

**Constraints on the Foraging Behaviour of the
Threespine Stickleback (*Gasterosteus aculeatus* L.)**

**Thesis submitted for the degree of
Doctor of Philosophy
at the University of Leicester**

by

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THESIS ABSTRACT

Constraints on the Foraging Behaviour of the Threespine Stickleback (*Gasterosteus aculeatus* L.) by Andrew B. Gill

As feeding is fundamental to any animal, this thesis examined constraints on foraging behaviour from the point of view of a predatory fish, the threespine stickleback, encountering prey sequentially and simultaneously.

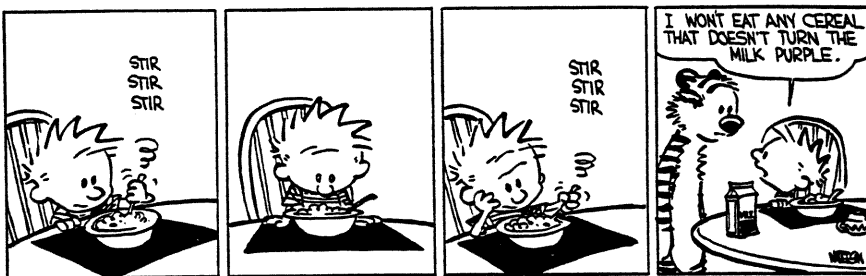
Subsequent to prey detection, the fish orientated towards the prey and then decided to attack. The probability of attack reduced with a decrease in fish size, an increase in the size of the prey and the fish's stomach fullness and was dependent on the presence of competitors. During the attack, if the fish hung midwater the probability of successful prey capture was greater. Hanging was more likely to occur with smaller fish and when larger prey were encountered and was also longer in duration when prey were encountered simultaneously.

When handling the prey, the fish made a decision to eat within the first few seconds. All of the fish ate to fill their stomachs, with the critical factors involved in prey choice being the size of the prey in relation to the size of the fish's mouth and the stomach fullness of the fish. With an empty stomach, the fish ate whatever prey was encountered. As stomach fullness increased the fish became selective against large prey with high handling costs, depending on the availability of alternative prey. Those prey selected for had low handling costs and were successfully captured whenever encountered. Prey with a width 0.6 of the fish's jaw width were found to be the best option in terms of costs and benefits to the fish. Selectivity was, however, also a function of the capacity of the fish's stomach.

The thesis demonstrates how the behavioural response of the foraging stickleback is dynamic, dependent on a number of factors external to and internal of the fish.

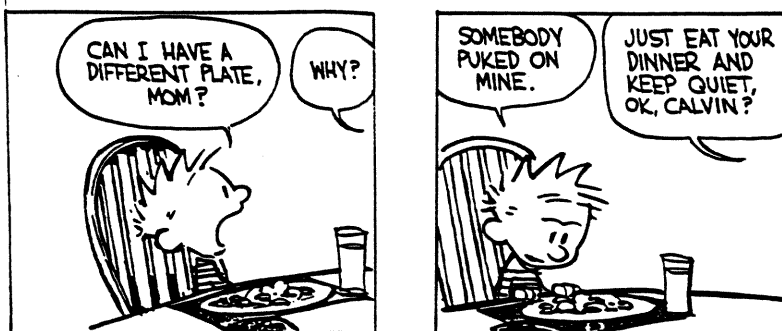
Little Known Constraints on:

Feeding Behaviour



&

Diet Choice



For me Mum and Dad,
there's too many reasons to say why.

ACKNOWLEDGEMENTS

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To Mike, Ian, Gavin, Mike and Jim, cheers for making the Faculty of Serendipity a happy and happenin' place to be (mine's a pint!).

