

THE INTERACTION OF FACTORS INFLUENCING  
THE PREDATORY BEHAVIOUR OF  
THE PIKE *Esox lucius* .L.

A thesis submitted for the degree of  
Doctor of Philosophy

by

Ian. S. Clarke

Department of Zoology  
University of Leicester  
1986

UMI Number: U001046

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.

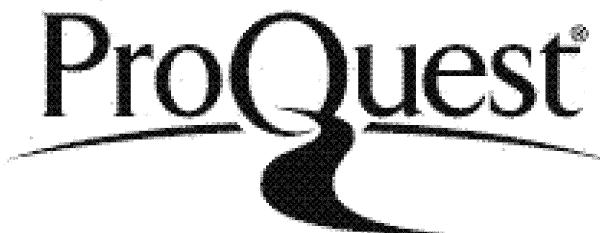


UMI U001046

Published by ProQuest LLC 2015. Copyright in the Dissertation held by the Author.

Microform Edition © ProQuest LLC.

All rights reserved. This work is protected against unauthorized copying under Title 17, United States Code.



ProQuest LLC  
789 East Eisenhower Parkway  
P.O. Box 1346  
Ann Arbor, MI 48106-1346



x750236786

## **ABSTRACT**

The work submitted in this thesis describes three investigations of the relationship between stimuli, the pike and the pike's inclination to feed. Consideration is given to the importance of relating internal and external factors to the causation of behaviour.

The effects of individual pike and the time lapsed after feeding on predatory behaviour are firstly assessed. Use of multivariate analysis determined key behaviours in the repertoire of pike that could be successfully employed in analysing prey-capture sequences.

The modifying influence of hunger, as categorised by stomach content, on prey capture sequences is presented and discriminant function analysis is used as a method of describing differences in predatory behaviour. A simple treatment of bout criteria is also given.

The interaction of the components of visual stimuli and its influence on predatory response revealed that particular movements and shape of a stimulus altered the attack behaviour of pike. The relative strength of a visual cue, for example, how "fish-like" a stimulus is, has dependence on how inclined an individual is to feed. A view of how these factors influence the behaviour of pike in a wider context is expressed.

DEDICATION

TO ALL THE FAMILY

Hic etiam Latio praenomine, cultor  
Stagnorum querulis vis infestissima ramis  
Lucius, obscuras ulva caenoque lacunas  
Obsidet: hic nullos mensarum lectus ad usus,  
Fervet fumosis olido nidore popinis.

Here also, under a name ridiculous in Latium,  
an inhabitant of the ponds, a most hostile  
power to the croaking frogs, the Pike haunts  
the pools dark with weed and mud: this fish,  
chosen for no uses of the table, steams with  
a bad smell in the smoking cookshops.

AUSONIUS. ID. X. 122.

## ACKNOWLEDGEMENTS

My thanks to all who have supported and encouraged me in this study. My gratitude to Dr. P.J.B.Hart for his supervision of this project. To Mr. S.Ison for his technical services and getting his feet wet, to Miss A.Hair and Mr. N.E.Street for making the laboratory work and fishing trips enjoyable and to the Zoology Department of Leicester University for support. I am indebted to Professor P. Freeman for help with statistics and to Mr. Howard Neale for all things electronic. Finally, to Ann for putting up with me. This study was funded by S.E.R.C Research Grant Number. 81312874.

## CONTENTS

<u>SECTION</u>	<u>TITLE</u>	<u>PAGE</u>
i	Abstract	
ii	Dedication	
iii	Acknowledgements	
iv	Contents	
v	Figures	
vi	Tables	
1	INTRODUCTION	1
2	EXPERIMENT ONE. A first investigation of the effects of motivation on the response of pike to a prey stimulus.	12
2.1	Introduction	12
2.2	Basic methods	14
2.3	Results	18
2.4	Discussion	24
3	EXPERIMENT TWO. The influence of hunger on the predatory behaviour of pike.	28
3.1	Introduction	28
3.2	Methods	30
3.2.1	Estimation of stomach content	30
3.3	Analysis of trials	33

3.3.1	Analysis of prey capture sequences	33
3.3.1.1	Stationary or "hanging" positions	33
3.3.1.2	Movements	34
3.3.1.3	Prey capture events	34
3.4	Results	34
3.4.1	Multivariate analysis	35
3.4.1.1	Results from discriminant function analysis	40
3.4.2	Behaviour and bout analysis	49
3.5	Discussion	60

4	EXPERIMENT THREE. An investigation of effective stimuli and their interaction with hunger states in the attack response of pike.	67
---	---	----

4.1	Introduction	67
4.2	Methods	71
4.2.1	Background	71
4.2.2	Considerations for the method	72
4.2.3	Basic methods	74
4.2.3.1	Apparatus for presenting stimuli	74
4.2.3.2	Stimuli presented	83
4.2.3.3	Method 1	85
4.2.3.4	Analysis of behavioural sequences	86
4.2.3.5	Method 2	87
4.3	Results	89
4.3.1	The effects of replication on the attack response of pike to four shadow treatments	89

4.3.2	The effects of movement and hunger on the attack response of pike towards different prey stimuli	93
4.3.2.1	Bar shadow stimuli	95
4.3.2.2	Fish shadow stimuli	106
4.3.2.3	Three dimensional stimuli	115
4.3.3	The effects of form and hunger on the attack responses of pike towards prey stimuli	120
4.3.3.1	The effect of form on the attack response of pike at an intermediate hunger state	123
4.3.3.2	The effect of form on the attack response of pike with increased hunger	129
4.3.4	Representation of attack responses by use of discriminant function analysis	133
4.3.5	Contrast measurements for stimuli presented	146
4.4	Discussion	148
5	GENERAL DISCUSSION	157

## APPENDIX

### REFERENCES

## FIGURES

<u>NUMBER</u>	<u>TITLE</u>	<u>PAGE</u>
1.	The relationship between internal and external factors and their influence on behavioural tendency.	5
2.	Arrangement of the aquarium for presentation of a live minnow stimulus in experiment 1.	15
3.	Fin coordination patterns for pike.	17
4.	Pectenoral fin beat rates expressed with the time in hours from last feed.	23
5.	Rates of eye movement expressed with the time in hours from last feed.	23
6.	Tank arrangement for filming prey capture sequences in experiment 2.	31
7.	Three dimensional plot of discriminant functions separating the responses of pike to a minnow school (stomach content of pike = 0 - 5g).	44
8.	Three dimensional plot of discriminant functions separating the responses of pike to a minnow school (stomach content of pike = 6 - 10g).	45
9.	Three dimensional plot of discriminant functions separating the responses of pike to a minnow school (stomach content of pike = 11 - 15g).	46
10.	Three dimensional plot of discriminant functions separating the responses of pike to a minnow school (stomach content of pike = 16 - 20g).	47
11.	Area map for the responses of pike in experiment 2 from the first two canonical discriminant functions for all trials.	48
12.	Frequencies of the behaviours Point, Approach, Stop, Strike and Capture at the four categories of hunger.	51
13.	Log survivorship curve with fitted regression line for the behaviour Point.	52

14.	Log survivorship curve with fitted regression line for the behaviour Attentive.	54
15.	Percentage frequency distributions for the durations of the behaviour Point for pike with stomach contents of 0 - 5g and 6 - 10g.	58
16.	Percentage frequency distributions for the durations of the behaviour Point for pike with stomach contents of 11 - 15g and 16 - 20g.	59
17.	The time course for overall satiation; A possible explanation for feeding behaviour exhibited in experiment 2.	65
18.	Diagram of the apparatus that produced moving stimuli in experiment 3.	77
19.	Tank arrangements for the presentation of stimuli, viewed from above and the side.	78
20.	Stimulus box used for presentation of a three dimensional stimulus and fish shaped shadow with a sinusodal-like component in its movement.	80
21.	Design of the electro-magnet box which created sinusoidal-like movement in stimuli that moved horizontally.	81
22.	Representations of how the stimuli appeared on the screens of tanks in experiment 3.	84
23.	Regression plot demonstrating the reduced responses of pike towards stimuli presented in successive trials.	92
24.	Frequency histograms for behaviours in the responses of pike to bar shadow stimuli for two hunger states and three movements.	100
25.	Times for descriptive parameters (TIN, TPT and TOPT for the responses of pike at two levels of hunger towards bar shadow stimuli with three movements.	104
26.	Times for descriptive parameters (TSC and TFIN) for the responses of pike at two levels of hunger towards bar shadow stimuli with three movements.	105
27.	Frequency histograms for the behaviours AT, IN, O and SN in the responses of pike at two hunger levels towards fish shadows with six types of movement.	108

28. Frequency histograms for the behaviours AP and PT in the responses of pike at two levels of hunger towards fish shadows with six types of movement. 109
29. Frequency histograms for the behaviour Strike and the total number of behaviours in the response of pike at two levels of hunger to fish shadow stimuli with six types of movement. 110
30. Times for descriptive parameters (TIN, TPT and TOPT) for pike at two levels of hunger responding to fish shadow stimuli with six types of movement. 113
31. Times for descriptive parameters (TSC and TFIN) for pike at two levels of hunger responding to fish shadow stimuli with six types of movement. 114
32. Frequency histograms for the behaviours (AT, IN, O and SN) in the response of pike at two levels of hunger to three dimensional fish stimuli with three types of movement. 117
33. Frequency histograms for the behaviours (AP and PT) in the response of pike at two levels of hunger towards three dimensional fish stimuli with three types of movement. 118
34. Frequency histograms for the behaviour Strike and the total number of behaviours exhibited by pike in response to three-dimensional fish stimuli with three types of movement. 119
35. Times for descriptive parameters (TIN, TPT and TOPT) for pike at two levels of hunger in response to three-dimensional fish stimuli with three types of movement. 121
36. Times for descriptive parameters (TSC and TFIN) for pike at two levels of hunger in response to three-dimensional stimuli with three types of movement. 122
37. Frequency histograms of the behaviours AT, IN, O and SN in the response of pike at an intermediate level of hunger towards stimuli with differing form and movement. 126
38. Frequency histograms of the behaviours AP and PT for the response of pike at an intermediate hunger level in response to stimuli with differing form and movement. 127
39. Frequency histograms for the behaviour Strike and the total number of behaviours in the response of pike at an intermediate level of

hunger in response to stimuli with differing form and movement.	128
40. Times for descriptive parameters (TIN, TPT and TOPT) in the response of pike at an intermediate level of hunger towards stimuli with differing form and movement.	131
41. Times for descriptive parameters (TSC and TFIN) in the response of pike at an intermediate hunger level to stimuli with differing form and movement.	131
42. Frequency histograms for the behaviours AT, IN, O and SN in the responses of hungry pike to stimuli with differing form and movement.	135
43. Frequency histograms for the behaviours AP and PT in the response of hungry pike to stimuli with differing form and movement.	136
44. Frequency histograms for the behaviour Strike and the total number of behaviours in the responses of pike to stimuli with differing form and movement.	137
45. Times for descriptive parameters (TIN, TPT and TOPT) for the response of hungry pike to stimuli with differing form and movement.	139
46. Times for descriptive parameters (TSC and TFIN) for the response of hungry pike to stimuli with differing form and movement.	140
47. Three dimensional plot for discriminant functions separating the responses of pike to bar shadow stimuli.	142
48. Three dimensional plot for discriminant functions separating the responses of pike to fish shadow stimuli.	143
49. Three dimensional plot for discriminant functions separating the responses of pike to three-dimensional stimuli.	144
50. The model of Wirtshafter and Davis (1977) that shows the influences on response to a feeding stimulus.	160
51. A model to show how a pike's response to a feeding stimulus may be modified.	161
52. Model proposed by McFarland and Sibly (1975) to predict motivational tendencies.	162
53. Hypothetical isocline of cue strength and hunger and its effect on the amount of time a pike spends pointing at a stimulus (TPT).	165

54. Hypothetical isocline of cue strength and hunger and its effect on the time when a pike finally becomes disinterested in a stimulus (TFIN). 166
55. Hypothetical isocline of cue strength and hunger and its effect on the amount of time a pike spends looking at the presentation screen (TSC). 167

## TABLES

<u>NUMBER</u>	<u>TITLE</u>	<u>PAGE</u>
1.	Possible factors influencing a pike's tendency to feed.	5
2.	Glossary of response variables in Experiment One.	20
3.	Multivariate tests of significance for effects in the results of Experiment One.	21
4.	Univariate F-tests for the effects of time on the response variables in Experiment One.	21
5.	The effect of time from last feed on pectoral fin beats.	22
6.	The effect of time from last feed on eye movements.	22
7.	Multivariate tests of significance for effects in the results of Experiment Two.	37
8.	Glossary of abbreviations for behaviours in the analysis of Experiment Two.	37
9.	Univariate F-tests for the effect of hunger on behaviours in Experiment Two.	38
10.	Univariate F-tests for the effect of pike on behaviours in Experiment Two.	39
11.	Selected behaviours for discrimination of prey capture responses at four categories of hunger.	41
12.	Canonical discriminant functions assigned to pike at four categories of hunger.	42
13.	Frequencies of selected behaviours for pike predating on a school of 3g minnows at four categories of hunger.	50
14.	Frequencies of bouts for four different categories of hunger.	55
15.	Mean durations of bouts for four different categories of hunger.	55
16.	Mean times to the start of the first bout at four categories of hunger.	57
17.	Mean handling times of 3g prey by pike at four categories of hunger.	57

18.	Possible combinations of stimulus treatments in Experiment Three.	88
19.	Numbers of behaviours exhibited in each of five trials for the response of five pike to four different shadow treatments.	90
20.	The effect of replication on the responses of pike to four shadow treatments. Regression coefficients are given for the log number of behaviours exhibited in each trial.	90
21.	Selected behaviours from stepwise discriminant function analysis for the classification attack responses of pike towards different stimuli.	94
22.	Response variables in the attack sequence of pike at two levels of hunger towards a bar shadow stimulus with three types of movement.	96
23.	Times for descriptive parameters for the response of pike at two hunger levels to bar shadow stimuli with three types of movement.	103
24.	Frequencies of behaviours performed by pike at two levels of hunger in response to fish shadow stimuli with six types of movement.	107
25.	Times for descriptive parameters for the response of pike at two levels of hunger to fish shadow stimuli with six types of movement.	1123
26.	Frequencies of behaviours displayed by pike at two levels of hunger to three-dimensional stimuli with three types of movement.	116
27.	Times for descriptive parameters for the response of pike at two levels of hunger to three-dimensional stimuli with three types of movement.	120
28.	Behaviours exhibited by pike at an intermediate level of hunger in response to stimuli with differing form and movement.	125
29.	Times for descriptive parameters for the response of pike at an intermediate level of hunger to stimuli with differing form and movement.	130
30.	Behaviours performed by hungry pike in	

response to stimuli with differing form and movement.	132
31. Significance table for changes in the frequency of behaviours due to the effects of stimulus form.	134
32. Times for descriptive parameters for the response of hungry pike to stimuli with differing form and movement.	138
33. Canonical discriminant functions assigned to the responses of pike to different stimulus treatments.	145
34. Mean contrast values for stimuli.	147

## 1 INTRODUCTION

Most studies of foraging behaviour are concerned with the ways in which animals select and eat their food and the rules that may determine this behaviour (Krebs et al 1983).

However it has become increasingly clear that animals show variation from the predictions of present theory and that foraging behaviour and the decisions an animal has to make cannot be considered in terms of function alone. Although this idea is not new, it is nevertheless a fundamental assumption in the course of this study. For example, optimality theory from the predictions of the Marginal Value Theorem (Charnov 1976) goes some way to demonstrating what criteria animals should use when foraging, but recently it has been suggested that the theory should consider the presence of factors that are immediately causal to the behaviour observed (McFarland and Houston 1981). Indeed, the internal state of an animal strongly influences whether it should feed or not and as a consequence the criteria often postulated by the ethological observer may be subject to change. Hunger is one factor of the internal state and may influence predictions for an animal's optimal diet (Richards 1983).

Having said that when an animal forages for food its behaviour may be influenced by hunger and prey characteristics or any combination of physiological fluctuations and environmental variables, this study attempts

to recognise such influences by evaluating the role of sensory cues in the feeding behaviour of the pike, *Esox lucius*. In particular observations were confined to those aspects of a pike's feeding tendency, where feeding tendency may be defined as the result of a trade-off between internal hunger and strength of feeding stimuli (McFarland and Houston 1981).

*Esox lucius* has a broad geographical distribution and is resident in Great Britain, Europe, Northern Asia and North America. It is found typically in lowland rivers and lakes especially where submerged and marginal vegetation is common. The pike is a solitary, opportunistic hunter (Nursall 1973) taking a wide range of food in its diet, predominantly fish, but ranging from invertebrates when young to many species of fish, small mammals, waterfowl and other aquatic animals when mature (Day 1880, Frost 1954, Lagler 1956, Johnson 1969, Mann 1982). As such the pike is a top carnivore in the aquatic ecosystem food chain.

The feeding ecology of the pike has been well documented by numerous workers with interest confined mainly to its diet (Kendal 1917, McNamara 1937, Frost 1954, Copland 1956, Buss 1961, Crossman 1962, Banks 1965, Lawler 1965, Willemsen 1967, Johnson 1969, Toner 1969, Mann 1973, Bialokoz 1979, Diana 1979) and its preferences or prey selection (Hoogland et al 1957, Popova 1967, Beyerle 1968, Mauck 1971, Coble 1973, Nursall 1973, Reist 1980, Mann 1982). Behavioural studies have focused principally on the hunting and strike tactics of the pike (Hoogland et al 1957, Baerends 1957, Ivanova 1969,

Nursall 1973, Neill 1974, Christiansen 1976, Kashin 1978, Webb 1980, Hart and Conellan 1984). Little work however has studied the proximate level of behaviour that influences prey-capture. Factors important at the proximate level may be those concerned with prey recognition and the internal homeostatic requirements of the pike in time (Curio 1976).

Perception of prey is thought to be the basic process underlying any predatory behaviour (Hinde 1970). A predator receives stimuli as it encounters prey which may initiate processes that lead to prey-capture. These stimuli may be a change in part of the animal's environment, for example, a change in contrast within the visual field, or they may be confined to an object that produces an observable response, perhaps some characteristic of the prey themselves. The requirement for recognition of prey is that the stimuli a predator receives must be readily discernable from those that elicit other types of behaviour (Hinde 1970). For example, any moving object smaller or equal in size to a predator may constitute a feeding stimulus, and any larger, a defensive stimulus (Protasov 1968).

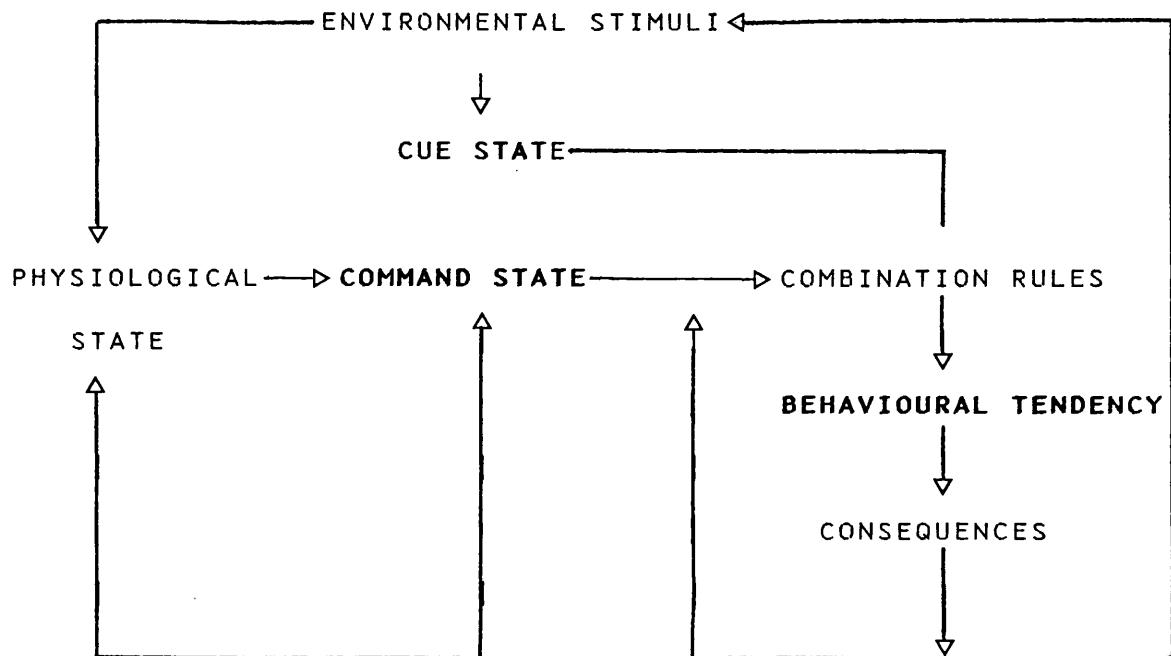
In fish, several external characteristics describe possible food items. These may be size, shape, colour, brightness, velocity and type of movement (Protasov 1968). The reaction to these, however, depends on the animal's motivational state. Motivation as a term may be considered in the above context to be a function of all possible internal variables that lead to an inclination to feed depending on its value.

The framework for such a consideration of feeding behaviour has been demonstrated by Colgan (1973) with work on the pumpkinseed sunfish, *Lepomis gibbosus*. In an analysis of possible factors affecting the motivation of the sunfish, it was found that variables of the fish's homeostatic system such as food deprivation and satiation, systemic need and gastric volume, influenced the preference and selectivity of the fish towards prey items. McFarland and Houston (1981) describe such combinations of factors in terms of external and internal states (Figure 1). They envisage a system by which an animal carries out a particular activity influenced by complex interactions between its internal state and stimuli from its environment. At any given time the overall state of an animal can be plotted on axes that represent independent physiological variables or independent but behaviourally relevant aspects of the environment. The resulting coordinates are part of a motivational space and their position from an optimum origin determines the behaviour performed by an animal. For a concise overview of this theory see Huntingford (1984).

Interpreting the ideas of McFarland and Houston, external stimuli that act on an animal to produce a state of arousal is called a cue state. This represents a point in a multidimensional cue space (coordinates in the motivational space) derived from axes corresponding to independent features of the external environment. These features act on an animal and contribute to an overall causal factor state which influences subsequent behaviour. Similarly they propose a command state which is due to physiological change

**FIGURE 1**

RELATIONSHIP BETWEEN INTERNAL AND EXTERNAL FACTORS AND THEIR INFLUENCE ON BEHAVIOURAL TENDENCY (McFarland & Houston 1981)



**TABLE 1**

POSSIBLE FACTORS INFLUENCING A PIKE'S TENDENCY TO FEED

<u>INTERNAL FACTORS</u>	<u>EXTERNAL FACTORS</u>	<u>PREY CHARACTERISTICS</u>
STOMACH CONTENT	TIME OF DAY	PHYSICAL APPEARANCE
DEPRIVATION TIME	TEMPERATURE	SHAPE
SYSTEMIC NEED	LIGHT INTENSITY	SIZE
HORMONES	WATER TURBIDITY	MOVEMENT
PREVIOUS EXPERIENCE		COLOUR
		ARMAMENT
		NOVELTY/ODDITY
		RELATIVE ABUNDANCE

from an animal's normal or acclimatized state. A physiological change produces motivating variables, or commands, for the mechanisms controlling behaviour. The cue and command states may combine additively or multiplicatively to give an overall feeding behaviour. The system may be considered in mechanical terms as one of input-output with the internal and external variables producing the energy to the system in order to do work. The amount of work done (feeding in this consideration) is the value of the combination of the internal and external variables. It is useful therefore to consider pike predatory behaviour in such a framework.

Factors of the cue state that affect pike predatory behaviour can be confined to two categories - those that are strictly environmental conditions and those that are direct features of the prey themselves. Factors of the command state are largely physiological variables not being specifically restricted to hunger (Dill 1983) but can include conditioned learning effects such as a pike's experience with prey.

(Table 1)

Mauck and Coble (1971) in selective feeding experiments with pike recognised that prey preference could be affected by innate inclination (now not generally accepted, see Hinde 1970 for a review), satiation and conditioning, also appearance, behaviour, relative abundance, size distribution and armament of prey. Coble (1973) surmised that prey perception could include differences in prey behaviour, manner of movements or physical appearance, for example,

form, colour and contrast (white against natural colour). His results indicated that shape and colour did not influence prey selection, nor did there appear to be any modification as a result of pike conditioning. It was also concluded that water turbidity had no effect on prey vulnerability.

The above findings have implications on the possible mechanisms by which prey are detected by pike. Coble (1973) asserted that visual stimuli are most important in prey recognition, as do Solman (1945) and Hoogland et al (1957).

Detection by the lateral line was considered as most prevalent by Wunder (1927) and Nikolsky (1963) who noted that blind pike could still successfully capture prey. The third mechanism, olfaction, has only been regarded as important by McNamara (1937) who stated that pike homed in on prey by this sense in still water. Christiansen (1976) concluded that both perception of prey by vision and the lateral line system were important and dependent on the physical properties of the water a pike inhabited.

Accepting the perception mechanisms concluded by Christiansen, a further observation from Coble's work was that diseased prey were more vulnerable. A possible explanation for this occurrence is that such fish are more easily caught or they move in such a way that pike pursue these instead of other fish.

The fact that movement may be important in the recognition of prey has been studied in pike. Meesters (1940) demonstrated that a moving dead-bait roach, *Rutilus rutilus*, produced a

markedly stronger predatory response in comparison to a motionless one, though a pike would strike at both baits. He also established that the orientation of the prey fish was important. Baerends (1957) stated that prey must be moving, whereas Nursall (1973), observed that prey could be swimming or motionless. Christiansen (1976) in the only quantitative work on this subject, found that rapidly swimming and abnormally moving fish had a greater probability of initiating the predatory act than fish that moved slowly and uniformly, and that stationary prey escaped predation in some cases.

There is evidently contradiction in the literature as regards sensory cues that elicit the prey-capture response in pike and although little is quantitative, it is generally agreed that moving prey strongly influences the predatory behaviour. Colour does not seem to be a major visual cue in terms of increasing pike selectivity or prey vulnerability, but, prey colour does affect the camouflage of prey and silvery sides may be difficult to detect as they match the brightness of the background (Denton 1965). Protasov (1968) quotes work of Herter (1959) in that pike appear to be responsive to shiny and to black and white foil strips. This source can only be traced to Herter (1929) with work on the eastern mudminnow, *Umbra pygmaea*, which is of the family Esocidae, but not a close relative of the pike, and therefore the significance of his observations must be in doubt.

Although the possible components of visual stimuli that elicit the prey-capture response has been demonstrated, none

has considered the influence of the internal or command state. The effect of the internal environment is important in this study as a pike's response (as in many animals) may rely on response thresholds. These thresholds are altered by both internal motivational state and by the nature of the external environment to give an animal flexibility when foraging (Dill 1983). Flexibility arises from the ability of fish to modify their behaviour in response to a fluctuating environment. Dill observed that hunger-motivated change could account for this adaptive flexibility.

Hunger is the most pervasive amongst the internal factors in initiating searching and hunting for prey, and after successful capture, in determining the amount eaten (Curio 1976). Hunger motivation has two components, that of gastric or stomach fullness and that of metabolic or systemic need. The former is commonly measured by the observer (Ware 1972) as fish can use stretch receptors to monitor gut fullness, and therefore gastric sensation of hunger may be a reliable cue to foraging behaviour (Dill 1983).

Though not documented for pike, the effects of hunger on foraging behaviour in other fish have been studied. Holst (1949) demonstrated with *Pterophyllum eimecki* that visual vigilance leading to prey-capture varied with hunger, and hunger tended to increase the range of objects recognized or accepted in the diet. Holst postulated a hunger dependent "central prey excitation" which is expressed as a short term rise of a general level of vigilance which must have a minimum level for capture to occur. This is analogous to the

concept of response thresholds (Dill 1983). Sticklebacks, *Gasterosteus aculeatus*, will fixate and take progressively less prey-like objects as hunger increases. In general, feeding behaviour appears to be subservient to nutritional homeostasis and as hunger decreases, searching, reactive distances and the transition probabilities for behaviours in prey-capture sequences decrease (see Dill 1983 for a review).

Hunger is not the single factor ruling predatory behaviour as there are fluctuations in the readiness to hunt which cannot be explained in terms of hunger. For example, it is well known that pike eat a broad range of food in their diet and are reputedly insatiable (Day 1880, Houghton 1890) although pike are often found with empty stomachs (McNamara 1937, Allen 1939, Johnson 1969) and not "on the feed". This occurrence may be due to a sparsity of prey or to the fact that pike are efficient converters of food so they need not be as gluttonous as common belief would have it (Johnson 1966, Buller 1981) or, that it is a result of a pike's previous experience with prey, for example pike learn to avoid fish with spines (Hoogland et al 1957). Much remains to be learned of the relationship between hunger and learning effects in the deployment of foraging tactics (Ringler 1983). Previous experience undoubtedly affects a pike's predatory behaviour and it has been shown to reduce the attractiveness of artificial lures, even after one capture's experience (Beukema 1969). Pike also avoid unpallatable prey such as sticklebacks in preference to other prey (Hoogland et al 1957) or morphs with less armament (Reist 1983).

Although the resultant behaviour of a pike from all possible factors of causation is likely to be complex this study investigates aspects of causation in a controlled, simplistic environment in order to provide a more complete understanding of a pike's predatory behaviour. This study assumes that the predatory response relies on some basic stimulus or cue that can be extracted from the overall background noise or environment. The work covers preliminary observations on pike to produce quantifiable measures of pike movements for assessing motivational states. This is taken further to evaluate the significance of hunger on subsequent prey capture and to recognise stimuli that elicit the prey-capture response and their relationship to a pike's internal state.

The pike used in this study were taken from local rivers in Leicestershire and Nottinghamshire by electric fishing. Individuals taken from the wild were acclimated to laboratory conditions for a minimum period of one month before use in experiments.

The pike were kept in holding tanks in rooms maintained at 15 °C and 13 hours daylength. They were fed on live fish caught by electric fishing from the River Welland, Leicestershire, or by small fish trap in the Queniborough Brook, Leicestershire.

The mean size of the pike used in all investigations was 141.2 g, SD  $\pm$  28.3.

2. EXPERIMENT ONE. A first investigation of the effects of motivation on the response of pike to a prey stimulus.

2.1 INTRODUCTION

In the study of relationships between an external stimulus and response, animals often exhibit varying degrees of reaction to the same stimulus (Halliday 1983). For example, animals do not always eat when presented with food, and this response must be regulated internally. Indeed, when investigating the foraging behaviour of animals in the field, the observer has little knowledge of how hungry an animal is or what previous experience it has gained which moves it to search for and acquire food.

A prerequisite, therefore, for the estimation of possible external factors eliciting the predatory response in pike is for an understanding of the relationship between behaviour and internal state. The ideal is for the observer to be able to look at an individual and by some simple means categorise the internal state of that animal at any time and explain its behaviour accordingly. That is, to gauge an animal's inclination or motivation in order to predict whether it will feed or not. Unfortunately, motivation cannot be readily described by a characteristic group of easily recognised actions (Halliday 1983).

Hinde (1982) describes three approaches to understanding motivation. The first is to observe changes in response to a constant stimulus, the second is to manipulate the internal state of an animal, and the third is by theoretical considerations of empirical observations or modelling. Each approach cannot be regarded as insular and for a complete understanding of motivation the three methods must be considered together. In this study and subsequent chapters emphasis will be mainly confined to the first two approaches.

Within the laboratory, factors influencing the behaviour of pike can be controlled to some extent by regulating the tank environment and the degree of hunger of individuals. In this way, measures of predatory response can be taken as an indication of the inclination of a pike to feed, influenced by the variable of hunger (a label for unknown physiological processes) and as such may be a description of motivation. This is a step towards evaluating the interaction of external and internal stimuli or causal factors (Lorenz 1950, McFarland and Houston 1981).

A common explanation for a change in response to a given stimulus is expressed by an animal's state of arousal (Andrew 1974). Arousal is generally thought to be related to the consciousness of an animal, whether it is sleeping, resting or alert, and therefore can influence a number of possible motivational systems. However, this term is biased through human experience and possibly it is better to express such changes in response by the term activation. Activation describes variable effects from different activities, for

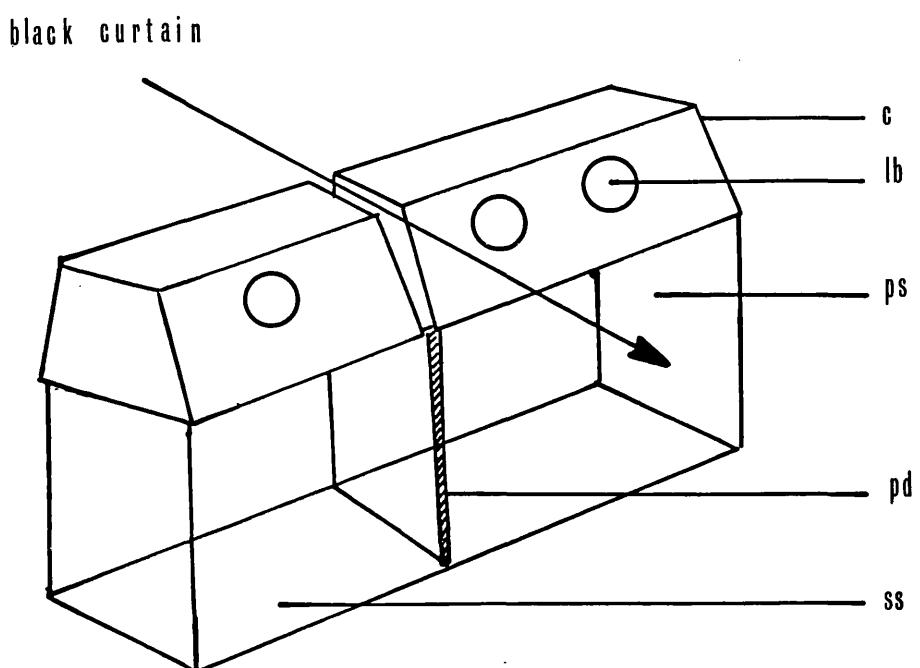
example, the variation in behaviour that may be caused by circadian rhythms (Brady 1979).

The behavioural responses that can be assessed as indicative of a pike's internal state are those initially evident before the capture of prey. In pike these are such things as eye movements and fin movements before the more conventional pointing, stalking, and axial tracking associated with the prey-capture sequence (Hoogland et al 1957, Nursall 1973). This section of the work was designed to relate quantifiable parameters of initial predatory response to the absence or presence of external stimuli and to examine the relationship between motivation and response to prey at a preliminary level with regard to this study.

## 2.2 BASIC METHODS

Trials were carried out in 1.0m x 0.32m x 0.38m aquarium tank with the interior divided into two sections by a clear perspex plate, enabling stimuli to be introduced on one side with a pike in the other. The tank was illuminated by two sets of 40w light bulbs that worked independently for each section. Pike were isolated from external interference by a screen made of black plastic curtains. This allowed the observation of the subject fish and the presentation of a live minnow, *Phoxinus phoxinus*, without the pike in the tank seeing the operator. (See figure 2)

**FIGURE 2** Arrangement of the aquarium for presentation of a live minnow stimulus.



KEY

c canopy

lb 40w light bulb

ps pike section

pd perspex divider

ss stimulus section

Pike were left to acclimate to the new tank for one week at the end of which they were fed to apparent satiation. Apparent satiation was taken when a pike refused food five minutes after the last take of prey. Live minnows were then presented to the pike, behind the perspex divider, and the behaviour of the pike filmed.

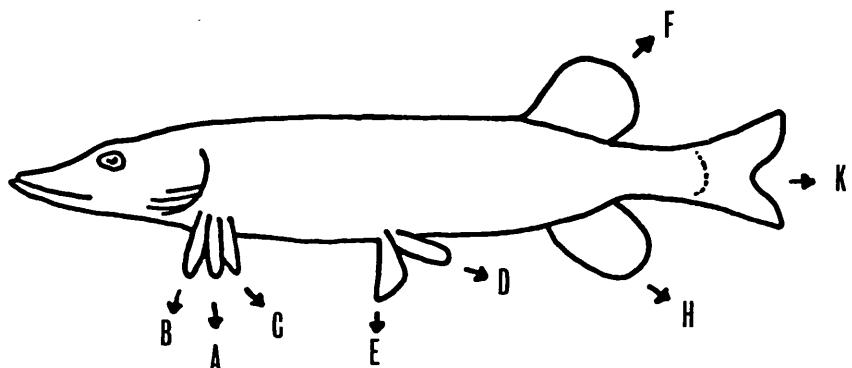
A video unit was used to record behavioural sequences and results were taken from video tapes. An Hitachi CCTV camera with viewfinder was used, coupled to a FOR-A video timer, all linked to a Sanyo 1100 video tape recorder using half inch high density video tape.

Pike were observed both before and during stimulus presentations and at times of 0.5, 1.0, 2.0, 4.0 and 24.0 hours after feeding.

Behavioural parameters (response variables) measured were those of eye movements, pectoral, pelvic and dorsal fin beats. Fin movements for measurement were selected from the description of fin co-ordination patterns by Hoogland et al (1957) for standing positions of pike which will be referred to as "hanging" states in this text.

Figure 3 shows fin positions for pike in a hanging state and for degrees of motion as observed by Hoogland et al (1957). The pectoral fins move as in A and B, and measurement of the beat was taken for the fin to move from A to B and back to A again. The dorsal fin moves in a sculling fashion producing the current F. Measurement of a beat was taken for the

**FIGURE 3** Fin coordination patterns for pike  
(after Hoogland et al 1957).



A, B, and C show possible positions for pectoral fins with currents (arrowed) having the opposite effects on the fish's movements. D shows the usual position for the pelvic fins but E may also be assumed, producing a downward and forward current. The dorsal fin undulates regularly to give the current F. The anal and caudal fin produce currents H and K respectively but were not included in the observations.

completion of one scull. The resultant forces of the beats of the pectoral and dorsal fins maintain the body of the pike in the horizontal plane. In some instances, the pectoral fins do not move greatly between A and B, but remain fixed in relation to the body with only the fin rays moving rhythmically. When this occurred, complete cycles of fin ray movement were measured. Beats and fin cycles were taken to be analogous for the recording of rates of fin movements, as the form of fin movement in the pectorals for example, was dependent on other body movements at the time of measurement. Hoogland et al state that the horizontal plane may also be maintained by movements of the other fins. Pilot work showed that with the escalation of "interest" in the stimulus, pelvic fins frequently were used in the hang state. These were therefore incorporated in the observation of the hanging state response. Measurement of the pelvic fin beats was similar to that of the pectoral fins, timing complete oscillations between E and D. Fine measurement of fin beat rates was facilitated by video recorder playback at one fifth normal speed.

Five pike were used with five replicates for each treatment. Within each replicate, fin beat and eye movement rates were taken every 30 seconds and the mean taken for analysis.

## 2.3 RESULTS

The response variables measured in this study are listed in

Table 2. Tables 3 and 4 are presented according to the main effects and interactions found in multivariate analysis of the response variables (MANOVA routine in the SPSS package, Hull and Nie 1981).

Table 3 gives values for the F statistic and its probabilities determined from the Wilks' lambda significance test. The results show that there are no effects of individual pike ( $F = 0.91$ ,  $p > 0.05$ ) but time since the last feed has a significant effect on the outcome of all response variables studied in the trials ( $F = 10.96$ ,  $p < 0.001$ ).

Table 4 presents results for the overall effect of time since the last feed. The results are given for univariate analyses of variance (ANOVA, Sokal and Rohlf (1981)) for each of the response variables. Only two of the response variables were not affected by time since the last feed. These were NPT ( $F = 2.16$ ,  $p > 0.05$ ,  $df = 5, 120$ ) and NET ( $F = 2.20$ ,  $p > 0.05$ ,  $df = 5, 120$ ). These results are important as the determination of a pike's inclination towards a stimulus relies on the comparison of the frequency of movements with a base line value, derived from pre-stimulus observations, that does not alter with time. The behavioural parameters of pectoral fin beats and eye movements only, therefore, satisfy the above conditions and were accordingly selected for further investigation.

Tables 5 and 6 demonstrate the effect of post feed times on pectoral fin beats and eye movements respectively. Results shown are for the mean and standard deviation for

TABLE 2      Glossary of response variables in Expt 1.

	<u>RESPONSE VARIABLE</u>	<u>DEFINITION</u>
1.	NPT	Pectoral fin beats before stimulus presentation
2.	PT	Pectoral fin beats with stimulus
3.	NPL	Pelvic fin beats before stimulus presentation
4.	PL	Pelvic fins with stimulus
5.	ND	Dorsal fin sculls before stimulus presentation
6.	D	Dorsal fin sculls with stimulus
7.	NET	Eye movements before stimulus presentation
8.	E	Eye movements with stimulus

TABLE 3      Multivariate tests of significance for  
effects in the results of Expt 1.

<u>MAIN EFFECTS</u>	F	p
Pike	0.91	0.609
Time	10.96	<0.001
Interaction	0.56	1.000

(F values and significance of F given are from Wilks' test)

TABLE 4      Univariate F-tests for effects of time on  
the response variables in Expt 1.

<u>RESPONSE VARIABLE</u>	F	p
NPT	2.16	>0.05
PT	41.21	<0.001
NPL	5.12	<0.001
PL	19.44	<0.001
ND	2.48	0.04
D	74.47	<0.001
NET	2.20	>0.05
E	14.78	<0.001

(F values and significance of F given for 5 & 120 degrees of freedom)

TABLE 5      The effect of time from last feed on pectoral fin beats (min<sup>-1</sup>).

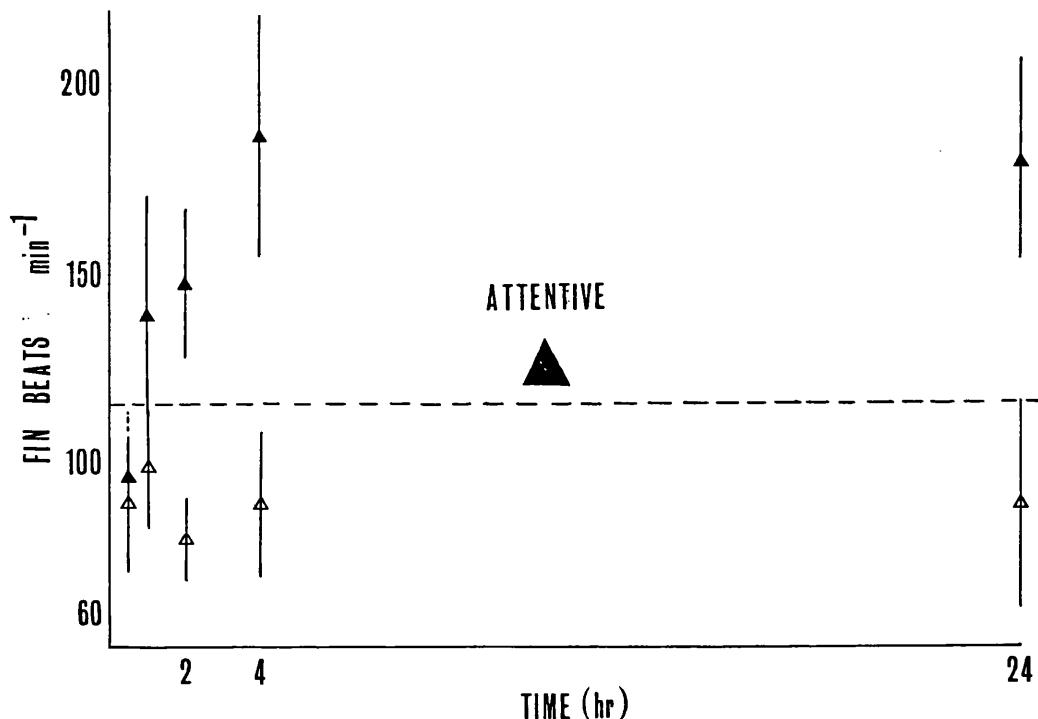
<u>TIME (hr)</u>	<u>PRE-STIMULUS</u>		<u>STIMULUS</u>	
	<u>MEAN</u>	<u>SD</u>	<u>MEAN</u>	<u>SD</u>
0.5	89.1	18.5	95.2	18.0
1.0	97.6	15.2	139.4	30.8
2.0	79.4	11.6	147.4	19.8
4.0	88.6	19.3	186.2	32.0
24.0	87.8	27.1	179.5	26.3

TABLE 6      The effect of time from last feed on eye movements (min<sup>-1</sup>).

