NOSESS*(NOBITE+
     ,NORESP)))
  468 CONTINUE
  456 WRITE(W,216)
      DO 467 I=1,INC
      WRITE(W,217) FQCODE(I), (STATS(I,II), II=1,14)
  467 CONTINUE
      WRITE(W,246) BUTTOT

C CALCULATE STATISTICS ON DURATIONS BETWEEN ATTACKS FOR ALL
C     SESSIONS
      WRITE(W,156)
      LG=1
      CALL FQFEED(200,FQBTCY,IN,IM2,OVR200)
      AN=FLOAT(IN)
```

```
      CALL STAT(1,AN,D1,D2,D3,D4,D5,D6,D7,D8,D9,D10,D11,D12)

C PRINT SPECIES FREQUENCY TABLE FOR DURATIONS BETWEEN ATTACKS
      WRITE(W,445)
  445 FORMAT('1FREQUENCY TABLE FOR DURATIONS BETWEEN',
     ,'ATTACKS:',11X,1H1,4X,1H2,4X,1H3,4X,1H4,4X,1H5,7X,1H6,
     ,4X,1H7,4X,1H8,4X,1H9,3X,2H10/)
      COLNB=-10
      IM=-9
      IN=0
      DO 446 IL=1,200,10
      COLNB=COLNB+10
      IM=IM+10
      IN=IN+10
      WRITE(W,447) COLNB, (FQBTCY(L), L=IM,IN)
  447 FORMAT( 28X,I4,3X,5I5,3X,5I5)
  446 CONTINUE
      STOP
      END
```

APPENDIX 11

COMPUTER PROGRAM TO ANALYSE FEEDING BEHAVIOUR OF FLATFISH
- PART TWO

```
C ****************************************************

C            BEHAVIOURAL ANALYSIS - PART TWO

C            USES SUBROUTINES : ADD, HISTO

C ****************************************************

C  NEW VARIABLES NOT DESCRIBED IN PART ONE
C  SECS     CUMULATIVE STORE OF TIME BLOCKS
C  INT      THE CHOSEN UNIT OF TIME BLOCK LENGTH
C  L        IN ANALYSIS - NUMBER OF BEHAVIOURS IN EACH BLOCK
C  CUMCTB   CUMULATIVE STORE OF NUMBER OF BEHAVIOURS PER BLOCK
C                                 THROUGHOUT THE SESSION
C
C  ORDINT   1-D ARRAY, ORDER OF BEHAVIOURAL INTERVALS WITHIN A
C                                                   BLOCK
C
C  COUNT    A COUNTER
C  NUM012   6 DIGIT SEQUENCE CODE
C  NUM345   6 DIGIT SEQUENCE CODE
C  FREQ     1-D ARRAY, FREQUENCY OF SEQUENCES
C  COD012   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C  COD345   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C  X        DECODE VARIABLE
C  DECODE   2-D ARRAY, NUMERIC STORAGE OF ALL SEQUENCES
C  C5-C4-C3-C2-C1-C0     6 VARIABLES STORING A SEQUENCE OF
C                                 BEHAVIOURAL ELEMENTS
C
C  TYPE     VARIABLE ENABLING GROUPING OF ATTACK RESPONSES
C  COUNTG   A COUNTER
C  GFREQ    1-D ARRAY, FREQUENCY OF SEQUENCES
C  GOD012   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C  GOD345   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C  GECODE   2-D ARRAY, NUMERIC STORAGE OF ALL SEQUENCES
C  START    DETECTOR VARIABLE
C  STOREL   1-D ARRAY, MULTI-SESSION STORE OF L
C  STOREC   1-D ARRAY, MULTI-SESSION STORE OF CUMCTB
C  SUB      SUBSCRIPT COUNTER
C  ELCENT   PERCENTAGE L VALUES
C  CMCENT   PERCENTAGE CUMCTB VALUES

C STATEMENT LABELS
C      500-531
C      600-631

C ELEMENTS OF FEEDING BEHAVIOUR
C  TURN               TN      01
C  SWIVEL TURN        SV      02
C  TURN AWAY          TA      03
C  LEAVE              LV      04
C  PALPATION          PP      05
C  SWIM               SW      06
C  DOWN               DN      07
```

APPENDIX 11

COMPUTER PROGRAM TO ANALYSE FEEDING BEHAVIOUR OF FLATFISH - PART TWO

```
C ********************************************************
C
C               BEHAVIOURAL ANALYSIS - PART TWO
C
C                USES SUBROUTINES : ADD, HISTO
C
C ********************************************************
C
C  NEW VARIABLES NOT DESCRIBED IN PART ONE
C  SECS     CUMULATIVE STORE OF TIME BLOCKS
C  INT      THE CHOSEN UNIT OF TIME BLOCK LENGTH
C  L        IN ANALYSIS - NUMBER OF BEHAVIOURS IN EACH BLOCK
C  CUMCTB   CUMULATIVE STORE OF NUMBER OF BEHAVIOURS PER BLOCK
C                                 THROUGHOUT THE SESSION
C
C  ORDINT   1-D ARRAY, ORDER OF BEHAVIOURAL INTERVALS WITHIN A
C                                                    BLOCK
C
C  COUNT    A COUNTER
C  NUM012   6 DIGIT SEQUENCE CODE
C  NUM345   6 DIGIT SEQUENCE CODE
C  FREQ     1-D ARRAY, FREQUENCY OF SEQUENCES
C  COD012   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C  COD345   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C  X        DECODE VARIABLE
C  DECODE   2-D ARRAY, NUMERIC STORAGE OF ALL SEQUENCES
C  C5-C4-C3-C2-C1-C0     6 VARIABLES STORING A SEQUENCE OF
C                                   BEHAVIOURAL ELEMENTS
C
C  TYPE     VARIABLE ENABLING GROUPING OF ATTACK RESPONSES
C  COUNTG   A COUNTER
C  GFREQ    1-D ARRAY, FREQUENCY OF SEQUENCES
C  GOD012   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C  GOD345   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C  GECODE   2-D ARRAY, NUMERIC STORAGE OF ALL SEQUENCES
C  START    DETECTOR VARIABLE
C  STOREL   1-D ARRAY, MULTI-SESSION STORE OF L
C  STOREC   1-D ARRAY, MULTI-SESSION STORE OF CUMCTB
C  SUB      SUBSCRIPT COUNTER
C  ELCENT   PERCENTAGE L VALUES
C  CMCENT   PERCENTAGE CUMCTB VALUES

C STATEMENT LABELS
C      500-531
C      600-631

C ELEMENTS OF FEEDING BEHAVIOUR
C  TURN                  TN       01
C  SWIVEL TURN           SV       02
C  TURN AWAY             TA       03
C  LEAVE                 LV       04
C  PALPATION             PP       05
C  SWIM                  SW       06
C  DOWN                  DN       07
```