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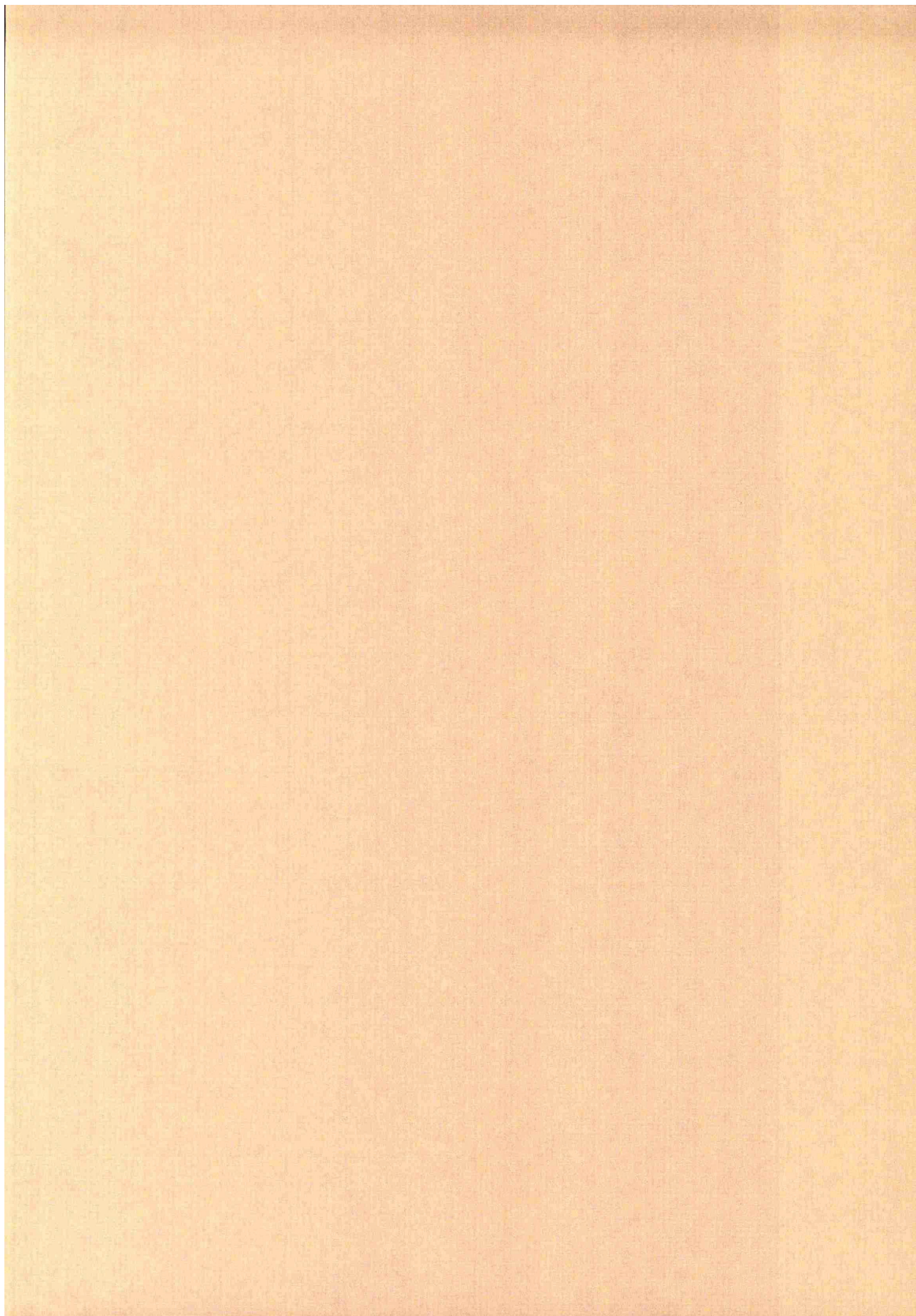
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CHAPTER 1