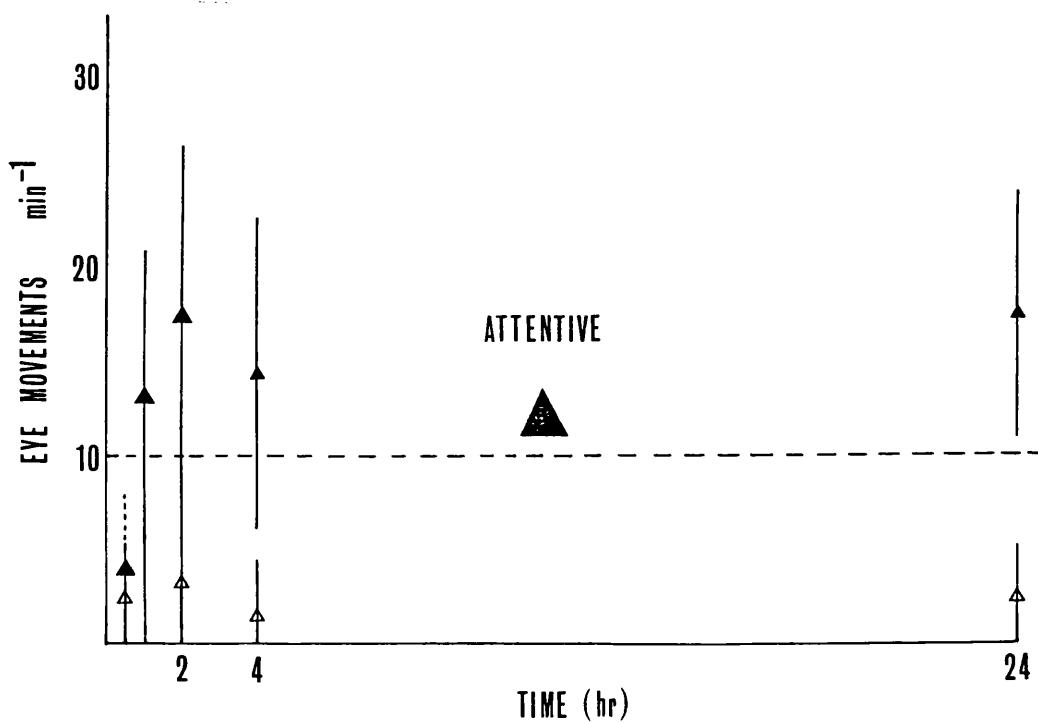
<u>TIME (hr)</u>	<u>PRE-STIMULUS</u>		<u>STIMULUS</u>	
	<u>MEAN</u>	<u>SD</u>	<u>MEAN</u>	<u>SD</u>
0.5	2.2	3.2	4.2	3.9
1.0	5.0	5.0	13.2	7.7
2.0	3.3	5.1	17.5	9.0
4.0	1.5	3.0	14.4	8.3
24.0	2.4	2.9	17.4	6.5

Pre-stimulus results are measurements before a minnow was presented. The time in hours denotes the period elapsed since pike were fed to apparent satiation.

**FIGURE 4** Pectoral fin beat rates expressed with time (hr)  
from last feed. (▲ denotes mean response to  
stimulus, △ = mean without)



**FIGURE 5** Rates of eye movement expressed with time (hr)  
from last feed. (Symbols as above)



pre-stimulus and stimulus presentations at five times from the last feeding of the pike. These are displayed as graphs in figures 4 and 5. Response levels were then seen to rise to an asymptote between 2 and 4 hours post feed, remaining unchanged at 24 hours.

Two states of the pike were deduced from the response curves for pectoral fin beats and eye movements, corresponding to the "interest" of pike towards the prey stimulus. A level of pectoral fin beats of greater than  $115 \text{ min}^{-1}$  and eye movements exceeding  $10 \text{ min}^{-1}$  were assigned to states termed "Attentive". Levels of response less than these were designated "Inattentive".

#### 2.4 DISCUSSION

In this investigation the overall response of a pike to the sight of prey is dependent on the interaction of several factors, this interaction being part of unobservable internal mechanisms which may be broadly encompassed in the term motivation. The time from when a pike last fed, the nature of the prey stimulus and the response of the individual describe the input and output to the system, and may through inference reveal the motivational state of a pike at a particular time. For example, it may be inferred that the escalation of pectoral fin beats with post feed time was a result of increasing hunger. However, there was no direct measurement of this possible increase in hunger, though the

results at 30 minutes post feed would suggest that hunger (or in this case apparent satiation) has a modulating affect on the response of a pike towards a prey item. Whether this explanation describes the motivational state of an individual pike at that time, or not, is dependent upon the amount of influence of other possible factors.

In 2.1, activation was suggested as an explanation for a change in an individual's response to a given stimulus (Brady 1979). Therefore, an increase in pectoral fin beat rate and the rate of eye movements might be ascribed to a change in state due to circadian rhythms or the time of day, rather than a change in hunger to explain motivational state. However this can be invalidated in this experiment because base line rates for eye and pectoral fin movements , in the absence of a stimulus, remained unchanged for observations taken in a 24 hour period.

The accountability for motivation being described in terms of hunger or activation does not mean that these factors are mutually exclusive of each other. It is not assumed that motivation, as a notion of internal state, has a hierarchy of influencing factors. Motivation is best considered as an interaction of factors within a homeostatic system (McFarland and Houston 1981).

The remaining factor in this investigation that may affect the response of individual pike is the nature of the prey stimulus given. As a live minnow was presented to pike, there was no control over the prey fish's behaviour.

Increased eye movements and fin beats could be explained if the minnow shows more activity in some trials than in others. A greater number of movements made by the prey fish could be correlated to an increase in the number of eye movements necessary for a pike to observe its potential prey item. Again, inference of motivational states in terms of hunger may be confounded by such an occurrence. However, though no quantifiable data is provided, as viewing of the stimulus section of the tank was not possible with this arrangement of the apparatus, minnows when introduced on their own to the tank environment tended to remain stationary, resting on the tank floor. It may be tentatively suggested that the nature of the stimulus remained constant enough to infer that increased levels of response were due to the effects of hunger.

Whatever the explanation for the response curves of fin beats and eye movements for pike responding to the presence of a prey item, the results provide a useful means of identifying the "interest" of pike to prey whilst in a hanging state. The hanging states, attentive and inattentive, as defined by the value of pectoral fin beats and eye movements, give an essential addition of two behaviours to the description of behaviours associated with prey capture detailed by Christiansen (1976) and Hart et al in prep. The behaviours provide an important description of the state of pike before the pursuit of prey commences, discussion of which will be expanded in subsequent chapters.

The complexity of describing responses of pike to prey in

terms of motivational states, as revealed in this experiment, requires a more refined approach to the identification and understanding of the internal mechanisms that influence behaviour. So too, for the recognition of the role of external causal factors that elicit the predatory response in pike.

### 3 EXPERIMENT TWO. The influence of hunger on the predatory behaviour of pike.

#### 3.1 INTRODUCTION

The behaviour of an animal may be described in two ways.

Firstly, behaviour can be related to its ecological consequences or function, for example, study of the costs and benefits of carrying out a particular activity. Secondly, a description of behaviour may be given by its form, that is, by the observation of a series or sequence of movements as an animal performs an activity (see Huntingford 1984 for a review). In this experiment the form of the predatory act as pike captured prey and its modification with varying degrees of hunger was studied.

The nature of the predatory behaviour in pike has been studied by several workers (Hoogland et al 1957, Nursall 1973, Neill and Cullen 1974, Christiansen 1976, Webb and Skadsen 1980, Hart and Connellan 1984). In general, these studies have described the repertoire of behaviours as pike pursue prey, either as a qualitative description or a listing of possible sequences of behavioural events leading up to prey capture. Hart and Connellan used the repertoire of behaviours to study the form of the predatory act as a pike pursued prey of different size classes (unpublished) and to

describe it functionally in terms of time budgeting and growth rates resulting from the different feeding regimes (Hart and Conellan 1984). However, no studies have been carried out to observe how hunger-motivated predatory behaviour in pike alters with respect to increasing satiation. Such investigation may assist in interpreting observations on food consumption and prey selection.

Traditionally, the hunger of an individual fish is estimated by the amount of food contained in the stomach at any particular time (Ware 1972). Stomach contents in pike have been estimated using evacuation times or rates of gastric emptying (Seaburg and Moyle 1964, Diana 1979). However, the way in which gastric evacuation occurs can be expressed by a number of different models (see Pitcher and Hart (1982) for a summary). Estimations of stomach content in this experiment were determined by the exponential evacuation rate equation as it best describes the evacuation of food from the stomach of pike (Diana 1979). It has also been shown to be the most realistic for passage of stomach contents in a variety of other fish (Elliott and Perrson 1978, Wirjoatmodjo 1980). The equation assumes that the rate of evacuation is proportional to the quantity (mass or volume) of food in the stomach.

The results of experiment one demonstrated the need for a more rigorous approach in the way that the interaction between a pike, its internal state and external stimuli, was investigated. The work in this section, therefore, was an extension of the previous one, using the rate of fin beating

as an index of a pike's internal state at the beginning of a trial and defining the hunger state in a more accurate way. The objective was to describe the form of the prey capture sequence and to derive an intermediate state of response for use in feeding tendency investigations (Experiment three).

### 3.2 METHODS

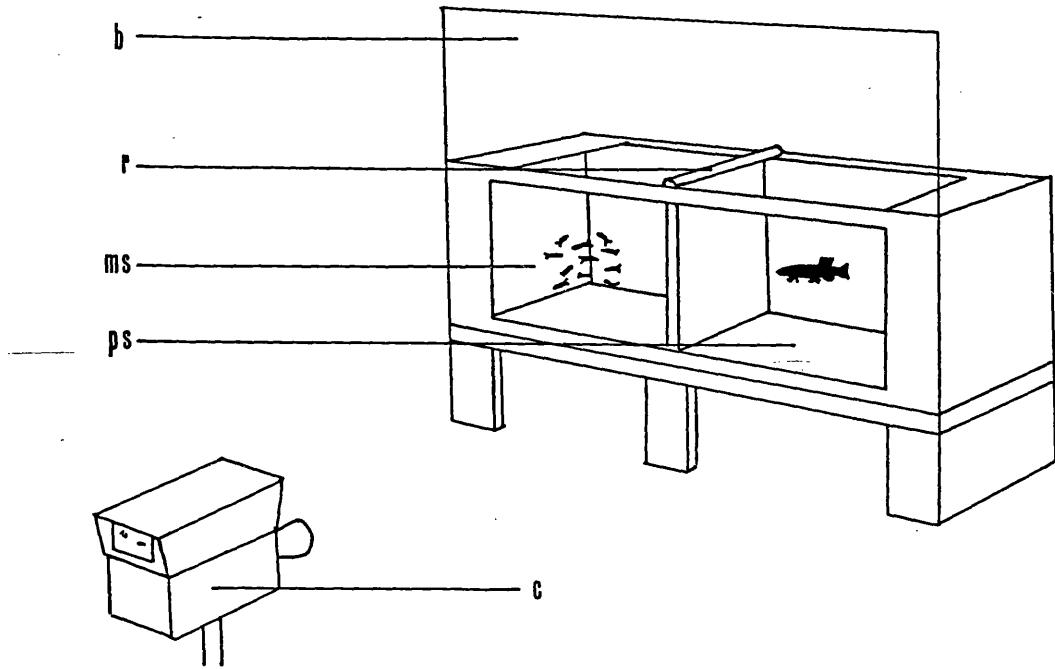
Trials were carried out in a large experimental tank of dimensions 1.7m x 1.5m x 0.5m<sup>3</sup>. The tank had a glass front marked in a grid system of 10 x 10 cm squares to assist in determining positions of fish when filming. The tank was divided into two halves by a net screen which could be rolled up to expose a school of 10 minnows, *Phoxinus phoxinus*, to a pike (Figure 6). The number of minnows for any trial was not allowed to fall below 5 in order to ensure adequate schooling behaviour. The size of the minnows was restricted to 3.0 - 3.5g weight and 7.0 - 8.0 cm fork length so that meal sizes could be determined easily and the physical appearance of the prey fish remained as constant as possible.

As in section 2.2 trials were of five minutes duration and filmed using video. Trials were carried out six times a day at one and a half hour intervals.

#### 3.2.1 ESTIMATION OF STOMACH CONTENT

Stomach content was estimated by use of the exponential evacuation rate equation described by Elliott and Persson

FIGURE 6 Tank arrangement for filming of prey capture sequences in Experiment 2.



KEY

b blackout cover

c CCTV camera

ms minnow section

ps pike section

r roller

(1978). It is assumed that the rate of gastric evacuation (R) is exponential and the rate of food consumption (F) is constant. The rate of change in stomach content (S) is given by -

$$\frac{dS}{dt} = F - RS \quad 1.$$

The actual amount of food present in the stomach ( $S_t$ ) after  $t$  hours is given by -

$$S_t = S_0 e^{-Rt} + \frac{F}{R} (1 - e^{-Rt}) \quad 2.$$

where  $S_0$  is the initial amount of food in the stomach.

This equation relies on the observer knowing the rate of feeding over a particular time period. However, in this experiment feeding stops at the end of a trial and starts at the beginning of the next. In such a case Elliott and Persson give the following equation for the amount of food in the gut after  $t$  time units -

$$S_t = S_0 e^{-Rt} \quad 3.$$

Equation 3, therefore, was used in determination of stomach contents.

In order to determine stomach contents at the start of any trial an estimate of the value of the exponent (R) was required. This was taken from the literature as 0.096 (Diana

1979).

### 3.3 ANALYSIS OF TRIALS

From determinations of stomach contents in section 3.2, four categories of stomach fullness were chosen. These were 0-5g, 6-10g, 11-15g and 16-20g stomach content. It was assumed that these four groups were indices of four different hunger levels. Analysis of trials on video tape was carried out using a Research Machines 380Z micro-computer programmed to function as an event recorder.

#### 3.3.1 ANALYSIS OF PREY CAPTURE SEQUENCES

The repertoire of behaviours used in the capture of prey were those listed by Hart and Connellan (1984) supplemented with additions independently observed. (See also Christiansen 1976).

##### 3.3.1.1 Stationary or " hanging " positions

- (i) Attentive - Pike stationary, elevated rate of fin beats and eye movements (section 2.3).
- (ii) Inattentive - Pike ignores prey, fin beats and eye at base rate (section 2.3).
- (iii) Point - A " hanging " position in proximity of prey. Body orientated towards prey and " bow " shaped.
- (iv) Stop - Short break in behavioural sequence which

cannot be readily defined as any of the above.

### 3.3.1.2 Movements

- (i) Chase - Fast swimming or gliding after prey caused by caudal propulsion.
- (ii) Approach - Overall movement of pike towards prey from a few caudal beats.
- (iii) Stalk - Movement in close proximity of prey with body held in either a " bow " shape or " S " shape, through fine adjustments of body position by pectoral, pelvic and dorsal fins.
- (iv) Back - Movement away from prey.

### 3.3.1.3 Prey capture events

- (i) Strike - Lunge at prey.
- (ii) Capture - Prey caught by pike.
- (iii) Hold - Pike holds prey transversely in mouth.
- (iv) Manipulate - Lateral head shakes which orientate the prey head or tail first down the throat.  
This is followed by swallowing.

## 3.4 RESULTS

Analysis of behavioural sequences may be performed by a number of methods, for example, by Markov chains (Ashby

1963), transition matrices and probabilities (Stokes 1962), multivariate analyses (Aspey and Blankenship 1977, 1978) and bout analysis (Slater 1974, Machlis 1977). The choice of which method to use relies on the form of the data set and the goals set by the investigator. In this experiment and in future work the use of multivariate analysis was extensively used.

### 3.4.1 MULTIVARIATE ANALYSIS

The application of multivariate analysis has become increasingly popular in recent years as it works on data which includes several variables and a number of groups. Multivariate analysis is useful in that it can reveal homogeneous sub-groups from heterogeneous samples and identifies relationships among multiple variables when the underlying source of variation is unknown (Aspey and Blankenship 1977).

Principal component and discriminant function analysis have been used to derive reliable functions to separate species (Josiak and Moore 1982) and environmental preferences of cyprinid fishes (Felley and Hill 1983). Multivariate analyses have also been applied to fish behaviour of the three spined stickleback (Huntingford 1976) and to goldfish and minnows (Magurran and Pitcher 1983).

In this experiment discriminant function analysis (DFA) was used. DFA was devised by Fisher (1936) as a means of classifying items or individuals, assuming that the

individuals to be classified belong to one of a finite number of groups. In this study pike were assigned to distinct categories of stomach content as indices of hunger.

As described in section 3.3.1, there is a repertoire of distinct behaviours in the predatory response of pike. DFA is a useful tool to the researcher as it takes the frequencies of these behaviours (or any parameter the investigator might choose) and allots weights to the behaviours according to their contribution to an optimum differentiation of group means (Hope 1969). The end result of a stepwise process leaves only those behaviours most useful in categorising the overall prey capture sequences displayed by pike at the four indices of hunger.

Table 7 presents overall effects within the data set from multivariate analysis on pike responses to prey at the four hunger indices. Values given are for the Wilks' lambda significance test (MANOVA routine in the SPSS package, Hull and Nie 1981). The results show that there are significant effects of hunger and of individual pike with a significant interaction.

df = 120).

Breakdowns for behaviours (glossary of abbreviations are given in Table 8) are represented in Table 9 and Table 10 for the effects of hunger and pike respectively, with corrections for significant interactions where necessary. It can be seen that individual pike affect all behaviours except IN, AP, ST and B, and that hunger affects all except IN and B.

**TABLE 7** Multivariate tests of significance for effects in the results of Experiment 2.

<u>MAIN EFFECTS</u>	<u>df</u>	<u>F</u>	<u>p</u>
HUNGER	30	4.06	< 0.001
PIKE	40	2.47	< 0.001
INTERACTION [H X P]	120	1.28	0.036

Complete details from which these results are derived are given in tables 9 and 10.

**TABLE 8** Glossary of abbreviations for behaviours in the analysis of Experiment 2.

<u>ABBREVIATION</u>	<u>BEHAVIOUR</u>
AT	ATTENTIVE
IN	INATTENTIVE
PT	POINT
SP	STOP
AP	APPROACH
SK	STALK
CH	CHASE
ST	STRIKE
CP	CAPTURE
B	BACK

**TABLE 9** Univariate F-tests for effects of hunger on  
on behaviours in Experiment 2.

<u>BEHAVIOUR</u>	<u>Sums of Squares</u>	<u>Mean Squares</u>	<u>F</u>	<u>p</u>
AT	97.63	32.54	12.91	< 0.001
IN	3.07	1.02	2.65	> 0.05 ♦
PT	1166.43	388.81	38.84	< 0.001
SP	842.56	280.85	16.63	< 0.001
AP	975.08	325.02	9.84	< 0.001 ♦
SK	103.63	34.54	12.33	< 0.001
CH	394.16	131.39	18.74	< 0.001
ST	221.36	73.79	14.14	< 0.001
CP	34.75	11.58	20.15	< 0.001
B	0.43	0.14	0.41	> 0.05 ♦

( ♦ indicates behaviours corrected for significant interaction)

Results are for univariate F-tests with 3/80 D.F.

**TABLE 10** Univariate F-tests for effects of pike on behaviours in Experiment 2.

<u>BEHAVIOUR</u>	<u>Sums of Squares</u>	<u>Mean Squares</u>	<u>F</u>	<u>p</u>
AT	107.66	26.91	10.68 < 0.001	
IN	3.26	0.82	0.39 > 0.05	♦
PT	211.46	52.87	5.28 < 0.001	
SP	599.54	149.88	8.88 < 0.001	
AP	167.76	41.94	1.27 > 0.05	♦
SK	109.36	27.34	9.76 < 0.001	
CH	149.50	37.38	5.33 < 0.001	
ST	21.20	5.30	1.02 > 0.05	
CP	13.14	3.28	5.71 < 0.001	
B	2.50	0.63	1.78 > 0.05	♦

( ♦ indicates behaviours corrected for significant interaction )

Results are for univariate F-tests with 4/80 D.F.

### 3.4.1.1 Results from discriminant function analysis

Realising the effects of hunger and pike on the behavioural sequences, stepwise discriminant function analysis was used to select statistically those behaviours most useful in describing the overall predatory behaviour.

The mathematical objective of DFA is to weight and linearly combine discriminating variables so that groups (in this cases indices of hunger) are forced to be as statistically distinct as possible (Hope 1969, Nie et al 1975). The statistical theory of DFA assumes a multivariate normal distribution but in practice is robust enough for the assumption to be violated to some degree. The data in this experiment shows good homogeneity (Cochran's C test showed non-significance) justifying the use of DFA.

The stepwise procedure selected the single best discriminating variable and then those of decreasing importance that help to separate (or discriminate) between indices of hunger. Table 11 lists those behaviours most useful in describing the prey capture response from DFA accounting for hunger and individuals (DISCRIMINANT sub-routine in MANOVA, SPSS, Hull and Nie 1981).

Further to the selection of discriminating behaviours, DFA produces functions which may be used to separate hunger and pike. Canonical correlation determined that the first three

**TABLE 11** Selected behaviours for discrimination of  
prev capture responses at four indices  
of hunger.

<u>ORDER OF DISCRIMINATION</u>	<u>BEHAVIOUR</u>
1	POINT
2	CAPTURE
3	BACK
4	APPROACH
5	STOP
6	INATTENTIVE
7	STRIKE

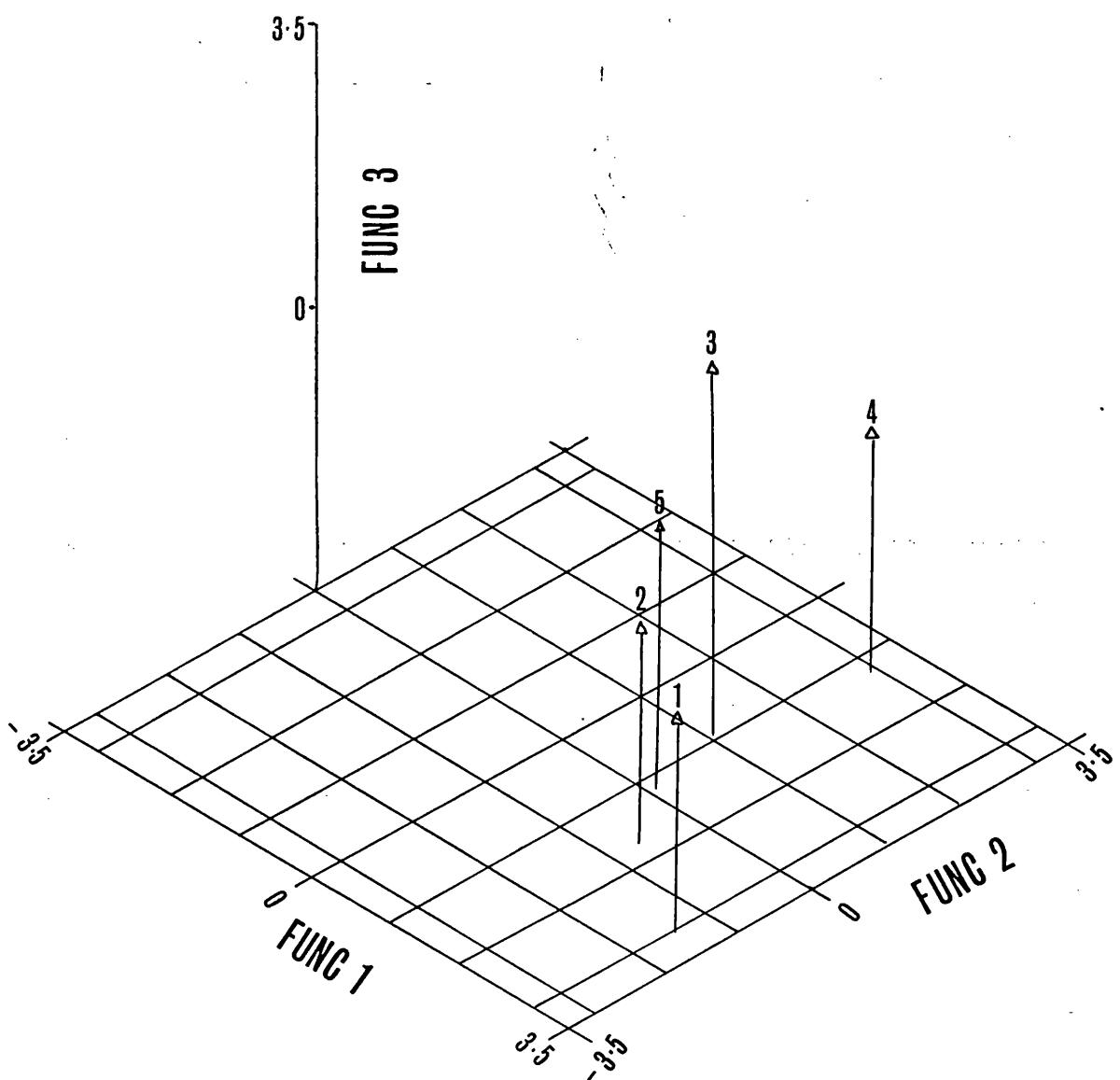
**TABLE 12** Canonical discriminant functions assigned to pike at four categories of hunger.

<u>STOMACH CONTENT</u>	<u>PIKE</u>	<u>FUNC 1</u>	<u>FUNC 2</u>	<u>FUNC 3</u>
0 - 5g	1	3.1224	-1.4770	-0.9187
	2	1.7983	-0.6737	-0.9453
	3	0.9731	1.5772	0.9032
	4	1.2627	3.0750	-0.6680
	5	1.2314	0.1205	-0.3418
6 - 10g	1	1.5947	-0.7578	1.6408
	2	2.1816	-0.8109	-0.4112
	3	0.0835	0.1281	-0.4539
	4	0.2621	1.3403	-1.0845
	5	-0.1968	0.4594	-0.3658
11 - 15g	1	1.0619	-0.5642	2.0212
	2	0.0695	0.5572	0.2906
	3	-1.8038	-0.4736	-0.2220
	4	-1.7505	-0.4483	-0.2506
	5	-1.7505	-0.4483	-0.2506
16 - 20g	1	-0.9714	-0.9164	0.0861
	2	-1.6434	0.7723	0.4505
	3	-1.8038	-0.4736	-0.2220
	4	-1.8038	-0.4736	-0.2220
	5	-1.9172	-0.0932	0.3628

discriminant functions were to be used. (Wilks' lambda = 0.307, p = 0.12, df = 85 after 3rd function). These functions accounted for 89% of the variance in the data that could be described by discriminating functions. Table 12 shows the first three canonical discriminant functions assigned to five pike at each of the four chosen indices of hunger. These are reproduced as three dimensional plots in Figures 7, 8, 9, 10. The presentation of results in this form facilitates the separation of feeding tendencies in pike, classified into groups of response, the strength of which depends on the first discriminant function (FUNC 1). FUNC 2 and FUNC 3, representing the second and third discriminant functions, serve to demonstrate variability in response by positioning individual pike in a three dimensional space. A response line for dividing non predatory and attack responses may be surmised corresponding to the axis of FUNC 2. Those points that lie to the right hand side of this axis show a strong predatory response compared to those that are positioned to the left.

Figure 11 is a "territorial" map for all trials plotted from coordinates of the first two discriminant functions (DISCRIMINANT, Nie et al, 1975). Whereas the three dimensional representation separates the response of pike by producing a single point, the mapping plot demonstrates the amount of overlap that occurs in responses from the four indices of hunger. The amount of overlap by areas corresponding to more satiated pike with that of hungry pike (0 - 5g stomach content), decreases as satiation approaches.

FIGURE 7 3 - Dimensional plot for discriminant functions  
separating responses of pike to a minnow school  
(stomach content = 0 = 5g).



**Figure 8** 3 - Dimensional plot for discriminant functions  
separating responses of pike to a minnow school  
(stomach content  $\leq 6 = 10g$ ).

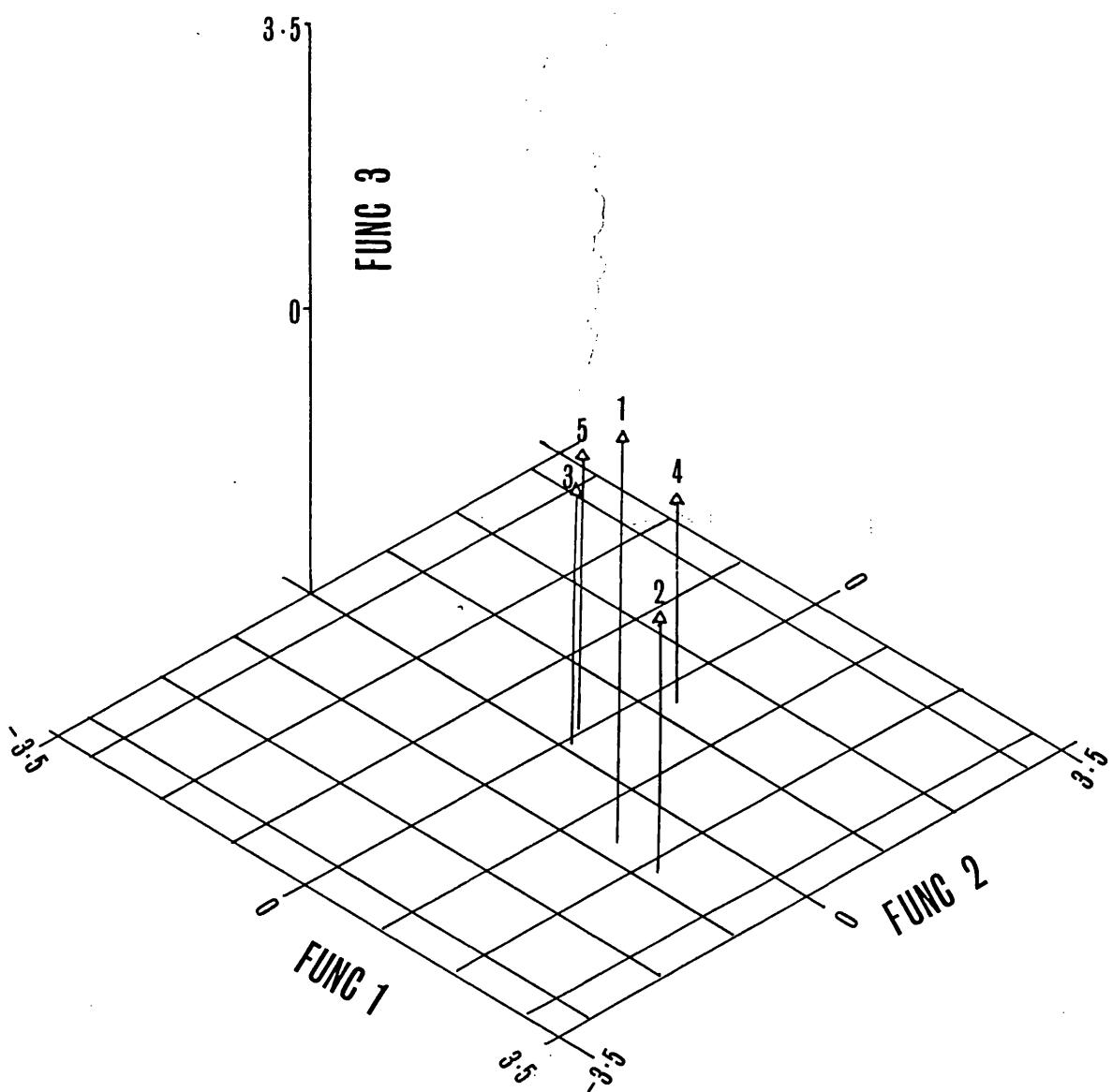
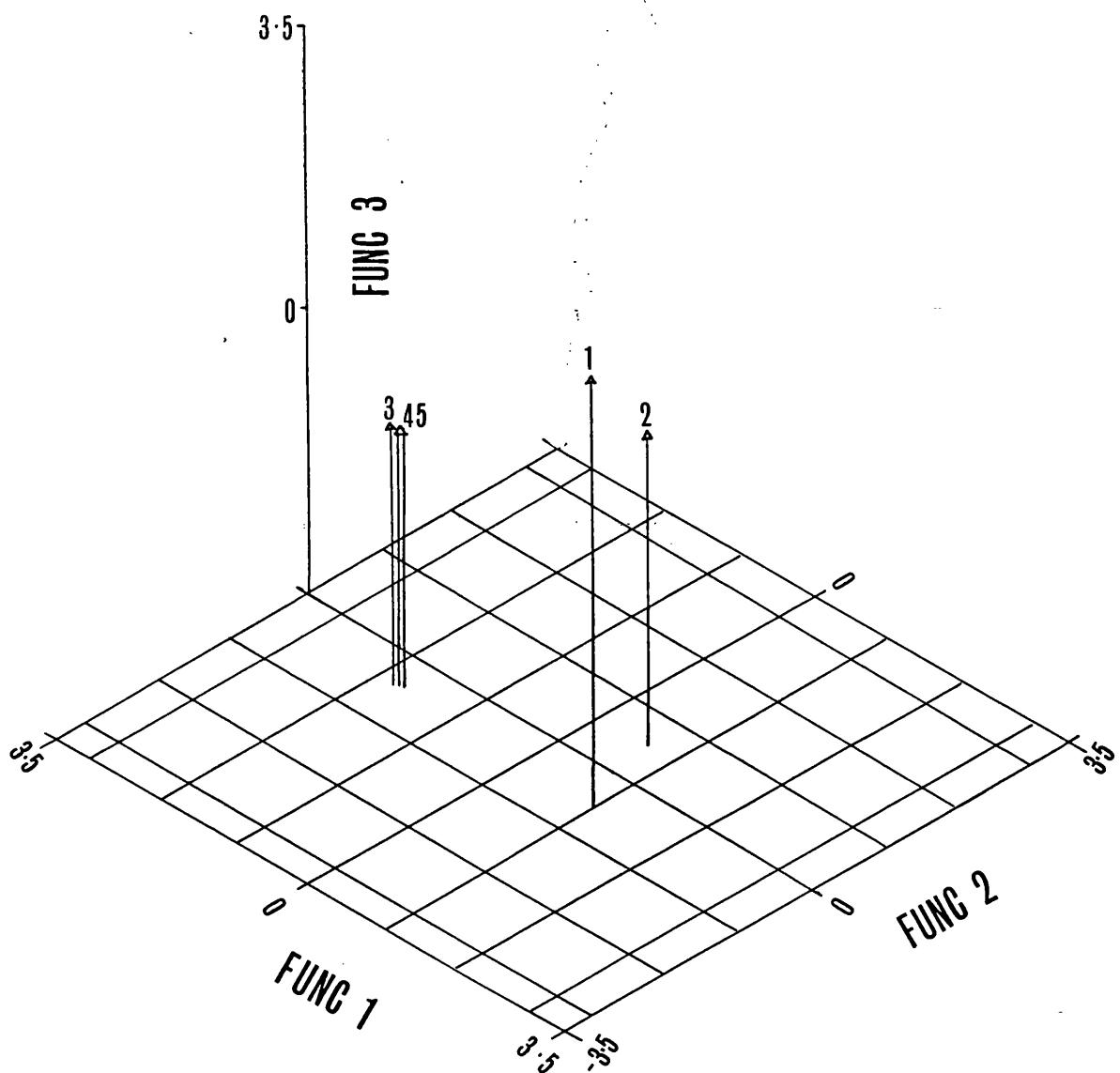


Figure 9 3 - Dimensional plot for discriminant functions  
separating responses of pike to a minnow school  
(stomach content = 11 ± 15g).



**FIGURE 10** 3 - Dimensional plot for discriminant functions separating responses of pike to a minnow school (stomach content = 16 = 20g).

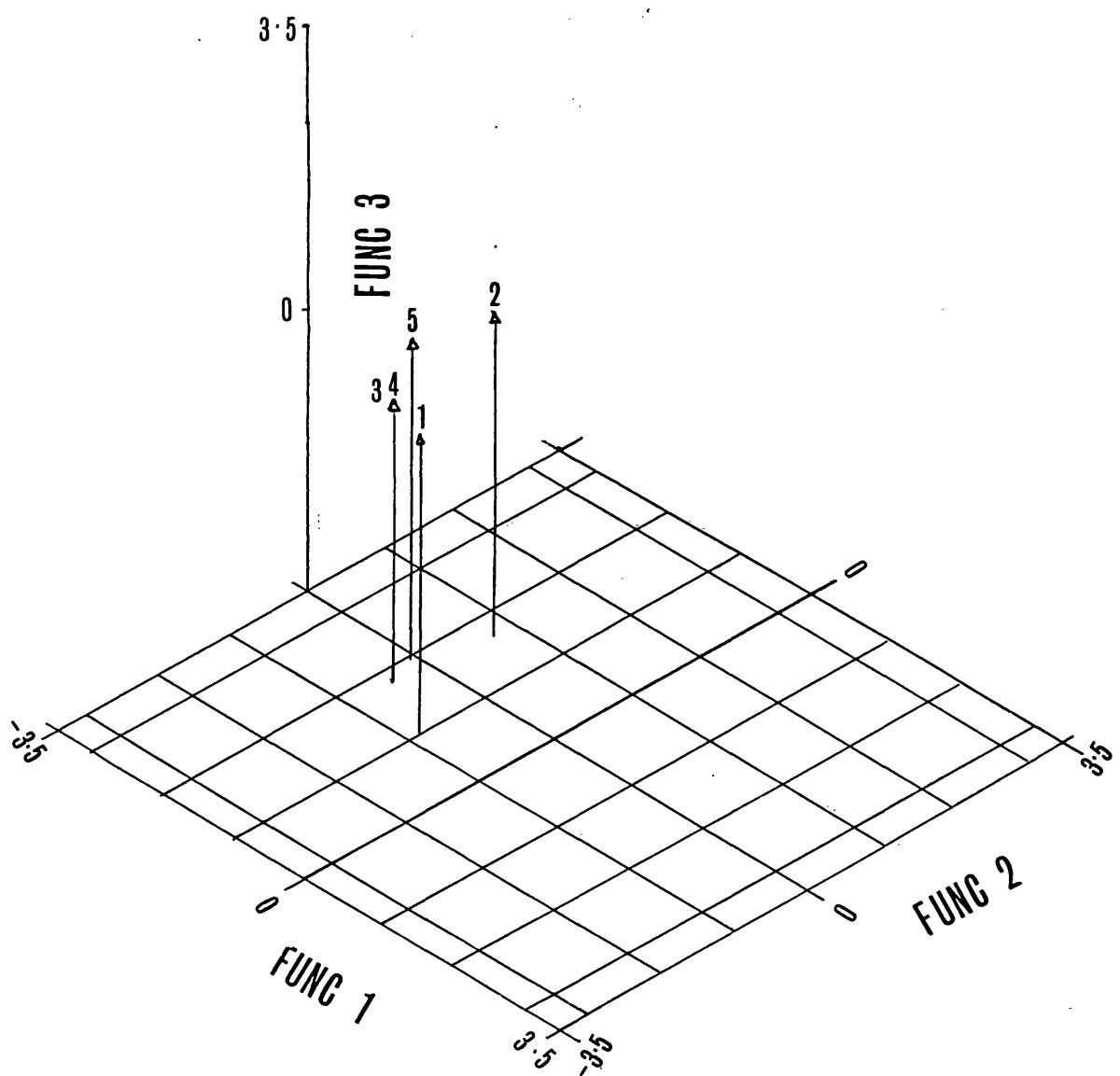
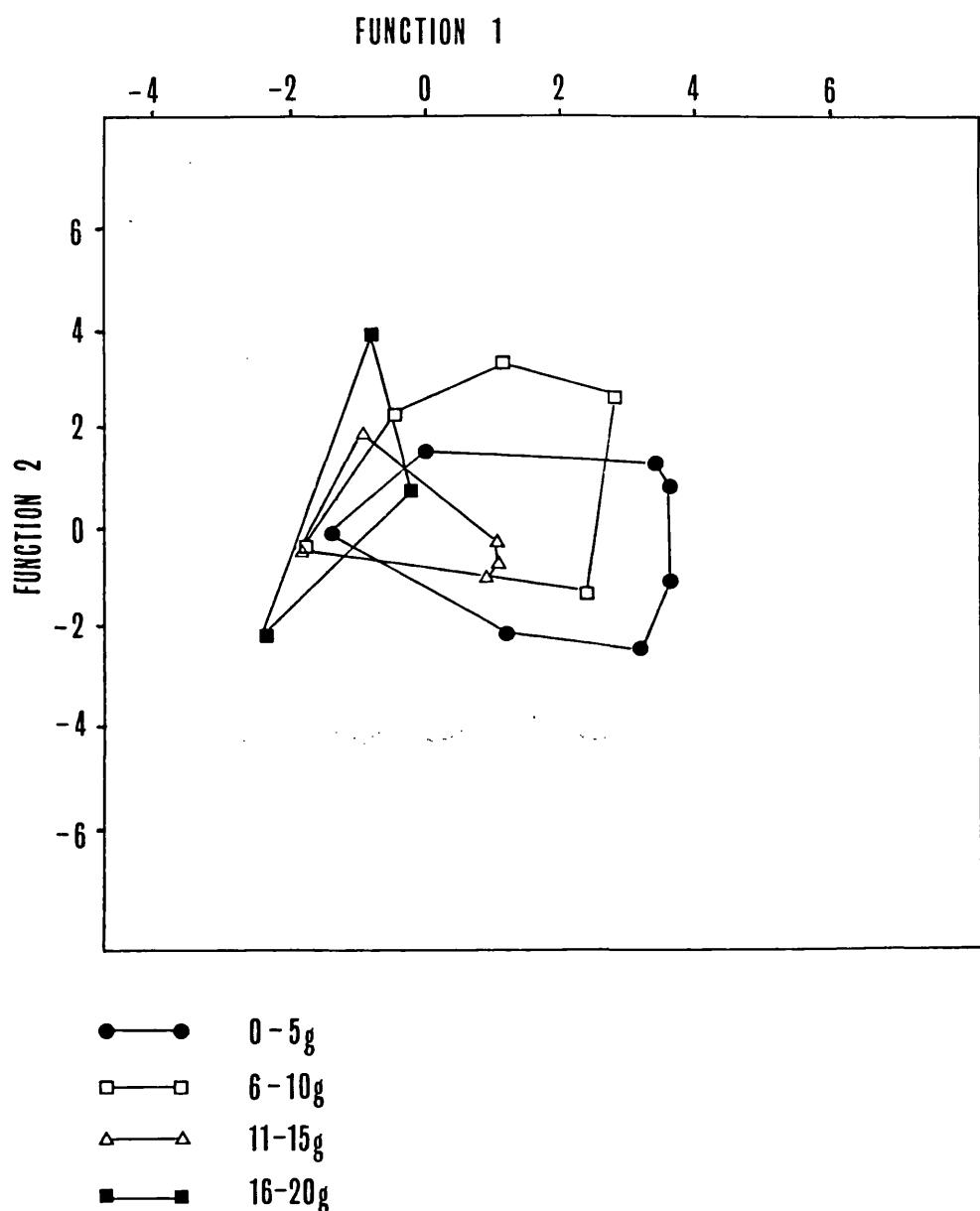


Figure 11 Area map for responses of pike in Experiment 2  
from first two canonical discriminant functions  
for all trials.



### 3.4.2 BEHAVIOUR AND BOUT ANALYSIS

The analysis of the form of the prey capture sequence was taken further by incorporating the results of sections 3.4.1 and 3.4.2, studying particular aspects of those behaviours selected by discriminant function analysis. From Table 10, Back and Inattentive were omitted from further analysis as the frequency of these was not influenced by hunger or individuals.