```
C  SKIM                 SK      08
C  SHUFFLE              SF      09
C  CREEP                CR      10
C  FORWARD              FD      11
C  REVERSE              RV      12
C  PAUSE                PS      13
C  SETTLE               ST      14
C  FLAP SWIM            FS      15
C  BURY                 BY      16
C  FLAP                 FP      17
C  UNDULATE             UN      18
C  BODY ARCH            AR      19
C  BODY RELAX           RX      20
C  ARC                  AC      21
C  HOVER                HV      22
C  LUNGE                LG      23
C  BITE                 BT      24
C  MISS                 MS      25
C  CHEW                 CW      26
C  SPIT                 SP      27
C  HEAD RAISE           HR      28
C  HEAD LOWER           HL      29
C  YAWN                 YN      30
C  OMEGA JUMP           JP      31
C  SWIM-TURN           STN      32
C  SWIM-LUNGE          SLG      33
C  SWIM-BITE           SBT      34
C  SWIM-MISS           SMS      35
C  SWIM-TURN AWAY      STA      36
C  SWIM-LEAVE          SLV      37
C  SWIM-CHEW           SCW      38
C  REVERSE-CHEW        RCW      39
C  SWIM-YAWN           SYN      40
C  QUIVER               QV      41
C  CREEP-BODY ARCH     CAR      42
C  TURN-BODY ARCH      TAR      43
C  ARCH-REVERSE        ARV      44
C  ARCH-TURN AWAY      ATA      45
C  ARCH-HEAD LOWER     AHL      46
C  ARCH-HEAD RAISE     AHR      47
C  HEAD LIFT-CREEP     HCR      48
C  END OF SESSION      END      99
C  GAP IN DATA         GAP

C TYPE STATEMENTS
      REAL  SESCOD(3), SCODES(30,3)
      INTEGER  OPTOUT, BLK, DETECT, BEHAV(1200), TIMVAL(1200),
     ,IELEM(20), INUM(20), ITIME(40), MINTOS(20), TIMSEC(20)
      INTEGER  SECS, CUMCTB, SUB, ORDINT, STOREC, STOREL
      INTEGER  COUNT, NUM012, NUM345, C0, C1, C2, C3, C4, C5,
     ,COD012(300), COD345(300), FREQ(300), DECODE(6,300),
     ,GOD012(1000), GOD345(1000), GFREQ(1000), GECODE(6,1000),
     ,COUNTG, START, ELCODE(49), TYPE(4), R, W, X

      COMMON  CUMCTB, L, ORDINT(500), SUB, STOREC(60),
     ,STOREL(60), W

      DATA TYPE(1), TYPE(2), TYPE(3), TYPE(4)/24,25,34,35/
```

```
      DATA    ELCODE(1),  ELCODE(2) / 3H TN  , 3H SV  /
      DATA    ELCODE(3),  ELCODE(4) / 3H TA  , 3H LV  /
      DATA    ELCODE(5),  ELCODE(6) / 3H PP  , 3H SW  /
      DATA    ELCODE(7),  ELCODE(8) / 3H DN  , 3H SK  /
      DATA    ELCODE(9),  ELCODE(10)/ 3H SF  , 3H CR  /
      DATA    ELCODE(11), ELCODE(12)/ 3H FD  , 3H RV  /
      DATA    ELCODE(13), ELCODE(14)/ 3H PS  , 3H ST  /
      DATA    ELCODE(15), ELCODE(16)/ 3H FS  , 3H BY  /
      DATA    ELCODE(17), ELCODE(18)/ 3H FP  , 3H UN  /
      DATA    ELCODE(19), ELCODE(20)/ 3H AR  , 3H RX  /
      DATA    ELCODE(21), ELCODE(22)/ 3H AC  , 3H HV  /
      DATA    ELCODE(23), ELCODE(24)/ 3H LG  , 3H BT  /
      DATA    ELCODE(25), ELCODE(26)/ 3H MS  , 3H CW  /
      DATA    ELCODE(27), ELCODE(28)/ 3H SP  , 3H HR  /
      DATA    ELCODE(29), ELCODE(30)/ 3H HL  , 3H YN  /
      DATA    ELCODE(31), ELCODE(32)/ 3H JP  , 3HSTN  /
      DATA    ELCODE(33), ELCODE(34)/ 3HSLG  , 3HSBT  /
      DATA    ELCODE(35), ELCODE(36)/ 3HSMS  , 3HSTA  /
      DATA    ELCODE(37), ELCODE(38)/ 3HSLV  , 3HSCW  /
      DATA    ELCODE(39), ELCODE(40)/ 3HRCW  , 3HSYN  /
      DATA    ELCODE(41), ELCODE(42)/ 3H QV  , 3HCAR  /
      DATA    ELCODE(43), ELCODE(44)/ 3HTAR  , 3HARV  /
      DATA    ELCODE(45), ELCODE(46)/ 3HATA  , 3HAHL  /
      DATA    ELCODE(47), ELCODE(48)/ 3HAHR  , 3HHCR  /
      DATA    ELCODE(49)/4H    /

      W=2
      R=37
      NUMEL=48
      INT=30
      IZ=2


C.....INITIALISE MULTI-SESSION VARIABLES BEFORE BEGINNING

  450 DO 521 I=1,1000
      GOD012(I)=0
      GOD345(I)=0
  521 CONTINUE
      START=0
      NOSESS=0
      ITOT=0

      DO 627 I=1,60
      STOREC(I)=0
      STOREL(I)=0
  627 CONTINUE


C.....SESSION ANALYSIS

C.....FIRST PART OF PROGRAM CONVERTS ALPHA ELEMENT BEHAVIOURAL
C     CODE TO A NUMERICAL ONE AND TIME FROM MINS AND SECS TO
C     SECONDS
C READ & WRITE SESSION CODE
  132 READ(R,1)SESCOD(1),SESCOD(2),SESCOD(3)
    1 FORMAT(/3A8)
      NOSESS=NOSESS+1
```

```
      SCODES(NOSESS,1)=SESCOD(1)
      SCODES(NOSESS,2)=SESCOD(2)
      SCODES(NOSESS,3)=SESCOD(3)
C LOOK FOR 'ANALYSE' TO INITIATE MULTI-SESSION ANALYSIS
      IF(SESCOD(1).EQ.8H ANALYSE) GOTO 517
      WRITE(W,2)SESCOD(1),SESCOD(2),SESCOD(3)
    2 FORMAT(5H1    ,3A8,//)
C   INITIALISE STORAGE ARRAYS
      DO 157 KKI=1,1200
      BEHAV(KKI)=0
      TIMVAL(KKI)=0
  157 CONTINUE
      BLK=0
      J=0
      OPTOUT=0
      LLN=0
      NOTIME=0
  128 DETECT=0
      MINS=00
      LAST=00
C READ 20 BEHAVIOURAL ELEMENTS AND WRITE
  100 READ(R,3)(IELEM(I),I=1,20)
    3 FORMAT(20A4)
      IF(IELEM(1).NE.4H  NO) GOTO 155
      WRITE(W,154)
  154 FORMAT(36HOFISH GAVE NO RESPONSE IN 30 MINUTES)
      GOTO 132
  155 WRITE(W,4)(IELEM(I),I=1,20)
    4 FORMAT(/10A6,5X,10A6)

C CONVERT ALPHA ELEMENT CODES TO NUMERICAL CODES
      N=0
      DO 101 I=1,20
      N=N+1
      IF(IELEM(I).NE.4H  TN) GOTO 102
      INUM(I)=01
      GOTO 101
  102 IF(IELEM(I).NE.4H  HR) GOTO 103
      INUM(I)=28
      GOTO 101
  103 IF(IELEM(I).NE.4H  SW) GOTO 104
      INUM(I)=06
      GOTO 101
  104 IF(IELEM(I).NE.4H  SK) GOTO 105
      INUM(I)=08
      GOTO 101
  105 IF(IELEM(I).NE.4H  SF) GOTO 106
      INUM(I)=09
      GOTO 101
  106 IF(IELEM(I).NE.4H  CR) GOTO 107
      INUM(I)=10
      GOTO 101
  107 IF(IELEM(I).NE.4H  FD) GOTO 108
      INUM(I)=11
      GOTO 101
  108 IF(IELEM(I).NE.4H  RV) GOTO 109
      INUM(I)=12
      GOTO 101
  109 IF(IELEM(I).NE.4H  AR) GOTO 110
```