GENERAL INTRODUCTION

Energy is a basic currency of living organisms (Harold, 1986), providing the organism with the potential to do the work required for the maintenance of life, growth and reproduction (Wootton, 1993). Predators obtain this currency via the food ingested which can be conceptualized as discrete packages of energy. The main constraint on a predator gaining energy is time (Curio, 1983). As the food is discrete in nature, the predator needs to have the facility for finding and then consuming the prey within the time available. The facilities available to the predator can be analysed by studying aspects of the foraging behaviour in relation to energetic and time limitations (see Schoener, 1971). The basic behavioural foraging sequence of a predator can be separated into five different categories, those of searching, detecting, attacking, handling and finally eating or rejecting the prey. Once the prey has been detected, the predator can break off the behavioural sequence at any step and resume searching (Figure 1).



Figure 1. The five basic components to the foraging behaviour of a predator. The large arrows indicate the main sequence of events, the small arrow shows where the sequence can be interrupted with the predator resuming searching.

The study documented here, deals specifically with an investigation of the foraging behaviour of predatory fish, using the three spine stickleback (*Gasterosteus aculeatus* L.), as a model fish species.

Searching for Prey

For a predacious fish there are two options available for obtaining food, either to sit and wait or to actively search for it. Many fish species, such as the three spine stickleback come somewhere between these two extremes, by adopting a saltatory pattern of searching, by which they swim in stops and starts (O'Brien *et al*, 1990). Depending on how long these respective stops and starts are changes the foraging mode of the fish. Altering the mode of foraging means that different food resources can be exploited (Helfman, 1990). At each stop, the fish is assumed to be searching in a previously unscanned area. When searching for prey, sticklebacks rely on their pectoral fins for propulsion (Linsey, 1978; Taylor & McPhail, 1986; Delbeck & Williams, 1987), known as labriform swimming (Blake, 1983). The modes of swimming available for a foraging fish to actively search are dependent on the body form of the fish (Blake, 1983; Webb, 1984).

Detection of Prey

The prey will only be found during the search if the fish has the means by which to detect it. Detection can be either visual, chemical or mechanical, or a combination of these stimuli. In the stickleback, the eyes are a prominent feature constituting about 25% of the head length (Scott & Crossman, 1973), which means that the retina of the eye takes up about 3.5% of the body surface of the fish (Beukema, 1968). The olfactory organ of the stickleback constitutes only 0.5% of the fishes body surface, which suggests that olfaction does not have a major role in prey detection. The role of the lateral line is important for mechanoreception of the prey (Bleckman, 1993), but this factor has been neglected in fish foraging studies. Its importance in the detection of prey by the stickleback is unknown. However, it is known that sticklebacks feed predominantly in the light, indicating the importance of vision to this fish for detecting prey (Wootton, 1984).

Aspects of the prey increase or decrease the chances of detection by the fish. Avoidance behaviour of prey reduces the rate of encounter between predators and prey (Blake & Hart, 1993). Prey are often associated with a particular substrate (Engel, 1985), which makes them patchily distributed. Being associated with a substrate decreases the availability of the prey due to cover (Stein, 1977; Engel, 1985; Hargeby, 1990) or

blending in with the background (Ibrahim & Huntingford, 1989a) so the chances of detection are reduced. Fish are known to have reduced foraging efficiency as the habitat becomes more complex (Mittlebach, 1981), sometimes requiring the fish to change foraging mode (Savino & Stein, 1989). One reason for the lower chance of detection due to habitat association is that the prey will be less likely to be moving (Convey, 1988). Movement has been identified as a main stimulus to a foraging stickleback, with the colour, size and shape of the prey being other determining factors in detection (Ibrahim & Huntingford, 1989b).