Table 13 presents mean frequencies for PT, CP, AP, SP and ST for each of the chosen indices of hunger. In all cases the number of behaviours decreased as satiation approached (Figure 12).

As a pike pursued prey, it was apparent to the observer that behaviours in the prey capture sequence occurred in bursts of activity, or bouts. A bout may be defined as a change in behaviour where a burst of one behaviour finishes and another one begins, or, where a sequence of behaviours is ended by a criterion interval ( $X_t$ ). All durations or intervals of behaviour less than or equal to  $X_t$  are assigned as within bout intervals and those greater are between bout intervals. (See Lehner 1979 for a summary).

In the sequence of behaviours when a pike is in pursuit of its prey indigenous end of bout markers are present. These are Inattentive and Capture. Other natural breaks in a burst of behaviours are those of Point and Attentive. However, to

**TABLE 13** Frequencies of selected behaviours for pike predating on 3g minnows at four categories of hunger.

<u>BEHAVIOUR</u>	<u>STOMACH CONTENT (g)</u>	<u>MEAN</u>	<u>S.D</u>
POINT	0 - 5	9.08	4.20
	6 - 10	7.04	3.97
	11 - 15	2.28	3.53
	16 - 20	0.68	1.82
CAPTURE	0 - 5	1.60	1.00
	6 - 10	1.12	0.93
	11 - 15	0.44	0.91
	16 - 20	0.08	0.28
APPROACH	0 - 5	9.08	5.03
	6 - 10	6.88	2.68
	11 - 15	2.52	3.49
	16 - 20	1.44	3.15
STOP	0 - 5	8.68	5.31
	6 - 10	7.48	4.76
	11 - 15	3.00	4.76
	16 - 20	1.80	4.02
STRIKE	0 - 5	3.80	3.02
	6 - 10	3.12	2.20
	11 - 15	0.76	1.74
	16 - 20	0.32	1.41

**FIGURE 12** Frequencies of Point, Approach, Stop, Strike  
and Capture at 4 categories of hunger.  
(Means and S.D drawn).

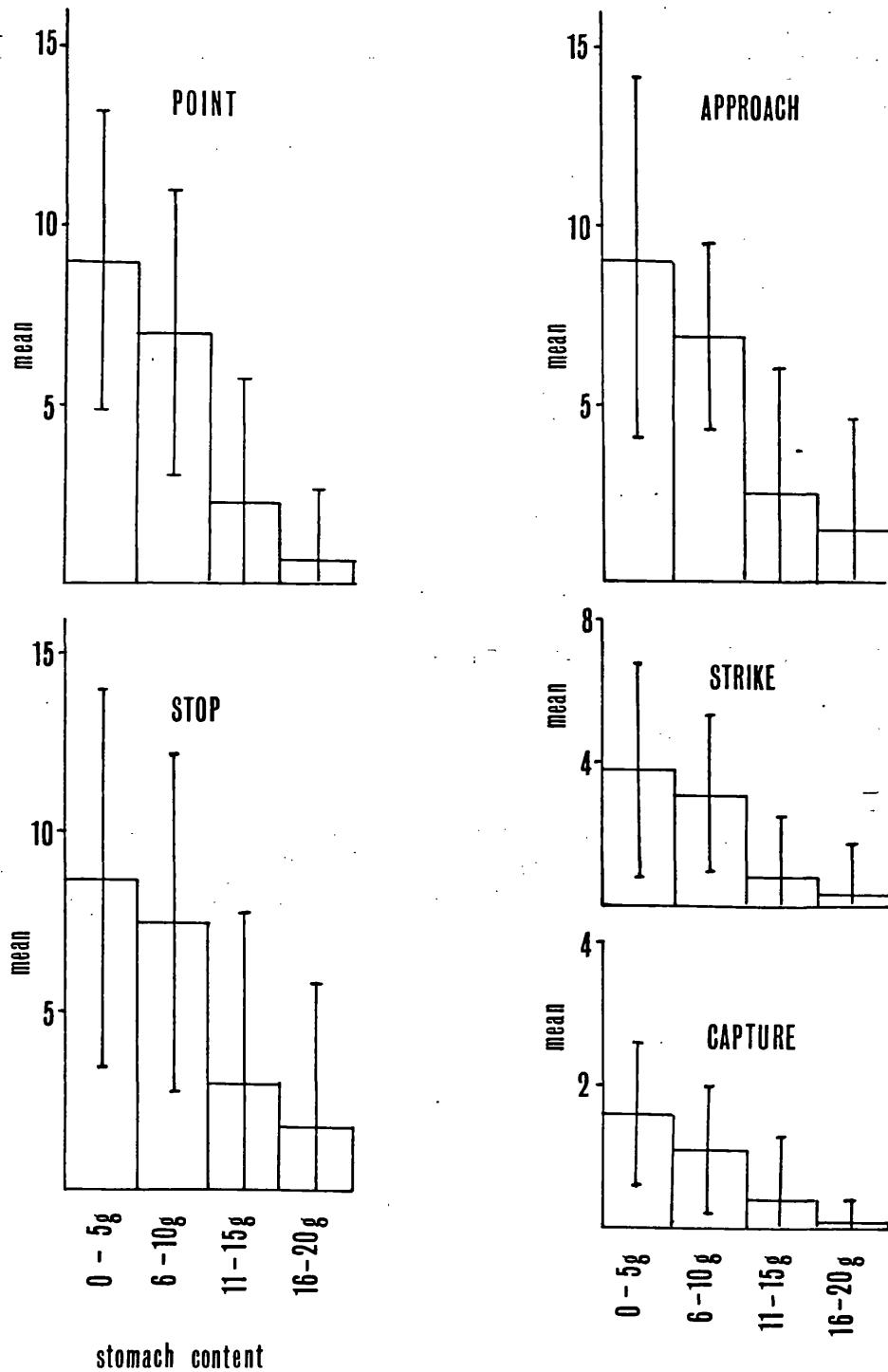
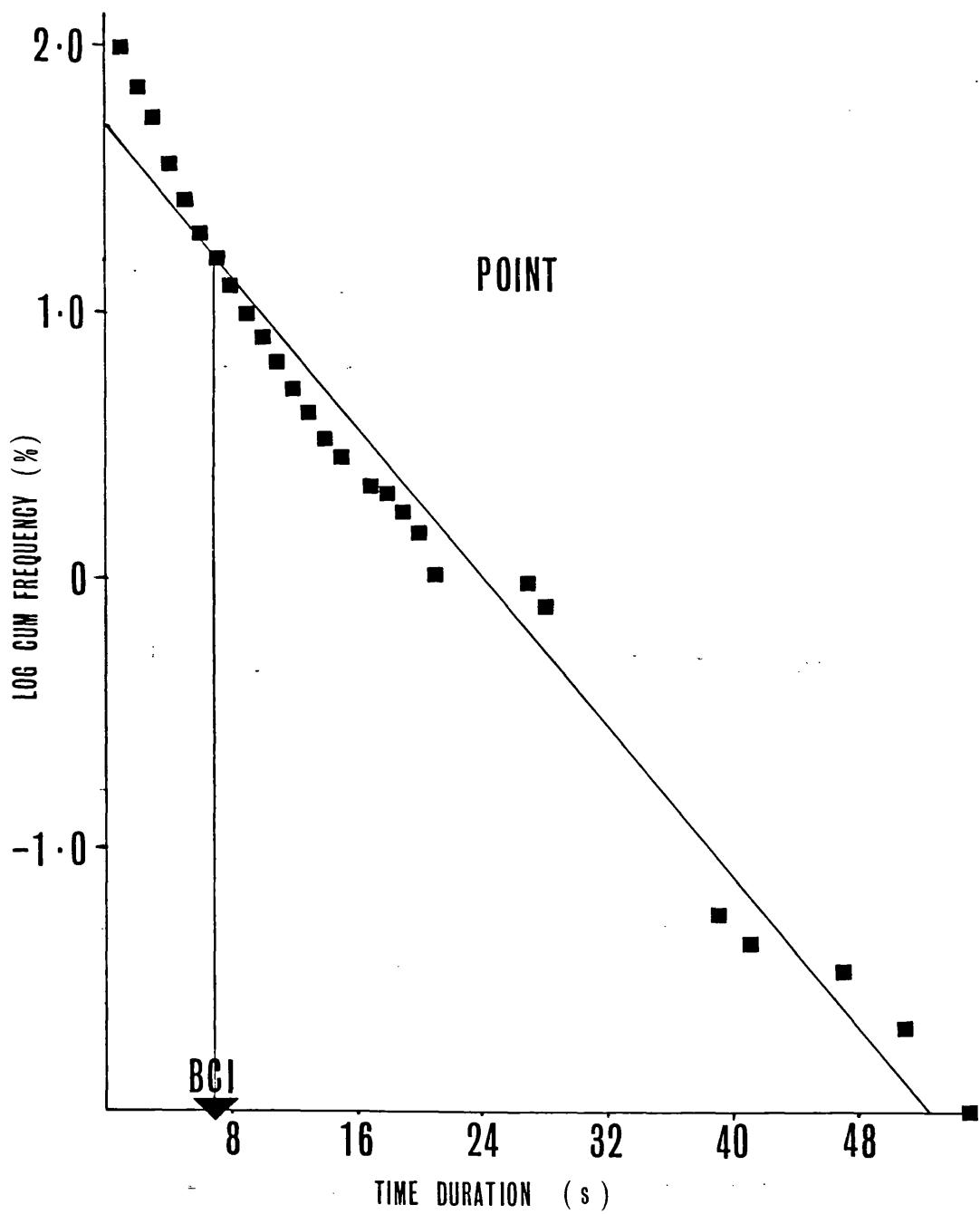


FIGURE 13 Log Survivorship curve with fitted regression line  
for the behaviour Point.



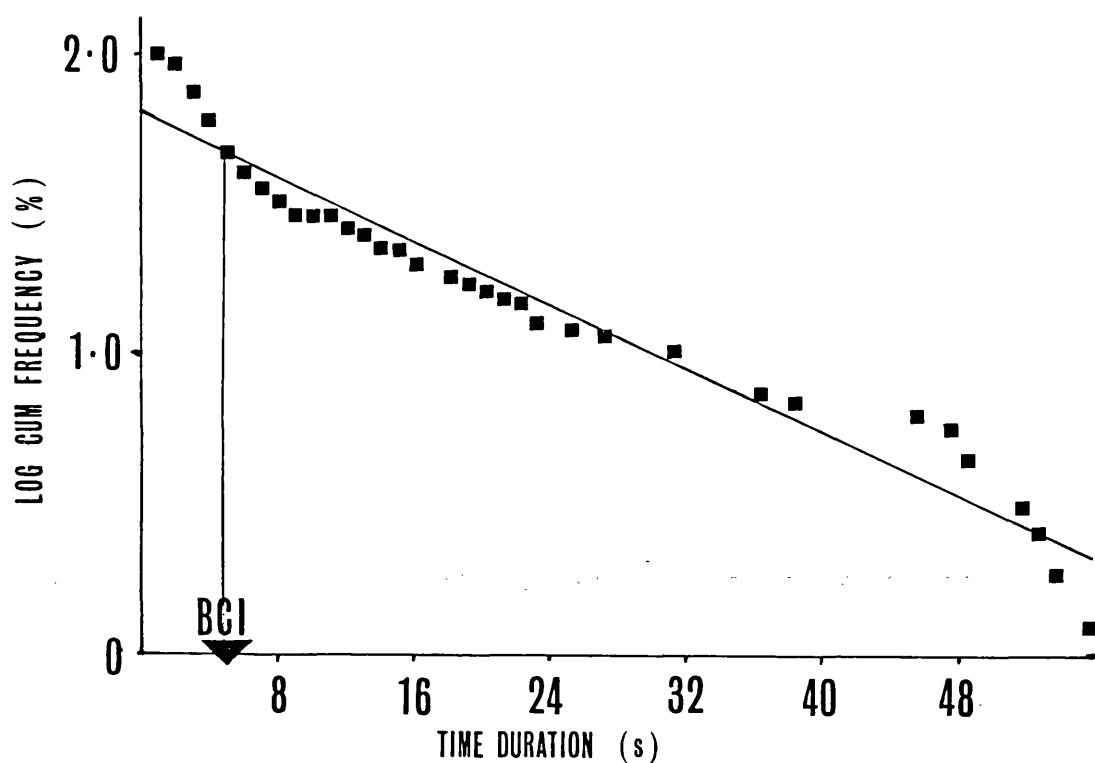
determine whether or not Point and Attentive were part of a bout, bout criterion intervals had to be calculated. This was performed by producing log survivorship curves (Slater 1974, Machlis 1977) with a regression line fitted through the points (Figures 13 and 14). A log survivorship plot gives the probability of a behavioural event occurring for the time elapsed since the last event. The method adopted in this study was to plot a regression line through the points in order to standardise a way in which the bout criterion interval (BCI) could be determined easily. Methods for producing BCIs involve either estimations by eye or the fitting of exponential curves from the Poisson distribution (Machlis 1977). These methods have a degree of misassignment of interval values (Slater and Lester 1982). BCIs were 7 seconds for Point and 6 seconds for Attentive.

The objective of bout analysis was to investigate the temporal form of the predatory act. Table 14 shows that the number of bouts decreases with approaching satiation (ANOVA  $F = 21.64$ ,  $p < 0.001$ ,  $df = 3/225$ , Sokal and Rohlf 1981).

Table 15 presents bout lengths. Bout duration remains constant for the first three indices of hunger but significantly rises for a stomach content of 16-20g ( $t = -3.14$ ,  $p = 0.006$ ,  $df = 3/$  ).

Times to the commencement of the first bout (Table 16) increases with stomach content (ANOVA  $F = 10.04$ ,  $p < 0.001$ ,  $df = 3/225$ ).

**FIGURE 14** Log Survivorship curve with fitted regression line  
for the behaviour Attentive.



**TABLE 14** Mean frequencies of bouts for 4 different categories of hunger.

<u>STOMACH CONTENT (g)</u>	<u>MEAN</u>	<u>S.D</u>
0 - 5	4.08	1.68
6 - 10	3.24	1.98
11 - 15	1.44	2.31
16 - 20	0.40	0.91

**TABLE 15** Mean duration of bouts (s) for 4 different categories of hunger.

<u>STOMACH CONTENT (g)</u>	<u>MEAN</u>	<u>S.D</u>
0 - 5	35.7	25.0 (99)
6 - 10	43.1	34.1 (81)
11 - 15	32.2	25.9 (36)
16 - 20	86.5	55.2 (10)

(Values in brackets indicate the total number of bouts in analysis)

Handling times remain constant over all indices of hunger (ANOVA  $F = 0.12$ ,  $p > 0.05$ ,  $df = 3/81$ ). Results are displayed in Table 17.

The overall trend of these results is that there were more bursts of activity, occurring more quickly, when pike were hungry and that for the first three hunger categories bout lengths remained the same. Prey fish, once caught, take the same time to handle but the pursuit time increases as pike become more satiated (ANOVA  $F = 4.65$ ,  $p < 0.001$ ,  $df = 3/81$ ).

The frequency and distribution of the durations of Point from log survivorship data shows that when points occur in the behavioural sequence they tend to be of a short length and are mostly classed as within bout intervals. However, there is a skew towards within bout intervals at 0-5g stomach content which is reduced as stomach content increases (Figure 15, Figure 16). The frequency distribution for the stomach content of 16-20g exhibits the least range of point durations with most confined to within bout intervals. This result should be considered apart from the rest of the distributions as the number of points that occurred at this index of hunger was considerably smaller than other sample sizes ( $N=17$ ).

Methods of analysis in this part of the study demonstrated that in nearly all cases a significant change in the frequency of behaviours occur between 6 - 10g and 11 - 15g stomach content (t-test on PT, AP and CP;  $p = < 0.001$ ,  $< 0.001$  and 0.003 respectively). The change in state as defined by overt behaviour corresponds to a range of food

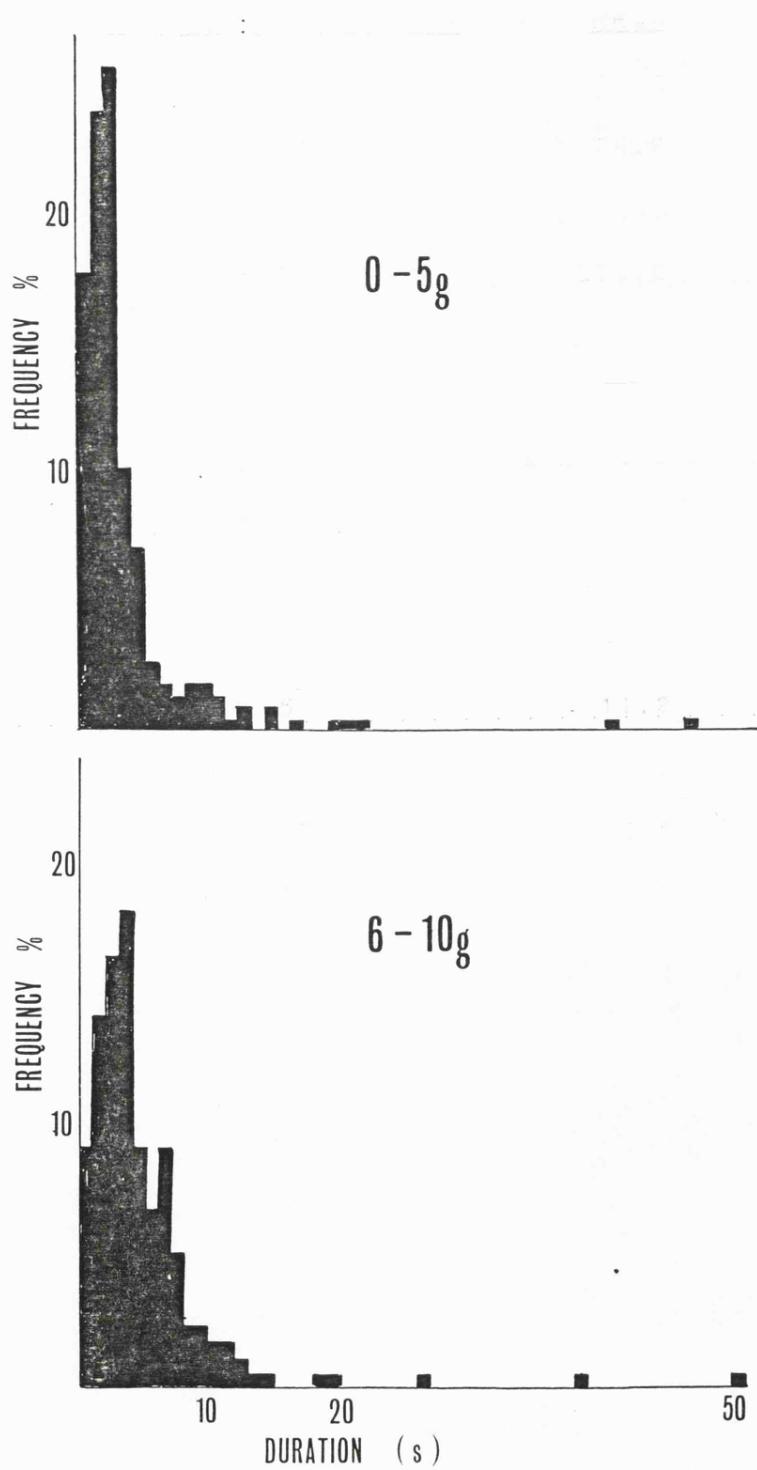
**TABLE 16** Mean times (s) to start of the first bout for 4 different categories of hunger.

<u>STOMACH CONTENT (g)</u>	<u>MEAN</u>	<u>S.D</u>
0 - 5	31.2	85.5
6 - 10	76.6	114.0
11 - 15	206.0	137.0
16 - 20	213.0	134.0

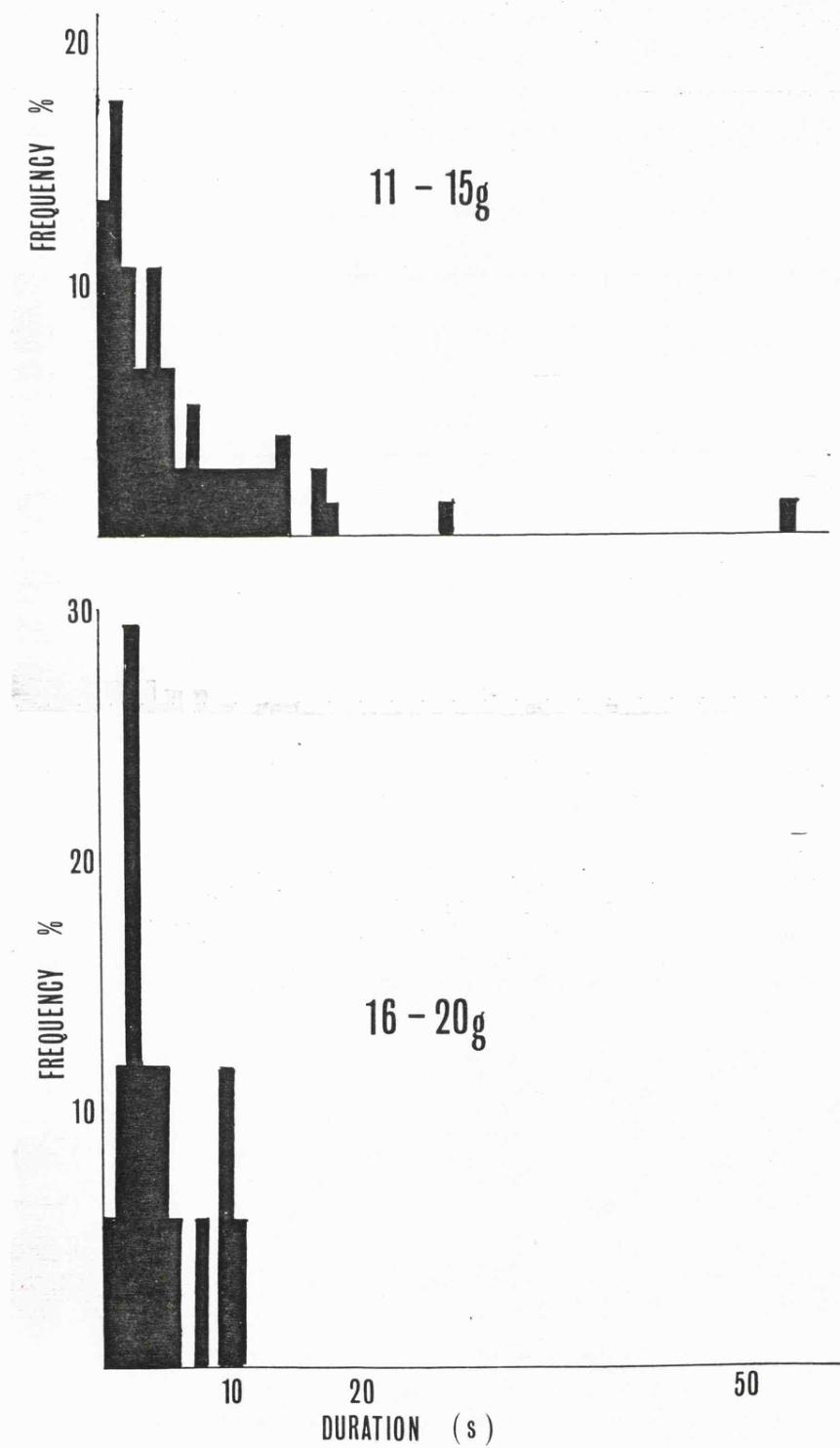
**TABLE 17** Mean handling times (s) for 3g prey at 4 different categories of hunger.

<u>STOMACH CONTENT (g)</u>	<u>MEAN</u>	<u>S.D</u>
0 - 5	11.2	11.5
6 - 10	12.9	8.3
11 - 15	12.7	12.6
16 - 20	11.1	10.3

FIGURE 15 Percentage frequency distributions for durations  
of Point for pike with stomach contents of  $0 \pm 5g$   
and  $6 \pm 10g$ .



**FIGURE 16** Percentage frequency distributions for durations  
of Point for pike with stomach contents of  
11 - 15g and 16 - 20g.



weight in the stomach equivalent to 6.28% and 9.42% of pike body weight. It was assumed that the intermediate state be set at the middle of this range (7.85% pike body weight). This value would then be used in future work.

### 3.5 DISCUSSION

In Experiment 1 an attempt was made to relate initial predatory response to the internal state of an individual pike. This had disadvantages in that although hunger affected an animal's readiness to feed, this response did not necessarily define the hunger state of an individual. For example, the responsiveness of an animal may be nil when the amount of food eaten reaches a certain level or it may reach a level beyond which no increase in response is seen with rising hunger. Ruiter (1963, 1967) suggested, therefore, that it is advisable to define hunger in terms of the feeding regime of an animal rather than in terms of overt behaviour. The results of this investigation achieved this by firstly controlling for the amount of food consumed by a pike and then relating its behaviour to the amount of food contained in the stomach at any particular time.

A full consideration of the foraging behaviour of pike was neither intended nor studied, with interest primarily confined to the representation of feeding behaviour and a pike's hunger. A mid point of response could then be used to satisfy conditions necessary for evaluating the interaction between external stimuli and internal state (Experiment 3).

As Hinde (1970) stated "the skill of the experimenter lies in selecting animals in an intermediate state in which the differences in models will be shown up to the best advantage". The intermediate state derived is such that pike will still respond to prey but not with the probability found for greater degrees of hunger. The use of discriminant function analysis is recommended to identify the region where overall changes in response occur markedly within a range of hunger motivated behaviours. This can then be followed up by the use of significance tests on selected behaviours to identify changes in response more precisely.

The approach in this study, then, is not dissimilar to other investigations of hunger, in that, the effect of hunger on feeding behaviour was examined by recording changes in response as pike became more satiated. Dill (1983) summarised a set of predictions for the foraging behaviour of fishes as satiation approached. These were that the amount of searching and the conditional probabilities of consecutive behaviours, such as strike/capture, would decrease and that handling times would increase with approaching satiation.

Frequencies of behaviours performed by pike decreased with increasing satiation (analogous to consecutive behaviour probabilities decreasing) and times to the commencement of bouts decreased with which a similar comparison can be made to observations quoted by Dill (1983) for the discovery of prey by 3-spined stickleback (Beukema 1968) and approaches towards prey in sunfish (Chiszar and Windell 1973). Handling times of pike remained constant over all categories of

hunger and therefore does not conform to Dill's prediction. However the reason for this is probably due to the way in which handling time is defined. Handling time was taken as the time from capture of prey to swallowing whereas Dill's handling time included the time taken to capture prey as well. This difference often causes misunderstanding in considerations of handling time (Street et al 1984). The fact that handling time remains constant in pike implies that the speed with which pike handle their prey is probably related to the physical size of prey and the morphology of a pike's jaw.

As in experiment 1, prey capture sequences were not affected by hunger alone but were also modified by the interaction of the pike, of internal state and the actions of the minnow school. Individual pike influenced the frequency with which behaviours in the sequences were exhibited. Influence on the behaviours was the same as for the effects of hunger, with the exception of the behaviours approach and strike. Approach and strike were not influenced by the individual and it may be suggested that these two behaviours are hunger motivated and prey specific. That is, satiation has a modulating influence on the appearance of these behaviours in the prey capture sequence and that the reactions and nature of the minnow school were likely to determine the approach and strike of prey.

The variation in the behaviour of individual pike was emphasized in the results for discriminant function analysis. Seven out of ten original behaviours in analysis were

selected, demonstrating the complexity of the attack sequences. When a stepwise process for the influence of hunger alone was carried out, only three behaviours were selected. This confirmed that the interaction between hunger and individuals could not be treated separately. It must be clarified here that individual effects include pike - prey interactions and not the variability in the performance of individuals alone. The variability in response at each of the hunger categories was further shown in the three dimensional plots where pike 1 and 2 were still demonstrating strong feeding responses at a hunger category of 11 - 15g stomach content. The influence of these pike affect the appearance of the data at the two more satiated indices of hunger and may account for the deviations from the mean for behaviours exhibited. Explanation of such deviation can be attributed to the individual differences in behaviour or the minnow school as the size class of pike used in this experiment was similar.

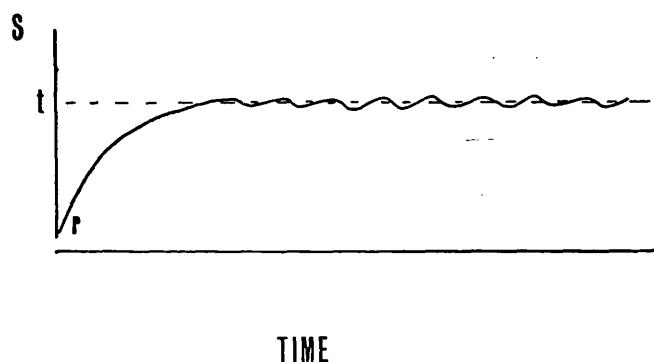
Beukema (1968) recognised that hunger was determined by at least two components. These were a gastric component relating to the amount of food present in the gut and a systemic one relating to metabolic conditions within the animal. These components of hunger were both dependent upon the interval of fasting (deprivation time). Although overall deprivation had no effect on the total amount of food consumed in a day by 3-spined sticklebacks, the rate of initial consumption was higher than average in the first hour of feeding with longer deprivation times. Colgan (1973) also supports the the influence of deprivation time on subsequent

feeding behaviour and for this reason, deprivation time was controlled in this experiment. The influence of deprivation time, therefore, may not be attributed to the variation in predatory behaviour seen.

A greater number of captures occurred at categories of 0 - 5g and 6 - 10g stomach content. Ruiter (1967) plotted a time course for fish feeding responses with satiation (Figure 17). The relevance of this time course to this experiment is that the response line follows, essentially, the course of trials and the sequence in which trials were filmed in relation to the hunger of an individual. The feeding pattern of fish is such that after the stomach is empty the rate of feeding is fast and satiation is reached quickly (this may correspond to results from 0 - 5g and 6 - 10g stomach contents). This is then followed by intermittent feeding (11 - 15g and 16 - 20g stomach content) with individuals not deviating far from the point of satiation. Wherever a trial occurred in relation to this feeding line might determine the degree of response at more sated categories of hunger. This curve may explain the frequency of behaviours seen and account for the variability of pike within a chosen hunger category.

The general form of a pike's predatory behaviour was modified by increasing satiation with a general reduction in the number of behaviours elicited, which in consequence affected the number of bouts seen. The duration of bouts, when they occurred at the first three indices of hunger, remained unchanged suggesting that bursts of activity in the pursuit of prey were stereotyped for pike and the actions of the

**FIGURE 17** The time course for overall satiation (S) is  
A possible explanation for feeding behaviour  
exhibited in Experiment 2. (After Ruiter 1967)



( t = threshold of satiation after which feeding responses cease; r = the time pattern of feeding responses )

minnow school. The frequency of bouts and their duration at varying degrees of hunger is different to findings of Hart and Connellan, pers comm, in that the number of bouts was seen to increase and be of shorter duration as satiation increased in their experiments. The implication from their findings is that pike appeared more "indecisive" whether or not to pursue prey at more satiated indices of hunger and that periods of prey assessment interrupted the overall pursuit of prey. The results of this experiment imply that once a pike is alerted to the presence of prey, pursuit follows in bouts, the durations of which appear to be fixed temporally and the frequency with which they occur being dependent on the individual and the action of the prey school.

This experiment shows the effects of hunger and the individual on the nature of the predatory behaviour of pike. The omission from the work so far is the influence that the appearance and actions of prey have on subsequent feeding behaviour. The determination of an intermediate hunger state, as demonstrated by predatory responses, facilitated the study of the role of external stimuli and their interaction with internal state to be carried out in future work.

#### **4 EXPERIMENT THREE. An investigation of effective stimuli and their interaction with hunger states in the attack response of pike.**

##### **4.1 INTRODUCTION**

In the sequence of events that may make up the predatory behaviour of an animal, actions such as the capture, killing and eating of prey may be controlled by the nature of the stimuli that the animal perceives. In experiments one and two the influence of internal state and its modifying affect on pike predatory behaviour was identified. In this experiment the role and significance of prey characteristics was determined.

As an animal receives information from its environment it selects which part of the environment to respond to and that which to ignore through a process of stimulus filtering (Manning 1979). The way in which information is filtered is of no direct importance to this study but the influence of a change in part of the environment on the state of a pike has important implications on the way in which the effects of stimuli are studied. A change in the environment can influence an animal in three ways. Firstly, a change may alter an animal's physiological state, secondly it may change the outcome of the relationship between a particular behaviour and its consequences and finally a change in the

environment may provide stimuli that an animal can evaluate perceptually (McFarland and Houston 1981). These considerations of the influence of environmental change lead to the conclusion that stimuli and motivation almost always interact to determine the nature and strength of an animal's response (Manning 1979). The objective of this part of the study, therefore, was to determine the interaction between stimuli and motivation in bringing about the attack response of pike.

The study of effective stimuli that may elicit the prey capture response in pike has not been considered in depth. Early works such as those of Meesters (1940) and Hoogland et al (1957) and more recently that of Christiansen (1976) demonstrated that the nature of prey objects could influence the attack response of pike. Most consideration has been devoted to the selection of prey items by pike (Mauck and Coble 1971, Coble 1973, Nursall 1973, Hart and Conellan 1984) but none have taken into account the interaction between stimuli and hunger-motivated processes (see general introduction for a review). This study therefore attempts to identify some specific components of prey stimuli and to demonstrate how the response of pike towards such stimuli is subject to change with degrees of hunger.

The investigation of response specificity to certain stimuli has been extensively carried out on other animals. The classic work of Tinbergen (1951) showed that male three-spined sticklebacks produced a greater number of attacks on crude red-bellied models than on accurate fish

representations that lacked the red colouration. Baerends and Kruijt (1973) demonstrated similar selective responses in the retrieval of eggs by herring gulls with the birds responding to size, shape and colouration of eggs. Stimuli evoking these responses have been called 'sign stimuli'. However, different aspects of the same object may elicit different responses depending on the motivation or activity being carried out by an animal at that time. For example, gulls showed different responses to a range of egg shape and colouration depending on whether they were feeding or incubating (Baerends and Kruijt 1973). In a similar manner it may be hypothesized that the response of pike to prey items may alter with degrees of satiation. Although this investigation was designed to extract effective stimuli from a complexity of possible prey characteristics, no inference will be made to 'sign stimuli' as degrees of response to prey made by an animal when feeding is probably due to the heterogeneous summation of diverse stimuli (Manning 1979).

Fish can recognise prey by one or more of three sensory modalities, vision, olfaction and the use of the lateral line. In this study emphasis was confined to the visual sense in pike for two reasons. Firstly, the visual sense in pike is deemed most prevalent (Solman 1945, Hoogland et al 1957, Coble 1973, Christiansen 1976) and secondly for logistic reasons in that manipulation of prey characteristics could be more easily carried out.

Studies of the visual sense in fish have been numerous, ranging from investigations of the discriminative

capabilities of fish towards colour, form, shape and size of objects, to the histological and electrophysiological examinations of the structure of the visual organs (Hester 1969). From such studies it is possible to summarise the nature of vision in fish, with attention to pike in particular, as a necessary background for formulating a method for determining effective stimuli.

Fish perceive light in the  $400 - 750 \times 10^{-6}$  m wavelength range and can detect objects at light intensities of  $10^4$   $10^5$  down to  $10^{-5} - 10^{-7}$  luxes. Most fish have well developed colour vision which may vary between species (pike can perceive the whole range) and all fish can perceive motion. The reader is referred to texts such as Protasov (1968) and Hoar and Randall (1971) for detailed accounts. The perception of motion is characterized by the capacity of a fish to distinguish objects moving successively through the visual field in n seconds. This ability varies with daylight and temperature. Perception of movement is expressed in optical moments ( $1/n$ ). Pike have a highly developed capacity to detect motion with optical moments of  $0.04 \text{ s}^{-1}$  compared to slower moments for non-predatory herbivore feeders. These factors must be taken into account when evaluating the significance of visual stimuli.

## 4.2 METHODS

### 4.2.1 BACKGROUND

The work carried out in this investigation can be divided into two parts, namely the nature of the stimulus (shape and movement) and the affects of hunger on the responsiveness of a pike to stimuli.

The apparatus used in this series of investigations was adapted from work by Gandolfi et al (1968) and Fehring (1974), the requirement being that components of stimuli be easily altered, for example, the shape and nature of movements, and each presentation of a stimulus be a true replicate of the one before. The need, therefore, was an apparatus that could be both adaptable and also consistent in its presentation of stimuli.

Gandolfi et al (1968) used models of fish which could be stationary, moving rectilinearly or wriggling. The models were presented to fish from behind a screen and were moved by mechanical means. Fehring (1974) took Gandolfi's system and adapted it for the production of shadows which represented different feeding stimuli to largemouth black bass, *Micropterus salmoides*. He produced shadows of different natured stimuli by means of rear projection onto opaque albanene paper and movement was created mechanically by a system of booms, cams and pivots. This type of apparatus was adapted for this study but the descriptions and dimensions of

Fehring's apparatus were not sufficiently detailed to allow his equipment to be reconstructed.

The end result was an adaptation of the two systems. The apparatus built could present both shadows and three-dimensional models and was designed so that presentations took place outside the tanks that the pike were in.

The adoption of shadow casting as a means of showing feeding stimuli to pike was justified by the fact that nearly all fish respond to a moving shadow (Protasov 1968) and that such a technique offered the possibility of creating a wide range of stimuli in a convenient way.

#### 4.2.2 CONSIDERATIONS FOR THE METHOD

The rationale behind this investigation was that pike were presented with stimulus situations differing in known physical characters, and any difference in response to these would suggest that these characters were significant for the feeding response in question (Hinde 1970).

In an investigation of the effectiveness of a stimulus, the first stage of the method is to compare naturally occurring situations which do and do not affect the response in question (attack response) and to form an hypothesis about the nature of the effective stimulus. A background to this was gained from the performance of prey fish in experiment two.

The characters of a complete stimulus eliciting a particular response can be found by systematically varying the situation and assessing the response. A comparison between response strengths to differing stimuli indicates whether or not the difference is significant to the response in question.

The results from experiment one provided observable parameters for assessing response strengths and those of experiment two enabled pike of an intermediate state of hunger motivation to be used for initial stimulus presentation; a requirement in determining effective stimuli (Hinde 1970). Pike were selected from the criteria of section 3.4.2 at a hunger state where an individual would still capture prey but not with the probability of a starved pike.

An artefact of stimulus work is that, in general, high intensity stimuli are more likely to be responded to than those of lower intensities (Hinde 1970). Therefore, in this experiment, physical properties such as the size of the stimuli was kept constant, the maximum length of any silhouette or model being less than one third the body length of an individual pike in compliance with the observations of Hoogland et al (1957) and Nursall (1973) on the optimal prey size for pike. Also, properties of the colour of the stimulus and the background were also controlled and will be detailed later.

#### 4.2.3 BASIC METHODS

The experimental method adopted here is similar to other stimulus investigations in that models or silhouettes were presented successively to individual pike and those that produced the strongest response were determined statistically from the number of behaviours recorded on video tape.

##### 4.2.3.1 APPARATUS FOR PRESENTING STIMULI

The apparatus consisted of an aluminium boom held in a block that facilitated vertical movements. This block was attached to a rotating drum shaft of a kymograph so that the boom revolved over a plate which could be ridged in order to produce irregular vertical movements. Silhouettes were suspended on thin electrical wire and shadows cast by a 60w gun lamp. (For further arrangement and dimensions see Figure 18 and 19).

Pike were kept in aquarium tanks of dimensions 32 x 38 x 100 cm with an 'ozatex' paper screen at one end for shadow casting and screens of MSC safety film for three-dimensional presentations. The safety film acted as a one way mirror system so that a pike could see a prey fish without the prey fish altering its behaviour due to recognising the presence of a predator.

FIGURE 18 Diagram of the apparatus that produced moving stimuli in experiment 3.

(see overleaf)

KEY

Diagram A. Top view of the boom mounting

ds	drum shaft of a kymograph
mt	metal block mounting
p	pivot
b	boom

Diagram B. Arrangement of boom and wheel

b	boom
s	securing screw
w	wheel

Diagram C. Whole apparatus viewed from the side

b	boom
ds	drum shaft
k	kymograph base
m	model
pl	plate leg
w	wheel
wr	wheel rod

**FIGURE 18** Diagrams of the converted kymograph that produced different movements in the stimuli presented to pike in experiment 3.

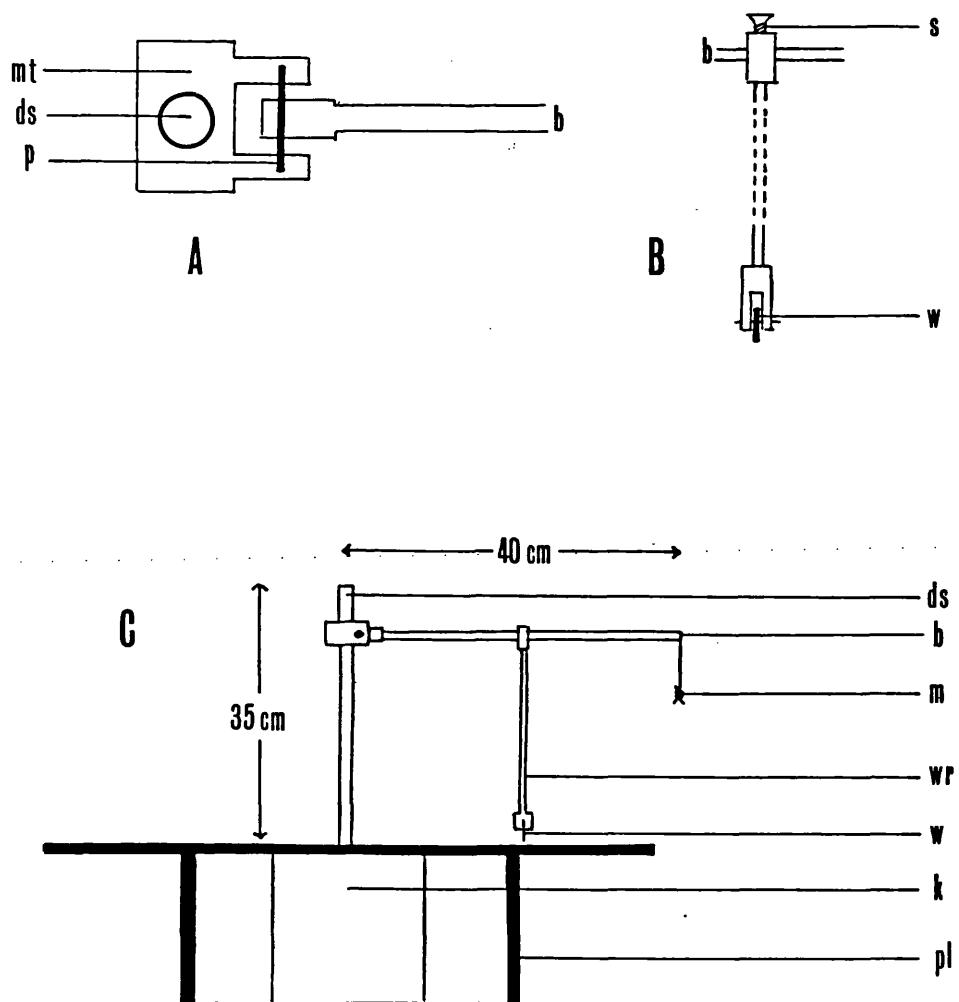
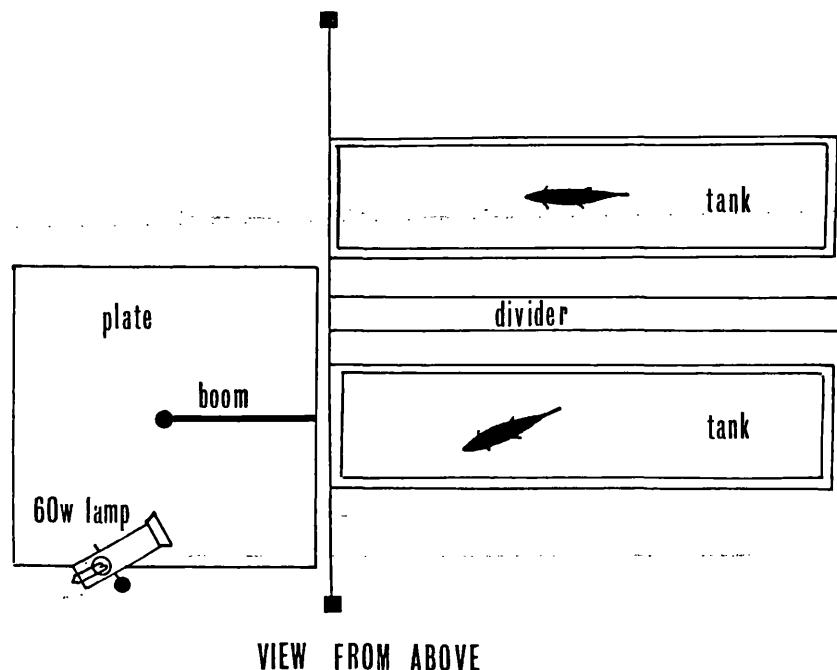
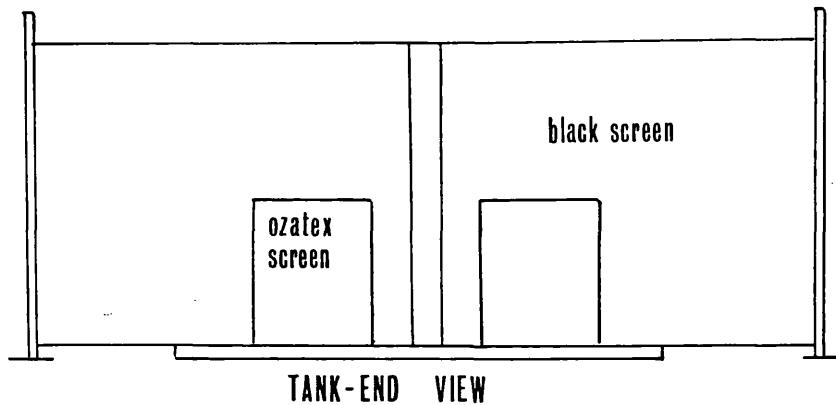


FIGURE 19 Tank arrangements for the presentation of moving stimuli, viewed from the side and above.