```
      INUM(I)=19
      GOTO 101
  110 IF(IELEM(I).NE.4H  HV) GOTO 111
      INUM(I)=22
      GOTO 101
  111 IF(IELEM(I).NE.4H  LG) GOTO 112
      INUM(I)=23
      GOTO 101
  112 IF(IELEM(I).NE.4H  BT) GOTO 113
      INUM(I)=24
      GOTO 101
  113 IF(IELEM(I).NE.4H  MS) GOTO 114
      INUM(I)=25
      GOTO 101
  114 IF(IELEM(I).NE.4H  CW) GOTO 115
      INUM(I)=26
      GOTO 101
  115 IF(IELEM(I).NE.4H  SP) GOTO 116
      INUM(I)=27
      GOTO 101
  116 IF(IELEM(I).NE.4H  PS) GOTO 117
      INUM(I)=13
      GOTO 101
  117 IF(IELEM(I).NE.4H  BY) GOTO 118
      INUM(I)=16
      GOTO 101
  118 IF(IELEM(I).NE.4H  DN) GOTO 119
      INUM(I)=07
      GOTO 101
  119 IF(IELEM(I).NE.4H  HL) GOTO 120
      INUM(I)=29
      GOTO 101
  120 IF(IELEM(I).NE.4H  TA) GOTO 121
      INUM(I)=03
      GOTO 101
  121 IF(IELEM(I).NE.4H  LV) GOTO 122
      INUM(I)=04
      GOTO 101
  122 IF(IELEM(I).NE.4H  FS) GOTO 123
      INUM(I)=15
      GOTO 101
  123 IF(IELEM(I).NE.4H  FP) GOTO 124
      INUM(I)=17
      GOTO 101
  124 IF(IELEM(I).NE.4H  YN) GOTO 125
      INUM(I)=30
      GOTO 101
  125 IF(IELEM(I).NE.4H  SV) GOTO 133
      INUM(I)=02
      GOTO 101
  133 IF(IELEM(I).NE.4H  RX) GOTO 126
      INUM(I)=20
      GOTO 101
  126 IF(IELEM(I).NE.4H  PP) GOTO 140
      INUM(I)=05
      GOTO 101
  140 IF(IELEM(I).NE.4H  ST) GOTO 141
      INUM(I)=14
      GOTO 101
```

```
141 IF(IELEM(I),NE,4H  UN) GOTO 142
    INUM(I)=18
    GOTO 101
142 IF(IELEM(I),NE,4H  AC) GOTO 143
    INUM(I)=21
    GOTO 101
143 IF(IELEM(I),NE,4H HCR) GOTO 145
    INUM(I)=48
    GOTO 101
145 IF(IELEM(I),NE,4H  JP) GOTO 146
    INUM(I)=31
    GOTO 101
146 IF(IELEM(I),NE,4H STN) GOTO 158
    INUM(I)=32
    GOTO 101
158 IF(IELEM(I),NE,4H SLG) GOTO 159
    INUM(I)=33
    GOTO 101
159 IF(IELEM(I),NE,4H SBT) GOTO 160
    INUM(I)=34
    GOTO 101
160 IF(IELEM(I),NE,4H SMS) GOTO 161
    INUM(I)=35
    GOTO 101
161 IF(IELEM(I),NE,4H STA) GOTO 162
    INUM(I)=36
    GOTO 101
162 IF(IELEM(I),NE,4H SLV) GOTO 163
    INUM(I)=37
    GOTO 101
163 IF(IELEM(I),NE,4H SCW) GOTO 164
    INUM(I)=38
    GOTO 101
164 IF(IELEM(I),NE,4H RCW) GOTO 165
    INUM(I)=39
    GOTO 101
165 IF(IELEM(I),NE,4H SYN) GOTO 166
    INUM(I)=40
    GOTO 101
166 IF(IELEM(I),NE,4H  QV) GOTO 167
    INUM(I)=41
    GOTO 101
167 IF(IELEM(I),NE,4H CAR) GOTO 168
    INUM(I)=42
    GOTO 101
168 IF(IELEM(I),NE,4H TAR) GOTO 169
    INUM(I)=43
    GOTO 101
169 IF(IELEM(I),NE,4H ARV) GOTO 170
    INUM(I)=44
    GOTO 101
170 IF(IELEM(I),NE,4H ATA) GOTO 171
    INUM(I)=45
    GOTO 101
171 IF(IELEM(I),NE,4H AHL) GOTO 172
    INUM(I)=46
    GOTO 101
172 IF(IELEM(I),NE,4H AHR) GOTO 173
    INUM(I)=47
```

```
      GOTO 101
  173 IF(IELEM(I),NE,4H GAP) GOTO 147
      N=N-1
      GOTO 129
  147 IF(IELEM(I),NE,4H END) GOTO 134
      INUM(I)=99
      DETECT=1
      GOTO 129
  134 IF(IELEM(N),NE,4H    ) GOTO 127
      INUM(I)=00
      GOTO 101
C WRITE NATURE OF ERROR (IF ANY)
  127 WRITE(W,12)IELEM(I)
      OPTOUT=1
   12 FORMAT(5X,8HERROR = ,A4)
  101 CONTINUE
C WRITE NUMERICAL CODES OF N BEHAVIOURAL ELEMENTS
  129 WRITE(W,6)(INUM(I),I=1,N)
    6 FORMAT(20I6,5X,10I6)

      IF(NOTIME,EQ,1) GOTO 177


C  READ TIME DATA FOR N BEHAVIOURAL ELEMENTS
      READ(R,7)(ITIME(K),K=1,40)
    7 FORMAT(40I2)
      IF(ITIME(1),EQ,77,AND,ITIME(2),EQ,77) NOTIME=1
      IF(NOTIME,EQ,1) GOTO 177
C CONVERT TIMES TO SECONDS AND WRITE
  176 DO 131 M=1,20
      MINTOS(M)=0
      TIMSEC(M)=0
  131 CONTINUE
      N=N+2
      L=0
      DO 130 K=1,N,2
      L=L+1
C IF A VALUE FOR MINS HAS NOT BEEN WRITTEN IN ITIME ASSUME
C     THE PRECEEDING VALUE
      IF(ITIME(K),EQ,2H  )ITIME(K)=MINS
      MINTOS(L)=ITIME(K)*60
      J=K+1
      IF(IELEM(L),NE,2H  ) GOTO 39
      ITIME(K)=0
      GOTO 130
   39 TIMSEC(L)=MINTOS(L)+ITIME(J)
      MINS=ITIME(K)
  130 CONTINUE
C WRITE  RAW TIME DATA FOR N BEHAVIOURAL ELEMENTS
      WRITE(W,8)(ITIME(K),K=1,N)
    8 FORMAT(10(1X,I2,1H:,I2),5X,10(1X,I2,1H:,I2))
      N=N/2
C CHECK CALCULATED TIMES FOR A PROGRESSIVE NUMERICAL INCREASE
C     AND WRITE ERROR IF THIS IS NOT THE CASE
      IF(TIMSEC(1),GT,LAST) GOTO 139
      WRITE(W,11) TIMSEC(1)
      OPTOUT=1
  139 NN=N-1
```