Attacking the Prey

Once the prey has been detected, fifteen spine stickleback (*Spinachia spinachia*) orientate towards the prey to fixate with both eyes (Croy & Hughes, 1991a). This may be used to judge the distance with binocular vision. In order to reach the prey, the fish need to have the ability to swim fast if the prey has a mobile escape response. Three spine stickleback are able to fast start by using the whole body (Webb, 1978). Even when the fish gets near to the prey the escape response is important as it can change the availability of prey for capture (Sih, 1987). Often before the final stage of attack the fish will stop, a behaviour which has been found to increase the chances of prey capture through directed attack (Kaiser *et al*, 1992a). Sticklebacks possess protrusible jaws (Alexander, 1967), which allow them to get their mouths close to the prey in a very short space of time and also reduces the dependence on their swimming ability.

Handling the Prey

With the prey successfully caught, the fish needs to have the ability to process it. Sticklebacks eat their prey whole, so there is an upper prey size limit determined by the maximum dimensions of the jaws. The gape of the jaw is an important influence on the size of prey that can be taken by sticklebacks (Lavin & McPhail, 1986). At this point in the foraging sequence, the fish may choose not to eat the prey. This choice could be a reflection of taste or of the defences of the prey, alternatively the choice could be based on energetic and time considerations (see next section). The capacity of the stomach is also important when eating prey. Sticklebacks have a simple straight gut with a true stomach which is capable of considerable distension (Hale, 1965).

Choosing to Eat a Prey

The fish need to acquire a minimum amount of energy per day to survive, any excess energy can be committed to growth and reproduction. Many fish are known to feed until they have achieved their energetic requirement (Bromley, 1980; Jobling, 1981; Fris & Horn, 1993). The energy requirement changes throughout the year due to temperature effects and sexual condition. These fluctuating energetic needs have to be accounted for in any analysis of prey choice.

It is obvious from stomach content analyses that there are some basic food choices being made by the fish. Some prey constitute a different proportion of the stomach content than the proportion in which they are found in the environment (Hangelin & Vuorinen, 1988; Ibrahim & Huntingford, 1989a). Other prey are abundant but ignored by the fish (Delbeek & Williams, 1988), which may be due to the unpalatability (Ibrahim & Huntingford, 1989a) or distribution of the prey.

It is known that many fish are selective in their feeding (Ivlev, 1961). The term 'selective' can be thought of as the fish choosing which prey to eat. The advent of optimal foraging theory stimulated analyses of how animals were selecting between prey items (MacArthur & Pianka, 1966). Basic optimal foraging theory uses the relationship between the energy content of the prey (E), the amount of time that it takes for the predator to deal with the prey, known as the handling time (H), and the encounter rate with the prey (λ). These identified variables have made it possible to examine the feeding choices of animals in terms of the food value gained per unit handling time, known as the profitability. This profitability judgement takes as a basic premise that the animal will forage selectively in an optimal manner so as to maximise the long term average rate of energy return (Stephens & Krebs, 1986). The profitability of a prey however, is dynamic, affected by many variable factors.

Prey type

Fish have to alter their predatory behaviour depending on prey type (Nyberg, 1971; Kaiser *et al*, 1992a). Prey types differ in many ways due to factors such as, habitat association (Engel, 1985), crypsis (Feltman & Williams, 1989), accessibility (Main, 1985), vulnerability (Jeffries, 1988), activity (Macchiusi & Baker, 1991), escape response

(Sih, 1987; Kaiser *et al*, 1992a), morphology (Stein *et al*, 1984; Hoyle & Keast, 1986; Eklöv & Hamrin, 1989) and digestibility (Kaiser *et al*, 1992b). A combination of any of these factors increases the cost to the predator in terms of the balance between the time and energy invested and the energetic benefit received, hence changing the profitability of the prey.