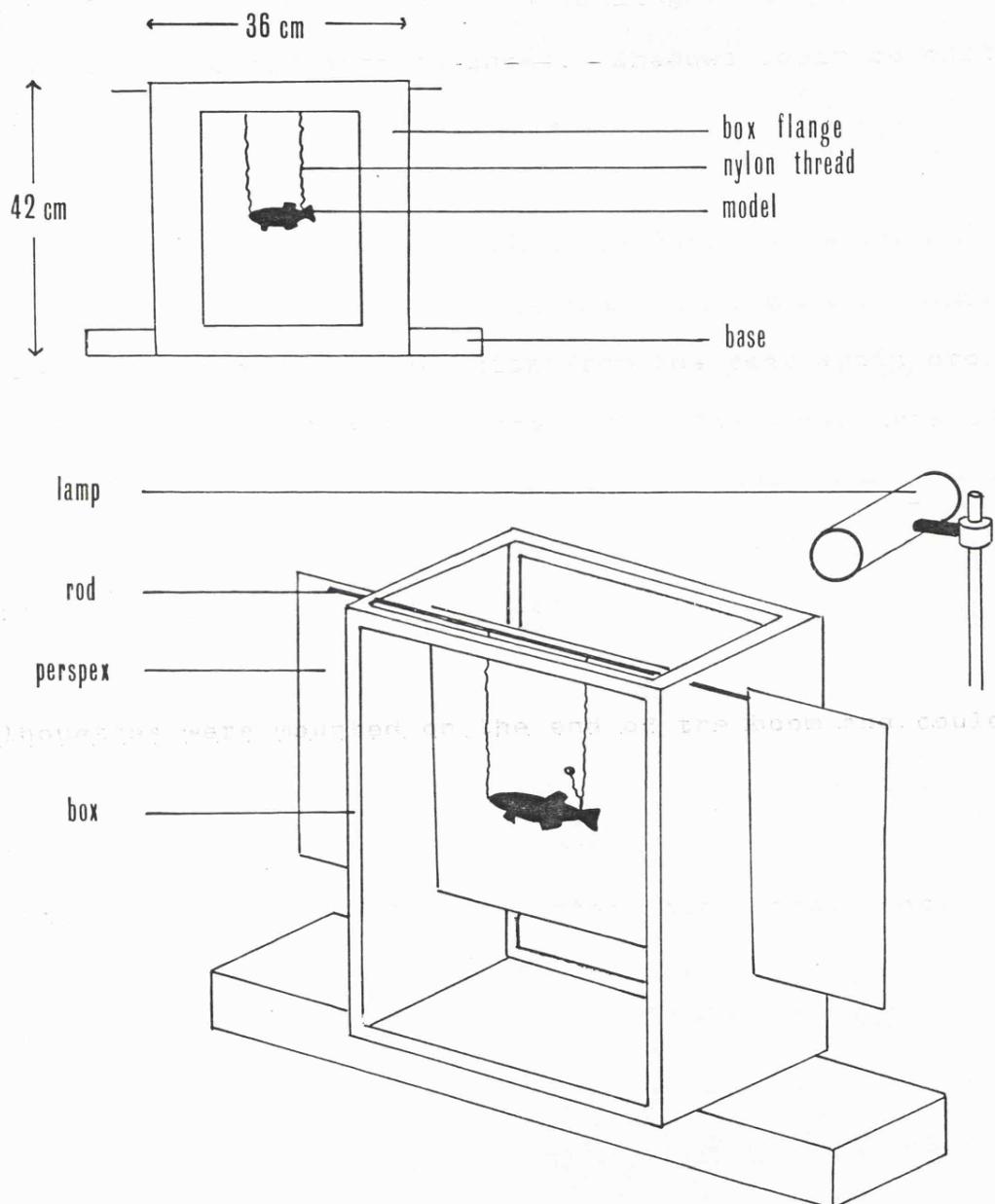
VIEW FROM ABOVE

Three-dimensional presentations were by means of a presentation box acting as a false end to the tanks. Models were suspended from a metal rod by transparent nylon thread and movement could be induced by pulling on the thread that ran through a clear perspex sheet. Shadows could be cast by illumination from the rear of the box (Figure 20).

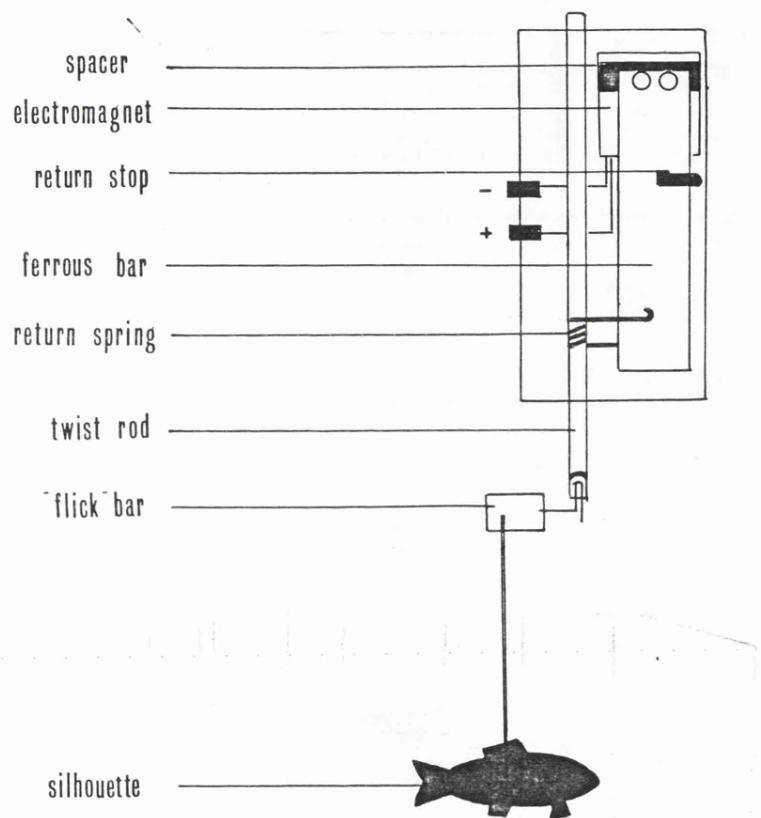
Shadows of live fish swimming were created by using the false end system with a glass tank (dimensions 32 x 38 x 7 cm) filled with water. Illumination from the rear again produced a shadow as the fish swam in the tank. The dimensions of the tank were such that the prey fish had sufficient room to turn around but were restrictive enough for clear shadows to be cast onto the ozatex paper screen.

Silhouettes were mounted on the end of the boom and could be made to move by having the boom rotate about the central shaft. The speed of horizontal movement was  $0.16 \text{ ms}^{-1}$ . Inevitably this method lead to intermittent appearance of the shadow. A rod, mounted on a wheel, supported the horizontal boom. The wheel could travel over a smooth or ridged surface causing the silhouette to move up and down or remain static. Vertical movements on the screen were approximately 1 cm in amplitude. Sinusoidal movements of the shadows were brought about by a multi-vibrator communicating with an electro-magnet box. The electro-magnet box was fixed to the end of the boom and as the multi-vibrator produced pulses of current silhouettes were caused to twist at a rate of  $1 \text{ s}^{-1}$ . (Figure 21)

**FIGURE 20** Stimulus box used for presentation of a three dimensional stimulus and fish shaped shadows with sinusoidal-like movements.



**FIGURE 21** Design of the electro-magnet box which created sinusoidal-like movement in stimuli that moved horizontally.



The flick speed was a pre-set oscillation in the machinery of the equipment and not determined by any calculation for an average caudal fin movement in a prey species. The movement created was that of caudal movements of a fish and not that of cetacean swimming.

Direct light to the screen and illumination inside the tank were kept as constant as possible. Light readings measured on a Gossen luna-pro light meter were taken when lights were being set up in the trials.

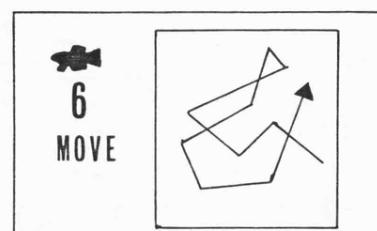
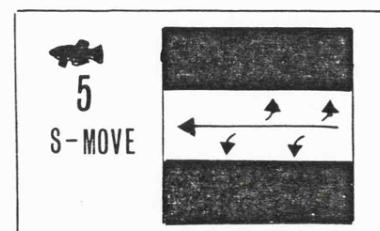
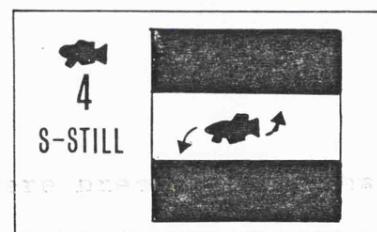
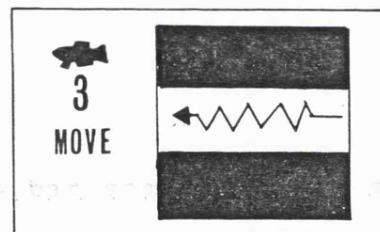
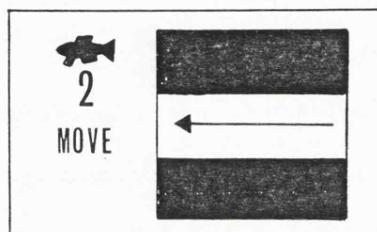
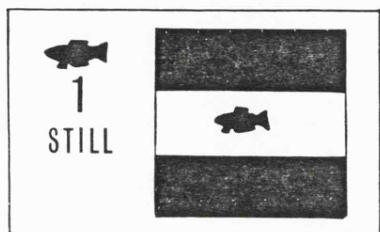
#### 4.2.3.2 STIMULI PRESENTED

Silhouettes and models used had the same surface area of 9.5 cm<sup>2</sup> and were of length 7.0 cm and height 1.5 cm. These dimensions were chosen from the size of fish selected for model production. The three-dimensional models were made from latex, cast in Plaster of Paris moulds. Silhouettes were cut from card and painted black. The size and shape of the live fish used in shadow presentations was kept to the dimensions of the model fish as far as was possible, in order to keep the intensity of the stimulus constant.

Two shapes were used for stimulus presentations; a fish shape and a bar shape. These shapes were presented in shadow and three-dimensional forms within a range of six possible movements. The treatments were as follows -

- (1) Shadow (or model) held stationary on the screen.
- (2) Intermittent shadow moving horizontally across the screen.
- (3) Intermittent shadow moving horizontally with irregular vertical components.
- (4) Shadow moving sinusoidally about a fixed point with respect to the x axis.
- (5) Intermittent shadow moving horizontally with sinusoidal components.
- (6) Shadow of a live fish swimming.

**FIGURE 22** Representations of how the stimuli appeared on the screens of tanks in experiment 3. (For full details of treatments refer to 4.2.3.2)



Representations of how these stimuli appeared on the presentation screen are given in figure 22. In the following text movements will be referred to by the numbers listed above and treatments of shape (form), movement and hunger are detailed in Table 18 in 4.2.3.5.

Light intensity and contrast measurements for the silhouettes and models were recorded using a Soligor Spot Sensor 11. This enabled fine measurements of light intensity to be taken for silhouettes and the background in a  $1^{\circ}$  angle of incidence. Results of these readings were used for the interpretation of responses of pike to the different stimuli. An exposure value conversion table is given in the appendix plus the method for working out contrast.

#### 4.2.3.3 METHOD 1

Five pike were used initially. Four tanks were occupied for observation at any one time thereby allowing one pike to be in a "time-out" state at some time during the course of stimulus presentations. Time-out was a period designed to allow fish to forget so that the conditioning and habituation effects incurred from trials would be lost. Trials consisted of:

- (1) SET UP TIME : The clock, camera and trial card were set up. The clock was started and the pike allowed to settle down.

(2) PRE-STIMULUS OBSERVATION : After 15 minutes from the start of the clock, pike in a resting state were filmed for two minutes.

(3) STIMULUS OBSERVATION : The kymograph was switched on and the stimulus presented twenty times at a frequency of 4  $\text{min}^{-1}$  for moving presentations. After 5 minutes a trial end and filming stopped. In the case of stationary presentations, the stimulus remained on the screen for the duration of a trial.

The responses of individual pike to the stimuli presented were recorded by the video unit using a wide angle lens on the camera to encompass the whole of the aquarium tank.

#### 4.2.3.4. ANALYSIS OF BEHAVIOURAL SEQUENCES

In principle this was the same as described in experiment two with a few alterations for the new experimental system. Again trials were recorded by video-tape machine and event recorder. As no prey could be caught in this set up, the behaviours 'capture', 'hold' and 'manipulate' were removed from the analysis, as were 'stop', 'chase' and 'stalk'. The rest of the behavioural repertoire remained as defined in section 2 but with three new additions.

The new additions to the behavioural repertoire were,

- (i) Orientate - The turning of a pike towards the stimulus.
- (ii) Snap - Rapid jaw movement opening and closing whilst pike is still in 'point'.
- (iii) Snake - Sinusoidal movements of tail region whilst in point.

Analysis of trials and behavioural sequences was as outlined in experiment two.

At the end of the series of trials described in method 1, a control for the effects of habituation to stimuli was carried out. Nine pike were used, all were at an intermediate hunger motivated state. All pike were subjected to a live fish stimulus at day 0. On day 3, pike A, B and C were given the stimulus again. On day 10 and day 14, individuals D, E and F and G, H and I were exposed to the stimulus respectively.

It may also be mentioned here that no sexing of the fish was carried out and although size differences are present in the adult which can influence feeding, the pike in this experiment were considered immature enough to negate sex influence.

#### 4.2.3.5 METHOD 2

This was the same as section 4.2.3.3 but allowances were made for the effects of negative reinforcement incurred in stimulus presentations. Five new pike were added to the system bringing the number to ten. First time presentations were now only taken for analysis. As far as possible the

TABLE 18 Possible combinations of stimulus treatments in Experiment 3. (\* indicates trials performed)

The form of stimuli presented were of three types:

F1 = Bar shadow, F2 = Fish shadow, F3 = 3-D fish model.

Movements were of six types numbered 1 to 6 and are described in 4.2.3.2 and Figure 22.

There were two categories of hunger used:

H1 = stomach content of 7.85% body weight of pike,

H2 = empty stomach

	MOVEMENT 1	2	3	4	5	6	
	1	2	3	4	5	6	
F1	*		*	*			H1
	*		*	*		*	H2
F2	*	*	*	*	*		H1
	*		*	*	*		H2
F3	*			*		*	H1
						*	H2

least effective stimuli (those combinations of form and movement which were less like real prey) were presented first in a sequence of presentations. Table 18 presents the treatments of stimuli given to the pike. Stimuli were presented to pike firstly at a hunger state corresponding to a stomach content of 7.85% pike body weight and then when pike were hungry after one week's deprivation of food to ensure gastric evacuation.

In the event of a pike striking at stimuli, that individual was removed from the experimental system for a minimum of 14 days to allow conditioning effects to be lost. Such a regime appreciably reduced the number of trials that could be performed, hence some of the matrix of possible stimulus combinations was not completed. This fact was coupled with complications in the later trials whereby deconditioning of individuals could not be guaranteed. To reduce this effect as much as possible the order of trials was such that presentations to hungry pike followed the series of presentations of stimuli to pike at an intermediate hunger state.

#### 4.3 RESULTS

##### 4.3.1 The effects of replication on the attack response of pike to four shadow treatments.

Table 19 presents the results obtained from method 1 (4.2.3.3) for the response of pike to four fish shadow

TABLE 19 Mean number of behaviours exhibited in each of five trials for the response of five pike to four different fish shadow treatments.

	SHADOW 1		SHADOW 2		SHADOW 3		SHADOW 4	
<u>TRIAL</u>	<u>MEAN</u>	<u>S.D</u>	<u>MEAN</u>	<u>S.D</u>	<u>MEAN</u>	<u>S.D</u>	<u>MEAN</u>	<u>S.D</u>
1	4.0	6.0	10.6	19.2	14.6	17.2	72.8	20.9
2	9.2	7.6	1.0	0.0	3.6	5.2	29.8	10.4
3	3.4	3.0	4.2	4.1	3.8	5.6	18.0	7.8
4	6.8	3.4	6.0	3.6	1.0	0.0	21.0	8.1
5	9.2	8.9	3.8	3.8	3.2	3.1	16.0	5.8

(Shadow 1 = stationary fish shape, Shadow 2 = horizontally moving fishshape, Shadow 3 = fish shape moving horizontally with irregular vertical components, Shadow 4 = swimming fish)

TABLE 20 The effect of replication on the responses of pike to four different shadow treatments. Regression coefficients are given for the log number of behaviours exhibited in each trial.

<u>SHADOW</u>	<u>R</u>	<u>P</u>
1	0.16	0.63
2	-0.13	0.88
3	-0.41	0.04
4	-0.70	<0.001

(Shadows as numbered in table 19)

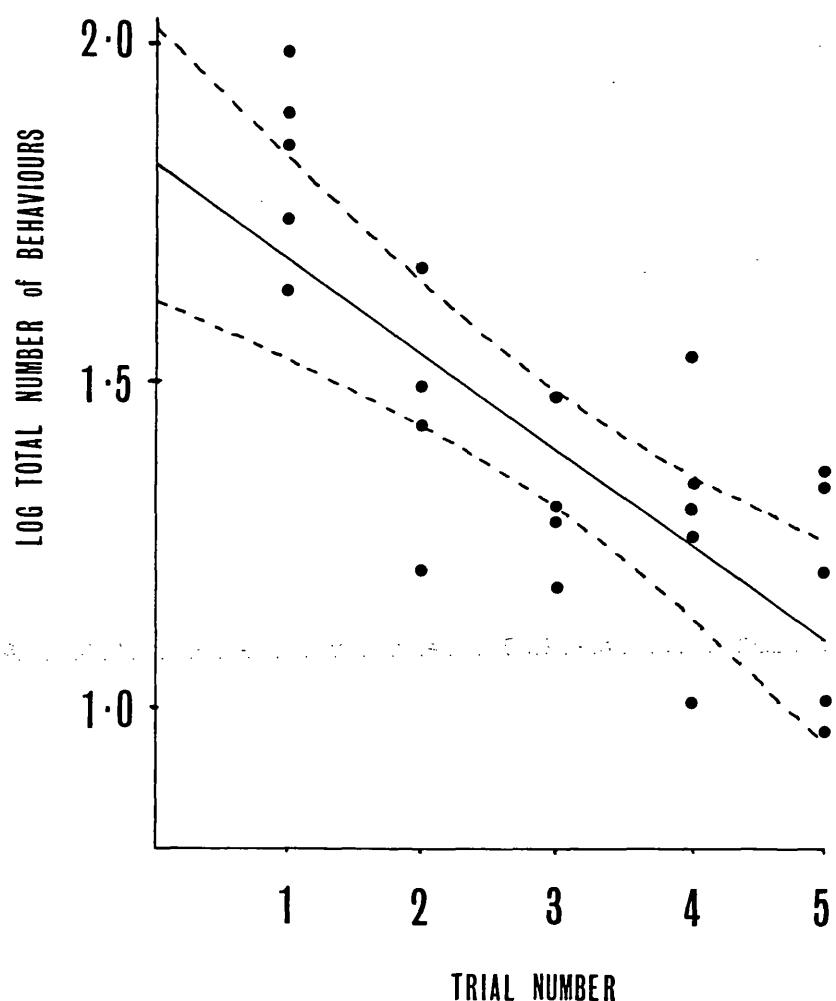
stimuli. The influence of replication was derived from plots of the total number of behaviours performed in a trial against trial number for each of the shadow presentations. Regression analysis was then used to describe the trend in behaviours performed in successive trials (SPSS PLOT procedure, Hull and Nie 1981).— Table 20 displays regression coefficients for each of the four stimuli presented.

The stimulus of a fish shadow held stationary on the screen produced a regression of slight positive slope but with no effect of replication (Anova, Sokal and Rohlf 1981,  $F = 0.63$ ,  $p > 0.05$ ). The response of pike to the horizontally moving fish shadow was also unaffected by replication (Anova,  $F = 0.02$ ,  $p > 0.05$ ). The total number of behaviours shown in trials for fish shadow stimuli that were moving horizontally with irregular vertical components, decreased with successive trials (Anova,  $F = 4.70$ ,  $p = 0.04$ ), so too for the response to a shadow of a live, swimming fish (Anova,  $F = 22.50$ ,  $p < 0.001$ ).

The trend in number of behaviours seen for the last two of the shadow presentations and the decrease in response in trials thereafter may be attributed to habituation effects from negative reinforcement when pike struck at the more effective shadows. Figure 23 shows a regression plot for pike responding to a live fish shadow stimulus.

In the following sections the effects of movement and hunger and then the effects of form and movement at two hunger states will be analysed.

FIGURE 23 Regression plot demonstrating the reduced response  
of pike towards stimuli presented in successive  
trials. (Values plotted for responses to a live  
fish stimulus)



4.3.2 The effects of movement and hunger on the attack response of pike towards different prey stimuli.

The form of the data obtained from method 2 (4.2.3.5) consisted of a large number of response variables (behaviours in the attack sequence) and sets of prey stimuli and the two hunger-motivated states of pike under consideration. This arrangement of data warranted the implementation of multivariate statistical analysis to locate relationships within the inter-related groupings of behaviours and dependent variables. However, tests for homogeneity in the data (Cochran's C test, SPSS MANOVA routine, Hull and Nie 1981) revealed that the data were not normally distributed, even when the data had been transformed to log, square root or arcsin (Sokal and Rohlf 1981). This meant that the assumptions for multivariate analysis could not be satisfied.

Statistical analysis was therefore confined to the use of non-parametric methods. However the use of discriminant function analysis (DFA) was still used to classify the overall attack responses to different stimuli. DFA is sufficiently robust enough to successfully sort the response variables in question, even though homogeneity does not exist (Freeman pers comm). However classification statistics involving levels of significance cannot be quoted from DFA as they assume normality in the data.

A list of the variables for the classification of groups of response are given in table 21. These were obtained from

**TABLE 21** Selected behaviours from stepwise discriminant function analysis for classifying the attack responses of pike to different stimuli.

<u>ORDER OF DISCRIMINATION</u>	<u>BEHAVIOUR</u>
1	POINT
2	ATTENTIVE
3	ORIENTATE
4	APPROACH
5	SNAP
6	BACK
7	INATTENTIVE
8	STRIKE

step-wise DFA (SPSS, DISCRIMINANT routine, Nie et al 1975) on frequencies of behaviours performed in trials for all treatments of stimuli. As such a large number of behaviours were selected (eight out of nine behaviours in the repertoire) statistical analysis was inherently complex involving multiple usage of Kruskal-Wallis oneway anovas (Sokal and Rohlf 1981) allowing for the effects of movement, form and hunger. The output from DFA will be described in a later section.

The eight behaviours selected by DFA were studied for patterns in frequency and in the time periods for selected responses such as the time spent looking at the stimulus and giving up times in trials of five minutes duration, in relation to each of the stimuli presented.

#### 4.3.2.1 Bar shadow stimuli.

Frequencies of behaviours in the attack response to bar shadow stimuli are given in table 22 for the two hunger-motivated states of pike. (For a description of treatments refer to table 18).

Figure 24 displays frequency histograms for bar shadow data. Significance tables for overall and between variable effects are given in the appendix. The tables are for Kruskal Wallis one way anovas (SPSS, NPAR TESTS, Hull and Nie 1981). This test works on ordinal numbers ranking the data and assesses differences between ranks for two or more groups (Sokal and Rohlf 1981). For between variable effects Mann Whitney 'U'

**TABLE 22** Response variables in the attack sequence of pike towards a bar shadow stimulus. Median values for the number of behaviours with ranges are given for two hunger states and three movements.

	MOVEMENT 1		MOVEMENT 3		MOVEMENT 4	
<u>VARIABLE</u>	<u>H1</u>	<u>H2</u>	<u>H1</u>	<u>H2</u>	<u>H1</u>	<u>H2</u>
ATTENTIVE	0.1	0.0	0.3	0.3	1.2	1.8
	(1.0)(0.0)		(1.0)(2.0)		(2.0)(3.0)	
INATTENTIVE	1.1	1.0	1.2	0.9	1.2	0.7
	(1.0)(0.0)		(1.0)(1.0)		(2.0)(2.0)	
ORIENTATE	0.1	0.0	0.1	0.1	0.8	0.5
	(1.0)(0.0)		(1.0)(1.0)		(1.0)(2.0)	
SNAP	0.0	0.0	0.0	0.0	0.0	0.0
	(0.0)(0.0)		(0.0)(0.0)		(0.0)(0.0)	
APPROACH	0.0	0.0	0.1	0.1	0.7	1.0
	(0.0)(0.0)		(1.0)(2.0)		(1.0)(3.0)	
POINT	0.0	0.0	0.1	0.1	1.5	0.5
	(0.0)(0.0)		(1.0)(3.0)		(3.0)(4.0)	
STRIKE	0.0	0.0	0.0	0.0	0.1	0.0
	(0.0)(0.0)		(0.0)(0.0)		(1.0)(0.0)	
BACK	0.0	0.0	0.2	0.0	1.0	0.3
	(0.0)(0.0)		(1.0)(0.0)		(3.0)(2.0)	
TOTAL	1.2	1.0	1.3	1.5	6.5	5.0
	(3.0)(0.0)		(6.0)(10.0)		(10.0)(14.0)	

(H1 = intermediate hunger state; H2 = hunger state after pike had been deprived of food for one week)

## FIGURES 24 to 36

The following figures describing the results of sections 4.3.2 and 4.3.3 all have the format as given below where the numbers of dots and triangles describe degrees of significance between results.

### 1. Between movement effects.

● < 0.05

●● < 0.01

●●● < 0.001

### 2. Between hunger effects.

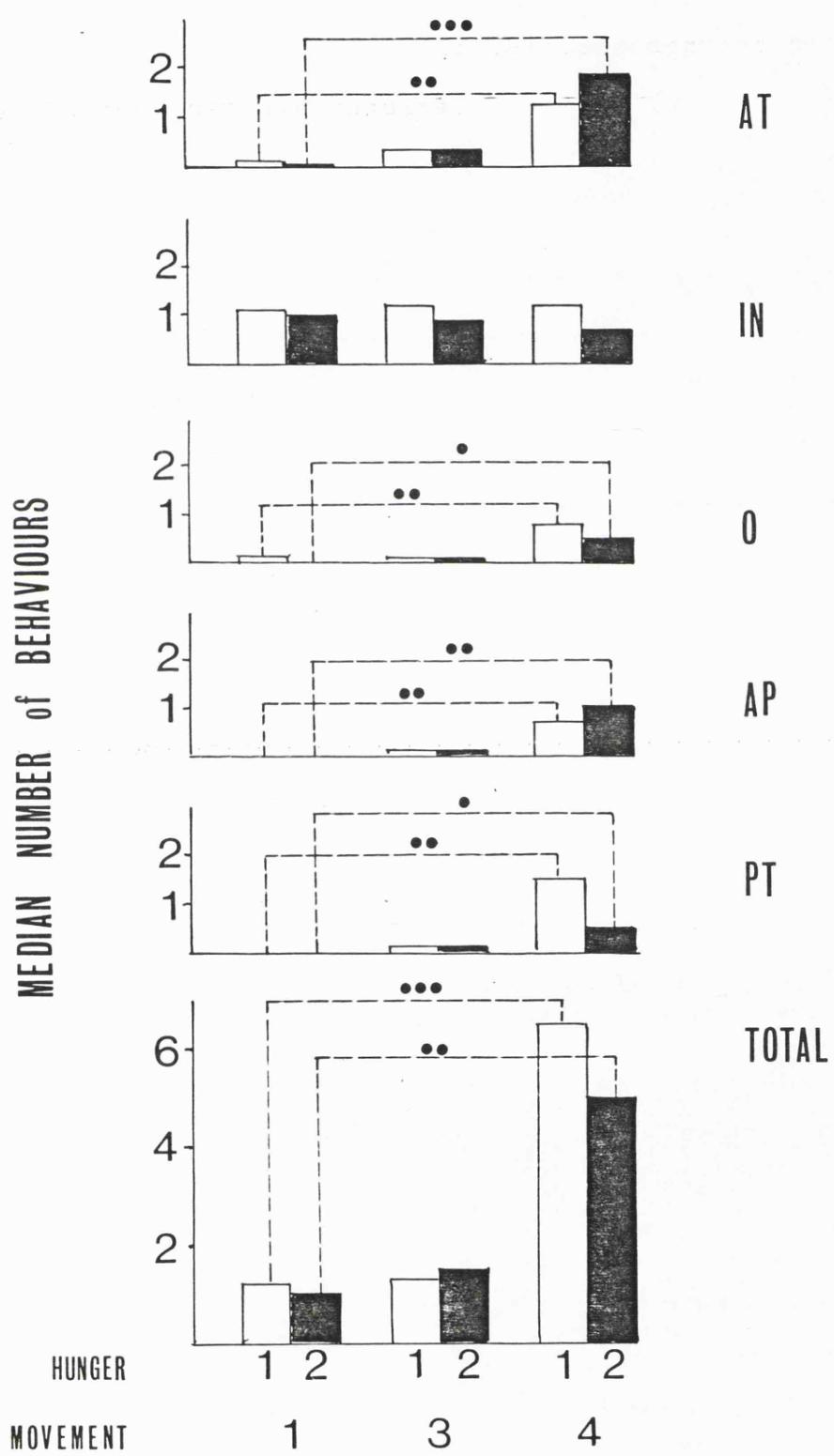
▼ < 0.05

▼▼ < 0.01

▼▼▼ < 0.001

All significance values are from Kruskal Wallis or Mann Whitney tests and the median numbers of behaviours are drawn.

**FIGURE 24** Frequency histograms for behaviours in the responses of pike to bar shadow stimuli for two hunger states and three movements.



tests were often used as this test specifically works on one dependent variable and two groups. The outcome of this test was equivalent in all cases to a Kruskal Wallis. The Kruskal Wallis test was used when there were more than two groups to be compared as a matter of convenience.

To make the following text more readable the intermediate hunger state and the most hungry state of pike will be referred to as H1 and H2 respectively.

Overall effects of movement on the median frequency of behaviours were found for attentive, orientate, approach and point for both hunger states of pike. In all cases there was a significant increase in response to a sinusoidal-like movement.

A change in hunger-motivated state did not influence the frequency with which behaviours occurred for each of the three types of bar shadow movements presented.

In the majority of cases, there were significant differences in the number of behaviours found between the intermittent, horizontally moving stimulus and that of the sinusoidally moving bar shadow that remained on the screen throughout. For ease of analysis the stimuli that appear intermittently (movements 2, 3 and 5) will be treated as a prey characteristic and not as noise in the system. However, to make comparisons between those stimuli that are intermittent and those that are not in a valid way, a different set of criteria was employed. Parameters were used to indicate the

degree of interest and speed of reaction towards a stimulus as a measure of response and are not specifically related to the frequency of appearance of a stimulus on the presentation screen.

Table 23 presents the temporal-parameters investigated and these are drawn as histograms in figures 25 and 26.

Analysis of the effects of movement demonstrated a decrease in the time that pike were disinterested in stimuli when they were more hungry. Accompanying increased interest were corresponding increases in times spent looking at the screen and in giving up times, particularly for the bar shadow with the sinusoidal-like movement.

There were movement effects for the time taken for pike to point at the stimulus and its duration at the intermediate state of hunger and, as above, was due to the shadow with a sinusoidal-like component to its movement.

A change in hunger state affected the response of pike to the shadows with movement 3 for TPT and movement 4 for TIN, TSC and TFIN.

The results suggest that a bar shadow with the sinusoidal-like component in its movement elicits a greater degree of interest by pike and that the response can be amplified when pike are more hungry.

**TABLE 23** Timed parameters for the responses of pike to bar shadow stimuli. Median values and ranges are given for two hunger states of pike.

	MOVEMENT 1		MOVEMENT 3		MOVEMENT 4	
<u>VARIABLE</u>	<u>H1</u>	<u>H2</u>	<u>H1</u>	<u>H2</u>	<u>H1</u>	<u>H2</u>
TIN	293.0	300.0	298.4	262.5	241.2	17.3
	(125.1)	(57.2)	(128.0)	(300.0)	(300.0)	(300.0)
TPT	0.0	0.0	0.8	5.1	23.1	0.5
	(0.0)	(0.0)	(21.0)	(84.2)	(183.9)	(120.3)
TOPT	301.0	301.0	300.8	298.8	11.4	115.1
	(0.0)	(0.0)	(295.5)	(292.1)	(295.9)	(295.5)
TSC	0.9	0.0	1.6	37.5	58.8	268.2
	(125.1)	(0.0)	(128.0)	(300.0)	(300.0)	(300.0)
TFIN	8.0	0.0	2.6	37.6	62.6	294.0
	(125.1)	(0.0)	(128.0)	(301.0)	(301.0)	(301.0)

TIN = time spent inattentive of stimulus; TPT = time pike spend in point; TOPT = time taken for pike to make the first point at stimuli; TSC = total time spent looking at the presentation screen; TFIN = time to pike become finally disinterested in stimuli. (All times are given in seconds). H1 and H2 are as described for table 23.

**FIGURE 25** Times for descriptive variables (TIN, TPT and TOPT) for the responses of pike at two levels of hunger towards bar shadow stimuli with three movements.

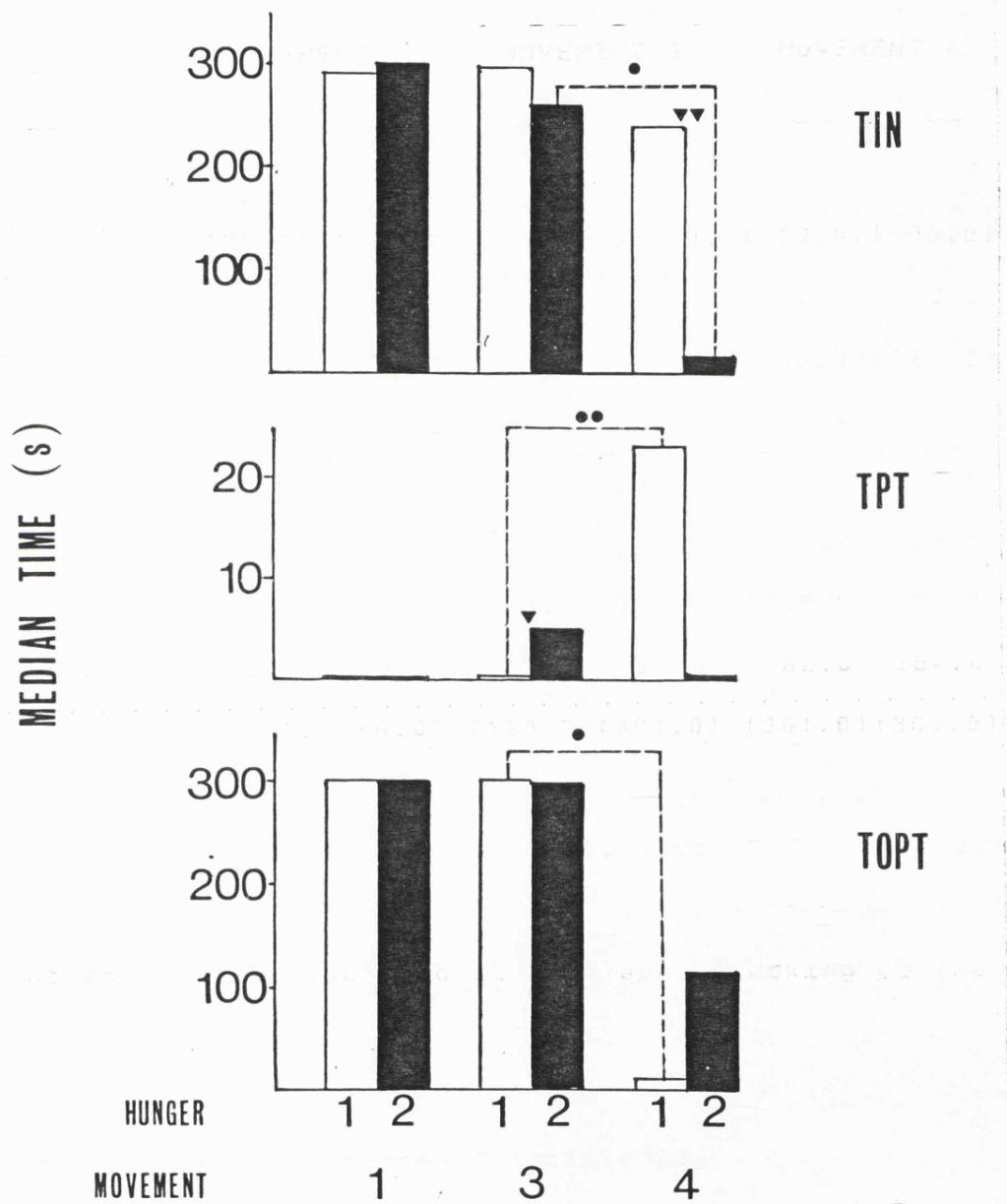
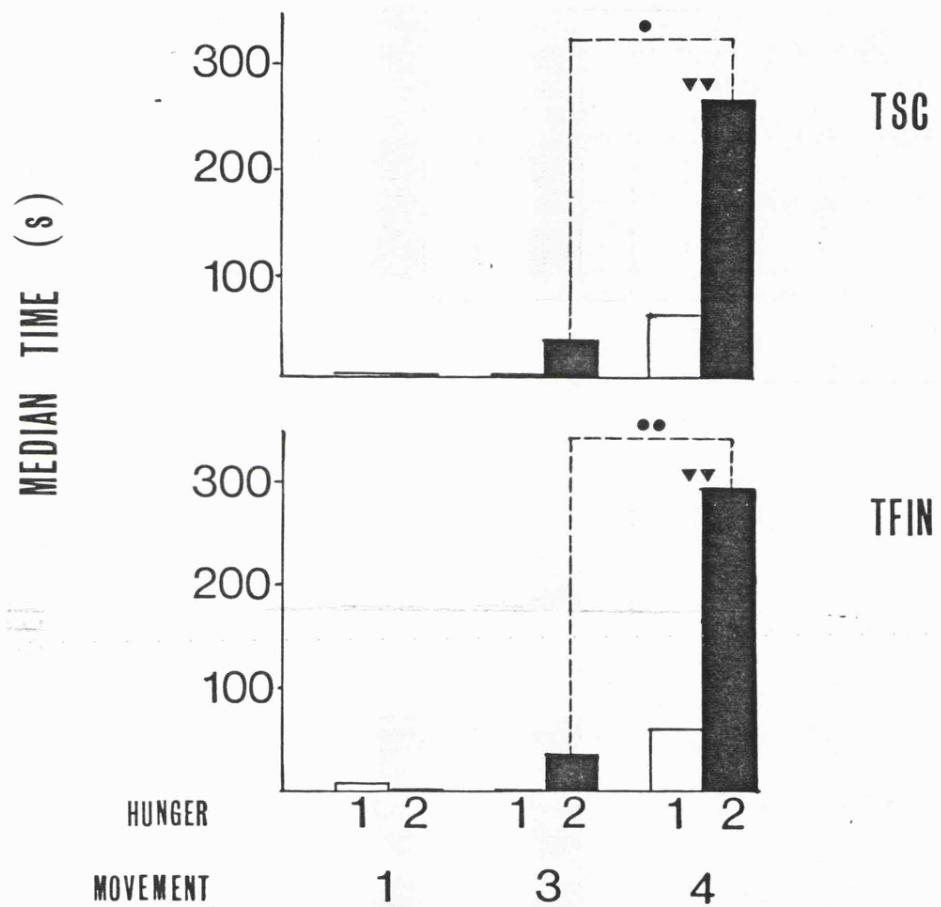


FIGURE 26 Times for descriptive variables (TSC and TFIN)  
for the responses of pike at two levels of hunger  
towards bar shadow stimuli with three movements.



#### 4.3.2.2 Fish shadow stimuli.

The results provided in table 24 are for frequencies of behaviours performed in the attack sequences to a fish shadow with a range of six movements. There were overall movement effects at both hunger-motivated states except for "inattentive" at H2 (refer to appendix for significance tables). Frequency histograms are again provided in figures 27, 28 and 29.

Once more between movement effects were found for like presentations of stimuli, that is, those that appeared intermittently and those that remained on the screen for the duration of a trial. Effects for the behaviours AT, AP and PT were located between movements 1 and 4 and for 3 and 5, when pike were at H1. These effects described increases in the frequency of behaviours related to increased responses to stimuli with movements that more closely resembled a living fish. There were no corresponding effects when pike were more hungry.

Between movement effects for stimuli with movements 4 and 6 showed that the frequency of IN and PT increased significantly at H1. When pike were more hungry the frequency of AP and PT increased. It is noted here that the number of strikes increased at H1 but decreased for H2, this fact will be discussed later.

Looking at movements specifically, a change in hunger state

TABLE 24 Frequencies of behaviours performed by pike in response to fish shadow stimuli. Medians and ranges given for the two hunger states of pike.