```
137 IF(N.EQ.1) GOTO 138
    DO 136 L=1,NN
    IF(TIMSEC(L+1).NE.0) GOTO 174
    IF(TIMSEC(L)-TIMSEC(L+2)) 136, 135, 135
174 IF(TIMSEC(L).LT.TIMSEC(L+1)) GOTO 136
    IF(TIMSEC(L).EQ.1800.OR.IELEM(L+1).EQ.4H GAP) GOTO 138
135 WRITE(W,11)TIMSEC(L)
    OPTOUT=1
 11 FORMAT(5X,8HERROR = ,I4)
136 CONTINUE
C WRITE TIME DATA IN SECONDS FOR N BEHAVIOURAL ELEMENTS
138 WRITE(W,9)(TIMSEC(L),L=1,N)
  9 FORMAT(10I6,5X,10I6)
C STORE NUMERICAL CODES & TIME DATA IN ARRAYS BEHAV & TIMVAL
177 JI=BLK+1
    JL = JI+(N-1)
    DO 148 I = JI , JL
    LLM=I-BLK
    LLN=LLN+1
    IF(INUM(LLM).NE.0) GOTO 175
    LLN=LLN-1
    GOTO 148
175 BEHAV(LLN)=INUM(LLM)
    IF(NOTIME.EQ.1) GOTO 148
    TIMVAL(LLN)=TIMSEC(LLM)
148 CONTINUE
    BLK=BLK+N
C DETECT END OF SESSION
    IF(DETECT.EQ.1) GOTO 200
    LAST=TIMSEC(N)
C PROCEED TO NEXT PAIR OF DATA CARDS
    GOTO 100



C.....THIS PART OF PROGRAM ANALYSES QUINTUPLETS PRECEEDING
C     AN ATTACK
200 GOTO 514
512 DO 513 I=1,COUNT
    GOD012(I)=COD012(I)
    GOD345(I)=COD345(I)
    GFREQ(I)=FREQ(I)
    WRITE(W,1004) I, GOD345(I), GOD012(I)
1004 FORMAT(3(2X,I6))
 513 CONTINUE
    COUNTG=COUNT
    GOTO 524

C  SCAN BEHAV ARRAY FOR 'BT' 'SBT' 'MS' & 'SMS'
514 COUNT=1
    C0=49
    C1=49
    C2=49
    C3=49
    C4=49
    C5=49
    DO 502 I=1,300
```

```
      COD345(I)=0
      COD012(I)=0
      FREQ(I)=0
  502 CONTINUE

      NELSES=LLN
      WRITE(W,1000) LLN
 1000 FORMAT(//3HLLN,5X,I4//)
       WRITE(W,1001) (BEHAV(LX), LX=1,LLN)
 1001 FORMAT(5HBEHAV,1X,(20I6),/(7X,(20I6)))
      WRITE(W,1002) (TIMVAL(LX), LX=1,LLN)
 1002 FORMAT(7HOTIMVAL,(20I6),/(7X,(20I6)))

  500 DO 501 I=1,NELSES
      IF(BEHAV(I),EQ,99) GOTO 516
      IB=BEHAV(I)
      IF(IB,NE,24,AND,IB,NE,25,AND,IB,NE,34,AND,IB,NE,35)
     ,GOTO 501
      C0=BEHAV(I)
      C1=BEHAV(I-1)
      IF(I,EQ,2) GOTO 526
      C2=BEHAV(I-2)
      IF(I,EQ,3) GOTO 526
      C3=BEHAV(I-3)
      IF(I,EQ,4) GOTO 526
      C4=BEHAV(I-4)
C.....(TRUNCATION TO FOUR ELEMENTS PRECEEDING A BITE)
      GOTO 526
      IF(I,EQ,5) GOTO 526
      C5=BEHAV(I-5)

C CONSTRUCT A FREQUENCY TABLE OF SEQUENCES
  526 NUM012=C0+100*(C1+100*(C2))
      NUM345=C3+100*(C4+100*(C5))
      DO 503 J=1,COUNT
      IF(NUM012,NE,COD012(J),OR,NUM345,NE,COD345(J)) GOTO 503
      FREQ(J)=FREQ(J)+1
      GOTO 504
  503 CONTINUE
      COD012(COUNT)=NUM012
      COD345(COUNT)=NUM345
      FREQ(COUNT)=1
  504 WRITE(W,1003) NELSES, COUNT, I, BEHAV(I), C5, C4, C3,
     ,C2, C1, C0, NUM345, NUM012, COD345(COUNT),
     ,COD012(COUNT), FREQ(COUNT)
 1003 FORMAT(4I5,6I3,2X,2(2I6,2X),2X,I3)
      COUNT=COUNT+1
  501 CONTINUE

C MULTI-SESSION STORAGE
  516 START=START+1
      COUNT=COUNT-1
      IF(START,EQ,1) GOTO 512
      DO 511 I=1,COUNT
      DO 510 J=1,COUNTG
      IF(COD012(I),EQ,0,AND,COD345(I),EQ,0) GOTO 511
      IF(COD012(I),NE,GOD012(J),OR,COD345(I),NE,GOD345(J))
     ,GOTO 510
      GFREQ(J)=GFREQ(J)+FREQ(I)
```

```
      GOTO 511
  510 CONTINUE
      COUNTG=COUNTG+1
      GOD012(COUNTG)=COD012(I)
      GOD345(COUNTG)=COD345(I)
      GFREQ(COUNTG)=FREQ(I)
      WRITE(W,1004) COUNTG, GOD345(COUNTG), GOD012(COUNTG)
  511 CONTINUE

C NOW DECODE FREQUENCY TABLE
  524 DO 505 I=1,COUNT
      C5=COD345(I)/10000
      X=C5*10000
      COD345(I)=COD345(I)-X
      C4=COD345(I)/100
      X=C4*100
      COD345(I)=COD345(I)-X
      C3=COD345(I)
      C2=COD012(I)/10000
      X=C2*10000
      COD012(I)=COD012(I)-X
      C1=COD012(I)/100
      X=C1*100
      COD012(I)=COD012(I)-X
      C0=COD012(I)
      DECODE(1,I)=C5
      DECODE(2,I)=C4
      DECODE(3,I)=C3
      DECODE(4,I)=C2
      DECODE(5,I)=C1
      DECODE(6,I)=C0
  505 CONTINUE

C WRITE FREQUENCY TABLE
      WRITE(W,508)
  508 FORMAT(30H1FREQUENCY OF ATTACK SEQUENCES)
  509 FORMAT(//30X,17HORDER OF ELEMENTS,9X,9HFREQUENCY,
     ,'   PERCENT'///)
      WRITE(W,509)
      DO 515 K=1,4
      DO 506 I=1,COUNT
      IF(DECODE(6,I),NE,TYPE(K)) GOTO 506
      C0=DECODE(6,I)
      C1=DECODE(5,I)
      C2=DECODE(4,I)
      C3=DECODE(3,I)
      C4=DECODE(2,I)
      C5=DECODE(1,I)
      WRITE(W,507)ELCODE(C5), ELCODE(C4), ELCODE(C3),
     ,ELCODE(C2), ELCODE(C1), ELCODE(C0), FREQ(I)
  507 FORMAT(30X,6A4,5X,I3,3X,F10.4)
  506 CONTINUE
  515 CONTINUE
      WRITE(W,528) COUNT
  528 FORMAT(49X,'TOTAL',I8)
      GOTO 522