Prey size

The size of the prey is extremely important in determining its profitability to the fish predator (Werner, 1974; Gardner, 1981; Eggers, 1982; Milinski, 1982; Bence & Murdoch, 1986; Wetterer, 1989; Ranta & Lindström, 1990; Hart & Ison, 1991). Figure 2 shows the general relationship between prey size and profitability (E/H). On the prey size continuum shown in Figure 2, there is a size which gives the best energetic return for the amount of time needed to deal with it, known as the optimal prey size. The majority of fish foraging studies have dealt with fish feeding on prey at the small end of the relationship shown in Figure 2. This means that as prey size increases the profitability increases (Werner, 1974; Gardner, 1981; Eggers, 1982; Milinski, 1982; Wetterer, 1989; Ranta & Lindström, 1990). An investigation of the effect of large prey on prey choice constitutes a main theme of this thesis. Profitability goes down as prey size increases when looking at the top end of the relationship (Bence & Murdoch, 1986). The relationship between the size of the prey and the jaw size of the fish has obvious implications for the profitability of the prey. As the prey get larger their energetic value increases, but with this increase in size comes an exponential increase in the prey handling time (Werner, 1974; Kislalioglu & Gibson, 1976; Hoyle & Keast, 1986). A number of studies into fish feeding have found that the optimal prey width for a fish is around 0.6 of the jaw width (Werner, 1974; Kislalioglu & Gibson, 1976; Moore & Moore, 1976; Wankowski, 1979). Some studies have also shown that this size of prey is also the most preferred (Scott, 1987; Prejs *et al*, 1990).

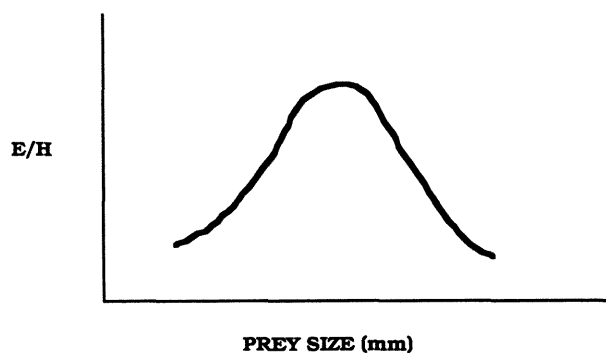


Figure 2. The general relationship between profitability (E/H) and prey size (mm). Upper and lower limits of the relationship will be determined by the morphological relation between the predator and the prey. The degree of skewness and kurtosis of the graph will be a function of the prey specific energy content and handling time.

Encounter rate

The encounter rate with prey is also of fundamental importance in prey selection by a predator (MacArthur & Pianka, 1966; Krebs, 1978; Stephens & Krebs, 1986) and is a function of the fishes reactive field, prey size, shape and colour and water clarity (Eggers, 1982). Predictions from foraging theory are that as the encounter rate with prey increases the predator can become choosy, neglecting those prey which have lower profitability. However, continued increases in the encounter rate eventually leads to an information processing constraint due to confusion effects of such a large number of potential prey (Milinski, 1977a; Ohguchi, 1981). The profitability of less preferred prey is changed by the increased cost of confusion generated by the high density of preferred prey (Visser, 1982). It is easier for a fish to track and capture rarer prey as the density increases (Heller & Milinski, 1979; Ohguchi, 1981).

Stomach fullness

Stomach fullness, known also as the satiation level, is a basic factor to consider when studying the foraging of the fish, as it determines the motivation of the fish to feed. As

the predator gets hungry so the profitability of prey changes, they become more valuable (Croy & Hughes, 1991b). A joule of energy is of more benefit to a hungry fish than to a fish which is sated. Hunger is critical in controlling the behaviour and prey choice of a fish (Hart & Ison, 1991). Whenever hunger is mentioned in feeding studies, it is always important to define it in its proper context. Hunger is a combination of the amount of time that the predator has been deprived of food and the stomach fullness (Beukema, 1968). Conventional optimal diet models do not account for a change in costs with increasing satiation (Stephens & Krebs, 1986). It is now recognised that dynamic changes in state need to be applied when attempting to model the feeding of fish (Stephens & Krebs, 1986; Houston *et al*, 1988; Mangel & Clark, 1988; Godin, 1990; Hart & Gill, 1993). Fish have been shown to become more selective in the prey eaten as satiation increases (Ivlev, 1961; Kislalioglu & Gibson, 1976; Heller & Milinski, 1979; Visser, 1982; Godin, 1990). The level of satiation is monitored by stretch receptors in the wall of the stomach (Hamilton, 1965). As the effect of stomach fullness is such a fundamental but not well understood empirical aspect of prey choice by fish, it constitutes the other major theme of study in this thesis.