VARIABLE	MOVEMENT 1		MOVEMENT 2		MOVEMENT 3		MOVEMENT 4		MOVEMENT 5		MOVEMENT 6	
	H1	H2	H1	H2	H1	H2	H1	H2	H1	H2	H1	H2
ATTENTIVE	0.1	1.1	0.5	*	0.8	2.2	1.7	1.5	5.5	1.6	0.8	3.0
	(2.0)	(3.0)	(6.0)		(3.0)	(6.0)	(4.0)	(4.0)	(5.0)	(2.0)	(2.0)	(5.0)
INATTENTIVE	0.9	0.5	0.9	*	0.9	1.0	1.1	1.1	0.8	1.7	2.0	0.8
	(1.0)	(2.0)	(3.0)		(1.0)	(3.0)	(2.0)	(3.0)	(3.0)	(1.0)	(4.0)	(5.0)
ORIENTATE	0.1	0.7	0.2	*	0.5	1.2	1.8	0.8	1.5	2.2	5.0	5.5
	(2.0)	(2.0)	(6.0)		(4.0)	(4.0)	(3.0)	(3.0)	(6.0)	(2.0)	(10.0)	(7.0)
SNAP	0.0	0.3	0.0	*	0.1	0.3	0.2	0.0	0.0	0.1	3.8	1.5
	(0.0)	(6.0)	(0.0)		(13.0)	(4.0)	(5.0)	(0.0)	(0.0)	(1.0)	(6.0)	(5.0)
APPROACH	0.3	1.5	0.1	*	0.2	1.5	4.5	2.2	5.5	3.5	9.5	9.8
	(6.0)	(7.0)	(8.0)		(7.0)	(12.0)	(11.0)	(8.0)	(9.0)	(6.0)	(12.0)	(11.0)
POINT	0.1	2.5	0.4	*	0.2	4.0	6.5	4.8	6.0	4.8	17.5	16.0
	(5.0)	(10.0)	(14.0)		(9.0)	(21.0)	(25.0)	(13.0)	(11.0)	(5.0)	(25.0)	(20.0)
STRIKE	0.0	0.1	0.0	*	0.5	0.5	0.2	0.5	0.0	1.0	5.0	2.2
	(0.0)	(2.0)	(0.0)		(9.0)	(6.0)	(12.0)	(2.0)	(0.0)	(4.0)	(18.0)	(7.0)
BACK	0.1	1.0	0.1	*	0.5	1.5	2.0	2.0	2.0	2.3	9.0	5.5
	(1.0)	(3.0)	(12.0)		(6.0)	(6.0)	(11.0)	(6.0)	(3.0)	(3.0)	(11.0)	(8.0)
TOTAL	1.6	9.5	1.3	*	3.0	15.0	20.0	16.5	23.5	16.5	57.5	41.5
	(15.0)	(22.0)	(48.0)		(41.0)	(58.0)	(71.0)	(41.0)	(25.0)	(12.0)	(89.0)	(52.0)

\* = trials not carried out due to conditioning of pike.

FIGURE 27 Frequency histograms for the behaviours AT, IN, O and SN in the responses of pike at two hunger levels towards fish shadows with three types of movement.

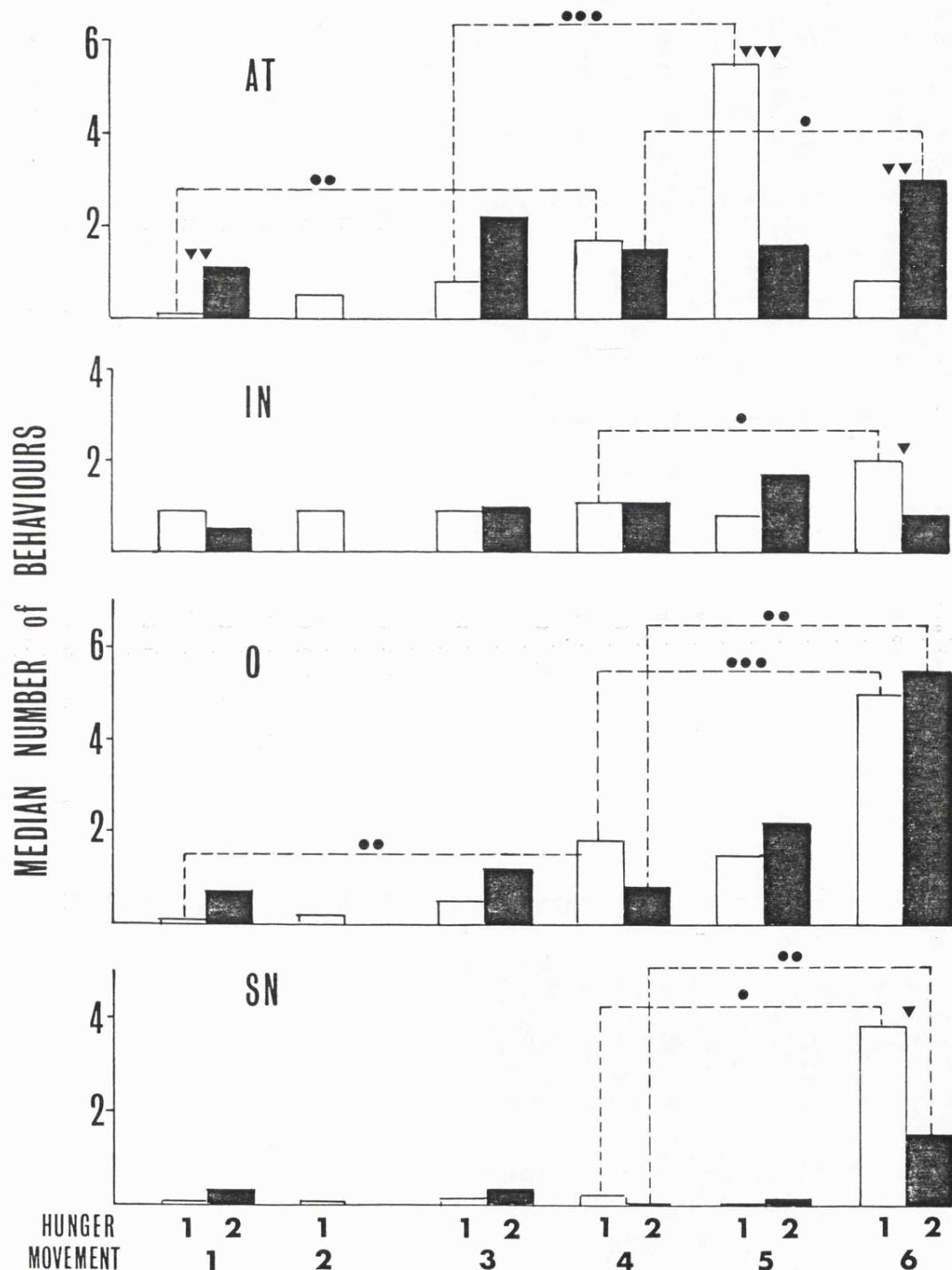


FIGURE 28 Frequency histograms for the behaviours AP and PT in the responses of pike at two levels of hunger towards fish shadows with six types of movement.

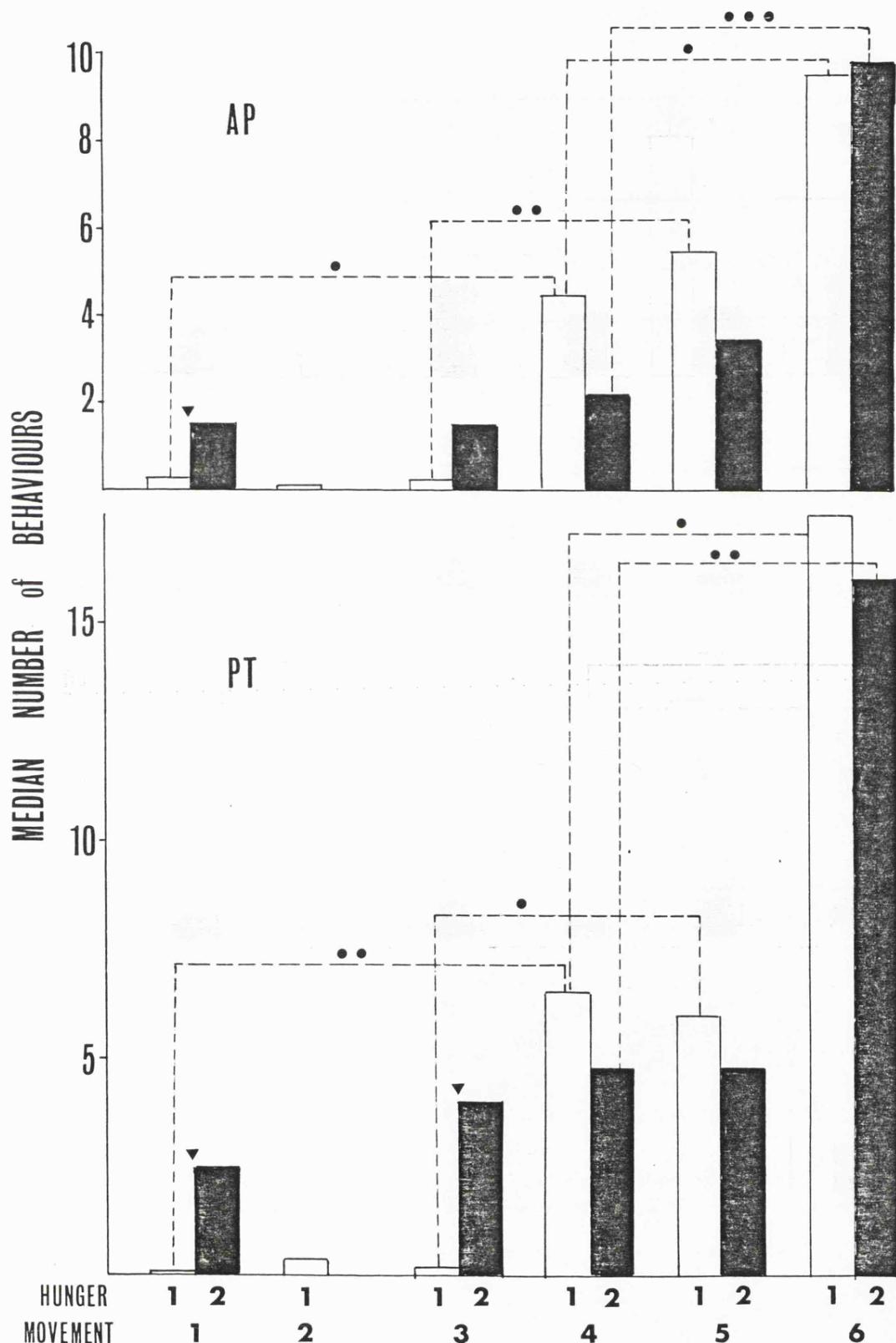
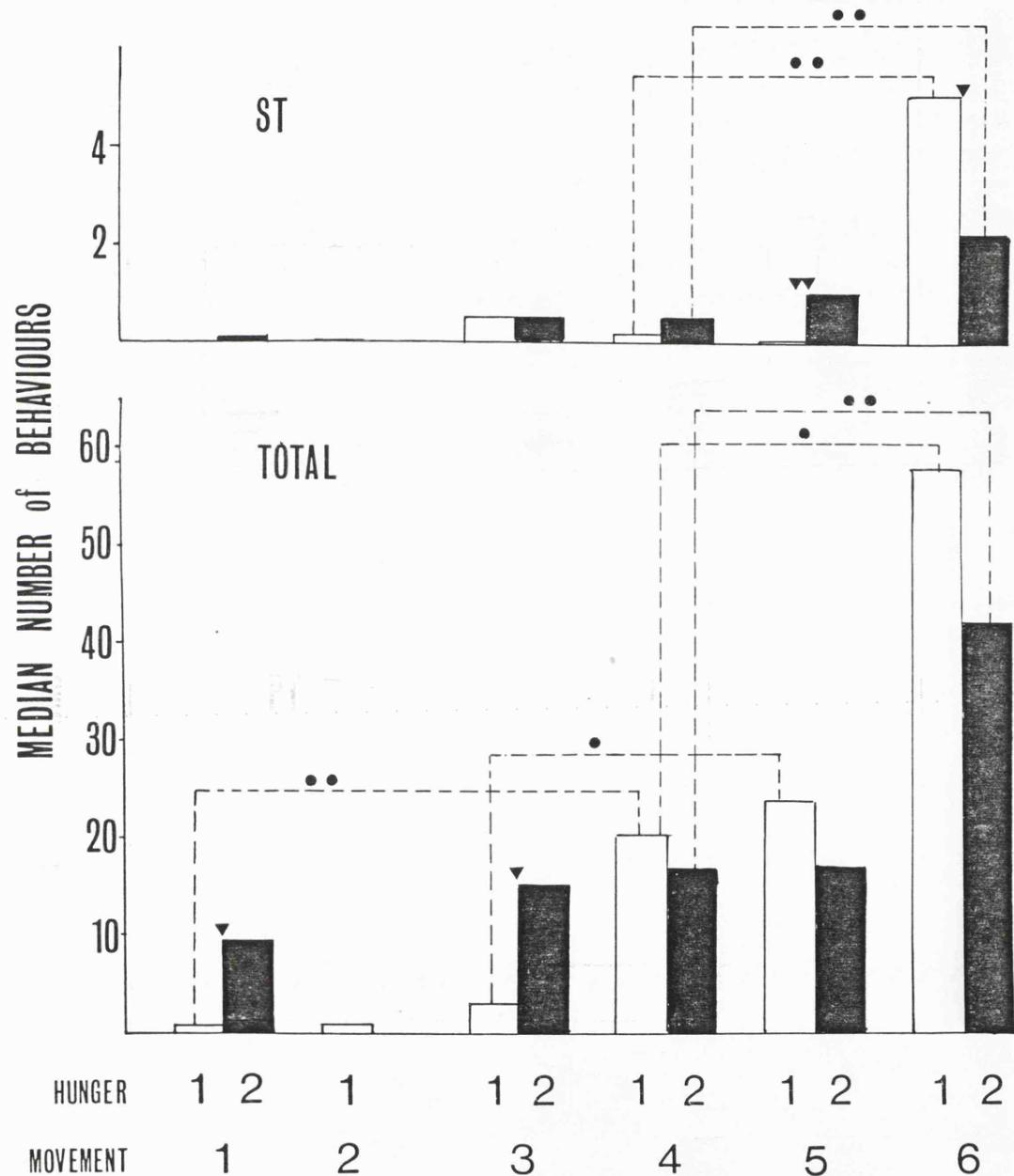


FIGURE 29 Frequency histograms for the behaviour Strike and the total number of behaviours in the responses of pike at two levels of hunger to fish shadow stimuli with six types of movement.



affected the frequency with which certain behaviours occurred. For the stationary fish shadow and for the live swimming fish shadow there was an increase in the frequency of AT but a decrease for responses to a fish shadow moving horizontally with sinusoidal-like components. IN increased in frequency with increased hunger for movement 6. The behaviours AP and PT increased in number for movement 1 and the frequency of PT increased for movement 3 when pike were more hungry.

The total number of behaviours that were performed in the responses of pike to the various stimuli embody the trends already described above. As stimuli are presented with greater degrees of moving components there are increases in the numbers of behaviours exhibited. Hunger increased the total number of behaviours made in response to the stationary stimulus and one that moved horizontally with irregular vertical components.

Timed variables of the attack sequences to fish shadow stimuli are given in table 25 and in histogram form in figures 30 and 31.

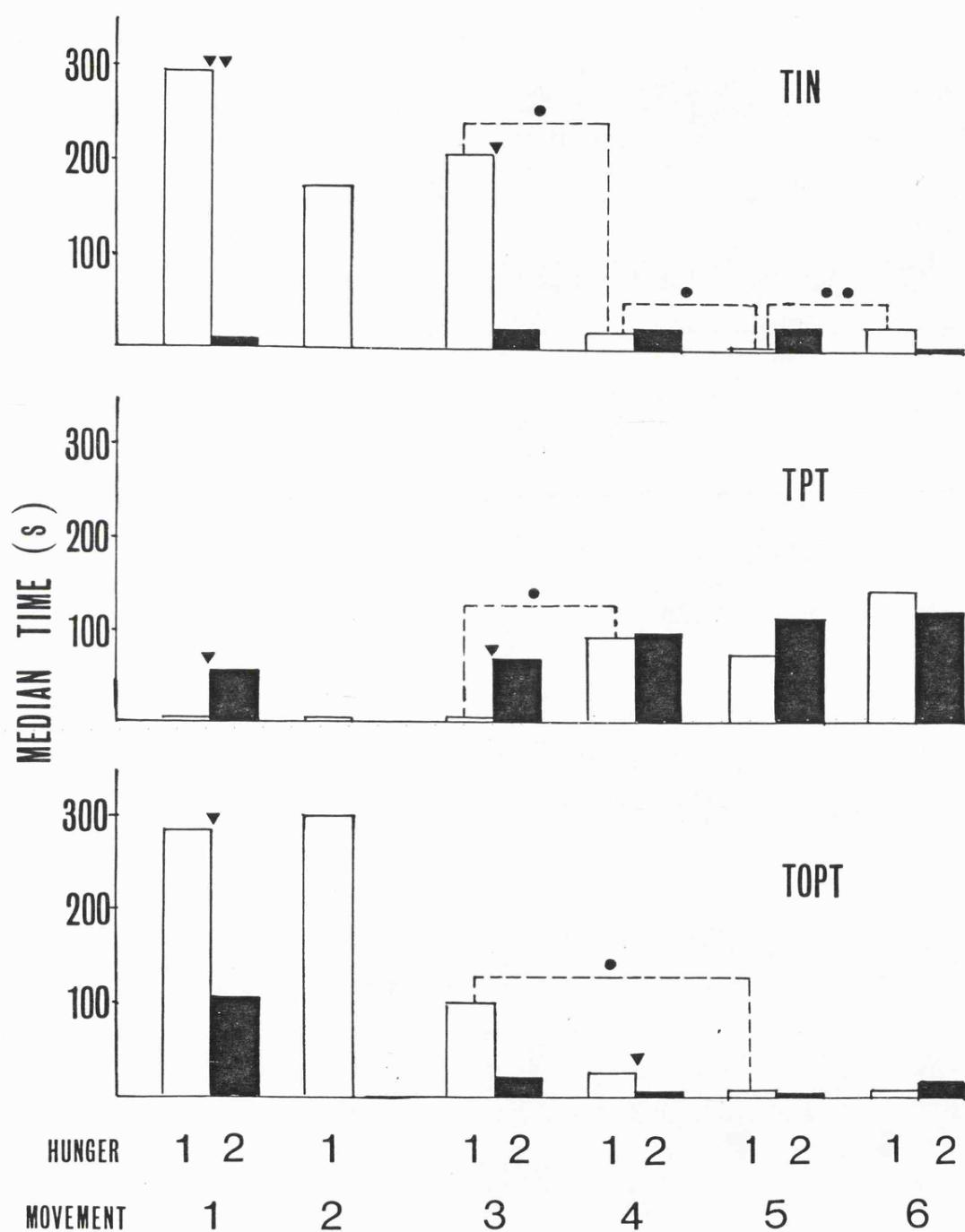
Overall effects of movement were only located for pike at an intermediate state of hunger. There were decreases in the time that pike were inattentive and the speed with which pike reacted to a stimulus as the characteristics became more like those of a living fish. Accompanying this trend, therefore, were associated increases in the time that pike spent pointing and looking at the presentation screen.

TABLE 25 Timed variables for pike responding to fish shadow stimuli. Medians and ranges given are in seconds.

VARIABLE	MOVEMENT 1		MOVEMENT 2		MOVEMENT 3		MOVEMENT 4		MOVEMENT 5		MOVEMENT 6	
	H1	H2	H1	H2	H1	H2	H1	H2	H1	H2	H1	H2
TIN	294.7	7.7	174.1	*	211.1	23.1	17.0	23.4	1.7	27.2	26.4	2.9
	(296.5)	(300.0)	(300.0)		(271.5)	(300.0)	(300.0)	(300.0)	(23.9)	(113.1)	(225.2)	(168.5)
TPT	2.6	56.5	3.6	*	3.7	67.3	91.5	95.5	70.8	111.9	141.3	119.0
	(105.8)	(169.0)	(134.3)		(111.2)	(240.1)	(214.4)	(258.9)	(166.6)	(100.6)	(268.6)	(170.6)
TOPT	284.7	105.4	300.5	*	98.6	18.5	26.2	6.2	7.1	5.2	8.8	18.4
	(293.7)	(295.8)	(297.6)		(295.7)	(291.7)	(292.1)	(298.4)	(298.3)	(30.7)	(43.6)	(30.4)
TSC	7.3	282.5	1.6	*	63.6	218.3	282.6	222.5	299.4	272.8	256.5	294.7
	(296.5)	(300.0)	(300.0)		(271.5)	(300.0)	(300.0)	(300.0)	(6.8)	(113.1)	(225.2)	(168.5)
TFIN	0.3	297.8	5.8	*	88.2	284.3	300.7	225.2	301.0	301.0	300.4	294.6
	(300.0)	(301.0)	(301.0)		(301.0)	(301.0)	(301.0)	(301.0)	(0.0)	(0.0)	(46.0)	(169.5)

\* = Trials not carried out due to conditioning of pike.

FIGURE 30 Times for the descriptive variables (TIN, TPT and TOPT) for pike at two levels of hunger responding to fish shadow stimuli with six types of movement.



There were no similar trends when pike were more hungry, that is to say that there were no significant differences between timed variables for each of the movements apart from the time to become disinterested in the stimulus (TFIN) which differed between movements 3 and 4, so too for movements 4 and 5.

In general, a change in hunger state (pike become more hungry) affected the response to the least effective stimuli as determined from the responses of pike when at H1. There was a decrease in the time that pike were inattentive of movements 1 and 3. Movement 5 is anomalous in the results in that a significant increase was found. The time in which pike spent pointing at the stimuli increased when they were more hungry for movements 1 and 2.

#### 4.3.2.3 Three dimensional stimuli.

Table 26 shows the frequencies of behaviours for pike responding to a three dimensional fish model and a natural fish stimulus. Histograms are provided in figures 32, 33 and 34. The possible combinations of movements and hunger are incomplete due to the pike becoming habituated.

Effects of movement could only be determined for H1. Significant effects were located for O, AP, PT and ST. The effects found for O, AP and PT were attributable to the difference in the characteristics of movements 1 and 4

**TABLE 26** Frequencies of behaviours displayed by pike in response to three-dimensional stimuli at two hunger-motivated states. (Median and ranges given).

	MOVEMENT 1		MOVEMENT 4		MOVEMENT 6	
<u>VARIABLE</u>	<u>H1</u>	<u>H2</u>	<u>H1</u>	<u>H2</u>	<u>H1</u>	<u>H2</u>
ATTENTIVE	2.0	*	2.2	*	2.0	2.2
	(6.0)		(3.0)		(4.0)	(5.0)
INATTENTIVE	0.9	*	0.4	*	0.3	0.5
	(2.0)		(2.0)		(4.0)	(2.0)
ORIENTATE	0.4	*	2.7	*	2.5	4.2
	(1.0)		(4.0)		(4.0)	(8.0)
SNAP	0.0	*	0.1	*	0.1	1.5
	(0.0)		(2.0)		(3.0)	(8.0)
APPROACH	0.8	*	4.0	*	6.2	10.5
	(6.0)		(9.0)		(10.0)	(15.0)
POINT	0.4	*	4.0	*	9.3	17.0
	(5.0)		(4.0)		(18.0)	(21.0)
STRIKE	0.0	*	0.2	*	0.5	2.5
	(0.0)		(2.0)		(12.0)	(16.0)
BACK	1.0	*	2.0	*	3.2	7.5
	(5.0)		(5.0)		(10.0)	(11.0)
TOTAL	5.0	*	14.0	*	28.5	57.0
	(22.0)		(32.0)		(65.0)	(88.0)

(H1 and H2 are as described in table 23. \* indicates where trials were not carried out due to conditioning effects)

FIGURE 32 Frequency histograms for the behaviours (AT, IN, O and SN) in the responses of pike at two levels of hunger to three-dimensional fish stimuli with three types of movement.

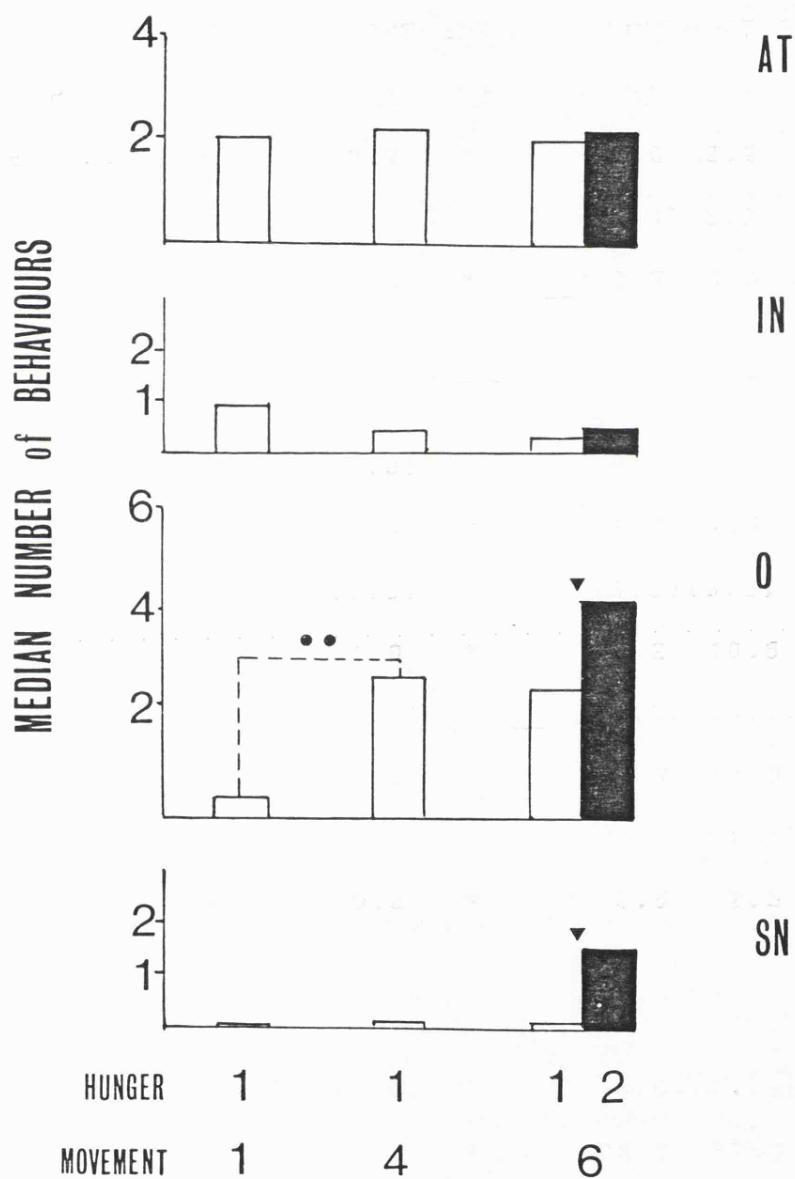


FIGURE 33 Frequency histograms for the behaviours AP and PT in the responses of pike at two levels of hunger to three-dimensional fish stimuli with three types of movement.

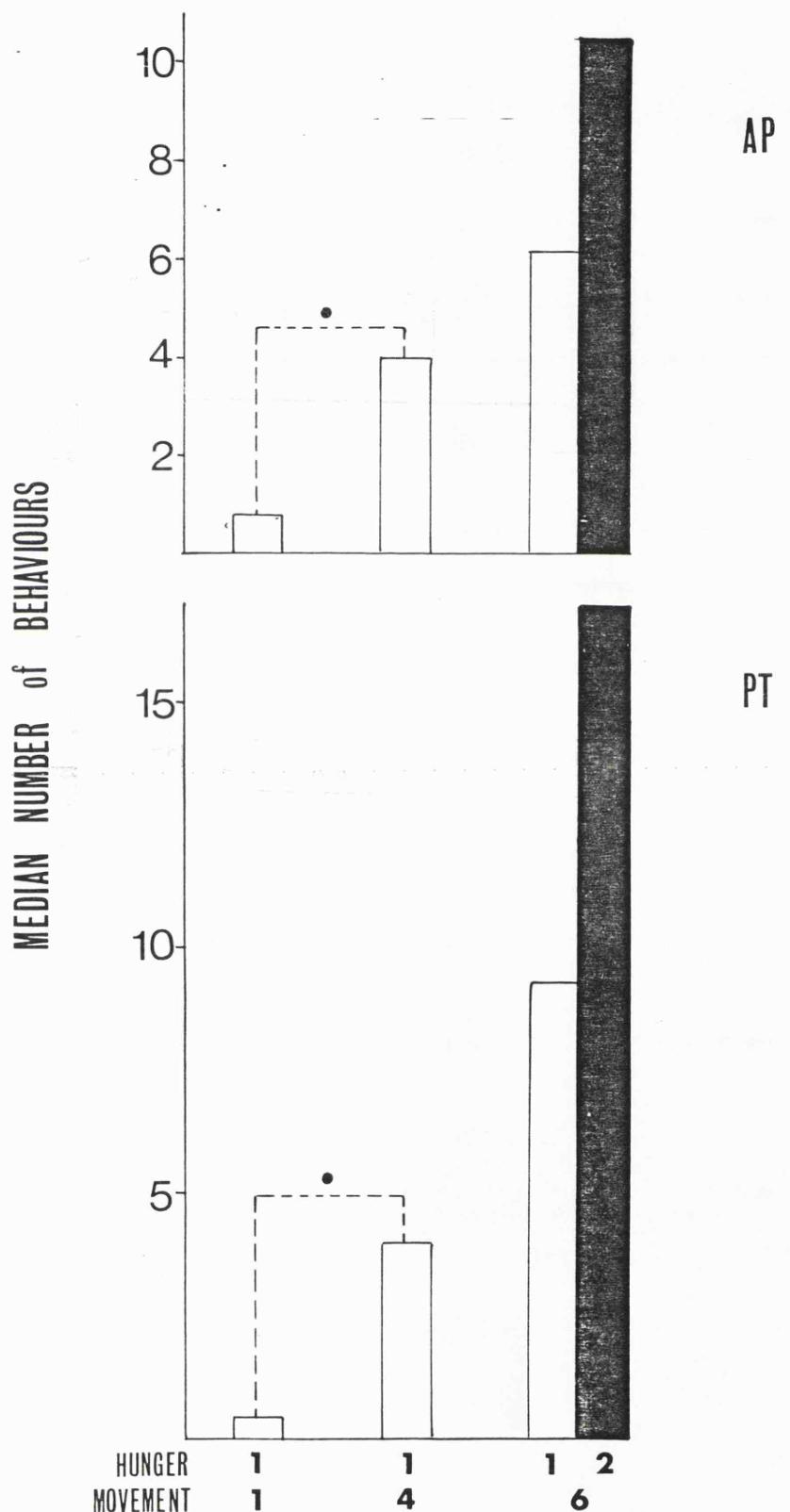
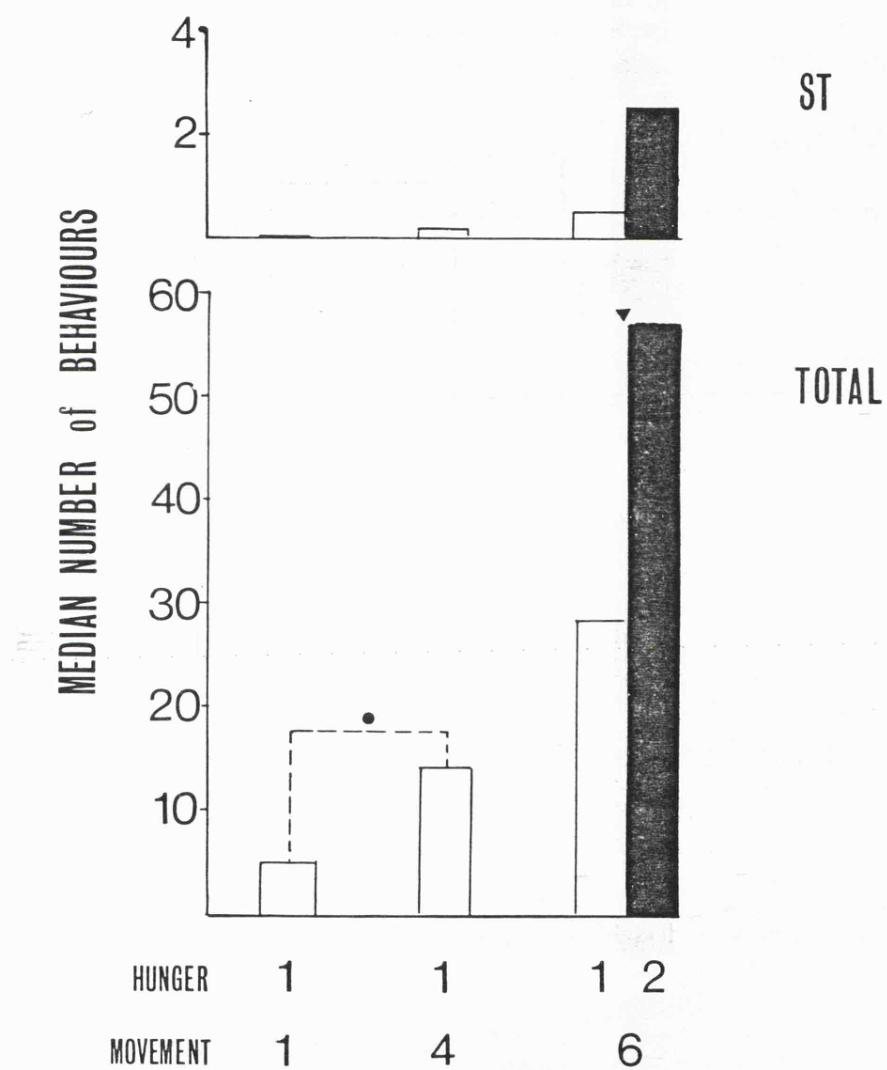


FIGURE 34 Frequency histograms for the behaviour Strike and the total number of behaviours exhibited by pike in response to three-dimensional fish stimuli with three types of movement.



whereas for ST the difference was located between movements 4 and 6.

The frequency with which strikes occurred was greatest for the live fish stimulus. Similar effects were found in the total number of behaviours produced in the attack responses.

The investigation of hunger effects could only be carried out on the live fish trials. Significant increases were found for the behaviours "orientate", "snap", "back" and in the total numbers of behaviours exhibited.

Results for timed variables are given in table 27. Figures 35 and 36 present histograms for these results.

Hunger did not influence the time for the various variables associated with the live fish stimulus. There were however increases in the amount of time pike spent pointing at more moving stimuli and decreases in reaction time to stimuli that moved, with accompanying increases in the times to final disinterest in stimuli. All these trends are described for pike at an intermediate state of hunger.

#### 4.3.3 The effects of form and hunger on the attack responses of pike towards prey stimuli.

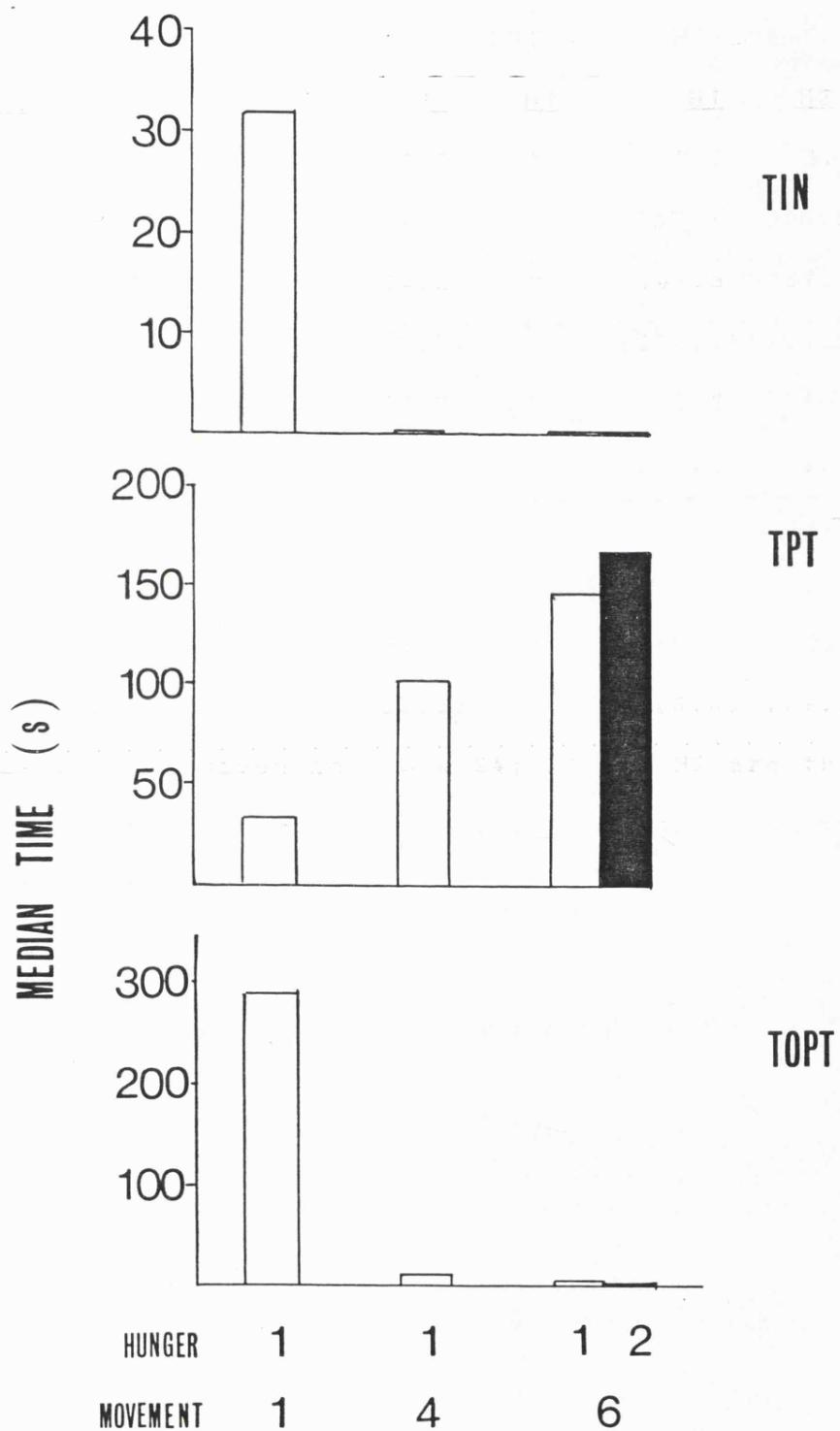
The effects of form, namely the influence of a bar shadow, a fish shadow and a three-dimensional fish on the results, were considered for the two hunger-motivated states of pike

**TABLE 27** Timed parameters of attack sequences for pike reacting to three-dimensional stimuli. (Medians and ranges given for times in seconds).

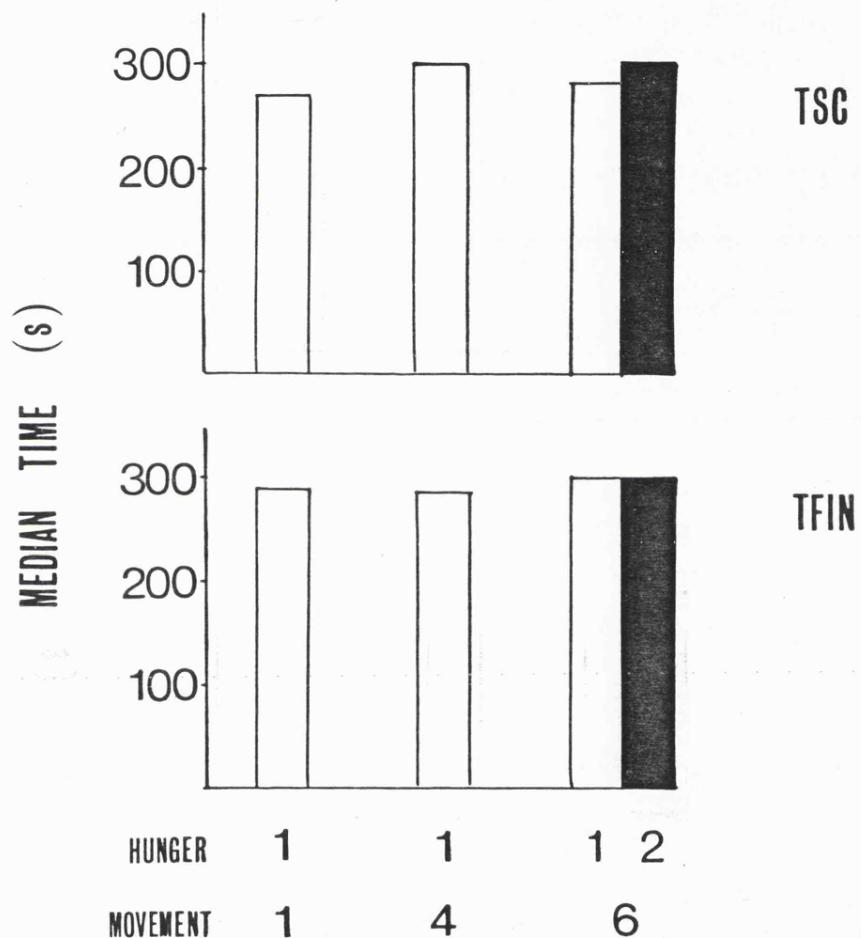
<u>VARIABLE</u>	MOVEMENT 1		MOVEMENT 4		MOVEMENT 6	
	<u>H1</u>	<u>H2</u>	<u>H1</u>	<u>H2</u>	<u>H1</u>	<u>H2</u>
TIN	31.8	*	0.2	*	0.6	0.1
	(300.0)		(227.0)		(57.1)	(70.5)
TPT	36.9	*	104.3	*	144.9	167.9
	(301.0)		(207.7)		(208.0)	(134.2)
TOPT	288.5	*	11.3	*	5.6	4.6
	(292.7)		(64.1)		(31.2)	(16.1)
TSC	268.2	*	299.9	*	281.6	299.6
	(300.1)		(227.0)		(147.9)	(70.5)
TFIN	289.9	*	286.9	*	301.0	300.8
	(301.0)		(225.2)		(0.0)	(71.5)

(Variable list is given in table 24; H1 and H2 are the same as in table 23; \* indicates where trials were not carried out due to conditioning effects)

**FIGURE 35** Times for descriptive variables (TIN, TPT and TOPT) for pike at two levels of hunger in response to three-dimensional stimuli with three types of movement.



**FIGURE 36** Times for descriptive variables TSC and TFIN for pike at two levels of hunger in response to three-dimensional with three types of movement.



employed in this study. The form of statistical approach was necessitated by not being able to employ standard multivariate analysis on the data.

#### 4.3.3.1 The effect of form on the attack response of pike at an intermediate hunger-motivated state.

Table 28 provides frequency data for the eight variables examined in earlier sections and are represented in figures 37, 38, and 39 for a comparison of the effects of form. Significance levels are given in the appendix.

There was no universal trend in the effects of form across all the behaviours selected for analysis. Where there were significant effects this finding was attributable to increases in the frequencies of behaviours resulting from the responses of pike in presentations where stimuli that more closely resembled a live fish were given.

The results do illustrate however that there was a reduced response towards an actual fish stimulus than that of its shadow counterpart. Reasons for this may be due to the fact that a fish shadow constitutes a supernormal stimulus or that pike had become habituated in the trials when real fish were presented.

The distribution for the total number of behaviours performed in the attack sequences reflected the general trend in behaviours.

## **FIGURES 37 TO 46**

The following diagrams show effects of form on the results in experiment 3 and all have the format given below where the numbers of dots and triangles denote degrees of significance between results.