C ANALYSE & DECODE MULTI-SESSION STORAGE
```

```
517 DO 518 I=1,COUNTG
    C5=GOD345(I)/10000
    X=C5*10000
    GOD345(I)=GOD345(I)-X
    C4=GOD345(I)/100
    X=C4*100
    GOD345(I)=GOD345(I)-X
    C3=GOD345(I)
    C2=GOD012(I)/10000
    X=C2*10000
    GOD012(I)=GOD012(I)-X
    C1=GOD012(I)/100
    X=C1*100
    GOD012(I)=GOD012(I)-X
    C0=GOD012(I)
    GECODE(1,I)=C5
    GECODE(2,I)=C4
    GECODE(3,I)=C3
    GECODE(4,I)=C2
    GECODE(5,I)=C1
    GECODE(6,I)=C0
    ITOT=ITOT+GFREQ(I)
518 CONTINUE

C WRITE MULTI-SESSION FREQUENCY TABLE
    WRITE(IZ,525)
525 FORMAT(30H1MULTI-SESSION FREQUENCY TABLE///)
    NOSESS=NOSESS-1
    WRITE(IZ,527) NOSESS
527 FORMAT(' NUMBER OF SESSIONS =',I4//'0','SESSION CODES:')
    DO 529 J=1,NOSESS
    WRITE(IZ,530) (SCODES(J,K), K=1,3)
530 FORMAT(' ',3A8)
529 CONTINUE
    WRITE(IZ,509)
    DO 519 K=1,4
    DO 520 I=1,COUNTG
    IF(GECODE(6,I),NE,TYPE(K)) GOTO 520
    C0=GECODE(6,I)
    C1=GECODE(5,I)
    C2=GECODE(4,I)
    C3=GECODE(3,I)
    C4=GECODE(2,I)
    C5=GECODE(1,I)
    PRCENT=GFREQ(I)*100./FLOAT(ITOT)
    WRITE(IZ,507) ELCODE(C5), ELCODE(C4), ELCODE(C3),
   ,ELCODE(C2), ELCODE(C1), ELCODE(C0), GFREQ(I), PRCENT
520 CONTINUE
519 CONTINUE
    WRITE(IZ,531) COUNTG, ITOT
531 FORMAT(14X,'NUMBER OF STRINGS =',I4,14X,'TOTAL =',I4)

    WRITE(IZ,622) INT
    WRITE(IZ,628)
628 FORMAT(2X,8HINTERVAL,2X,8HCUM FREQ,3X,7HPERCENT,6X,
   ,4HFREQ,3X,7HPERCENT/)
    JJ=1800/INT
    DO 630 SUB=1,JJ
    CMCENT=100.*(FLOAT(STOREC(SUB)))/STOREC(JJ)
```

```
      ELCENT=100.*(FLOAT(STOREL(SUB)))/STOREC(JJ)
      WRITE(IZ,629) SUB, STOREC(SUB), CMCENT, STOREL(SUB),
     ,ELCENT
  629 FORMAT(4X,I6,2(2X,I8,F10.4))
  630 CONTINUE
      CALL HISTO(STOREL,JJ)

      STOP



C.....BEHAVIOURAL INTERVAL/ TIME BLOCK ANALYSIS
  522 WRITE(W,622) INT
  622 FORMAT('1BEHAVIOURAL INTERVAL/TIME BLOCK ANALYSIS',15X,
     ,13HTIME BLOCK = ,I4,2X,7HSECONDS//)
      WRITE(W,623)
  623 FORMAT(6HCUMCTB,4X,1HL,9X,7HPERCENT,3X,6HORDINT/)
      WRITE(W,624)
  624 FORMAT(44X,1H5,13X,2H10,13X,2H15,13X,2H20,13X,2H25,13X,
     ,2H30/)

      L=0
      SECS=INT
      CUMCTB=0
      SUB=0

      DO 600 I=1,NELSES
  626 IF(TIMVAL(I)-SECS) 601,602,603
  601 L=L+1
      IF(I.NE.1) GOTO 608
      ORDINT(L)=TIMVAL(I)
      GOTO 600

  608 ORDINT(L)=TIMVAL(I)-TIMVAL(I-1)
      IF(I.EQ.NELSES) GOTO 619
      GOTO 600

  602 L=L+1
      IF(I.NE.1) GOTO 609
      ORDINT(L)=INT
      CALL ADD
      L=0
      SECS=SECS+INT
      GOTO 600

  609 ORDINT(L)=SECS-TIMVAL(I-1)
      CALL ADD
      L=0
      SECS=SECS+INT
      IF(I.EQ.NELSES.AND.SECS.GT.1800) GOTO 600
      IF(I.EQ.NELSES) GOTO 617
      GOTO 600

  603 L=L+1
      IF(I.NE.1) GOTO 610
      ORDINT(L)=INT
      CALL ADD
```

```
607 IF(TIMVAL(I)-(SECS+INT)) 604,605,606
604 ORDINT(L)=TIMVAL(I)-SECS
    SECS=SECS+INT
    GOTO 600

605 SECS=SECS+INT
    L=0
    GOTO 626

606 ORDINT(L)=INT
    CALL ADD
    SECS=SECS+INT
    IF(SECS.GE.1830) GOTO 600
    GOTO 607

610 ORDINT(L)=SECS-TIMVAL(I-1)
    CALL ADD
    L=1
614 IF(TIMVAL(I)-(SECS+INT)) 611,612,613
611 ORDINT(L)=TIMVAL(I)-SECS
    SECS=SECS+INT
    IF(I.EQ.NELSES) GOTO 619
    GOTO 600

612 ORDINT(L)=TIMVAL(I)-SECS
    CALL ADD
    L=0
    SECS=SECS+(INT*2)
    IF(I.EQ.NELSES) GOTO 621
    GOTO 600

613 ORDINT(L)=INT
    CALL ADD
    L=1
    SECS=SECS+INT
    IF(SECS.GE.1830) GOTO 600
    GOTO 614
619 L=L+1
615 ORDINT(L)=SECS-TIMVAL(I)
    CALL ADD
621 L=1
    SECS=SECS+INT
    IF(SECS.GE.1830) GOTO 600
    GOTO 618
617 L=L+1
618 ORDINT(L)=INT
    CALL ADD
    SECS=SECS+INT
    IF(SECS.GE.1830) GOTO 600
    GOTO 618
600 CONTINUE
    WRITE(W,631) SUB
631 FORMAT('0','SUB = ',I4)
    GOTO 132
    END


    SUBROUTINE ADD
```

```
      INTEGER  W, SUB, CUMCTB, ORDINT, STOREC, STOREL
      COMMON  CUMCTB, L, ORDINT(500), SUB, STOREC(60),
     ,STOREL(60), W
      CUMCTB=CUMCTB+L
      WRITE(W,625) CUMCTB, L, (ORDINT(K), K=1,L)
  625 FORMAT(I4,4X,I4,18X,30I3,/(30X,30I3))
      SUB=SUB+1
      IF(SUB.GT.60) RETURN
      STOREC(SUB)=STOREC(SUB)+CUMCTB
      STOREL(SUB)=STOREL(SUB)+L
      RETURN
      END


      SUBROUTINE HISTO(FQNUMB,N)
      INTEGER FQNUMB(500), W, CODE(125)
      DATA  W/2/,     CODE/125*1HX/
      LGEST=FQNUMB(1)
      DO 10 I=2,N
      IF(FQNUMB(I).GT.LGEST) LGEST=FQNUMB(I)
   10 CONTINUE
      ITRANS=0
      STAND=LGEST/125.
      IF(STAND.LE.1.) GOTO 40
      DO 20 I=1,N
      FQNUMB(I)=FQNUMB(I)/STAND
      ITRANS=1
   20 CONTINUE
   40 WRITE(W,5) ITRANS, LGEST
    5 FORMAT('1FREQUENCY HISTOGRAM',10X,'TRANSFORMATION = ',
     ,I1,5X,'LARGEST FREQUENCY = ',I4/)
      DO 30 I=1,N
      J=FQNUMB(I)
      WRITE(W,15) I, (CODE(K), K=1,J)
   15 FORMAT(' ',I4,2X,125A1)
   30 CONTINUE
      RETURN
      END
```

APPENDIX 12

COMPUTER PROGRAM TO ANALYSE FEEDING BEHAVIOUR OF FLATFISH - PART THREE

```
C ****************************************************************

C PROGRAM SELECTS STRINGS OF BEHAIOURAL ELEMENTS OF A
C SPECIFIED LENGTH, 'NEVENT', FROM SEQUENTIAL DATA.
C FREQUENCY TABLES OF STRINGS ARE CONSTRUCTED FOR EACH
C SEQUENCE AND FOR ALL SEQUENCES COMBINED. THE SHANNON
C INDEX OF INFORMATION IS CALCULATED FROM THE STRING
C FREQUENCIES.