Competition

Competition for resources has an effect on prey choice by fish. The phenotype of individual sticklebacks is known to be a determinant of the competitive ability of the fish (Milinski, 1984a). The ability of an individual to compete influences the choice of prey (Milinski, 1982). A competitor can have an adverse effect on the choice of food either by getting to the prey first, monopolising the resource (Grant & Kramer, 1992) or stealing prey. In view of these facts, this thesis examines the dependence of the foraging behaviour and diet choice on the phenotypic attributes of an individual fish.

Parasites

Parasites affect the foraging behaviour of sticklebacks by lowering swimming speeds and feeding performance (Milinski, 1984b). Due to body cavity constraints, sticklebacks with gut parasites have been found to eat half as much as healthy fish (Milinski, 1985). The presence of eye flukes (*Diplostomum* spp.) reduces the reactive distance of the stickleback (Owen *et al*, in press). It has also been demonstrated that the parasites alter the feeding behaviour, causing the fish to eat different prey types

compared to healthy fish (Reimchen, 1982; Giles, 1983; Milinski, 1985; Jakobsen *et al.*, 1988). Due to the metabolic demands of the parasite, infected sticklebacks are hungrier and swimming is energetically more costly than in non-infected fish (Lester, 1971). Parasitized fish are more likely to feed unselectively and take greater risks in terms of exposure to predation (Giles, 1983; Milinski, 1985; Godin & Sproul, 1988).

Predation

Predation is yet another factor which influences the profitability of the prey to the fish (Milinski, 1985; Godin & Sproul, 1988; Pitcher *et al.*, 1988; reviewed by Milinski, 1993). Milinski & Heller (1978) showed that by introducing a predator, sticklebacks changed their diet choice accordingly, to reduce the cost of confusion so reducing the predation risk. It has been shown that when the risk of predation is perceived, large prey are dropped from the diet of sticklebacks (Ibrahim & Huntingford, 1989c) and of guppies (*Poecilia reticulata*) (Godin, 1990). Hungry fish are more likely to take risks (Godin, 1986; Godin & Smith, 1988) and less likely to detect a predator (Milinski, 1984c).

Study Aims

With all these factors influential on the foraging of a fish taken into consideration, the basic aim of this study was to elucidate how important the size of the prey and the body size and level of stomach fullness of the predator are to the predatory feeding behaviour and prey selection of the three spine stickleback. Further to this, the aim was to use the results from sticklebacks to predict the importance of these factors to fish foraging behaviour in general.

GENERAL MATERIALS AND METHODS

The Predator

The threespine stickleback was the fish central to the studies in this thesis. Due to numerous studies much is known of the biology of this particular fish (Wootton 1976, 1984; Bell & Foster, 1993). This enables the research to focus on a specific area of interest. The stickleback is a convenient species for study in the laboratory and is readily available in Leicestershire, where it appears to be a major component of the foodwebs of the aquatic environments. The experimental sticklebacks were all obtained from the River Welland, Leicestershire. The fish were caught by using plastic lemonade bottles pierced with aeration holes and the neck end cut off and inverted. The traps work in a similar way to lobster pots/creels without needing to be baited. Traps were laid out during the day and retrieved 24 hours later. In the river, the traps need to have the open end pointing downstream.

There are known to be three specific stickleback morphotypes (Wootton, 1984), which feed either in the benthic or limnetic zones or intermediate between these two. The morphotypes are identified in part by the number of lateral plates along the body, gill raker number and length, and mouth morphology (Larson, 1976; Lavin & McPhail, 1986; McPhail, 1993). These morphological attributes contribute to the foraging success of the fish in their appropriate habitats (Lavin & McPhail, 1986). All the fish used in this study were identified to be of the low plated leleus morph and benthic feeders.