### **1. Overall effects of form.**

- <0.05
- ● <0.01
- ● ● <0.001

### **2. Between form effects.**

- ▼ <0.05
- ▼▼ <0.01
- ▼▼▼ <0.001

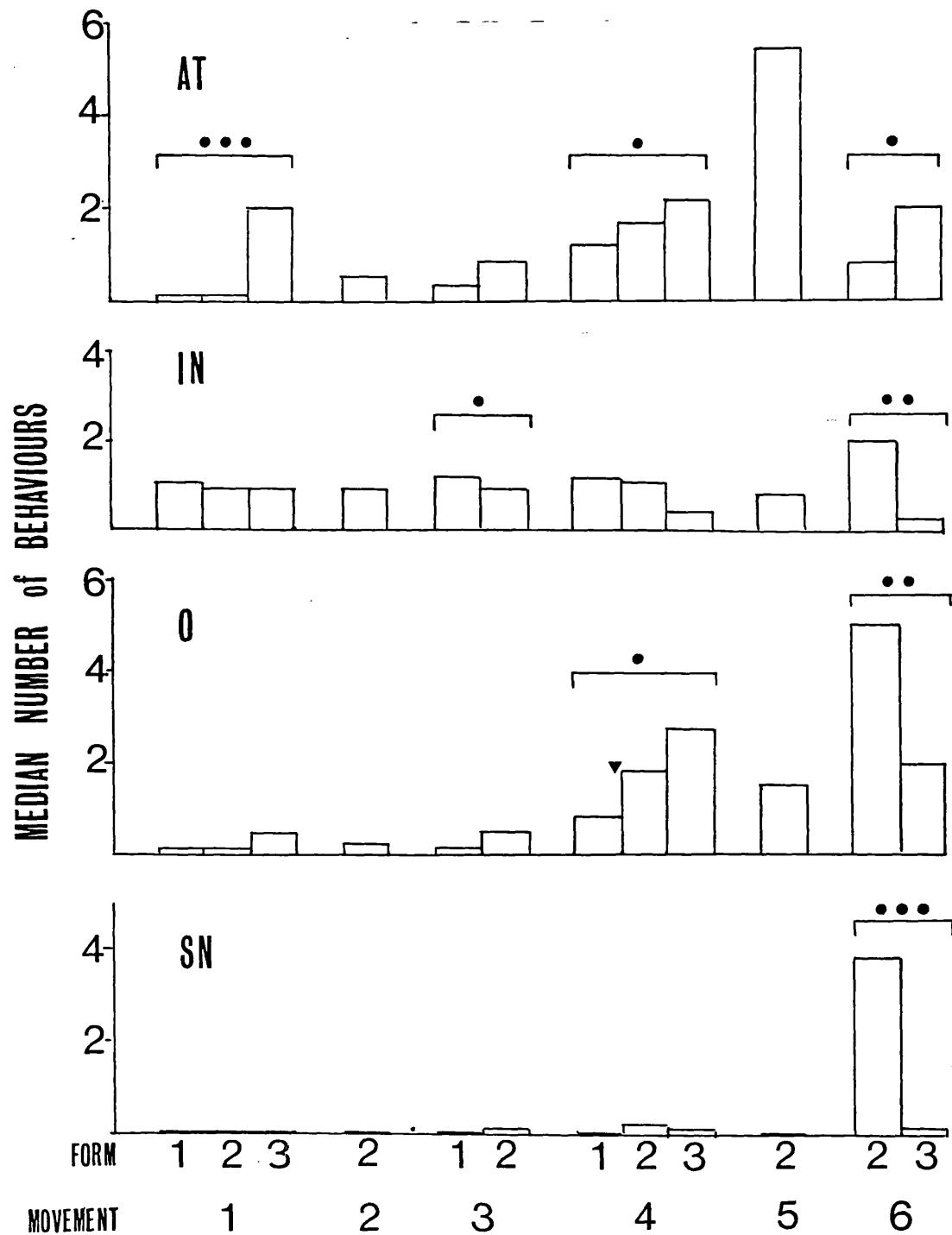
Median values are once more drawn and significance values quoted are from Kruskal Wallis and Mann Whitney tests.

TABLE 28 Behaviours exhibited by pike at the hunger state H1 in response to different forms and movements of stimuli. Medians and range given.

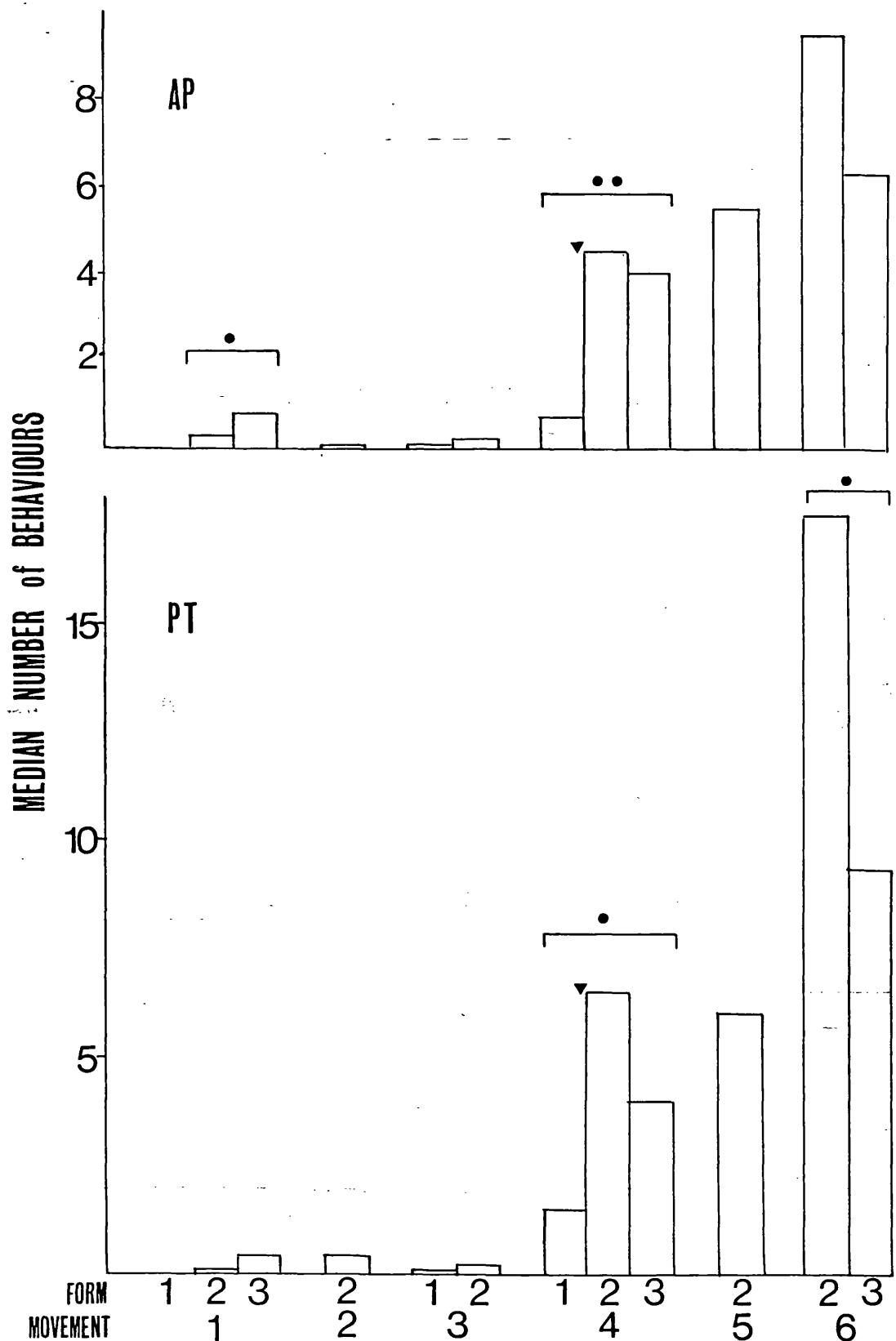
VARIABLE	MOVEMENT 1			MOVEMENT 2			MOVEMENT 3			MOVEMENT 4			MOVEMENT 5			MOVEMENT 6		
	E1	E2	E3	E1	E2	E3	E1	E2	E3	E1	E2	E3	E1	E2	E3	E1	E2	E3
ATTENTIVE .1 .1	2.0	0.5	0.3	0.8	1.2	1.7	2.2	5.5	0.8	2.0								
(11) (2)	(6)	(6)	(11)	(3)	(2)	(4)	(3)	(5)	(2)	(4)								
INATTENTIVE 1.1 .9	0.9	0.9	1.2	0.9	1.2	1.1	0.4	0.8		2.0	0.3							
(11) (1)	(2)	(3)	(11)	(1)	(2)	(2)	(2)	(3)	(1)	(4)								
ORIENTATE .1 .1	0.4	0.2	0.1	0.5	0.8	1.8	2.7	1.5		5.0	2.5							
(11) (2)	(1)	(4)	(11)	(4)	(1)	(3)	(4)	(6)	(1)	(10)	(4)							
SNAP 0 0	0	0	0	0	0.1	0	0.2	0.1	0	3.8	0.1							
(0) (0)	(0)	(0)	(0)	(0)	(0)	(13)	(0)	(5)	(2)	(0)	(6)	(3)						
APPROACH 0 0.3	0.8	.0.1	0.1	0.2	0.7	4.5	4.0	5.5		9.5	6.2							
(0) (6)	(6)	(8)	(11)	(7)	(11)	(11)	(9)	(9)	(1)	(12)	(10)							
POINT 0 0.1	0.4	0.4	0.1	0.2	1.5	6.5	4.0	6.0		17.5	9.3							
(0) (5)	(5)	(14)	(11)	(9)	(3)	(25)	(12)	(11)	(25)	(18)	(18)							
STRIKE 0 0	0	0	0	0	0.5	0.1	0.2	0.2	0	5.0	0.5							
(0) (0)	(0)	(0)	(0)	(0)	(9)	(1)	(12)	(2)	(0)	(18)	(12)							
BACK 0 0.1	1.0	0.1	0.2	0.5	1.0	2.0	2.0	2.0		9.0	3.2							
(0) (1)	(5)	(12)	(1)	(6)	(3)	(11)	(5)	(3)	(11)	(11)	(10)							
TOTAL 1.2 1.6	5.0	1.3	1.3	3.0	6.5	20.0	14.0	23.5		57.5	28.5							
(3) (15)	(22)	(48)	(6)	(41)	(10)	(71)	(32)	(25)	(89)	(65)								

F1 = BAR SHADOW; F2 = FISH SHADOW; F3 = 3D MODELS

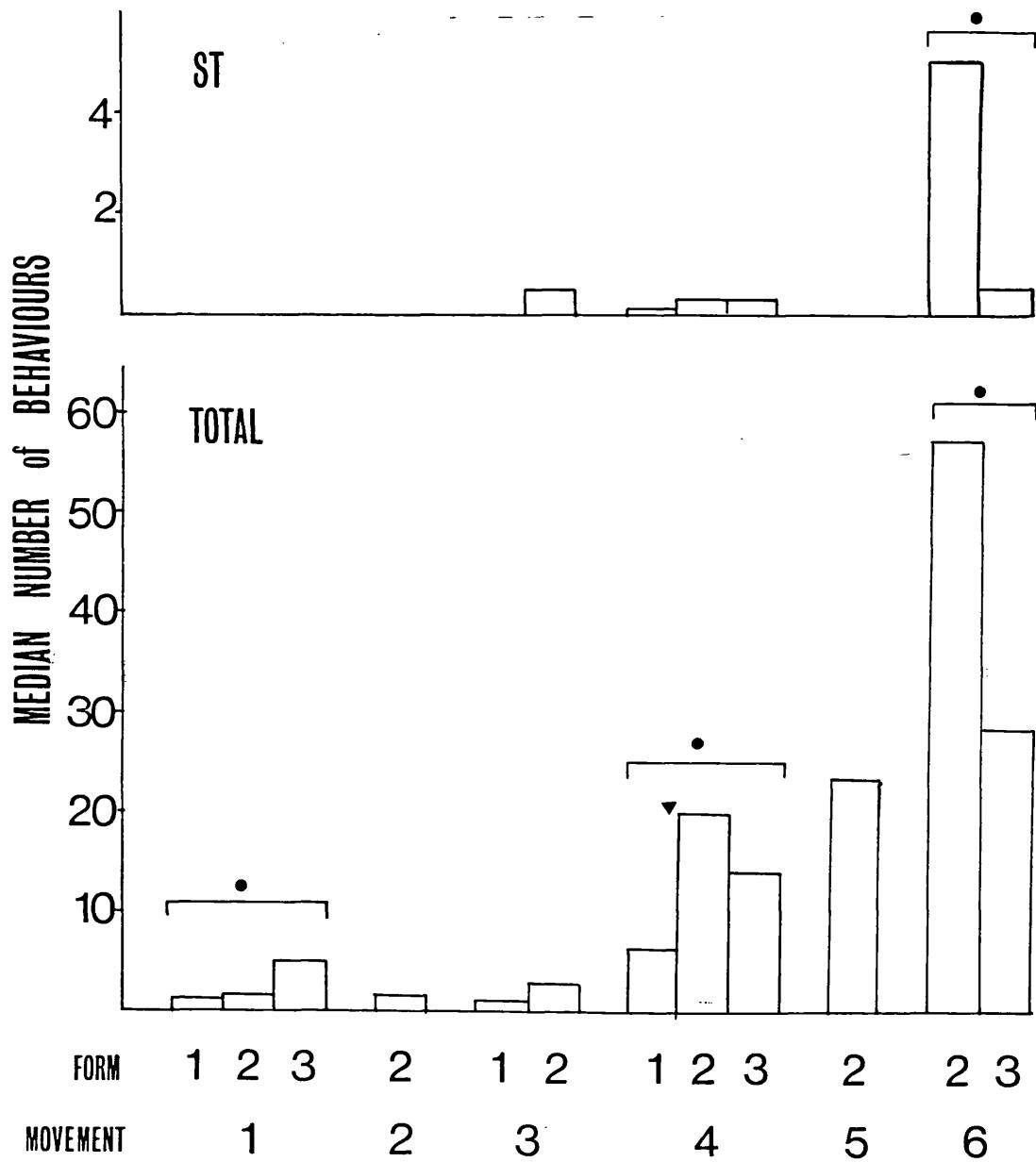
**FIGURE 37** Frequency histograms for the behaviours AT, IN, O and SN in the response of pike at an intermediate hunger to stimuli with differing form and movement.



**FIGURE 38** Frequency histograms for the behaviours AP and PT for the response of pike at an intermediate hunger level to stimuli with differing form and movement.



**FIGURE 39** Frequency histograms for the behaviour Strike and the total number of behaviours at an intermediate level of hunger in response to stimuli with differing form and movement.



The distribution for the total number of behaviours performed in the attack sequences reflected the above patterns. The response to a natural fish stimulus was reduced, there was an increase in total between the bar shadow and a fish shadow for movement 4 and an overall effect of form was demonstrated in the response to a stationary stimulus.

The timed variables associated with responses to form are given in table 29 and histograms in figures 40 and 41. Major effects were confined to the stationary stimulus and that with movement 4. For the stationary stimulus there was a large difference in response variables between a fish shadow and the three-dimensional presentations, for the time spent inattentive and for the overall time spent looking at the presentation screen, so too for the time to when pike became disinterested in the prey stimuli. For stimuli with movement 4 there were changes in response between bar and fish shadow forms, for times spent inattentive, for the time spent in point, for total interest in the stimulus and for times to final disinterest.

#### 4.3.3.2 The effect of form on the attack response of pike with increased hunger-motivation.

Most comparisons of form at this hunger-motivated state were between the bar shadow and fish shaped shadows. The results are presented in table 30.

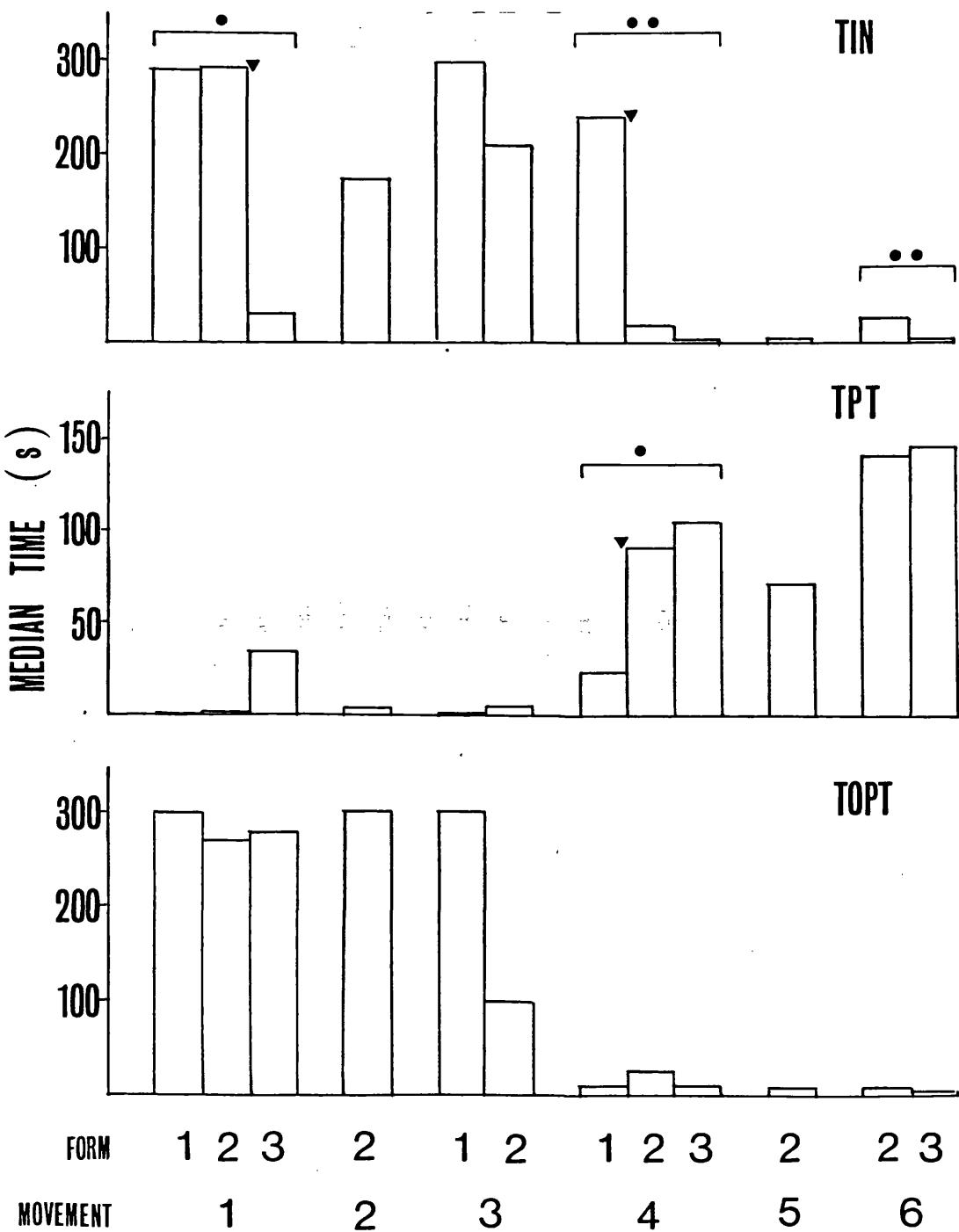
Unfortunately the comparisons of shape are not the same for

TABLE 29 Timed variables for form and movement in the attack sequences of pike at the hunger state H1. Medians and range are in seconds.

VARIABLE	MOVEMENT 1			MOVEMENT 2			MOVEMENT 3			MOVEMENT 4			MOVEMENT 5			MOVEMENT 6		
	E1	E2	E3	E1	E2	E3	E1	E2	E3	E1	E2	E3	E1	E2	E3	E1	E2	E3
TIN	293.	294.	31.	174.	298.	211.	241.	17.	.2	1.			26.	.6				
	(125)(296)(300)			(300)			(128)(271)			(300)(300)(227)			(225)	(57)				
TPT	0.	2.	36.	3.	.8	3.	23.	91.	104.	70.			141.	144.				
	(0)(105)(300)			(134)			(21)(111)			(184)(214)(207)			(166)					
TOPT	301.	284.	288.	300.	300.	98.	11.	26.	11.	7.			8.	5.				
	(0)(293)(292)			(297)			(295)(295)			(295)(292)(64)			(298)					
TSC	.9	7.	268.	1.		1.	63.	58.	282.	299.			256.	281.				
	(125)(296)(300)			(300)			(128)(271)			(300)(300)(227)			(6)					
TFIN	8.	.3	289.	5.		2.	88.	62.	300.	286.			300.	300.				
	(125)(300)(300)			(300)			(128)(300)			(300)(300)(225)			(0)					

F1 = Bar shadow; F2 = fish shadow; F3 = 3D models.

**FIGURE 40** Times for the descriptive variables (TIN, TPT and TOPT) in the response of pike at an intermediate level of hunger towards stimuli with differing form and movement.



**FIGURE 41** Times for the descriptive variables TIN and TFIN  
 in the response of pike at an intermediate hunger  
 level to stimuli with differing form and movement.

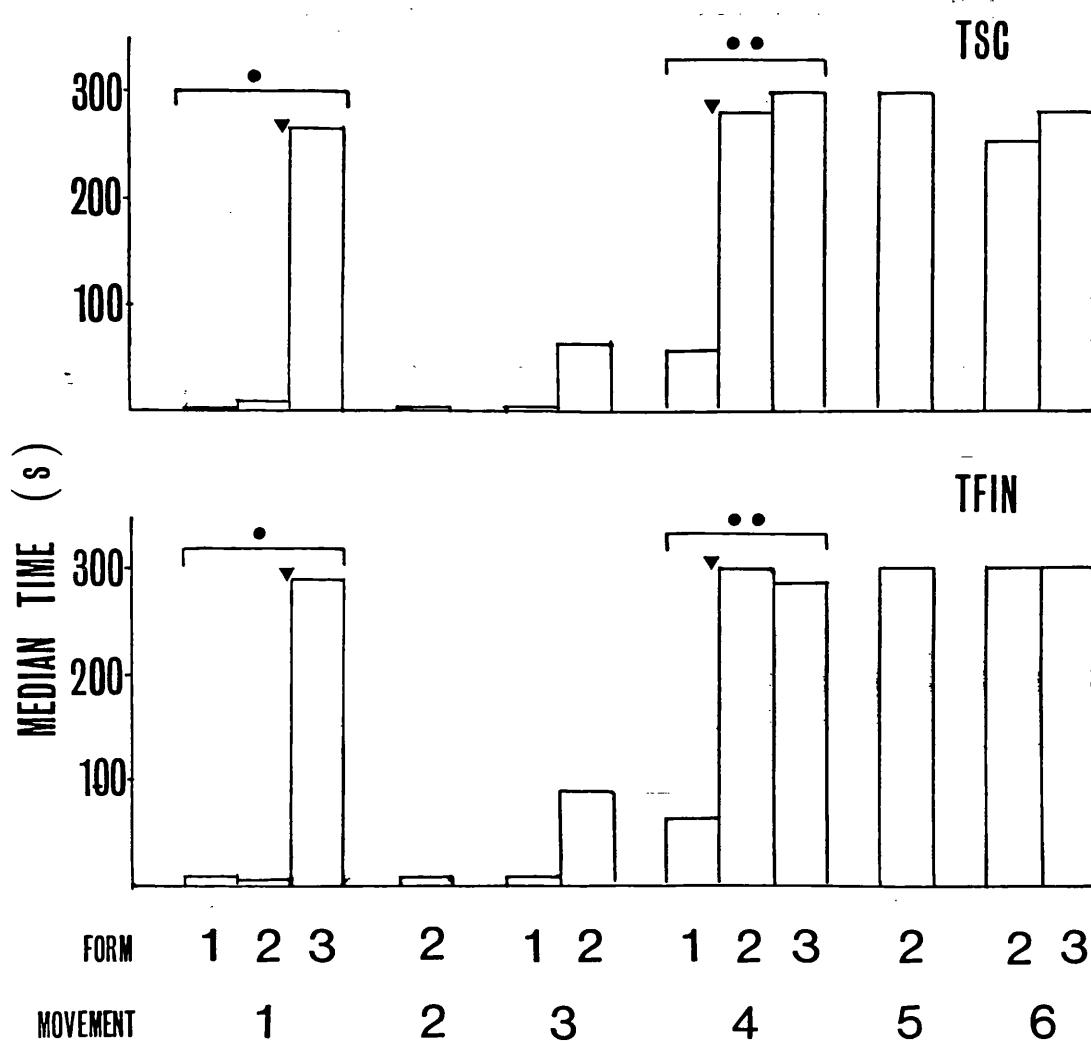


TABLE 30 Behaviours performed by pike for different forms and movement of stimuli at the hunger state H2. Medians and range given.

VARIABLE	MOVEMENT 1		MOVEMENT 3		MOVEMENT 4		MOVEMENT 5		MOVEMENT 6	
	E1	E2	E1	E2	E1	E2	E2	E3	E2	E3
ATTENTIVE	0.0	1.1	0.3	2.2	1.8	1.5	1.6		3.0	2.2
(0)	(13.0)	(2.0)	(6.0)	(3.0)	(4.0)	(2.0)		(5.0)	(5.0)	
INATTENTIVE	1.0	0.5	0.9	1.0	0.7	1.1	1.7		0.8	0.5
(0)	(12.0)	(11.0)	(3.0)	(2.0)	(3.0)	(2.0)		(5.0)	(2.0)	
ORIENTATE	0.0	0.7	0.1	1.2	0.5	0.8	2.2		5.5	4.2
(0)	(2.0)	(1.0)	(4.0)	(2.0)	(3.0)	(2.0)		(7.0)	(8.0)	
SNAP	0.0	0.3	0.0	0.3	0.0	0.0	0.1		1.5	1.5
(0)	(6.0)	(0)	(4.0)	(0)	(0)	(1.0)		(5.0)	(8.0)	
APPROACH	0.0	1.5	0.1	1.5	1.0	2.2	3.5		9.8	10.5
(0)	(17.0)	(2.0)	(12.0)	(3.0)	(8.0)	(6.0)		(11.0)	(15.0)	
POINT	0.0	2.5	0.1	4.0	0.5	4.8	4.8		16.0	17.0
(0)	(10.0)	(3.0)	(21.0)	(4.0)	(13.0)	(5.0)		(20.0)	(21.0)	
STRIKE	0.0	0.1	0.0	0.5	0.0	0.5	1.0		2.2	2.5
(0)	(2.0)	(0)	(6.0)	(0)	(2.0)	(4.0)		(7.0)	(16.0)	
BACK	0.0	1.0	0.0	1.5	0.3	2.0	2.3		5.5	7.5
(0)	(13.0)	(0)	(6.0)	(2.0)	(6.0)	(3.0)		(8.0)	(11.0)	
TOTAL	1.0	9.5	1.5	15.0	5.0	16.5	16.5		41.5	57.0
(0)	(22.0)	(10.0)	(58.0)	(14.0)	(41.0)	(12.0)		(52.0)	(60.0)	

F1 = BAR SHADOW; F2 = FISH SHADOW; F3 = 3D MODELS.

each treatment and hence it makes inter-movement comparison virtually impossible. In the majority of cases, significant changes in response to form were revealed in most behaviours in the attack sequences to stimuli with movements 1, 3 and 4. Significance values for stimuli with movements 1, 3 and 4 are given in table 31. Frequency histograms are drawn in figures 42, 43 and 44.

Timed variables for comparison of form are given in table 32 and represented in figures 45 and 46. Generally, the more effective stimuli (those considered to have some degree of sinusoidal-like moving components that approximate fish movement) elicited similar degrees of response regardless of whether or not the stimulus form was that of a bar or fish. Differences were still produced from stimuli that moved horizontally with irregular vertical components in all timed parameters ( $p > 0.05$ , see appendix). So too for the reaction of pike to stationary stimuli. No significance values are quoted as bar shadow results produced constant values for all parameters investigated which creates problems in ordering ranks in the non-parametric statistical tests (SPSS, NPAR TESTS, Hull and Nie 1981).

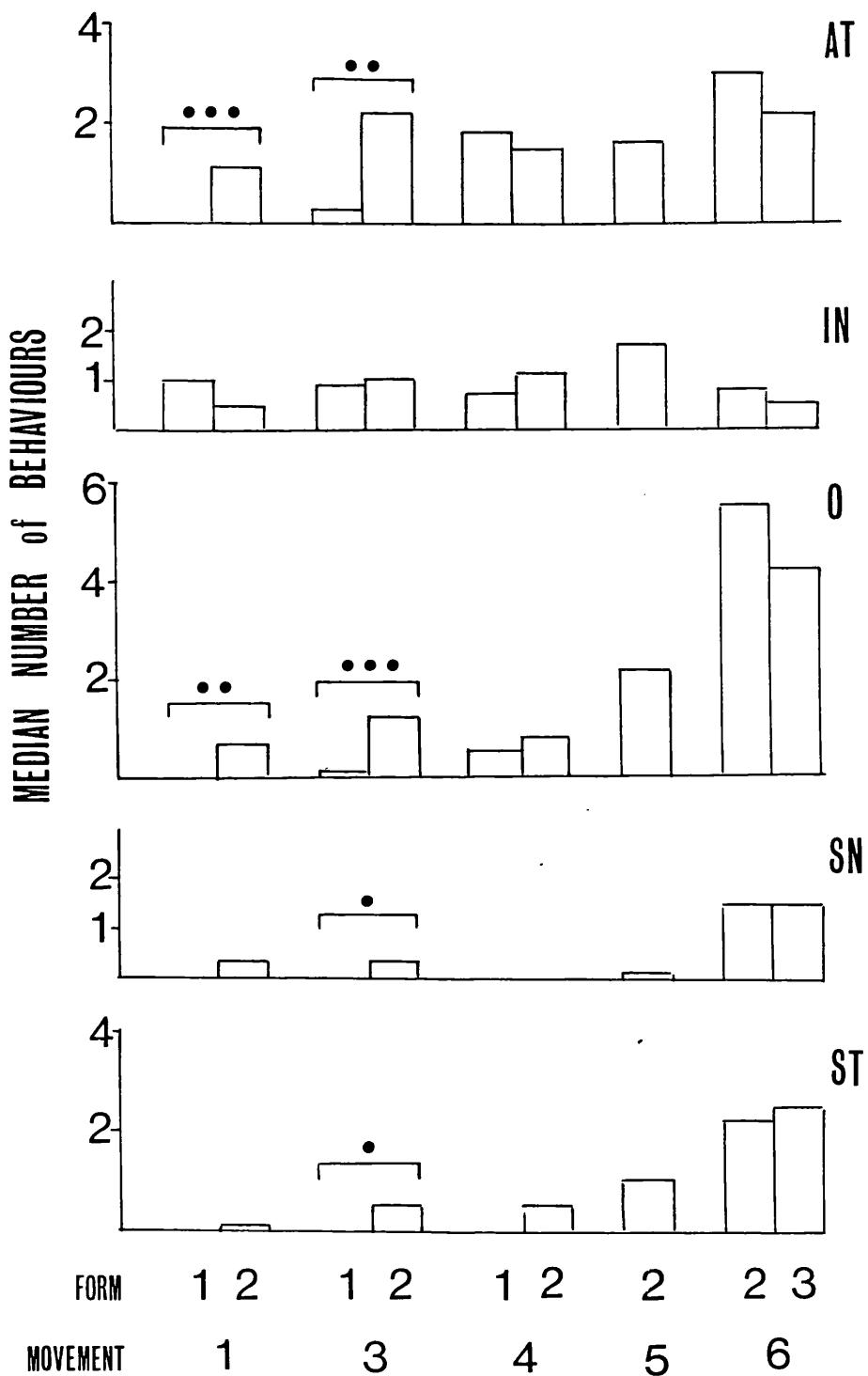
#### 4.3.4 Representation of attack responses by use of discriminant function analysis.

In 4.3.2 it was stated that the use of discriminant function analysis (DFA) could still be justified for the classification of responses, so long as parametric

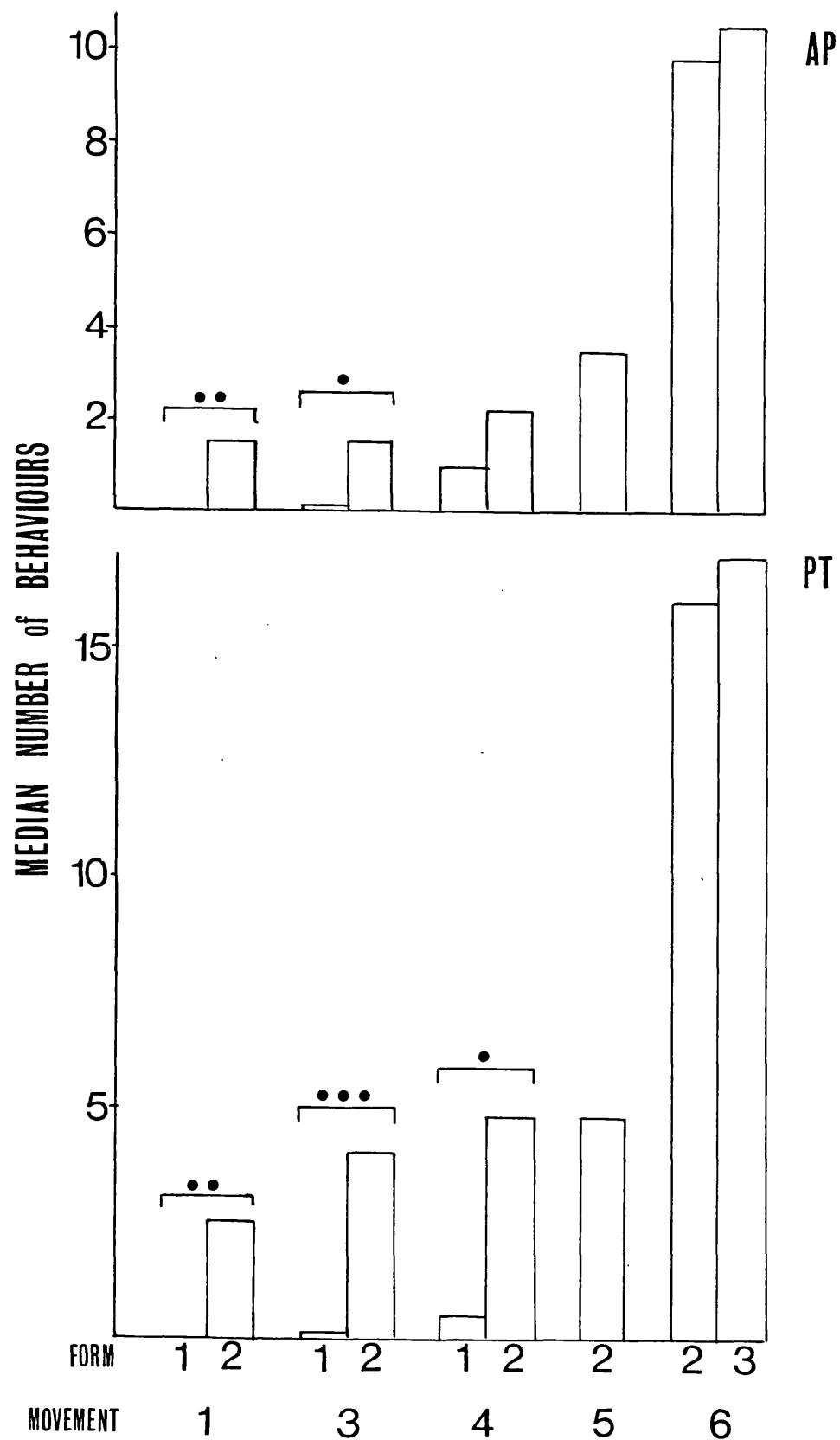
**TABLE 31** Significance table for changes in the frequency of behaviours due to the effects of stimulus form. Values of H and probability (p) are given from Kruskal Wallis one-way anovas.

	MOVEMENT 1		MOVEMENT 3		MOVEMENT 4	
<u>BEHAVIOUR</u>	H	p	H	p	H	p
ATTENTIVE	11.89	0.001	8.78	0.003	0.13	>0.05
INATTENTIVE	1.81	>0.05	0.16	>0.05	1.72	>0.05
ORIENTATE	8.00	0.005	11.80	0.001	0.59	>0.05
SNAP	1.00	>0.05	4.68	0.03		
APPROACH	9.66	0.002	5.59	0.02	2.39	>0.05
POINT	9.64	0.002	10.09	0.001	5.42	0.02
STRIKE	2.11	>0.05	6.18	0.01	6.25	0.01
BACK	7.86	0.005	7.83	0.005	3.66	>0.05
TOTAL	9.65	0.002	10.07	0.002	3.97	0.05

**FIGURE 42** Frequency histograms for the behaviours AT, IN, O and SN in the responses of hungry pike to stimuli with differing form and movement.



**FIGURE 43** Frequency histograms for the behaviours AP and PT in the response of hungry pike to stimuli with differing form and movement.



**FIGURE 44** Frequency histograms for the total number of behaviours in the responses of pike to stimuli with differing form and movement.

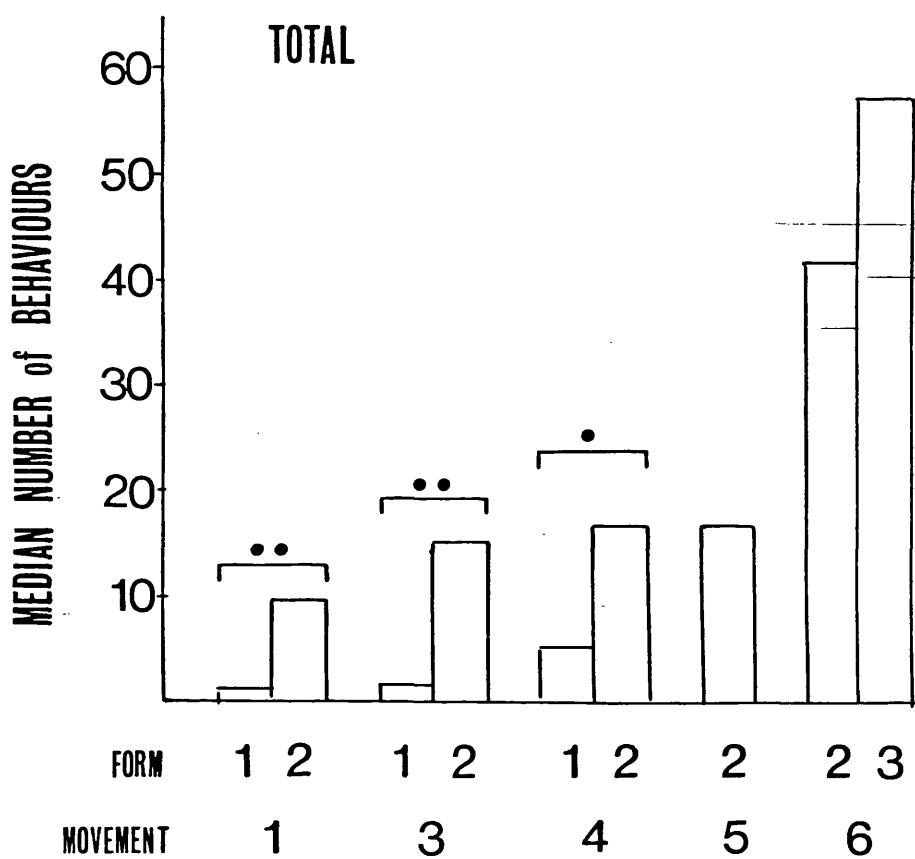
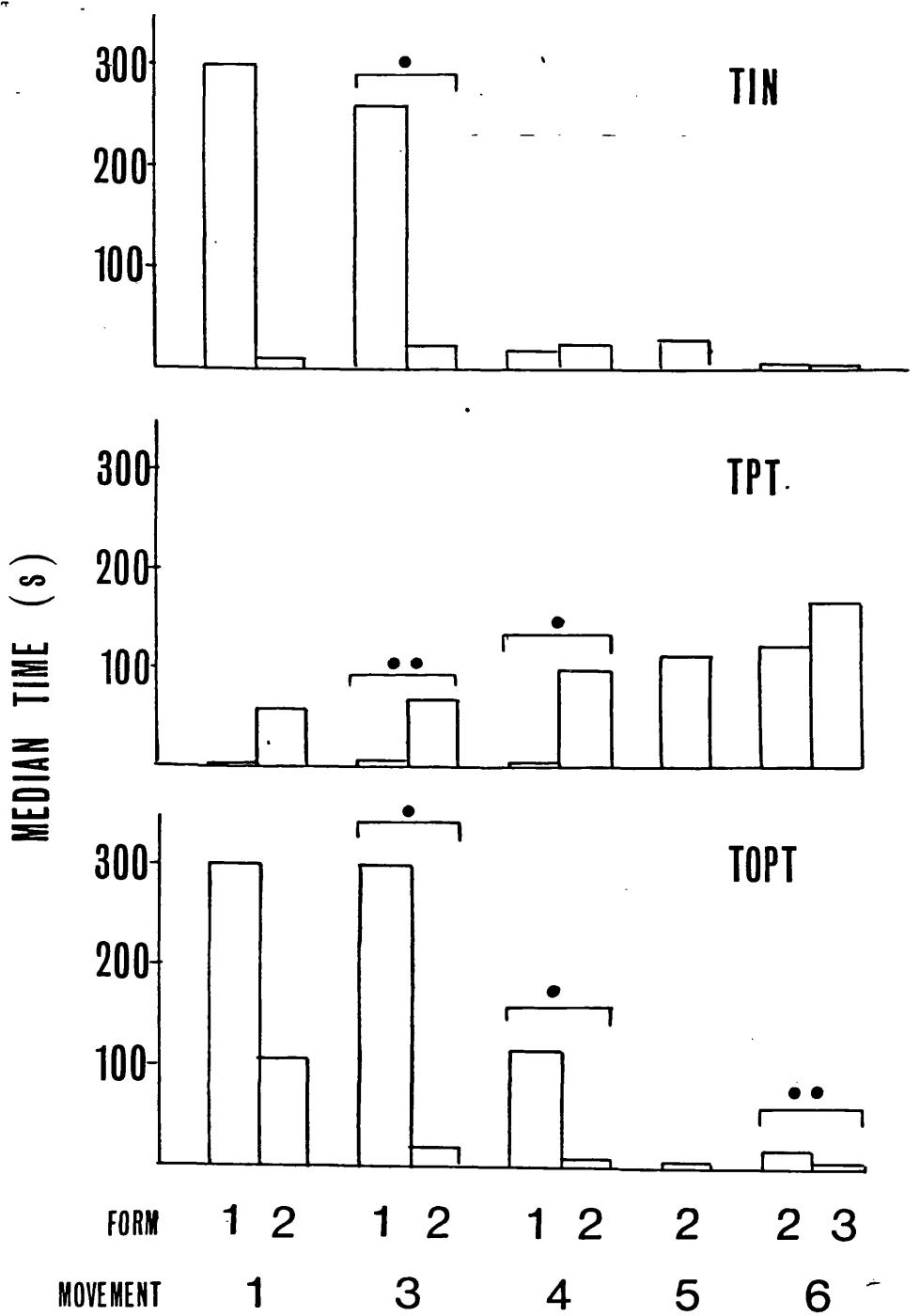


TABLE 32 Timed variables for form and movement in the attack sequences of pike towards stimuli at the hunger state H2. Medians and ranges are in seconds.