C ****************************************************************

C   KEY TO VARIABLES
C   COUNT    A COUNTER, A SESSION VARIABLE
C   NUM012   6 DIGIT SEQUENCE CODE
C   NUM345   6 DIGIT SEQUENCE CODE
C   FREQ     1-D ARRAY, FREQUENCY OF SEQUENCES
C   COD012   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C   COD345   1-D ARRAY, STORAGE OF ALL 6 DIGIT NUMBERS
C   X        DECODE VARIABLE
C   C5-C4-C3-C2-C1-C0      6 VARIABLES STORING A SEQUENCE OF
C                               BEHAVIOURAL ELEMENTS
C
C   COUNTG   A COUNTER, A MULTI-SESSION VARIABLE
C   GFREQ    1-D ARRAY, MULTI-SESSION FREQUENCY OF SEQUENCES
C   GOD012   1-D ARRAY, MULTI-SESSION STORAGE OF ALL 6 DIGIT
C                                         NUMBERS
C
C   GOD345   1-D ARRAY, MULTI-SESSION STORAGE OF ALL 6 DIGIT
C                                         NUMBERS
C
C   START    DETECTOR VARIABLE
C   TBEHAV   THE NUMBER OF ELEMENTS EXHIBITED
C   ICOUNT   1-D ARRAY, THE SESSION ELEMENT FREQUENCY TABLE
C   JCOUNT   1-D ARRAY, THE MULTI-SESSION ELEMENT FREQUENCY
C                                          TABLE
C
C   ITOT     THE NUMBER OF STRING TYPES (SESSION)
C   JTOT     THE NUMBER OF STRING TYPES (MULTI-SESSION)
C   NOSESS   THE NUMBER OF SESSIONS
C   H        THE SHANNON INDEX OF AVERAGE UNCERTAINTY
C   NELSES   THE TOTAL NUMBER OF SESSION ELEMENTS
C   JELSES   THE TOTAL NUMBER OF MULTI-SESSION ELEMENTS

C   STATEMENT LABELS:    500-552

C ELEMENTS OF FEEDING BEHAVIOUR
C   TURN                  TN      01
C   SWIVEL TURN           SV      02
C   TURN AWAY             TA      03
C   LEAVE                 LV      04
C   PALPATION             PP      05
C   SWIM                  SW      06
C   DOWN                  DN      07
C   SKIM                  SK      08
C   SHUFFLE               SF      09
C   CREEP                 CR      10
C   FORWARD               FD      11
C   REVERSE               RV      12
C   PAUSE                 PS      13
```

```
C   SETTLE              ST      14
C   FLAP SWIM           FS      15
C   BURY                BY      16
C   FLAP                FP      17
C   UNDULATE            UN      18
C   BODY ARCH           AR      19
C   BODY RELAX          RX      20
C   ARC                 AC      21
C   HOVER               HV      22
C   LUNGE               LG      23
C   BITE                BT      24
C   MISS                MS      25
C   CHEW                CW      26
C   SPIT                SP      27
C   HEAD RAISE          HR      28
C   HEAD LOWER          HL      29
C   YAWN                YN      30
C   OMEGA JUMP          JP      31
C   SWIM-TURN           STN     32
C   SWIM-LUNGE          SLG     33
C   SWIM-BITE           SBT     34
C   SWIM-MISS           SMS     35
C   SWIM-TURN AWAY      STA     36
C   SWIM-LEAVE          SLV     37
C   SWIM-CHEW           SCW     38
C   REVERSE-CHEW        RCW     39
C   SWIM-YAWN           SYN     40
C   QUIVER              QV      41
C   CREEP-BODY ARCH     CAR     42
C   TURN-BODY ARCH      TAR     43
C   ARCH-REVERSE        ARV     44
C   ARCH-TURN AWAY      ATA     45
C   ARCH-HEAD LOWER     AHL     46
C   ARCH-HEAD RAISE     AHR     47
C   HEAD LIFT-CREEP     HCR     48
C   END OF SESSION      END     99
C   GAP IN DATA         GAP
```

```
C.....TYPE STATEMENTS
      REAL   SESCOD(3), SCODES(30,3)
      INTEGER  R, W, BEHAV(1200), ELCODE(49)
      INTEGER  ICOUNT(48), JCOUNT(48), X
      INTEGER  COUNT, NUM012, NUM345, C0, C1, C2, C3, C4, C5,
     ,COD012(3000), COD345(3000), FREQ(3000), COUNTS, START,
     ,GOD012(5000), GOD345(5000), GFREQ(5000)

      DATA   ELCODE(1),  ELCODE(2) / 3H TN  , 3H SV  /
      DATA   ELCODE(3),  ELCODE(4) / 3H TA  , 3H LV  /
      DATA   ELCODE(5),  ELCODE(6) / 3H PP  , 3H SW  /
      DATA   ELCODE(7),  ELCODE(8) / 3H DN  , 3H SK  /
      DATA   ELCODE(9),  ELCODE(10)/ 3H SF  , 3H CR  /
      DATA   ELCODE(11), ELCODE(12)/ 3H FD  , 3H RV  /
      DATA   ELCODE(13), ELCODE(14)/ 3H PS  , 3H ST  /
      DATA   ELCODE(15), ELCODE(16)/ 3H FS  , 3H BY  /
      DATA   ELCODE(17), ELCODE(18)/ 3H FP  , 3H UN  /
      DATA   ELCODE(19), ELCODE(20)/ 3H AR  , 3H RX  /
      DATA   ELCODE(21), ELCODE(22)/ 3H AC  , 3H HV  /
      DATA   ELCODE(23), ELCODE(24)/ 3H LG  , 3H BT  /
```

```
      DATA   ELCODE(25), ELCODE(26)/ 3H MS  , 3H CW  /
      DATA   ELCODE(27), ELCODE(28)/ 3H SP  , 3H HR  /
      DATA   ELCODE(29), ELCODE(30)/ 3H HL  , 3H YN  /
      DATA   ELCODE(31), ELCODE(32)/ 3H JP  , 3HSTN  /
      DATA   ELCODE(33), ELCODE(34)/ 3HSLG  , 3HSBT  /
      DATA   ELCODE(35), ELCODE(36)/ 3HSMS  , 3HSTA  /
      DATA   ELCODE(37), ELCODE(38)/ 3HSLV  , 3HSCW  /
      DATA   ELCODE(39), ELCODE(40)/ 3HRCW  , 3HSYN  /
      DATA   ELCODE(41), ELCODE(42)/ 3H QV  , 3HCAR  /
      DATA   ELCODE(43), ELCODE(44)/ 3HTAR  , 3HARV  /
      DATA   ELCODE(45), ELCODE(46)/ 3HATA  , 3HAHL  /
      DATA   ELCODE(47), ELCODE(48)/ 3HAHR  , 3HHCR  /
      DATA   ELCODE(49)/4H    /