The Prey

The main prey used was *Asellus aquaticus*, a benthic freshwater isopod, obtained either from the River Welland or the River Soar in Leicester, depending on availability. *Asellus aquaticus* feed on filamentous algae and the flora of fungi and bacteria associated with decaying vegetation (Daoud, 1984). This species of *Asellus* was identified by the pigmentation pattern on the dorsal surface of the head and the abdomen (Daoud, 1984).

To measure the prey accurately, millimetre graph paper was attached to the underside of a plastic, transparent petri dish and the prey were restrained from moving

about with a smaller transparent petri dish. Only males or non-ovigerous females were used to keep down the variation of prey profitability. The energetic contents of each size of *Asellus* shown in Table I, were obtained from Daoud (1984).

Table I. The energetic contents of each millimetre size of *Asellus*, from Daoud (1984).

Prey Size (mm)	3	4	5	6	7	8	9
Energy Content (J)	7.90	15.70	58.60	80.00	122.40	171.70	264.50

For the final experiment (see Chapter 7) the prey used was *Daphnia* sp. These prey were obtained either from the Zoology Department field station in Leicester or from a local pet shop, depending on availability.

Experimental Apparatus and Methods

The experiments described in chapters 2, 3, 4 and 5, were performed with the apparatus shown in Figure 3 and described by Hart & Ison (1991). Individual prey of the required size (mm) and number were loaded into separate tubes fixed to the carousel which was mounted on top of the aquarium. An electric motor operated remotely allowed the carousel to be advanced one tube at a time. When opposite the delivery funnel the tube was tipped to discharge the prey and a water jet sprayed into the tube to ensure prey delivery down the funnel. Prey then entered the feeding arena where they were either eaten or rejected by the fish. Rejected prey sank into the funnel set into the arena floor and were collected in a net under the aquarium. For these experiments, the fish were exposed to only one prey at a time. New prey were introduced into the feeding arena only after the fish had finished handling the current prey. Each fish was assigned one of six holding tanks, which were labelled C1-C6. Access to food was controlled by compartment specific doors with attached wires operated by the experimenter. During the trials the fish were fed once a day between 09.00 and 12.00 hours. The laboratory had a day:night light regime of 12:12 hours. As temperature is a major influence on food intake (Beukema, 1968; Wootton *et al.*, 1980) the water temperature during the