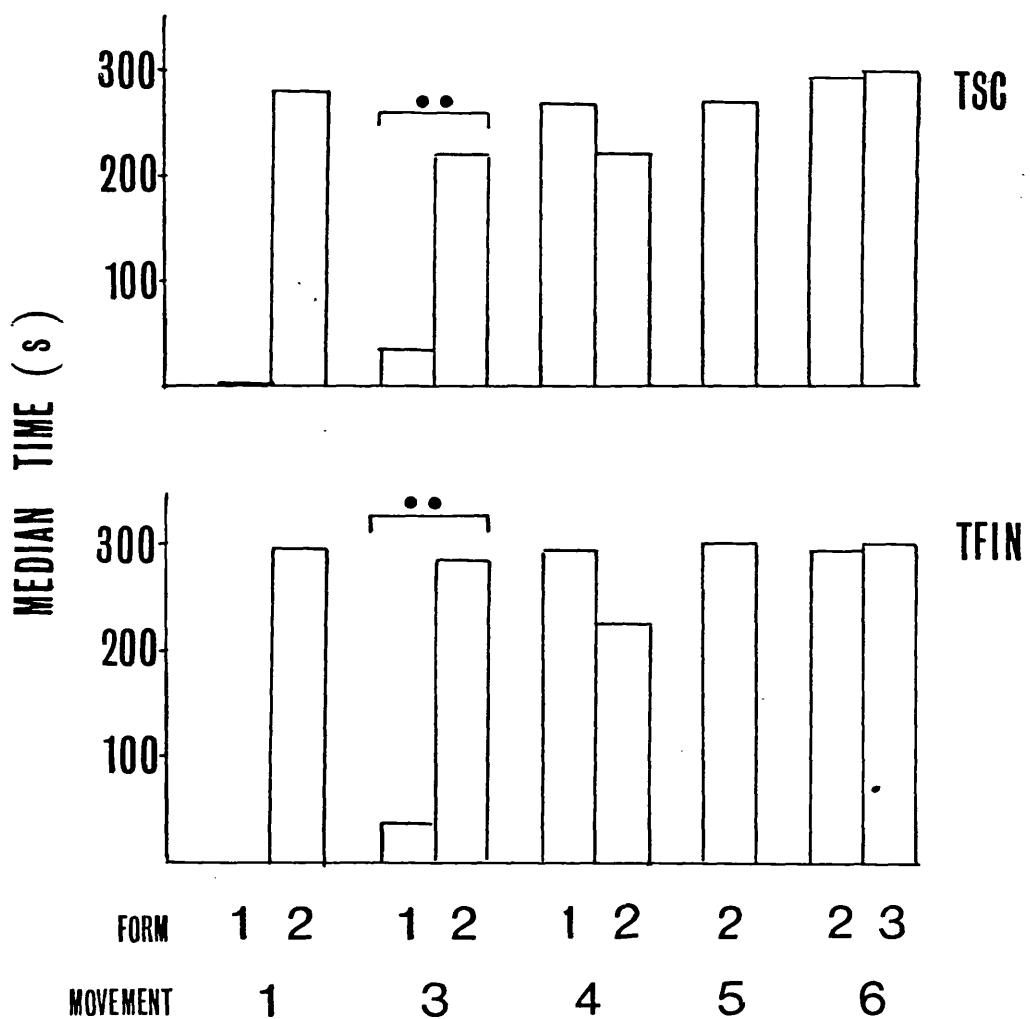
VARIABLE	MOVEMENT 1		MOVEMENT 3		MOVEMENT 4		MOVEMENT 5		MOVEMENT 6	
	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
TIN	300.0	7.7	262.5	23.1	17.3	23.4	27.2		2.9	0.1
	(0)	(300.0)	(300.0)	(300.0)	(300.0)	(300.0)	(113.1)		(168.5)	(70.5)
TPT	0.0	56.5	5.1	67.3	0.5	95.5	111.9		119.0	167.9
	(0)	(169.0)	(84.2)	(240.1)	(120.3)	(258.9)	(100.6)		(170.6)	(134.2)
TOPT	300.0	105.4	298.8	18.5	115.1	6.2	5.2		18.4	4.6
	(0)	(295.8)	(292.1)	(291.7)	(295.5)	(298.4)	(30.7)		(30.4)	(16.1)
TSC	0.0	282.5	37.5	218.3	268.2	222.5	272.8		294.7	299.6
	(0)	(300.0)	(300.0)	(300.0)	(300.0)	(300.0)	(113.1)		(168.5)	(70.5)
TFIN	0.0	297.8	37.6	284.3	294.0	225.2	301.0		294.6	300.8
	(0)	(301.0)	(301.0)	(301.0)	(301.0)	(301.0)	(0)		(169.5)	(71.5)

TIN, TPT, TOPT, TSC and TFIN are as described in table 24.

**FIGURE 45** Times for descriptive variables (TIN, TPT and TOPT) for the responses of hungry pike to stimuli with differing form and movement.



**FIGURE 46** Times for the descriptive variables TSC and TFIN  
for the responses of hungry pike to stimuli with  
differing form and movement.



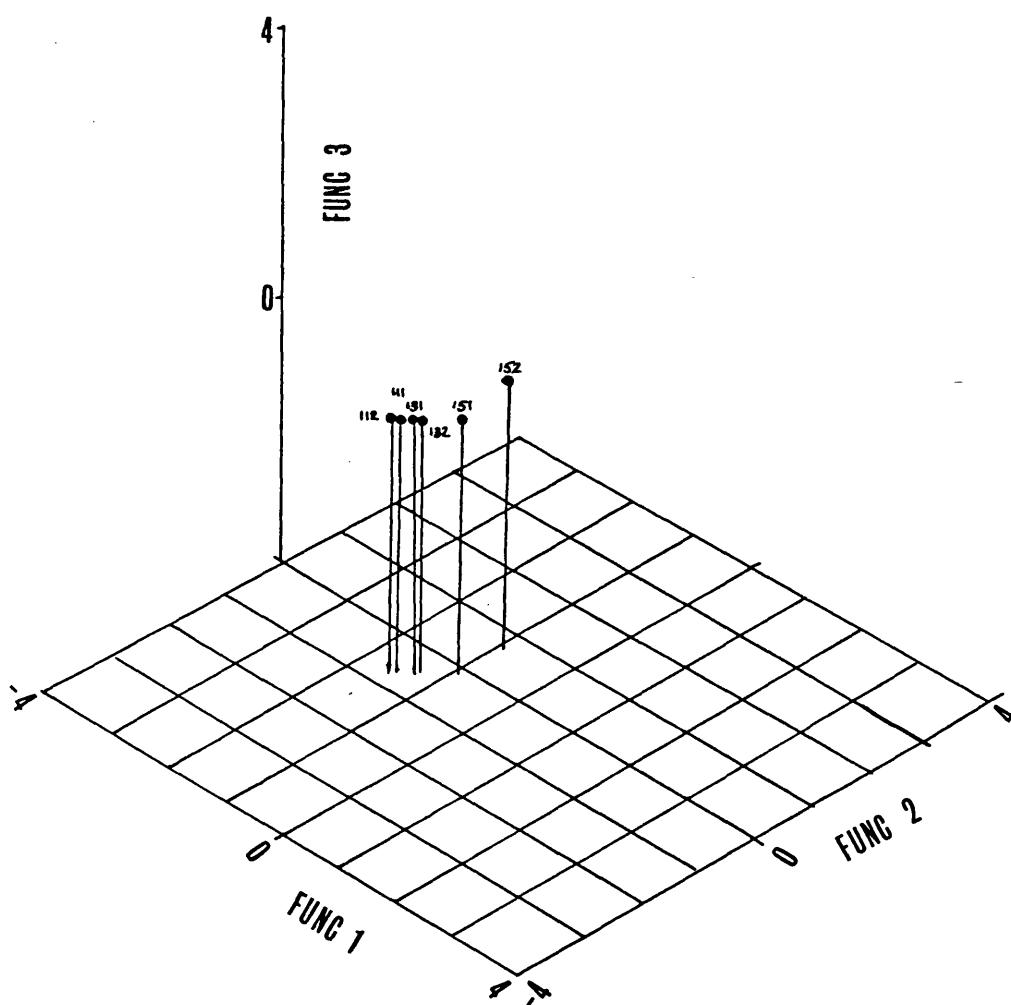
significance tests were ignored.

Figures 47, 48 and 49 provide three-dimensional plots of the responses to bar shadow, fish shadow and 3-D models respectively. Table 33 gives the three canonical discriminant functions used as coordinates for the mapping of positions representing attack sequences for each treatment of stimulus and hunger.

Response strengths may be derived from the extent to which the points plotted in the three-dimensional space lie either side of the axis of Func 2. Those points that have high positive and negative values of Func 1 demonstrate stronger and weaker attack responses respectively (refer to section 3.4.1.1). In this way, DFA offers a convenient method for assessing visually which combinations of form and movement were the most effective stimuli. DFA readily separates the responses of pike without involving the complex breakdown of multiple effects already described in the last sections. The three-dimensional plot may be used as a summary of the overall trends described in 4.3.2 but obviously for statements as to which stimuli are statistically different one needs the multiple use of KW and MW tests.

Figure 47 depicts the response strengths of pike towards the bar shadow stimuli. All points have a negative value of Func 1 with little separation of responses to a stationary shadow and one that moved horizontally with irregular vertical components. Points representing the reaction of pike to the bar shadow with a degree of sinusoidal-like

**FIGURE 47** Three dimensional plot for discriminant functions separating the responses of pike to bar shadow stimuli. (Numbers on dots denote form, movement and hunger as in table 33)



**FIGURE 48** Three dimensional plot for discriminant functions separating the responses of pike to fish shadow stimuli. (Numbers on dots denote form, movement and hunger as in table 33)

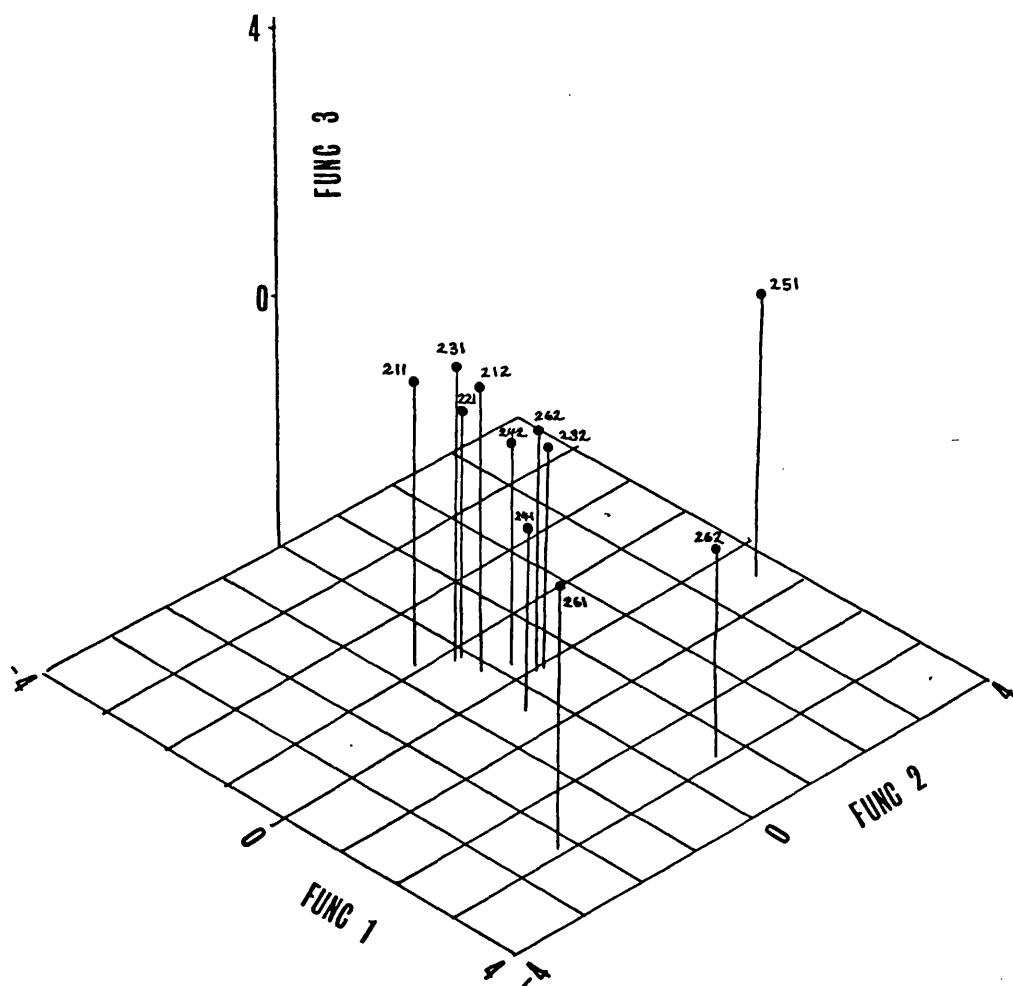
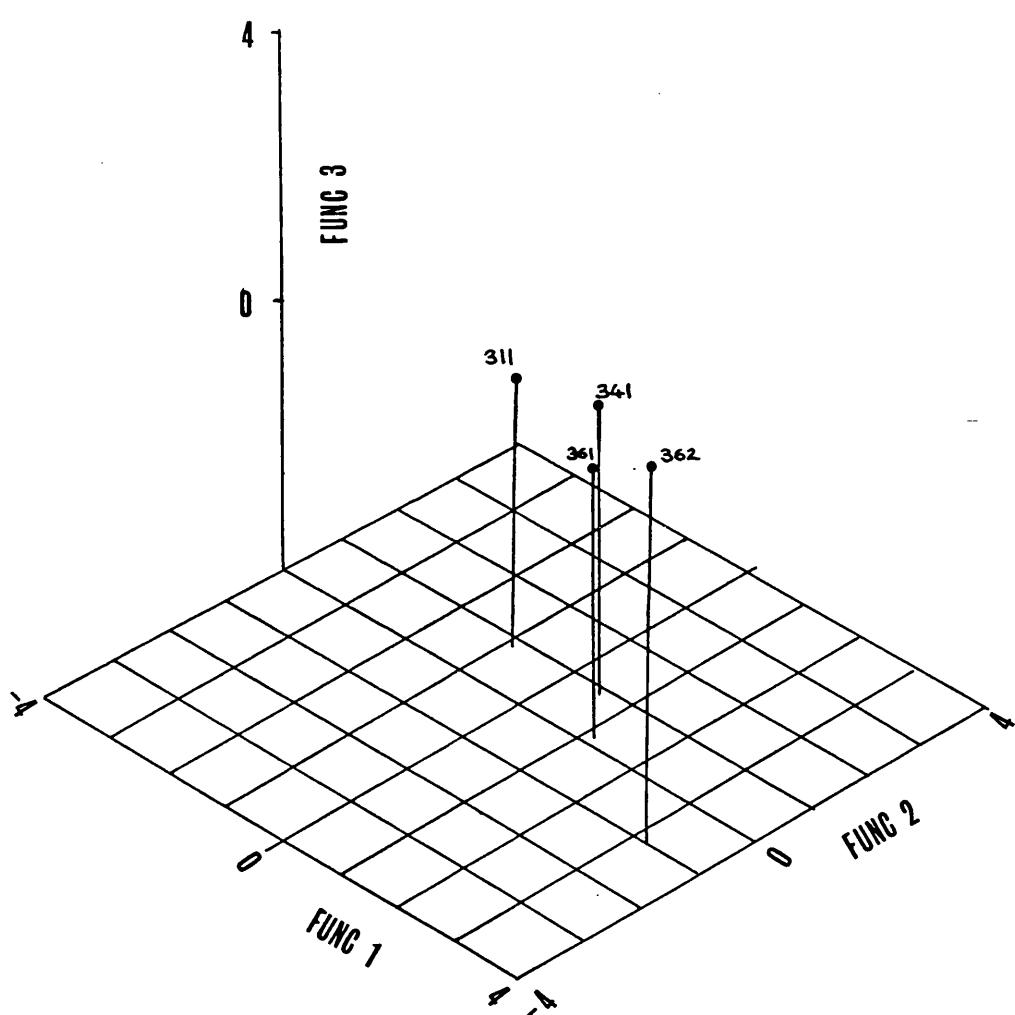


FIGURE 49 Three dimensional plot for discriminant functions  
separating the responses of pike to  
three-dimensional stimuli. (Numbers on dots  
donate form, movement and hunger as in table 33)



**TABLE 33** Canonical discriminant functions assigned to the responses of pike to different stimulus treatments.

<u>FORM</u>	<u>MOVEMENT</u>	<u>HUNGER</u>	<u>FUNC 1</u>	<u>FUNC 2</u>	<u>FUNC 3</u>
1	1	1	-1.3222	-0.8085	0.0321
1	1	2	-1.3424	-0.8973	0.0732
1	3	1	-1.2618	-0.6127	-0.0129
1	3	2	-1.2489	-0.5241	-0.0082
1	4	1	-0.9127	-0.1274	-0.1347
1	4	2	-0.8673	0.6926	0.0963
2	1	1	-1.0859	-0.7003	0.2999
2	1	2	-0.4500	-0.1508	0.3449
2	2	1	-0.8387	-0.1572	-0.1555
2	3	1	-0.7228	-0.2936	0.6221
2	3	2	-0.0630	0.6338	-0.7234
2	4	1	0.5928	-0.3310	-1.2689
2	4	2	-0.1765	0.1794	-0.5196
2	5	1	0.4902	3.8192	0.3887
2	5	2	0.1799	0.2459	-0.1380
2	6	1	3.0280	-2.2051	0.0958
2	6	2	2.9222	0.6521	-0.7583
3	1	1	-0.8437	0.7933	0.2175
3	4	1	0.5499	0.8991	0.4660
3	6	1	1.1959	0.2228	0.1261
3	6	2	2.8522	-0.4350	1.3442

(Numeration of form, movement and hunger is given  
in table 18)

movement lie closer to the postulated response axis Func 2. The values of Func 1 are still negative, indicating relatively weak response strengths compared to those for fish shadow and 3-D stimuli.

Figure 48 shows the response strengths for fish shadow stimuli. Those stimuli involving stationary or horizontally moving stimuli without sinusoidal components are located furthest to the left of the Func 2 axis. The influence of hunger moved these points closer to the Func 2 axis, describing an increased reaction to stimuli when pike were more hungry (see points corresponding to movements 1 and 3). Points associated with movements 4, 5 and 6 indicate stronger responses, values of Func 1 are more positive. The greatest reaction was to the live fish stimulus and this is separated markedly from the coordinates of other stimuli.

The responses for the three-dimensional stimuli are plotted in figure 49. As the stimulus become successively more "real" in appearance, points tend to the right hand side of the response axis Func 2.

#### 4.3.5 Contrast measurements for stimuli presented.

The contrast for stimuli presented are given in table 34. Contrast is determined as the ratio of the background luminance (BL) minus the stimulus luminance (SL) to the background luminance (Hester 1969).

**TABLE 34** Mean contrast values for stimuli expressed in  
luminance ( $\text{cd m}^{-2}$ ).

<u>STIMULUS</u>	<u>MEAN CONTRAST</u>	<u>S.D</u>
STATIONARY BS, FS	0.44	0.21
HORIZONTAL BS, FS	0.49	0.13
SINUSOIDAL BS, FS	0.52	0.10
HORIZ + SINUSOID FS	0.53	0.14
LIVE FS	0.42	0.13
STATIONARY 3DF	0.46	0.16
SINUSOIDAL 3DF	0.51	0.14
LIVE 3DF	0.44	0.13

( BS = bar shadow; FS = fish shadow; 3DF = three-dimensional  
models )

$$BL = \frac{BL - SL}{BL}$$

Details of the measurement of contrast is given in section 4.2.3.2: There were no significant differences in contrast values for all the stimuli presented to pike (analysis was by t-tests, Sokal and Rohlf 1981).

#### 4.4 DISCUSSION

The interaction between prey stimuli and individual pike was dependent on the various characteristics of form and movement of the stimuli and on the hunger-motivated states of the subject pike. The relationship between these factors could be further influenced by the physical properties of the stimuli presented, such as light intensities and contrast, so too by the individual pike used. The responses to stimuli may be strongly affected by the latter fact, in that those fish that respond strongly in one trial may not repeat the same performance in subsequent presentations of stimuli. Indeed, pike have been shown to learn very quickly (Beukema 1970, Christiansen 1976).

It is suggested, on the basis of results in 4.3.1, that pike are subject to negative reinforcement as they hit the aquarium panels when striking at the more effective stimuli. As a consequence, individuals could soon become habituated to the introduction of stimuli in any trial. The success of

this part of the study, therefore, relied on the selection of individuals that were likely to be responsive to the stimulus given. This selection was dependent on the amount of time that pike had spent in the experimental system and by the nature of the stimuli that individuals had experienced before.

Choosing suitable individuals in laboratory experiments is not a unique problem. Fuchs (1967) and Barmack (1970) realised that it was often difficult to extract optimum performance from individuals in a controlled laboratory situation. However, relaxing the conditions to give a more naturalistic setting in order to avoid complications such as those of negative reinforcement and individuals becoming "system tired" would have made the observation of response strengths considerably more difficult.

The solution to the problem encountered in section 4. was to use the ten pike and subject them once only to each stimulus treatment. This was accompanied by a progression from weaker stimuli to stronger stimuli to negate as far as possible the effects of negative reinforcement. It was anticipated that the use of first trial data might avoid some of the problems encountered in the first investigations. In addition it was hoped that deleterious affects would be reduced by the fact that responses were measured behaviourally and not at a more confined level such as a physiological investigation of retinal receptivity (Tamura 1957).

As later results suggested, the unconditioned state of pike could not be maintained indefinitely. Moving shadow stimuli evoked similar responses to three-dimensional presentations in later trials and a live fish shadow stimulus was better in terms of the number of behaviours seen, compared to its real counterpart in eliciting the attack behaviour of pike. The interpretation of this result was that either a fish shadow was indeed a more effective stimulus, or, that by the time a pike encountered real prey stimuli in the sequence of stimulus presentations, individuals were demonstrating degrees of negative conditioning. A performance check at this stage on the responses of pike towards a fish shadow stimulus revealed that there was a significant reduction in response which warranted the cessation of further stimulus presentations (see section 4.2.3.4).

A determination of which characteristics of prey stimuli were the most effective in eliciting attack responses necessitates the sorting of interactive factors. Having checked for conditioning effects and controlling the hunger-motivated states of individuals, it may be assumed that the responses elicited were attributable to the nature of the stimuli presented. However, even with as controlled an environment as possible, individual variation showed through in the results. This was reflected in the ranges for some behaviours in 4.3.2 and 4.3.3. A greater sample size would have been needed to reduce the effects of individual variation but was not possible due to limitations in tank space and time constraints at this stage of the study. The use of non-parametric statistics provided the most suitable

method for determining trends within a data set displaying heterogeneity.

Within the range of six possible prey movements and three forms of stimuli, there are differences in the stimulus presentations that must be taken into account. Firstly, the nature of stimuli that appear intermittently and those remaining on the screen for five minutes must be evaluated. As indicated in 4.3.2 intermitting stimuli can be treated as a stimulus characteristic in its own right but the use of a different timed variable facilitated a meaningful treatment comparison. Secondly, differences in physical properties of the stimuli that may have affected perception of stimuli must be assessed.

The contrast of an object is important when considering why certain stimuli elicit the responses they do. For example, objects in motion tend to be more conspicuous to an animal than when they are stationary. This is caused by the edges of an object being emphasized through an increase in contrast between stimulus and background (Hinde 1970, Treisman 198-). The intensity of a stimulus is therefore effectively changed and as in any sensory modality, stimuli of a higher intensity are more readily reacted to due to a greater amount of sensory nerve fibre excitation (Hinde 1970, Manning 1979). Light intensity is also important in an animal's ability to discriminate objects as it can alter the contrast of an object. This is particularly true for the natural water environment (Dabrowski 1982, 1984). If a fish responds greatly to differences in contrast this may imply choice by

perception rather than a choice of form or movement.

In this investigation, contrast measurements showed that there were no changes in contrast for all stimulus treatments. All changes in response may therefore be attributed to prey characteristics and hunger-motivated effects.

The general trend that emerged was that stimuli containing degrees of sinusoidal-like movement elicited stronger responses. This was demonstrated with the bar shadow movements in 4.3.2.1. The bar with sinusoidal movement was more quickly reacted to than one that moved across the screen in a horizontal fashion and pike remained interested for longer periods of time. The fact that a bar shadow moving sinusoidally arouses "interest" in pike demonstrates that movement can strongly influence responses to less prey-like objects. This has been shown also in work on the prey catching activity of salamanders (Roth 1978) and in toads (Borchers et al 1978). The significance of a certain type of movement was further emphasized in the results with fish shadow stimuli. A fish shadow moving horizontally with a sinusoidal-like "flicker" evoked a greater response from pike than one that was moving horizontally without it.

Irregularity of movement has been postulated by previous workers on pike predation as being a key factor in the elicitation of attack responses and the selection of prey items (Beyerle and Williams 1968, Christiansen 1976). In this study the fish shadow that moved horizontally with

irregular vertical components only produced a very weak response relative to those responses to stimuli with sinusoidal-like movements. It would appear from these results that a sinusoidal movement contributes more authentically to the illusion of a moving fish prey. The fact that a live fish shadow was most responded to may give some credence to the irregularity of movement postulation as live fish were unrestricted in their trajectory of movement. In other words, the pike has evolved in a way that enables it to pick out from the range of possible movement, those which are uniquely shown by swimming fish.

Christiansen (1976), in the only previous quantitative work on the nature of effective stimuli in the predatory behaviour of pike, stated that the type of movement was important in eliciting attack responses. In his work he presented a fish model to pike. The model was pulled through the water with three speeds,  $0.05 \text{ ms}^{-1}$ ,  $0.2 \text{ ms}^{-1}$  and  $0.5 \text{ ms}^{-1}$ . At the slowest speed all pike showed a weak interest in the model presented (this may be analogous to the weak response of pike to a stationary stimulus at H1 as shown in section 4.3.2.2). In Christiansen's experiment there was again little reaction to the second speed of model presentation but at the speed of  $0.5 \text{ ms}^{-1}$  80% of his subject pike attacked. Christiansen proposed that the increase in response was due to an increase in the frequency with which irregular movements of the model occurred. On the basis of this finding he negates any model deficiency that may have caused the weak responses at slow swimming speeds.

Moving stimuli presented in this investigation had a set speed of  $0.16 \text{ ms}^{-1}$ . This was sufficient to produce an attack response particularly when a sinusoidal-like movement was present. It would suggest therefore that Christiansen's model lacked an appropriate visual cue at slower speeds and that the pike in his experiment were responding more to the speed of movement than a specific character associated with his model's movement. Perhaps these models became less stable as they were towed faster developing a side to side wag at the highest speed. Pike are known to be well adapted to perceive movement and are capable of registering 25 stimulations on the retina in one second (Protasov 1968). This facility enables them to respond to fast moving objects and linked with the fact that objects moving faster increase the intensity of a stimulus it seems feasible that Christiansen's pike were responding to speed of movement. It is also worth commenting that Christiansen made no allowance for the possible modification of attack behaviour caused by the hunger-motivated state of individuals.

The acceptability of prey stimuli was influenced by hunger. Less prey-like stimuli, as described in terms of movement, were responded to differently with a change in hunger-motivated state. For very hungry pike a fish shadow stimulus, such as those which were either stationary or moving horizontally without sinusoidal-like components elicited similar responses to those with sinusoidal components. There was a general increase in the amount of time that pike were "interested" in the weaker stimuli and their speed of reaction was quickened when they were more

hungry. This conforms to previous works on the influence of hunger on the fixation and acceptance of less prey-like objects (see Curio 1976 for a detailed account). The increased acceptance of less prey-like stimuli as defined by the various movements, was not true for the form of stimulus when pike were hungry. Pike still showed increased responses to a fish shadow stimulus compared to a bar shadow at the most hunger-motivated state.

It is generally accepted that as predators approach satiation, they become more selective acting as if prey were more abundant (Schoener 1971, Pulliam 1974, Charnov 1976) and that hungry predators accept a wider variety of prey items (Schoener 1971). A good example of this in fish is that of the feeding of stickleback (Beukema 1958) where the fish snap up small inedible objects resembling prey as hunger increases. The results for the most satiated pike indicated that they were less ready to display "interest" in stimuli lacking sinusoidal-like movements, supporting the fact that satiation increases selectivity. The change in selectivity with hunger, as illustrated earlier, may explain why pike reputedly accept almost anything in their diet. When hungry, a sinusoidal movement of any object, such as a leg of a waterfowl when swimming, may be enough to elicit a strike from pike. (A consideration of cue strengths and hunger will be accounted for in the general discussion).

Although it is true to say that movement strongly influences the attack responses made by pike on specific stimuli, the summation of possible factors influencing the reaction of

pike towards prey can be made up by differing proportional effects. For example, the response of pike (at an intermediate hunger-motivated state) to a stationary stimulus without any movement was enhanced by a three-dimensional stimulus. Pike were seen to spend less time inattentive, remaining interested for longer periods of time. When the same stimuli moved sinusoidally there was no increase in response towards a three-dimensional form. Therefore, under different conditions, characters of stimuli summate heterogeneously.

As found in other animals, the reaction of pike to stimuli follow some general principles. These are that the response may change when stimuli are presented on different occasions, at different times pike show changing selective responses and that the strength of a stimulus required to produce a standard response is dependent on the internal state of the individual.

## 5 GENERAL DISCUSSION

The study of the influence of stimuli on the behaviour of animals has mostly been confined to the receptor level at which stimuli are first received (see Curio 1976 for a review). Recently there has been an awareness for relating sensory capabilities of animals to the way in which they carry out a particular activity, and, that there are important interactions between stimuli and the state of an animal which modify an individual's behaviour.

Stimuli from prey objects strongly influence the acceptability or palatability of food in the feeding response of animals. Predatory animals can distinguish the form of possible prey objects but rarely does this stimulus elicit the predatory response alone. Often other cues such as movement and patterning are needed in association with form for a predator to initiate an attack on prey (Curio 1976) and this leads to the description of eliciting stimuli in the context of the heterogeneous summation required to evoke particular responses as an animal carried out an activity.

In this discussion about pike, relating the interaction of cues and internal state to the more general field of food selection and prey preferences which have been well documented by ecologists, may be informative. Mann (1982), in a recent account of the prey preferences of pike, found that pike-prey relationships were complex in their nature. As suggested in other works (Ricker 1952, Frost 1954, Lawler

1965) factors such as food availability, vulnerability of prey species and the selective feeding of pike could all influence the diet of pike. In the light of such evidence, pike, although euryphagous, can be influenced in their predatory behaviour by the abundance of certain prey species in that such prey items may be predated on more. Mann's data show also that different prey species may be selected at various times of the year and that selection was linked to changes in the populations of prey species.

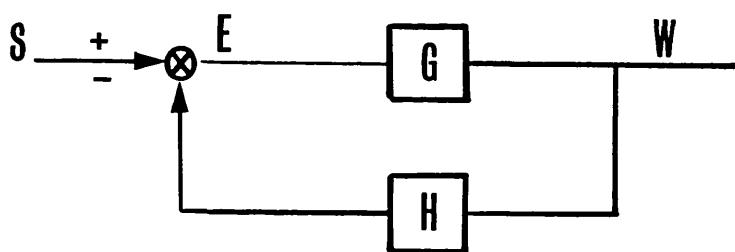
Mauck and Coble (1971) demonstrated that prey preference could be changed by the relative availability of prey items. Pike predating in closed ponds apparently took in their diet the last of one fish species before switching to eating fish of another species. Such a statement implies that although the relative abundance of prey is important in determining the diet of pike, pike nevertheless still are able to actively select their prey. The question therefore arises as to which mechanisms bring about such behaviour. It is hoped that this study may help in suggesting ways in which prey choice and diet may be further understood.

This study has been specifically concerned with the investigation of pike feeding, in that the goal, or purpose, of feeding is to maintain a state of nutritional balance and the behaviour that an animal carries out to achieve this balance is influenced by a homeostatic system. A deficit in the gut, for example, may determine the way in which feeding behaviour is directed and the intensity with which the activity is pursued.

In experiment 2 it was seen that as satiation approached, pike were less likely to pursue and capture prey. Satiation, as indexed by stomach content in 3.1, can be thought of as the inhibitor of feeding. In experiment 3 an investigation of the effects of prey stimuli-whether it be at the lower end of an hypothesized satiation scale or not, revealed that the same stimulus could elicit different strengths of response which were dependent on the degree of inhibition to the feeding tendency of pike. It was also shown that the same form of stimulus with various moving components could elicit different attack responses for a given stomach content value. In this scheme, therefore, stimuli can be considered as an excitation to the homeostatic system, the influence of which will depend on the values of other variables in the system.

The way in which motivation and response can be illustrated is often, due to the complex way in which factors interact, difficult to choose. An understanding of motivation is helped by looking at a model which describes the system being investigated. There are several ways in which this can be achieved (see Huntingford 1984). The system of feeding in pike in this study, as outlined in the previous paragraph, is essentially that of a scheme described by Wirtshafter and Davis (1977) and Bolles (1980) in their feeding models for rats and flies respectively. The models that they used are simple representations of a complex system. The model of Wirtshafter and Davis (1977) is given in Figure 50 with a pike's feeding system as determined by the experiments in this study, presented in figures 51 and 52.

Figure 50 The model of Wirtshafter and Davis (1977) that shows the influences on response to a feeding stimulus.



S = strength of feeding signal, E = difference between excitation and inhibition, G = set of internal factors, W = energy store and H = inhibitory influence

**Figure 51** A model to show how a pike's response to a feeding stimulus may be modified.

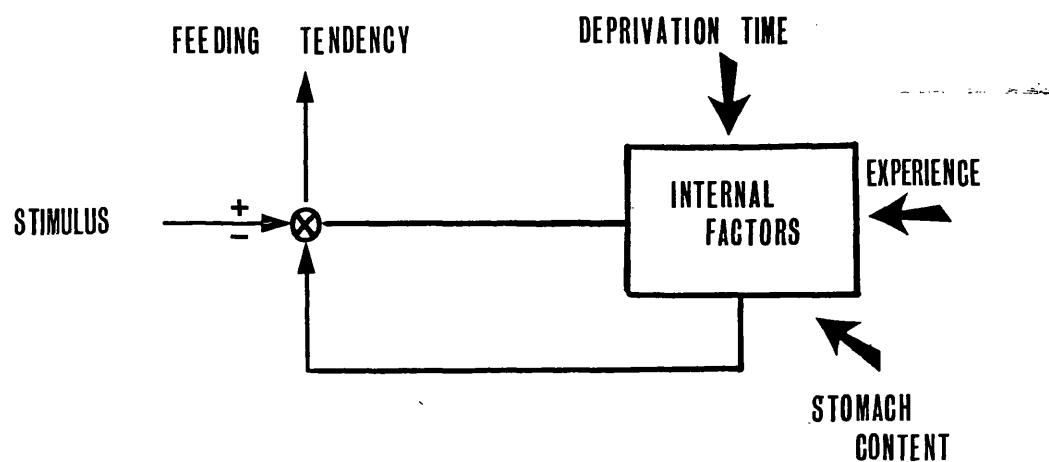
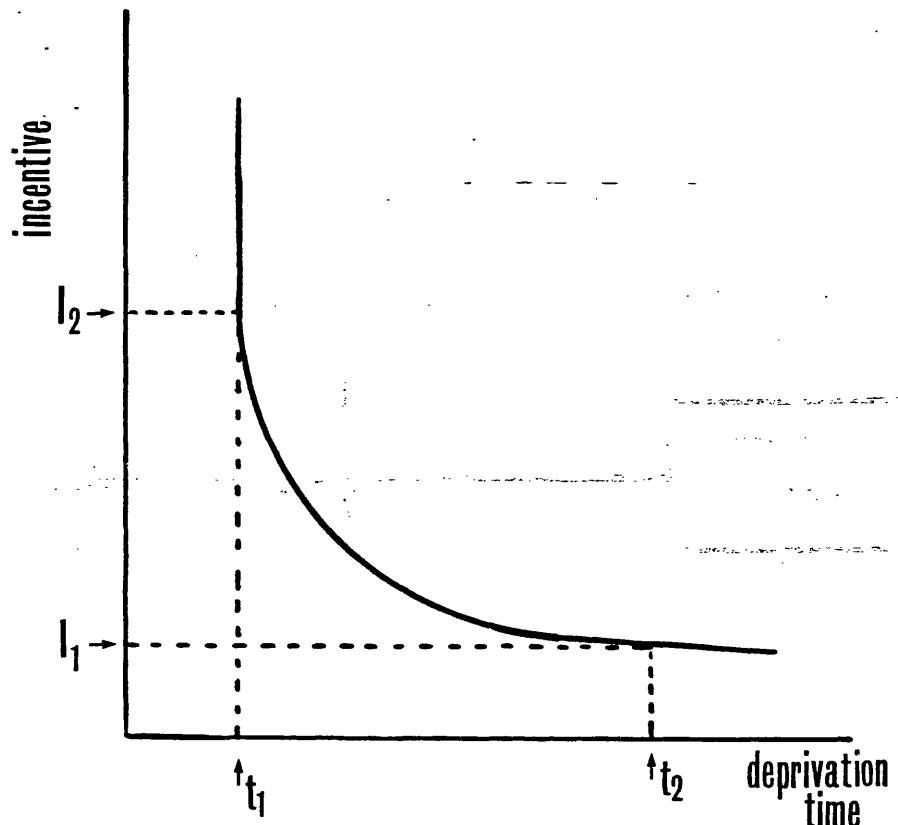


Figure 52 Model proposed by McFarland and Sibyl (1975)  
to predict motivational tendencies.



Each point on the curve has an equal strength of motivational tendency. Another curve would be needed to represent a combination having a higher motivational tendency.

The models assume that the amount of feeding carried out by an animal is dependent on the difference between excitation and inhibition. In simple terms, this is a trade-off between the strength of food cues and hunger, the value of which constitutes an animal's feeding tendency (McFarland and Houston 1981). However, as recognised from figure 51, factors such as deprivation time and previous experience can also influence the outcome. Such influences were encompassed in the terminology of a causal factor state by McFarland and Houston (1981) which was introduced Figure 1 of the general introduction. As has been continually emphasized throughout earlier chapters, it is the interaction of these internal or causal factors that evoke the concept of motivation to describe them.

McFarland and Sibly (1975) proposed a model that predicted motivational tendencies (Figure 52). The curve of McFarland and Sibly represents a relationship between an incentive to feed (food quality) and the hours from when an animal last fed (deprivation time) where they postulated that an animal would always perform an action for which the tendency was the greatest.

Baerends (1970) produced a model for the motivational system controlling egg incubation in gulls, with a hierarchy of response behaviours resulting from the influence of various internal states and external stimuli. To produce a simple model for the attack behaviour of pike to various treatments of stimuli is not easy. The elucidation of a hierarchy of

stimuli and their interactions with one motivational state (hunger) necessitates a calculation of how different characteristics of stimuli summate to elicit a given response.

Taking the results of 4.3 it is possible to adapt the curve to consider the relationship between cue strength (an increase in cue strength represents the progression from a stationary bar shadow stimulus to a swimming live fish shadow stimulus) and hunger (postulated from stomach content values). The scale for the cue strength axis may be determined from the temporal parameters of behaviours in 4.3 for the responses of pike to each stimulus at an intermediate level of hunger, on the assumption that the effectiveness of stimuli relative to each other are best determined at that state (Hinde 1970). These results are used to overcome the problems of stimulus presentation and the duration of which they were present in a pike's field of vision. The axis of deprivation time may be substituted by stomach content to represent hunger (see section 3.4.2 for a justification of this). Hunger may be presumed to affect the probability of eating an item; as hunger increases the probability of eating rises, approaching unity (Colgan 1973). Hunger is taken to be zero when the stomach is full and more than zero when the stomach is less than full.

The axis of hunger (stomach content) is represented as percentage body weight of pike (experiment 2) and it is possible to relate the two hunger-motivated states used in experiment 3 to those stimuli presented in order to form the

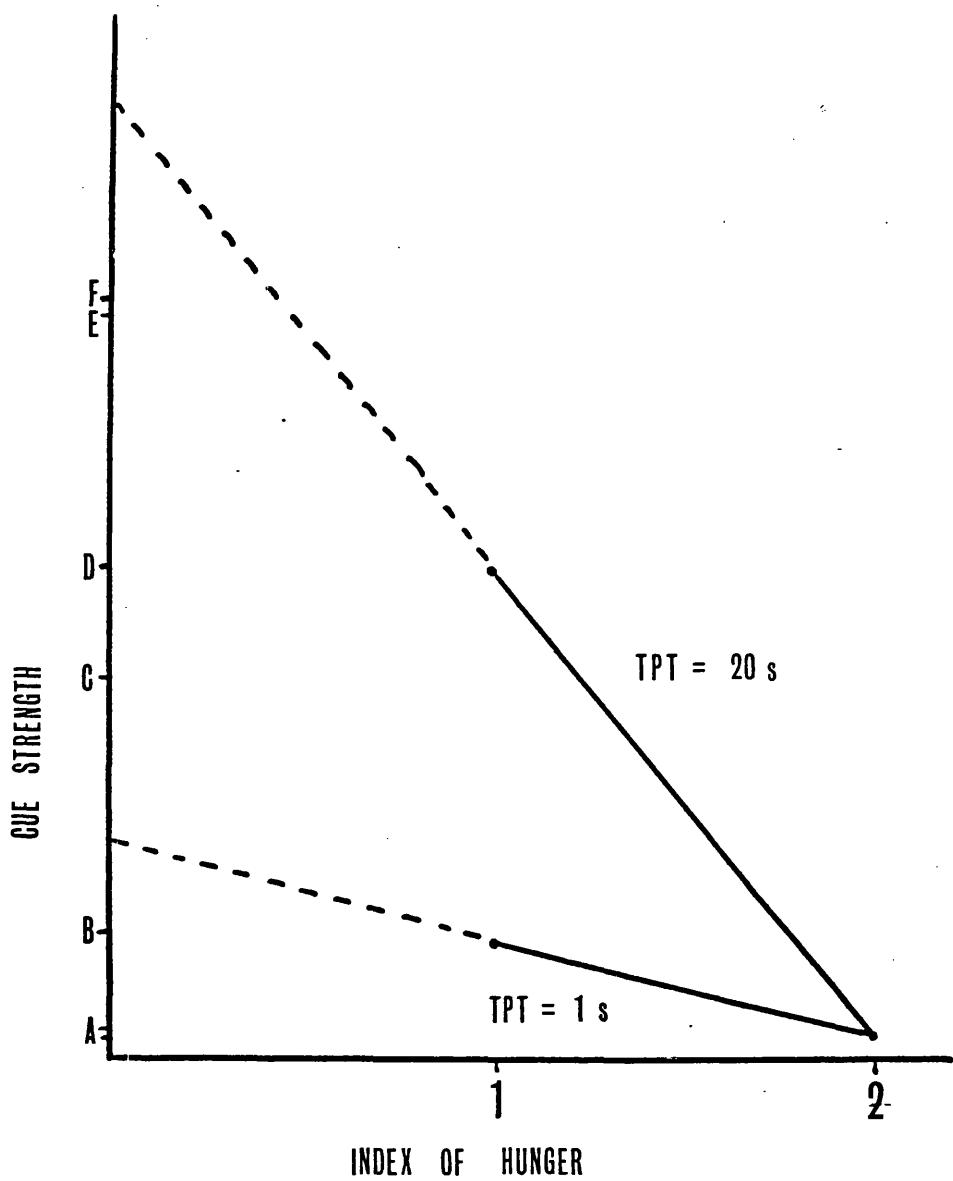
**Guide to figures 53 to 56**

The following graphs are hypothetical representations for the degree of effect of different stimuli on a pike's feeding behaviour.

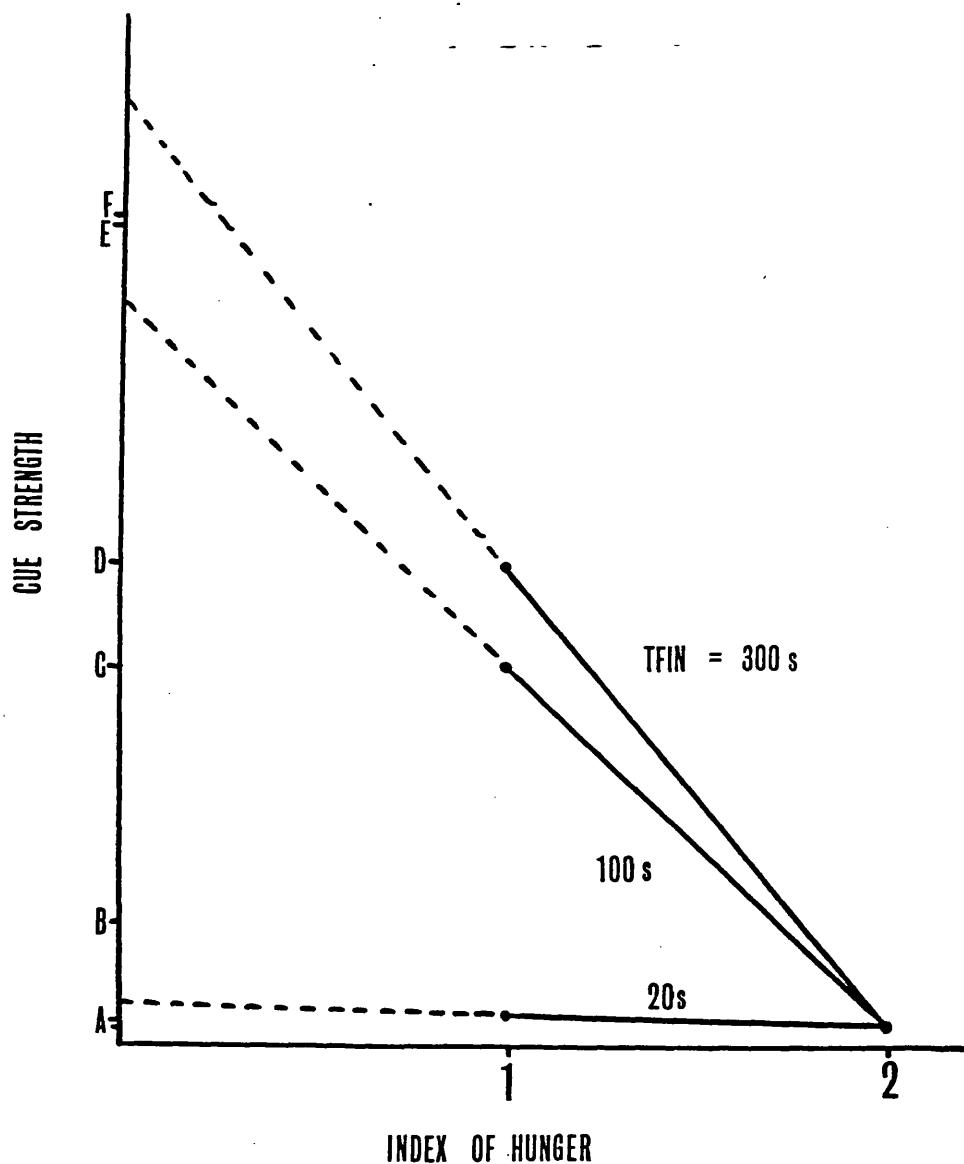
The combination of form and movement (cue strength) are given letters.