      R=37
      NUMEL=48
      IZ=2


C.....SET THE NUMBER OF ELEMENTS IN A STRING, 'NEVENT'
      DO 520 NEVENT=1,5
      REWIND 37

C.....INITIALISE MULTI-SESSION STORGAE VARIABLES
  450 DO 521 I=1,5000
      GOD012(I)=0
  521 GOD345(I)=0
      DO 537 I=1,NUMEL
  537 JCOUNT(I)=0
      START=0
      NOSESS=0
      JTOT=0
      JELSES=0



C.....READ INPUT DATA

C READ & WRITE SESSION CODE
  132 READ(R,1)SESCOD(1),SESCOD(2),SESCOD(3)
      NOSESS=NOSESS+1
    1 FORMAT(/3A8)
      SCODES(NOSESS,1)=SESCOD(1)
      SCODES(NOSESS,2)=SESCOD(2)
      SCODES(NOSESS,3)=SESCOD(3)
C LOOK FOR 'ANALYSE' TO INITIATE MULTI-SESSION ANALYSIS
      IF(SESCOD(1).EQ.8H ANALYSE) GOTO 400
      WRITE(IZ,2) SESCOD(1),SESCOD(2),SESCOD(3)
    2 FORMAT(5H1    ,3A8,//)
      READ (R,3) LLN
    3 FORMAT(I4)
      READ(R,4) (BEHAV(LK), LK=1,LLN)
    4 FORMAT(40I2)

C.....CHECK TO SEE IF AN ATTACK OCCURS IN THE SESSION
      DO 539 I=1,LLN
```

```
      IF(BEHAV(I).EQ.24.OR.BEHAV(I).EQ.34) GOTO 540
      IF(BEHAV(I).EQ.25.OR.BEHAV(I).EQ.35) GOTO 540
  539 CONTINUE
      WRITE(IZ,547)
  547 FORMAT('0THE FISH DID NOT MAKE AN ATTACK IN THIS SESSION')
      GOTO 132

C.....SELECT APPROPRIATE PATHWAY
  540 IF(NEVENT-1) 200, 200, 250



C.....IF 'NEVENT' = ONE

C.....CONSTRUCT A FREQUENCY TABLE, 'ICOUNT', FOR THE
C     OCCURRENCE OF ELEMENTS IN THE SESSION
  200 DO 541 KL=1,NUMEL
      ICOUNT(KL)=0
  541 CONTINUE
C DOES DATA VALUE DENOTE END OF SESSION (CODE 99), IF NOT ADD
C  VALUE TO ELEMENT FREQUENCY ARRAY AND PROCEED TO NEXT VALUE
      DO 549 I=1,1200
      IF(BEHAV(I).EQ.99)GOTO 515
  549 ICOUNT(BEHAV(I))=ICOUNT(BEHAV(I))+1
  515 NELSES=I-1

C.....ADD 'ICOUNT' STORE INTO MULTI-SESSION STORE, 'JCOUNT'
      JELSES=JELSES+NELSES
      DO 506 LA=1,NUMEL
  506 JCOUNT(LA)=JCOUNT(LA)+ICOUNT(LA)

C.....CALCULATE THE NUMBER OF ELEMENTS EXHIBITED, 'TBEHAV'
  552 TBEHAV=FLOAT(NUMEL)
      DO 519 KM=1,NUMEL
      IF(ICOUNT(KM).NE.0) GOTO 519
      TBEHAV=TBEHAV-1.
  519 CONTINUE

C.....CALCULATE 'H' VALUES
      CONST=1/ALOG10(2.)
      HMAX=ALOG10(TBEHAV)*CONST
      CALL SHANON (ICOUNT, NUMEL, NELSES, H)

C.....PRINT 'H' VALUES AND FREQUENCY TABLE OF ELEMENTS
      WRITE(IZ,532)
  532 FORMAT(///'FREQUENCY TABLE OF ELEMENTS'//'ELEMENT',3X,
     ,'FREQUENCY')

      DO 533 I=1,NUMEL
      IF(ICOUNT(I).EQ.0) GOTO 533
      WRITE(IZ,534) ELCODE(I), ICOUNT(I)
  534 FORMAT(4X,A4,7X,I5)
  553 FORMAT(2X,'TOTAL',8X,I5,10X,'NUMBER OF ELEMENT TYPES ',
     ,'EXHIBITED =',F4.0)
  533 CONTINUE
      WRITE(IZ,553) NELSES, TBEHAV
      WRITE(IZ,535) NEVENT, HMAX, H
  535 FORMAT(///'NUMBER OF ELEMENTS IN STRING =',I2,5X,
     ,'HMAX =',F14.8,5X,'H =',F14.8)
```

```
      IF(SESCOD(1),EQ,8H ANALYSE) GOTO 520
      GOTO 132


C.....IF 'NEVENT' = TWO OR MORE

C.....ADD THE FIRST SESSION INTO THE MULTI-SESSION STORE
  250 GOTO 514
  512 DO 513 I=1,COUNT
      GOD012(I)=COD012(I)
      GOD345(I)=COD345(I)
      GFREQ(I)=FREQ(I)
  513 CONTINUE
      COUNTG=COUNT
      GOTO 524

C.....INITIALISE SESSION VARIABLES
  514 COUNT=1
      NELSES=LL'=1
      ITOT=0
      C0=49
      C1=49
      C2=49
      C3=49
      C4=49
      C5=49
      DO 502 I=1,3000
      COD345(I)=0
      COD012(I)=0
  502 FREQ(I)=0

C.....SELECT THE APPROPRIATE PATHWAY
  500 DO 501 I=NEVENT,NELSES
      GOTO (200, 542, 543, 544, 545, 546), NEVENT
  546 C5=BEHAV(I=5)
  545 C4=BEHAV(I=4)
  544 C3=BEHAV(I=3)
  543 C2=BEHAV(I=2)
  542 C1=BEHAV(I=1)
      C0=BEHAV(I)

C.....CONSTRUCT A FREQUENCY TABLE OF SEQUENCES
  526 NUM012=C0+100*(C1+100*(C2))
      NUM345=C3+100*(C4+100*(C5))
      DO 503 J=1,COUNT
      IF(NUM012,NE,COD012(J),OR,NUM345,NE,COD345(J)) GOTO 503
      FREQ(J)=FREQ(J)+1
      GOTO 501
  503 CONTINUE
      COD012(COUNT)=NUM012
      COD345(COUNT)=NUM345
      FREQ(COUNT)=1
      COUNT=COUNT+1
  501 CONTINUE
      COUNT=COUNT-1

C.....CALCULATE 'ITOT' AND 'JTOT'
      DO 528 I=1,COUNT
```

```
  528 ITOT=ITOT+FREQ(I)
      JTOT=JTOT+ITOT

C.....MULTI-SESSION STORAGE
  516 START=START+1
      IF(START.EQ.1) GOTO 512
      DO 511 I=1,COUNT
      DO 510 J=1,COUNTG
      IF(COD012(I).EQ.0.AND.COD345(I).EQ.0) GOTO 511
      IF(COD012(I).NE.GOD012(J).OR.
                     COD345(I).NE.GOD345(J)) GOTO 510
     ,
      GFREQ(J)=GFREQ(J)+FREQ(I)
      GOTO 511
  510 CONTINUE
      COUNTG=COUNTG+1
      GOD012(COUNTG)=COD012(I)
      GOD345(COUNTG)=COD345(I)
      GFREQ(COUNTG)=FREQ(I)
  511 CONTINUE