- A Fish shadow moving horizontally with irregular vertical components
- B Bar shadow moving sinusoidally about a fixed point
- C Fish shadow moving horizontally with a sinusoidal flicker
- D Fish shadow moving sinusoidally about a fixed point
- E Shadow of a fish swimming
- F Real fish swimming

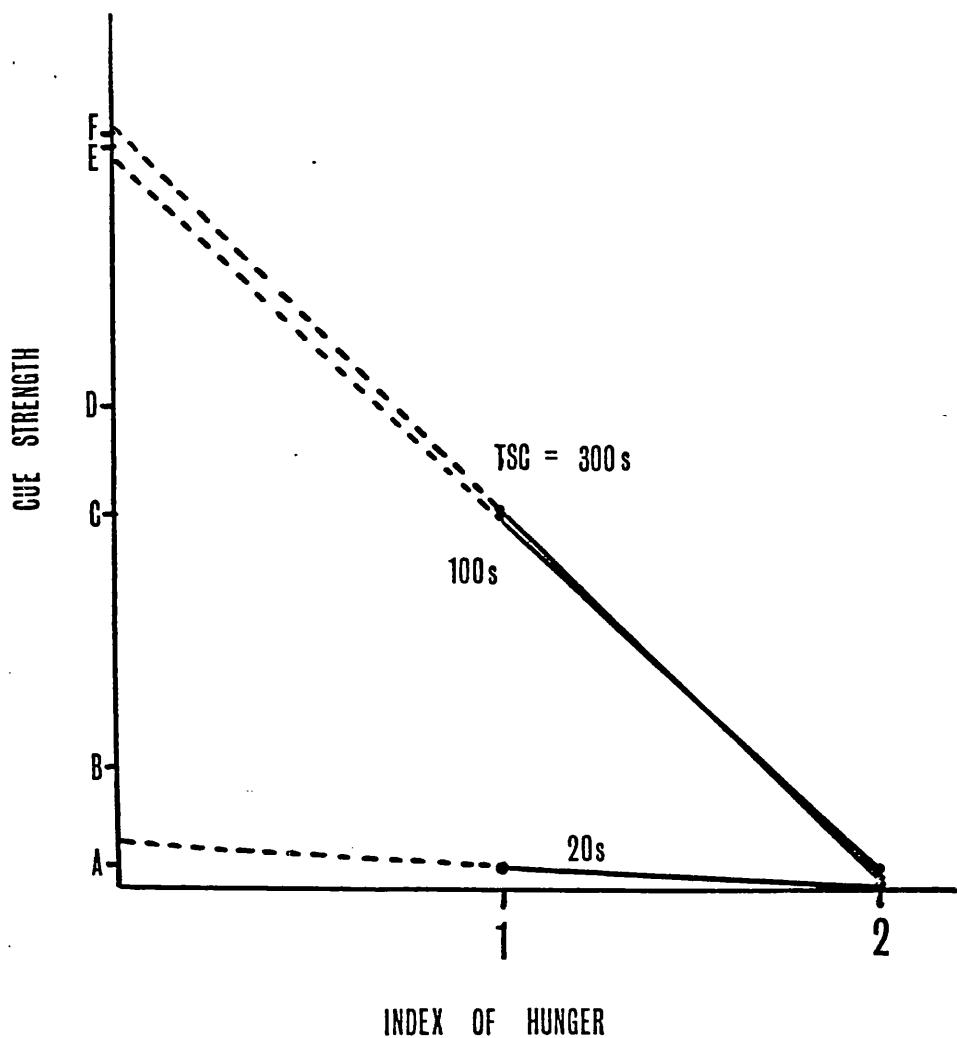
**Figure 53** Hypothetical isocline of cue strength and hunger  
and its effect on the amount of time a pike spends  
pointing at a stimulus (TPT).



**Figure 54** Hypothetical isocline of cue strength and hunger  
and its effect on the time when a pike finally  
becomes disinterested in a stimulus.



**Figure 55** Hypothetical isocline of cue strength and hunger  
and its effect on the time a pike spends looking  
at the presentation screen.



isocline of motivational tendency postulated by McFarland and Sibly (1975). The evaluation of the cue strength axis was made by finding combinations of form and movement that produced equivalent responses in time, for example, the duration of interest in stimuli for predetermined time intervals.

It is assumed in this discussion that the probability of pike capturing prey in any encounter (or more strictly, the degree of response to stimuli) approximates linearly as hunger increases. This assumption is taken from work on blue-gill sunfish (Colgan 1973). It is now possible to construct hypothetical isoclines in order to predict what may happen if the responses of pike to different stimuli had been investigated at hunger states closer to satiation. Figures 53, 54 and 55 present possible plots for TPT, TFIN and TSC. It can be seen that for a pike to point at a stimulus for 20 s when its stomach is full, would require stimuli more effective than the live, swimming fish stimulus. Similarly, this would be the case for a pike to remain interested in a stimulus for the duration of a trial. For a pike at satiation to be interested in a feeding stimulus for 20 s the presentation of a stimulus with a sinusoidal movement component is required.

Such reasoning may represent the weak feeding responses of pike to a shoal of minnows at the most satiated hunger state in experiment 2.

The legitimacy of these plots in terms of there only being two points of stomach content with which to draw the

isoclines is obviously questionable. Further work is necessary to define the shape of the complete isocline. However, the general deduction that more than effective stimuli (super-normal stimuli) are required to elicit equivalent responses at satiation would not be contradicted if the form of the isocline was changed due to further investigation. The reason for this is that there are only two forms of isocline possible due to the relationship between feeding response and hunger. The one form of isocline is linear as expounded above, the other is a curve. If the results plotted were part of a curve, then more effective stimuli would be required than already suggested for a linear relationship. It is possible that an isocline for the relationship between cue strength and hunger may indeed be a curve if the probability of feeding followed the exponential curve of gastric evacuation determined by Diana (1979). However, a much more defined set of stomach content values and response would be required to prove this and at this point no further inference can be made save only that the appearance of the isocline provides a basis for possible future investigation.

Returning to the simple model of hunger postulated earlier (figure 51), it may be realised that different levels or values of factors within the causal state may change the position of the isoclines describing feeding tendency. The isocline may be changed by systemic need, temperature, deprivation times, digestive rates and encounter rates with prey. The approach conjectured in this discussion may have relevance in understanding the real "willingness" of pike to

feed. It is worth noting that an interpretation of behavioural tendency in terms of motivational isoclines has been successfully related to the data of Baerends et al (1955), for the courtship display of male guppies, by McFarland and Houston (1981). It is envisaged that the selection of prey as regards to form, shape and movement can be represented in a similar way.

If it can be accepted that motivational isoclines may go some way to representing the feeding behaviour of pike then the question of how pike may choose food in the wild may also be considered in a similar way. If a food source diminishes then it can reasonably be assumed that a pike may be deprived of food as the encounter rate with prey items decreases. This alters the threshold of response to specific prey as hunger increases. This was demonstrated by the increased response of pike towards less fish-like stimuli in experiment 3.

When pike were feeding on dace in the River Frome, Dorset (Mann 1982) it may be suggested that because dace were abundant they constituted a strong feeding stimulus to pike as the frequency with which they were encountered was high. In other words, the development of a search image makes a species more stimulating. It may also be inferred that a pike's state of hunger would be one of satiation, or close to it. With such an interaction of factors, the combination of cue strength and hunger would mean that pike would always feed on dace if they always performed an action for which the tendency was the greatest, which would mean that dace are

taken at low levels of hunger as they constitute the most attractive feeding stimulus. A pike's motivational tendency, therefore, would lie in the region of the curve corresponding to large cue strengths and little hunger (refer to figure 52). With the seasonal variation in prey populations, deprivation of food would cause a position shift on the motivational isocline so that stimuli offered by other prey fish (relative cue strength is less as they had been encountered less) would cause pike to predate on them. This is analogous to the change in response of pike towards less prey-like stimuli at more hunger-motivated states in experiment 3. The shift from dace to other prey species may be dependent on cues such as form, colour and movement, though such information cannot be deduced from pure ecological surveys.

The suggestion is then, in this system, that the nature of a prey stimulus determines the feeding response when related to pike hunger. This interpretation has to be reconciled with the proposition that feeding behaviour maximises net energy gain. In terms of motivational isoclines once more, if the situation arises that hunger increases prey offering less attractive stimuli will be taken thereby reducing hunger. This is acceptable if one assumes that the objective of feeding is to obtain a predefined quota of food in a day (overall energy gain) and that the way in which this is achieved is not reliant on net energy gains at any moment in time but is dependant on where a pike's feeding tendency is aligned on the motivational isocline.

The description of a possible way in which pike change their choice of prey as exemplified here is not as simple as outlined. Mann did not suggest otherwise, and as do other workers it is generally accepted that pike are opportunistic predators feeding on a wide range of prey items. There must also be no confusion between what constitutes a long term response and those which are short term. For a pike to be truly opportunistic its predatory behaviour must be readily adaptable to changes in its environment. It may be postulated that a change in hunger coupled with a pike's increased response to objects with a sinusoidal component in its movement (experiment 3) is sufficient in motivational terms to initiate predation on a wide range of prey species. The extent that a simple sinusoidal-like cue, when pike are hungry, can evoke predatory attacks may suggest a feasible explanation for predation on swimming waterfowl and mammals due to similar movements made by their limbs.

It is not claimed that the results of this study explain exactly what may happen as a pike predares in the wild. In the laboratory situation many factors of the environment which would influence the behaviour of pike was kept constant. The simplicity of approach facilitated a progression of ideas in order to describe the predatory behaviour of pike and to overcome motivational problems that become inherently more complex as conditions become less restricted. Analysis of the immediate causes of behaviour was kept at the behavioural level, measuring the input and output from stimulus modification, though there are those who would argue that behaviour can only be understood by

determining what occurs at the neurophysiological level (Wilson 1975). A simple black box approach allowed aspects of feeding stimuli and possible motivational variables to be selected and their overall contribution to the intensity of pike predatory behaviour evaluated, the consequence being that as a motivational factor such as hunger increased, stimuli sharing fewer characters of the natural, and presumably optimal stimulus, were adequate in eliciting a given response.

Although the approach employed in this study was structured to maintain observations on interacting factors at a level that was as simple as possible, there is the desire to attempt to put some order into the results obtained.

A problem encountered in this study was that not all the information required for this approach was achieved. The main source of this problem that determined how much of the results could be relied on as useful information, was the fact that obtaining the details associated with effective stimuli were influenced by the experiences of the individual pike under investigation. As Ewert and Keul (1978) demonstrated, in the prey-catching behaviour of toads, replication of stimulus presentations led to the habituation of the predatory response. This was supported by the observations in 4.3.1.

In this study an alternative means of describing behaviour was used that did not require complex modelling. The objective was to overcome the problem of representing data

that described the various effects of stimuli and internal state on the frequency of ten behaviours in a pike's predatory repertoire. The use of discriminant function analysis facilitated the representation of behavioural sequences as values of the interaction of state and stimuli, which could be easily plotted in a three dimensional space. Sequences of these ten behaviours exhibited by pike in response to different stimuli presentations were separated and the ethological observer can readily look for trends or dissimilarities in the plots of the first three canonical discriminant functions (see 4.3.4).

The fact that discriminant function analysis selected most of the ten possible behaviours in the predatory sequence of pike responding to the various stimulus treatments, demonstrates that when motivational studies include more variables interpretation becomes more complex. This may be compared with the results from discriminant function analysis on behavioural sequences for pike predating on minnow shoals where the only variable being included in analysis was hunger (3.4.1).

Although three discriminant functions are required for the complete representation of predatory sequences, it is possible to construct a simple hierarchy of stimulus treatments from the values of the first discriminant function assigned to each treatment (refer to figures 47 - 49). The first discriminant function describes the major separating factor in determining between sequences of behaviours. As discussed in sections 3.4.1.1 and 4.3.4 the Func 1 axis may

be thought of as a scale for the response strength as a pike reacts to different stimuli. From the spatial separation of the first discriminant functions the hierachial order of stimuli for pike at an intermediate state of hunger is:-

WEAK RESPONSE 1. BS (1,3); FS (1)

2. BS (4); FS (2,3); 3D (1)

3. FS (4,5); 3D (4)

4. 3D (6)

STRONG RESPONSE 6. FS (6)

where BS= bar shadow, FS= fish shadow and 3D= fish model; numbers in brackets denote types of movement (see 4.2.3.1 for details).

The hierarchy makes it easier to understand the interaction of stimulus form and movement. The outcome is similar to the scale devised for the isocline treatment of cue strength and state. It must be remembered that the above list is one devised purely from spatial separation of first discriminant functions and that significant differences in response can only be assessed by reference to specific behaviours in the predatory sequence, as discussed earlier.

From the appreciation of interacting factors it is now possible to summarise the nature of stimuli presented in this study. Various aspects of the natural stimulus may influence the predatory behaviour of pike. Some of these characteristics are of greater importance than others, for example, fish shape and the presence of a sinusoidal-like

component of movement, and in general these are parameters which are most like the features of the natural stimulus. The selective response to these characters and their relative contribution to a given response may be altered by the state of pike at any given time.

The pike, from the results of this study, appears to be well adapted to the selection of particular visual cues which may be modified by how hungry the animal is.

## **APPENDIX**

The tables given in this appendix extend those results presented in section 4.3. The following abbreviations are assigned -

F Form of stimulus

M Movement

H Hunger state

Numbers relating to the differences in form, movement and hunger are the same as in section 4.3.

## 1 KRUSKAL WALLIS ONE WAY ANOVA TABLES

### 1.1 EFFECTS OF MOVEMENT

Table 3 E2, H=1, and H=2

Table 1 E1, H=1, and H=2.

VARIABLE	H1		H2		VARIABLE	H1		H2		VARIABLE	H1		H2		
	H	p	H	p	ATTENTIVE	27.87	0.000	9.71	0.046	ATTENTIVE	0.34	0.842	ATTENTIVE	0.34	0.842
ATTENTIVE	8.95	0.01	17.52	<.001	INATTENTIVE	14.51	0.013	6.77	0.148	INATTENTIVE	1.05	0.592	INATTENTIVE	1.05	0.592
INATTENTIVE	0.40	0.82	2.88	0.24	ORIENTATE	30.72	0.000	22.43	0.000	ORIENTATE	11.83	0.003	ORIENTATE	11.83	0.003
ORIENTATE	8.99	0.01	8.69	0.01	SNAP	36.01	0.000	12.36	0.015	SNAP	1.97	0.373	SNAP	1.97	0.373
APPROACH	11.17	0.004	9.50	0.009	APPROACH	32.38	0.000	17.63	0.001	APPROACH	10.82	0.004	APPROACH	10.82	0.004
POINT	13.14	0.001	6.92	0.03	POINT	31.90	0.000	19.94	0.001	POINT	13.32	0.001	POINT	13.32	0.001
STRIKE	2.00	0.37			STRIKE	40.44	0.000	12.95	0.012	STRIKE	6.63	0.036	STRIKE	6.63	0.036
BACK	14.02	0.001	8.88	0.01	BACK	30.37	0.000	18.73	0.001	BACK	3.42	0.181	BACK	3.42	0.181
<b>TOTAL</b>	<b>12.64</b>	<b>0.002</b>	<b>9.35</b>	<b>0.009</b>	<b>TOTAL</b>	<b>33.28</b>	<b>0.000</b>	<b>20.82</b>	<b>0.000</b>	<b>TOTAL</b>	<b>10.60</b>	<b>0.005</b>	<b>TOTAL</b>	<b>10.60</b>	<b>0.005</b>

Table 2 E1, H=1, and H=2.

VARIABLE	H1		H2		VARIABLE	H1		H2		VARIABLE	H1		H2		
	H	p	H	p	TIN	25.54	0.000	1.65	0.798	TIN	3.87	0.149	TIN	3.87	0.149
TIN	2.44	0.118	5.82	0.016	TPT	24.20	0.000	8.11	0.068	TPT	6.26	0.016	TPT	6.26	0.016
TPT	7.01	0.008	1.54	0.214	TOPT	17.99	0.003	8.34	0.068	TOPT	14.31	0.001	TOPT	14.31	0.001
TOPT	3.62	0.057	2.01	0.156	TSC	26.95	0.000	1.82	0.768	TSC	3.79	0.151	TSC	3.79	0.151
TSC	2.44	0.118	6.33	0.012	TFIN	27.03	0.000	10.33	0.035	TFIN	8.84	0.012	TFIN	8.84	0.012
TFIN	2.09	0.101	7.59	0.006											

Table 4 E2, H=1, and H=2

Table 5 E3, H=1

## 1.2 EFFECTS OF HUNGER.

Table 1 E1, M=3

VARIABLE	H	R	VARIABLE	H	R
ATTENTIVE	0.317	0.574	ATTENTIVE	2.24	0.135
INATTENTIVE	2.904	0.088	INATTENTIVE	2.68	0.102
ORIENTATE	0.373	0.542	ORIENTATE	0.06	0.801
APPROACH	0.448	0.503	APPROACH	0.94	0.331
POINT	0.012	0.914	POINT	0.35	0.553
BACK	3.53	0.067	STRIKE	1.00	0.317
TOTAL	0.556	0.456	BACK	2.12	0.145
			TOTAL	0.18	0.673

Table 2 E1, M=3

VARIABLE	H	R	VARIABLE	H	R
TIN	0.313	0.576	TIN	6.72	0.009
TPT	0.047	0.829	TPT	0.12	0.725
TOPT	0.047	0.829	TOPT	1.28	0.257
TSC	0.313	0.576	TSC	7.01	0.008
TFIN	0.313	0.576	TFIN	7.71	0.005

Table 10 E1, M=4

VARIABLE	H	R	VARIABLE	H	R
TIN	6.72	0.009	TIN	6.72	0.009
TPT	0.12	0.725	TPT	0.12	0.725
TOPT	1.28	0.257	TOPT	1.28	0.257
TSC	7.01	0.008	TSC	7.01	0.008
TFIN	7.71	0.005	TFIN	7.71	0.005

**Table 11** E2.. M=1

VARIABLE	H	R
ATTENTIVE	7.62	0.006
INATTENTIVE	0.91	0.340
ORIENTATE	2.44	0.118
SNAP	1.00	0.317
APPROACH	4.30	0.038
POINT	5.38	0.02
STRIKE	2.11	0.147
BACK	5.78	0.016
TOTAL	5.76	0.016

**Table 13** E2.. M=3

VARIABLE	H	R
ATTENTIVE	3.05	0.081
INATTENTIVE	0.56	0.453
ORIENTATE	1.98	0.159
SNAP	0.78	0.375
APPROACH	2.62	0.105
POINT	5.52	0.019
STRIKE	2.66	0.103
BACK	0.63	0.425
TOTAL	3.99	0.05

**Table 15** E2.. M=4

VARIABLE	H	R
ATTENTIVE	0.01	0.937
INATTENTIVE	0.06	0.607
ORIENTATE	0.81	0.367
SNAP	3.37	0.068
APPROACH	0.91	0.339
POINT	1.06	0.304
STRIKE	0.23	0.636
BACK	0.02	0.877
TOTAL	0.90	0.342

**Table 17** E2.. M=5

VARIABLE	H	R
TIN	6.74	0.009
TPT	4.99	0.025
TOPT	4.28	0.039
TSC	6.74	0.009
TFIN	6.60	0.009

**Table 18** E2.. M=1

VARIABLE	H	R
TIN	4.55	0.032
TPT	5.73	0.017
TOPT	2.47	0.116
TSC	4.23	0.040
TFIN	6.03	0.014

**Table 19** E2.. M=3

VARIABLE	H	R
TIN	0.12	0.732
TPT	0.00	0.970
TOPT	3.75	0.053
TSC	0.12	0.732
TFIN	1.16	0.261

**Table 19 E2, M=6**

VARIABLE	H	R	VARIABLE	H	R
ATTENTIVE	10.05	0.002	ATTENTIVE	0.21	0.646
INATTENTIVE	5.32	0.021	INATTENTIVE	0.02	0.882
ORIENTATE	0.05	0.818	ORIENTATE	3.59	0.055
SNAP	5.48	0.015	SNAP	3.89	0.049
APPROACH	0.18	0.676	APPROACH	2.50	0.107
POINT	0.63	0.427	POINT	3.22	0.073
STRIKE	4.39	0.036	STRIKE	1.73	0.188
BACK	2.67	0.102	BACK	4.22	0.040
TOTAL	1.20	0.272	TOTAL	3.76	0.050

**Table 20 E2, M=6**

VARIABLE	H	R	VARIABLE	H	R
TIN	2.30	0.129	TIN	0.15	0.696
TPT	0.14	0.705	TPT	0.13	0.722
TOPT	1.12	0.290	TOPT	0.39	0.534
TSC	2.30	0.129	TSC	1.01	0.314
TFIN	0.48	0.487	TFIN	2.65	0.104

**Table 22 E3, m=6**

VARIABLE	H	R	VARIABLE	H	R
TIN	0.15	0.696	TIN	0.15	0.696
TPT	0.13	0.722	TPT	0.13	0.722
TOPT	0.39	0.534	TOPT	0.39	0.534
TSC	1.01	0.314	TSC	1.01	0.314
TFIN	2.65	0.104	TFIN	2.65	0.104

### 1.3 EFFECTS OF FORM.

Table 23 H=1, H=1 and H=2

VARIABLE	H=1		H=2		
	H	R	H	R	
ATTENTIVE	13.78	0.001	11.88	0.001	
INATTENTIVE	1.15	0.568	1.81	0.179	
ORIENTATE	2.78	0.249	8.00	0.005	
APPROACH	7.18	0.028	9.65	0.002	
POINT	5.62	0.060	9.63	0.002	
STRIKE			2.11	0.147	
BACK	10.23	0.006	7.68	0.005	
TOTAL	8.45	0.015	9.65	0.002	

Table 24 H=1, H=1 and H=2

VARIABLE	H=1		H=2		
	H	R	H	R	
TIN	5.70	0.017			
TPT	2.88	0.09			
TOPT	0.98	0.322			
TSC	5.71	0.017			
TFIN	5.74	0.017			

Table 25 H=3, H=1 and H=2

VARIABLE	H=1		H=2		
	H	R	H	R	
ATTENTIVE	1.75	0.185	8.78	0.003	
INATTENTIVE	3.80	0.051	0.16	0.690	
ORIENTATE	2.32	0.128	11.80	0.001	
SNAP	2.15	0.147	4.68	0.030	
APPROACH	1.42	0.234	5.59	0.018	
POINT	0.49	0.486	10.09	0.001	
STRIKE	1.00	0.317	6.18	0.013	
BACK	1.27	0.259	7.83	0.005	
TOTAL	1.57	0.210	10.07	0.002	

Table 26 H=3, H=1 and H=2

VARIABLE	H=1		H=2		
	H	R	H	R	
TIN	2.61	0.106	4.97	0.026	
TPT	1.47	0.226	9.07	0.003	
TOPT	1.13	0.287	6.43	0.011	
TSC	2.35	0.125	4.96	0.026	
TFIN	2.62	0.106	9.40	0.002	

**Table 27**  $M=4$ ,  $H=1$  and  $H=2$ 

VARIABLE	$H$		$\Delta$		$H$	$\Delta$
	$H=1$	$H=2$	$H=1$	$H=2$		
ATTENTIVE	6.73	0.035	0.12	0.723		
INATTENTIVE	4.26	0.119	1.72	0.189		
ORIENTATE	6.70	0.035	0.58	0.444		
SNAP	4.04	0.133				
APPROACH	10.93	0.004	2.39	0.122		
POINT	10.23	0.006	5.42	0.020		
STRIKE	1.51	0.550	6.25	0.012		
TOTAL	7.90	0.019	3.97	0.046		

**Table 28**  $M=4$ ,  $H=1$  and  $H=2$ 

VARIABLE	$H$		$\Delta$		$H$	$\Delta$
	$H=1$	$H=2$	$H=1$	$H=2$		
TIN	11.47	0.003	0.92	0.338		
TPT	7.33	0.026	3.73	0.053		
TOPT	5.66	0.059	3.74	0.053		
TSC	11.47	0.003	1.43	0.231		
TFIN	11.77	0.003	1.86	0.172		

**Table 29**  $M=6$ ,  $H=1$  and  $H=2$ 

VARIABLE	$H$		$\Delta$		$H$	$\Delta$
	$H=1$	$H=2$	$H=1$	$H=2$		
ATTENTIVE	4.80	0.028	1.01	0.314		
INATTENTIVE	6.80	0.009	0.28	0.597		
ORIENTATE	8.06	0.005	0.34	0.561		
SNAP	12.16	0.000	0.41	0.52		
APPROACH	1.49	0.222	0.39	0.531		
POINT	6.28	0.012	0.01	0.929		
STRIKE	5.42	0.020	0.25	0.621		
TOTAL	6.22	0.012	1.25	0.264		

**Table 30**  $M=6$ ,  $H=1$  and  $H=2$ 

VARIABLE	$H$		$\Delta$		$H$	$\Delta$
	$H=1$	$H=2$	$H=1$	$H=2$		
TIN	6.78	0.009	0.70	0.403		
TPT	0.46	0.496	3.25	0.076		
TOPT	1.75	0.186	7.57	0.006		
TSC	1.85	0.173	0.70	0.403		
TFIN	2.11	0.147	0.20	0.653		

**Exposure Value Conversion Table**

ASA100 K=13	Nits (nt)	Stilb (Sb)	Radlux (rix)	Lamberts (L)	Foot lamberts	
EV: 1	cd/m <sup>2</sup>	cd/cm <sup>2</sup>	lin/m <sup>2</sup>	lin/m <sup>2</sup>	(ft-L)	cd/ft <sup>2</sup>
2	0.27986	0.000027986	0.87922	0.000087922	0.08168	0.026
3	0.55973	0.000055973	1.7584	0.00017584	0.16336	0.052
4	1.1195	0.00011195	3.5169	0.00035169	0.32672	0.104
5	2.2389	0.00022389	7.0338	0.00070338	0.65345	0.208
6	4.4978	0.00044978	14.068	0.0014068	1.3069	0.416
7	8.9557	0.00089557	28.135	0.0028135	2.6138	0.832
8	17.911	0.0017911	56.27	0.005627	5.2276	1.664
9	35.823	0.0035823	112.54	0.011254	10.455	3.328
10	71.645	0.0071645	225.08	0.022508	20.91	6.656
11	143.29	0.014329	450.16	0.045016	41.821	13.312
12	286.58	0.028658	900.32	0.090032	83.642	26.624
13	573.16	0.057316	1,800.64	0.180064	167.28	53.248
14	1,146.3	0.11463	3,601.3	0.36013	334.57	106.5
15	2,292.6	0.22926	7,202.6	0.72026	669.13	212.99
16	4,585.3	0.45853	14,405	0.4405	1,338.3	425.98
17	9,170.6	0.91706	28,810	2.881	2,676.5	851.97
18	18,341	1.8341	57,620	5.762	5,353.1	1,703.9
19	36,683	3.6682	115,241	11.5241	10,706	3,407.9
20	73,365	7.3365	230,482	23.0482	21,412	6,815.7
	146,730	14.673	460,964	46.0964	42,825	13,631

This exposure value conversion table enables luminance readings to be determined from light readings taken on a spot sensor.

The Soligor spot sensor measures an extremely narrow angle of incidence which allows accurate recording of light emitted from objects on a background.

REFERENCES

Allen, K. R. 1939. A note on the food of pike (Esox lucius .L.) in Windermere. J.Anim.Ecol., 8, 72-75.

Andrew, R. J. 1974. Arousal and the causation of behaviour. Behaviour., 51, 135-165.

Ashby, W. R. 1963. An introduction to cybernetics. London: Edward Arnold.

Aspey, W. P. & Blankenship, J. E. 1977. Spiders and snails and statistical tales: application of multivariate analyses to diverse ethological data. In: Quantitative methods in the study of behaviour (Ed. by B. A. Hazlett), pp. 75-120. New York: Academic Press.

Aspey, W. P. & Blankenship, J. E. 1978. Comparative ethometrics: congruence of different mulivariate analyses applied to the same ethological data. Behav.Proc., 3, 173-195.

Baerends, G. P., Brouwer. R. & Walterbolk. H. 1955. Ethological studies of Lebistes reticulatus (Peters). 1. An analysis of the male courtship pattern. Behaviour., 8, 249-334.

Baerends, G. P. 1957. The ethological analysis of fish behavior. In: The Physiology of Fishes (Ed. by M.E.Brown), pp. 229-269. New York: Academic Press.

Baerends, G. P. 1970. A model of the functional organisation  
of incubation behaviour in the herring gull.  
Behav. Suppl., 17, 261-312.

Barmack, N. H. 1970. Dynamic visual acuity as an index of eye  
movement control. Vision. Res., 10, 1377-1391.

Beukema, J. J. 1970. Acquired hook avoidance in pike (Esox  
lucius .L.) fished with artificial and natural baits.  
J. Fish Biol., 2, 155-160.

Beyerle, G. B. & Williams, J. E. 1968. Some observations of  
food selectivity by Northern pike (Esox lucius .L.) in  
aquaria. Trans. Am. Fish. Soc., 97, 28-31.

Bialokoz, W. & Krzywosz, T. 1979. An analysis of the food  
composition, availability of prey and food selectivity  
of pike (Esox lucius .L.) in Lake Dgal Wielki.  
Rocznik. Nauk Rolniczych. H., 99, 7-24.

Bolles, R. C. 1980. Some functionalistic thoughts about  
regulation. In: Analysis of Motivational processes  
(Ed. by F. M. Toates & T. R. Halliday), pp. 63-75.  
London: Academic Press.

Borchers, H. W., Burghagen, H. & Ewert, J. P. 1978. Key  
stimuli of prey for toads (Bufo bufo .L.):  
Configuration and movement patterns. J. Comp. Physiol.,  
128, 189-192.

Brady, J. 1979. Biological clocks. London: Edward Arnold.

Buller, F. 1981. Pike and the pike angler. London: Stanley Paul.

Buss, K. 1961. The Northern Pike. Special purpose report., Penn. Fish.Comm, Bonner Spring Fish Research Station. 52p.

Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. Am.Nat., 110, 141-151.

Chiszar, D. & Windell, J. T. 1973. Predation by bluegill sunfish (Lepomis macrochirus) upon mealworm larvae (Tenebrio molitor). Anim.Behav., 21, 536-534.

Christiansen, D. G. 1976. Feeding and behaviour of northern pike (Esox lucius .L.). MSc.thesis.Dept.Zool. Alberta, Edmonton.

Coble, D. W. 1973. Influence of apparence of prey and satiation of a predator on food selection by northern pike (Esox lucius .L.). J.Fish.Res.Bd.Can., 30, 317-320.

Colgan, P. 1973. Motivational analysis of fish feeding. Behaviour, 45, 38-66.

Copland, W. O. 1956. Notes of the food and parasites of pike

(Esox lucius .L.) in Loch Lomond. Glas.Nat., 17,  
230-235.

Crossman, E. J. 1962. Predator-prey relationships in pikes  
(Esocidae). J.Fish.Res.Bd.Can., 19, 979-980.

Curio, E. 1976. The ethology of predation. Zoophysiology and  
Ecology 7. Berlin: Springer-Verlag.

Dabrowski, K. R. 1982. The influence of light intensity on  
feeding of fish larvae and fry. 1. Coregonus pollan.  
(Thompson) and Esox lucius .L. Zool.Jb.Physiol., 86,  
341-351.

Dabrowski, K. R. & Jewson, D. H. 1984. The influence of light  
environment on depth of visual feeding by larvae and  
fry of Coregonus pollan (Thompson) in Lough Neagh.  
J.Fish.Biol., 25, 173-181.

Day, F. 1880. Fishes of Great Britain and Ireland. Vol 2.  
London: Williams and Norgate.

Denton, E. J. & Nichol, J. A. 1965. Reflection of light by  
external surfaces of the herring, Clupea harengus.  
J.Mar.Biol., 45, 711-738.

Diana, J. S. 1979. The feeding pattern and daily ration of a  
top carnivore, the northern pike.  
J.Fish.Res.Bd.Can., 57, 2121-27.

Dill, L. M. 1983. Adaptive flexibility in the foraging behaviour of fishes. Can.J.Fish.Aquat.Sci., 40, 398-408.

Elliott, J. M. & Persson, L. 1978. The estimation of daily rates of food consumption of fish. J.Anim.Ecol., 47, 977-999.

Fehring, W. K. 1974. Stimuli in the feeding behaviour of the largemouth black bass, Micropterus salmoides (Lacepede). Unpublished Ph.D Thesis. Cornell University.

Felley, J. D. & Hill, L. G. 1983. Multivariate assessment of environmental preferences of cyprinid fishes of the Illinois river, Oklahoma. Am.Mid.Nat., 109, 209-221.

Fisher, R. A. 1936. The use of multiple measurements in taxonomic problems. Ann.Eugen., 7, 179-188.

Frost, W. E. 1954. The food of pike (Esox lucius .L.) in Windermere.

Fuchs, A. F. 1967. Periodic eye tracking in the monkey. J.Physiol., 193, 161-171.

Gandolfi, D, Mainardi, A, & Rossi, C. 1968. La reazione di paura e lo svantaggio individual dei pesci allarmisti (perimenti con modelli). Zoologia., 102, 8-14.

Halliday, T. 1983. Motivation. In: Animal Behaviour 1 - Causes and Effects (Ed. by Halliday, T. & P. Slater), pp. 100-133. London: Blackwell.

Hart, P. J. B. & Connellan, B. 1984. Cost of prey capture, growth rate and ration size in pike, Esox lucius .L., as functions of prey weight. J.Fish.Biol., 25, 279-292.

Herter, K. 1929. Dressurversuche an fischen.  
Z.F.Vergl.Physiol., 10, 688-711.

Hinde, R. A. 1970. Animal behaviour. A synthesis of ethology and comparative psychology. New York: McGraw Hill.

Hinde, R. A. 1982. Ethology. London: Fontana.

Holst, E. 1948. Quantitative unterschungen über umstimmungsvorgange im Zentralnervensystem. 1. Der EinfluB des Appetits auf das Gleichgewichtsverhalten bei Petromyzon. Z.vergl.Physiol., 31, 134-148.

Hoogland, R, Morris,D. & Tinbergen, N. 1957. The spines of the stickleback (Gasterosteus pygosteus) as means of defence against predators (Perca fluviatilis and Esox lucius). Behaviour., 10, 205 - 236.

Hope, K. 1969. Methods of multivariate analysis. New York: Gordon & Breach.

Houghton, W. H. 1890. British freshwater fishes.

Hull, C. & N. H. Nie. 1981. SPSS Update 7-9. New York:  
McGraw-Hill.

Huntingford, F. 1976. An investigation of the territorial behaviour of 3-spined sticklebacks using principal components analysis. *Anim.Behav.*, 24, 822-834.

Huntingford, F. 1984. The study of Animal Behaviour. London:  
Chapman.

Ingle, D. 1971. Prey catching behaviour of anurans towards moving and stationary objects. *Vision.Res.Suppl.*, 447-456.

Ingle, D. 1971. The experimental analysis of visual behaviour In: *Fish Physiology* (Ed. by Hoar & Randall). New York:  
Academic Press.

Johnson, L. D. 1966. Experimental determination of food consumption of pike, Esox lucius .L., for growth and maintenance. *J.Fish.Res.Bd.Can.*, 23, 1495 - 1505.

Johnson, L. D. 1969. Food of angler-caught northern pike (Esox lucius .L.) in Murphy Flowage.  
*Wis.Dept.Natur.Res.Tech.Bull.*, 42, pp26.

Josiak, G. R. & Moore, W. S. 1982. Discriminant analysis of two cyprinid fishes, Phoxinus eos and Phoxinus erythrogaster. (Pisces: Cyprinidae). *Am.Mid.Nat.*, 108,

398-407.

Kendall, W. C. 1917. The pikes: their geographical distribution, habits, culture and commercial importance. U.S. Bureau of fish.Rept.Comm.Fish.App5., 1-45.

Lagler, K. F. 1956. The pike, Esox lucius .L., in relation to waterfowl on the Seney National Wildlife Refuge, Michigan. J.Wildl.Mgmt., 20, 114-124.

Lanchester, B. S. & Mark, R. F. 1975. Pursuit and prediction in the tracking of moving food by a teleost fish (Acanthaluteres spilometanurus). J.Exp.Biol., 63, 627-645.

Lawler, G. H. 1965. The food of pike, Esox lucius .L., in Heming Lake, Manitoba. J.Fish.Res.Bd.Can., 22, 1357-1377.

Lehner, P. N. 1979. Handbook of ethological methods. New York: Garland STPM Press.

Lorenz, K. 1950. The comparative method in studying innate behaviour patterns. Symp.Soc.Exp.Biol., 4, 221-268.

Machlis, L. 1977. An analysis of the temporal patterning of pecking in chicks. Behaviour., 63, 1-70.

Magurran, A. E. & Pitcher, T. J. 1983. Foraging, timidity and shoal size in minnows and goldfish.

Behav.Ecol.Sociobiol., 12, 147-152.

Mann, R. H. K. 1973. Observations on the age, growth, reproduction and food of the pike (Esox lucius) in two rivers in Southern England. J.Fish Biol., 5, 707-737.

Mann, R. H. K. 1982. The annual food consumption and prey preferences of pike (Esox lucius .L.) in the river Frome, Dorset. J.Anim.Ecol., 51, 81-95.

Manning, A. 1979. Introduction to animal behaviour. London: Edward Arnold.

Mauck, W. L. & Coble, D. W. 1971. Vulnerability of some fishes to northern pike predation. J.Fish.Res.Bd.Can., 28, 957-969.

McFarland, D. & Sibly, R. 1975. The behavioural final common path. Phil.Trans.Roy.Soc.Lond., B, 265-293.

McFarland, D. & Houston, A. 1981. Quantitative biology. London: Pitman.

Meesters, A. 1940. Über die organisation des gesichtsfeldes der fische. Z.Tierpsychol., 4, 84-149.

Neill, S. R. & Cullen, J. M. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. J.Zool.Lond., 172, 549-569.

Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H. 1975. SPSS. 2nd ed. New York: McGraw-Hill.

Nikolsky, G. V. 1963. The ecology of fishes. London: Academic Press.

Nursall, J. R. 1973. Some behavioural interactions of spottail shiners (Notropis hudsonius), yellow perch (Perca flavescens) and northern pike (Esox lucius .L.). J.Fish.Res.Bd.Can., 30, 1161-1178.

Pitcher, T. J. & Hart, P. J. B. 1982. Fisheries Ecology. London: Croom Helm.

Protasov, V. R. 1968. Vision and near orientation of fish. Jerusalem: Israel Program Scientific Translations.

Pulliam, H. R. 1974. On the theory of optimal diets. Am.Nat., 108, 59-74.

Reist, J. D. 1980. Selective predation upon pelvic phenotypes of brook stickleback, Culea inconstans, by northern pike, Esox lucius. Can.J.Zool., 58, 1245-1252.

Reist, J. D. 1983. Behavioral variation in pelvic phenotypes of brook stickleback, Culea inconstans, in response to predation by northern pike, Esox lucius .L. In: Predators and prey in fishes (Ed. by D.L.G.Noakes), The Hague. Neths. Dr.W.Junk. Publ.

Richards, L. J. 1983. Hunger and the optimal diet. Am.Nat.,  
122 , 326-334.

Ringler, N. H. 1983. Variation in foraging tactics of fishes.  
In: Predators and prey in fishes (Ed. by D.L.G.Noakes),  
The Hague. Neths. Dr.W.Junk. Publ.

Roth, G. 1978. The role of stimulus movement patterns in the  
prey catching behaviour of Hydromantes genei (Amphibia,  
Plethodontidae). J.Comp.Physiol., 123, 261-264.

Ruiter, L. 1963. The physiology of vertebrate feeding  
behaviour towards a synthesis of the ethological and  
physiological approaches to problems of behaviour.  
Z.Tierpsychol., 20, 498-516.

Ruiter, L. 1967. Feeding behaviour of vertebrates in the  
natural environment. In: Handbook of Physiology.  
Alimentary canal 7. (Ed. by Coda, C. F.)  
Am.Physiol.Soc.

Seaburg, K. G. & J. B. Moyle. 1964. Feeding habits, growth  
rates and digestion of some Minnesota warm water  
fishes. Trans.Am.Fish.Soc., 93, 269-285.

Slater, P. J. B. 1974. Bouts and gaps in behaviour of zebra  
finches, with special references to preening.  
Rev.Comp.Animal., 8, 47-61.

Solman, V. E. F. 1945. The ecological relations of pike, Esox  
lucius .L., and waterfowl. Ecol., 26, 157-170.

Sokal, R. R. & Rohlf, F. J. 1981. Biometry. 2nd ed. San  
Francisco: W.H.Freeman & Co.

Stokes, A. W. 1962. Agonistic feeding behaviour among blue  
tits at a winter feeding station. Behaviour., 19,  
118-138.

Street, N. E, Magurran, A. E. & Pitcher, T. J. 1984. The  
effects of increasing shoal size on handling time in  
goldfish, Carassius auratus .L. J.Fish.Biol., 25,  
561-566.

Tamura, T. 1957. A study of visual perception in fishes,  
especially resolving power and accommodation.  
Jap.Soc.Sci.Fish.Bull., 22, 536-557.

Toner, E. D. & Lawler, H. B. 1969. Synopsis of biological  
data on pike. F.A.O.Fish.Synop.U.N.Rome.

Ware, D. M. 1972. Predation by rainbow trout (Salmo  
gairdneri): the influence of hunger, prey density and  
prey size. J.Fish.Res.Bd.Can., 31, 1531-1536.

Webb, P. W. & Skadsen, J. M. 1980. Strike tactics of Esox.  
Can.J.Zool., 58, 1462-1469.

Willemse, J. 1967. Research on the feeding of pike. In:

Proc. 3rd. Brit. Coarse Fish Conf. Livpl., pp 33-36.

Wilson, E. O. 1975. *Sociobiology: The new synthesis*. Mass:  
Belknap Press.

Wirjoatmodjo, S. 1980. Growth, food and movement of a  
flounder, Platichthys flesus (L.), population in an  
estuary. DPhil thesis, New University of Ulster,  
Northern Ireland.

Wirtshafter, D. & Davis, J. D. 1977. Set points, settling  
points, and the control of body weight. *Physiol&Behav.*,  
19, 75-78.

Wunder, W. 1927. *Synnesphysiologische Untersuchungen über die  
Nahrungsaufnahme verschiedener Knochenfischarten*.  
*Z. Vergl. Physiol.*, 6, 67-98.