C.....DECODE AND PRINT SESSION FREQUENCY TABLE
  524 WRITE(IZ,508)
  508 FORMAT(///'FREQUENCY OF SEQUENCES')
  509 FORMAT(//8X,'ORDER OF ELEMENTS',5X,'FREQUENCY',3X,
     ,'PERCENT',25X,'ORDER OF ELEMENTS',5X,'FREQUENCY',
     ,3X,'PERCENT'/)
      WRITE(IZ,509)
      NBSTR=0

      DO 505 I=1,COUNT
      C5=COD345(I)/10000
      X=C5*10000
      COD345(I)=COD345(I)-X
      C4=COD345(I)/100
      X=C4*100
      COD345(I)=COD345(I)-X
      C3=COD345(I)
      C2=COD012(I)/10000
      X=C2*10000
      COD012(I)=COD012(I)-X
      C1=COD012(I)/100
      X=C1*100
      COD012(I)=COD012(I)-X
      C0=COD012(I)
      IF(C0.EQ.0) GOTO 505
      PRCENT=FLOAT(FREQ(I))*100./FLOAT(ITOT)
      NBSTR=NBSTR+1
      I2=(I/2)*2
      IF(I.EQ.I2) GOTO 523
      WRITE(IZ,507) ELCODE(C5), ELCODE(C4), ELCODE(C3),
     ,ELCODE(C2), ELCODE(C1), ELCODE(C0), FREQ(I), PRCENT
  507 FORMAT(1X,6A4,5X,I5,4X,F10.4)
      GOTO 505
  523 WRITE(IZ,522) ELCODE(C5), ELCODE(C4), ELCODE(C3),
     ,ELCODE(C2), ELCODE(C1), ELCODE(C0), FREQ(I), PRCENT
  522 FORMAT('+',66X,6A4,5X,I5,4X,F10.4)
  505 CONTINUE
      WRITE(IZ,531) NBSTR, ITOT
```

```
C.....CALCULATE 'H' VALUES
      CALL SHANON (FREQ, COUNT, ITOT, H)

C.....PRINT 'H' VALUES
      WRITE(IZ,548) NEVENT, H
  548 FORMAT(///'NUMBER OF ELEMENTS IN STRING =',I2,5X,
     ,'H =',F14.8)
      GOTO 132



C.....IF 'SESCOD(1)' = 'ANALYSE'.....
  400 WRITE(IZ,525)
  525 FORMAT('1MULTI-SESSION FREQUENCY TABLE OF SEQUENCES'///)
      NOSESS=NOSESS-1
      WRITE(IZ,527) NOSESS
  527 FORMAT(' ','NUMBER OF SESSIONS =',I4//'0','SESSION CODES:')
      DO 529 J=1,NOSESS
      WRITE(IZ,530) (SCODES(J,K), K=1,3)
  530 FORMAT(' ',3A8)
  529 CONTINUE

C.....SELECT APPROPRIATE PATHWAY
      IF(NEVENT-1) 551, 551, 517
  551 DO 536 I=1,NUMEL
  536 ICOUNT(I)=JCOUNT(I)
      NELSES=JELSES
      GOTO 552

C.....DECODE AND PRINT MULTI-SESSION FREQUENCY TABLE
  517 WRITE(IZ,509)
      DO 518 I=1,COUNTG
      C5=GOD345(I)/10000
      X=C5*10000
      GOD345(I)=GOD345(I)-X
      C4=GOD345(I)/100
      X=C4*100
      GOD345(I)=GOD345(I)-X
      C3=GOD345(I)
      C2=GOD012(I)/10000
      X=C2*10000
      GOD012(I)=GOD012(I)-X
      C1=GOD012(I)/100
      X=C1*100
      GOD012(I)=GOD012(I)-X
      C0=GOD012(I)
      IF(C0.EQ.0) GOTO 518
      PRCENT=FLOAT(GFREQ(I))*100./FLOAT(JTOT)
      I2=(I/2)*2
      IF(I.EQ.I2) GOTO 550
      WRITE(IZ,507) ELCODE(C5), ELCODE(C4), ELCODE(C3),
     ,ELCODE(C2), ELCODE(C1), ELCODE(C0), GFREQ(I), PRCENT
      GOTO 518
  550 WRITE(IZ,522) (LCODE(C5), ELCODE(C4), ELCODE(C3),
     ,ELCODE(C2), ELCODE(C1), ELCODE(C0), GFREQ(I), PRCENT
  518 CONTINUE
      WRITE(IZ,531) JOUNTG, JTOT
  531 FORMAT(2X,'NUMBER OF STRINGS =',I4,14X,'TOTAL =',I4)
```

```
C.....CALCULATE 'H' VALUE
      CALL SHANON (GFREQ, COUNTG, JTOT, H)

C.....PRINT 'H' VALUE
      WRITE(12,948) NEVENT, H

  520 CONTINUE
      STOP
      END


      SUBROUTINE SHANON (ISTORE, NUM, N, H)
C.....SUBROUTINE CALCULATES THE SHANNON INFORMATION INDEX FOR
C     A FREQUENCY DISTRIBUTION.
C     LOGS ARE TO THE BASE 2
      DIMENSION  ISTORE(3000)
      A=0.0
C     'CONST' IS A CONVERSION FROM LOG10 TO LOG2
      CONST=1/ALOG10(2.0)
      DO 5 I=1,NUM
      IF(ISTORE(I).EQ.0) GOTO 5
      STORE=FLOAT(ISTORE(I))
      A=A+STORE*(ALOG10(STORE)*CONST)
    5 CONTINUE
      B=FLOAT(N)
      H=(ALOG10(B)*CONST)- (A/N)
      RETURN
      END
```

ELEMENTS OF FEEDING BEHAVIOUR & THEIR CODE LETTERS

ARC	AC
BODY-ARCH	AR
BITE	BT
BURY	BY
CREEP	CR
CHEW	CW
DOWN	DN
FORWARD	FD
FLAP	FP
FLAP-SWIM	FS
HEAD-LOWER	HL
HEAD-RAISE	HR
HOVER	HV
OMEGA-JUMP	JP
LUNGE	LG
LEAVE	LV
MISS	MS
PALPATION	PP
PAUSE	PS
QUIVER	QV
REVERSE	RV
BODY-RELAX	RX
SHUFFLE	SF
SKIM	SK
SPIT	SP
SETTLE	ST
SWIVEL-TURN	SV
SWIM	SW
TURN AWAY	TA
TURN	TN
UNDULATE	UN
YAWN	YN
ARCH-HEAD LOWER	AHL
ARCH-HEAD RAISE	AHR
ARCH-REVERSE	ARV
ARCH-TURNAWAY	ATA
CREEP-BODY ARCH	CAR
HEAR RAISE CREEP	HCR
REVERSE-CHEW	RCW
SWIM-BITE	SBT
SWIM-CHEW	SCW
SWIM-LUNGE	SLG
SWIM-LEAVE	SLV
SWIM-MISS	SMS
SWIM-TURN AWAY	STA
SWIM-TURN	STN
SWIM-YAWN	SYN
TURN-BODY ARCH	TAR