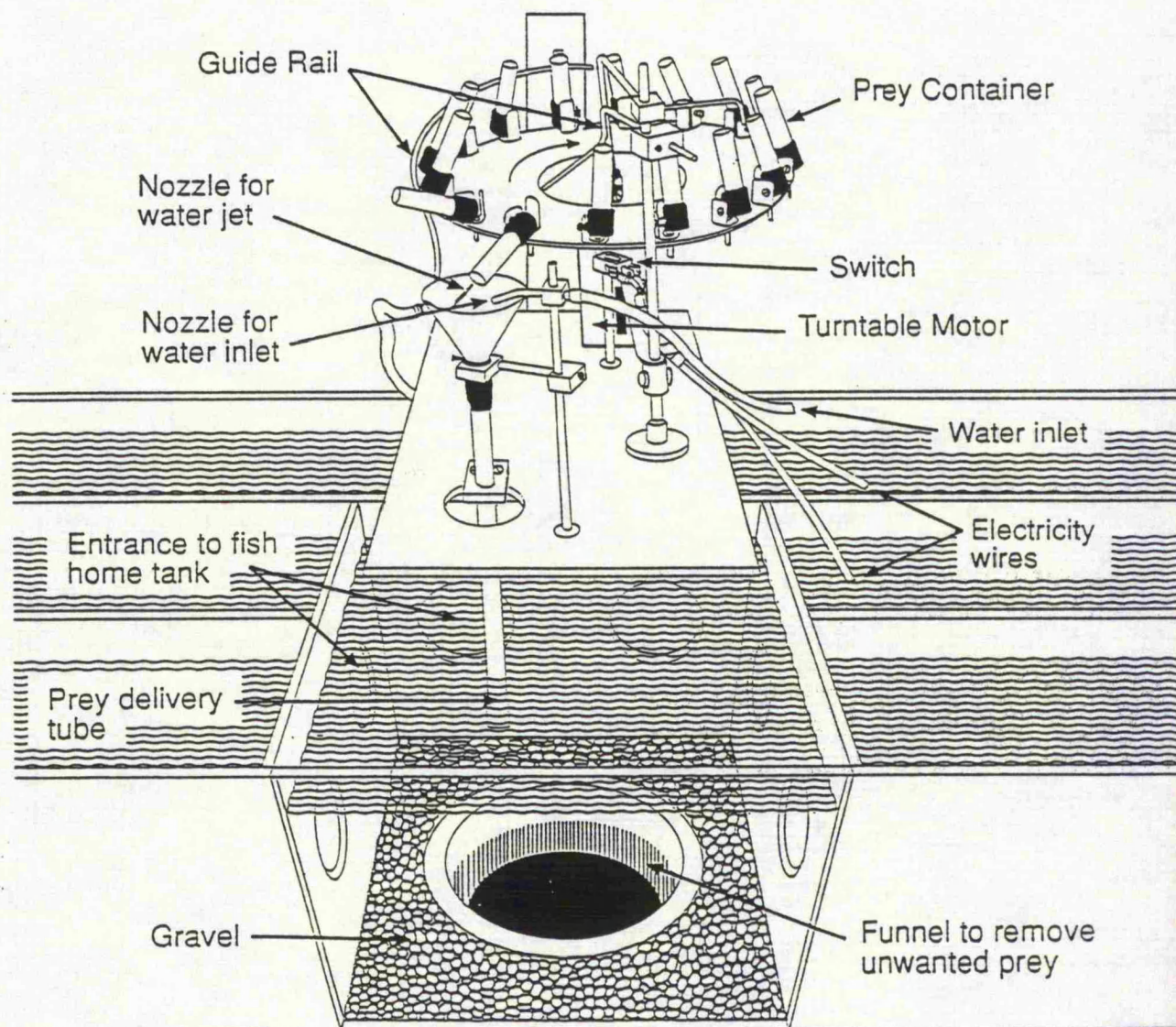


Figure 3. The experimental apparatus used for all the experiments. The dimensions of the central feeding arena were 29*33*18cm. In the diagram, the essential features which allowed prey to be presented sequentially are shown (see text for details).

experiments was kept at around 13 °C.

The size of the feeding arena was 29*33*18cm (length*breadth*depth). Therefore, the maximum distance that a fish could be away from the prey delivery tube was approximately 28cm or 6 fish body lengths. Beukema (1968) documents that sticklebacks of a comparable size to those used in most of this study, found *Tubifex* prey with a probability of 1.0 at 20cm and 0.9 at 25cm. The feeding arena also had a uniform dark background. These factors combined to reduce the searching requirements of the fish.

In the experiments of chapters 6 and 7, the basic aquarium was adapted to allow the simultaneous presentation of *Asellus* (Chapter 6) and the presentation of a different prey type, *Daphnia* (Chapter 7). Details of the methods can be found in the appropriate chapters.

All the fish were acclimatised to the experimental procedures for more than two weeks before the experiments began in order to minimise any learning effects. Threespine sticklebacks reared in the laboratory have been found to learn to handle prey to a level comparable with wild fish after a week (Ibrahim, 1988). It has also been demonstrated that fiftenspine stickleback have reduced handling times and increased foraging efficiency as an effect of learning (Croy & Hughes, 1991a).

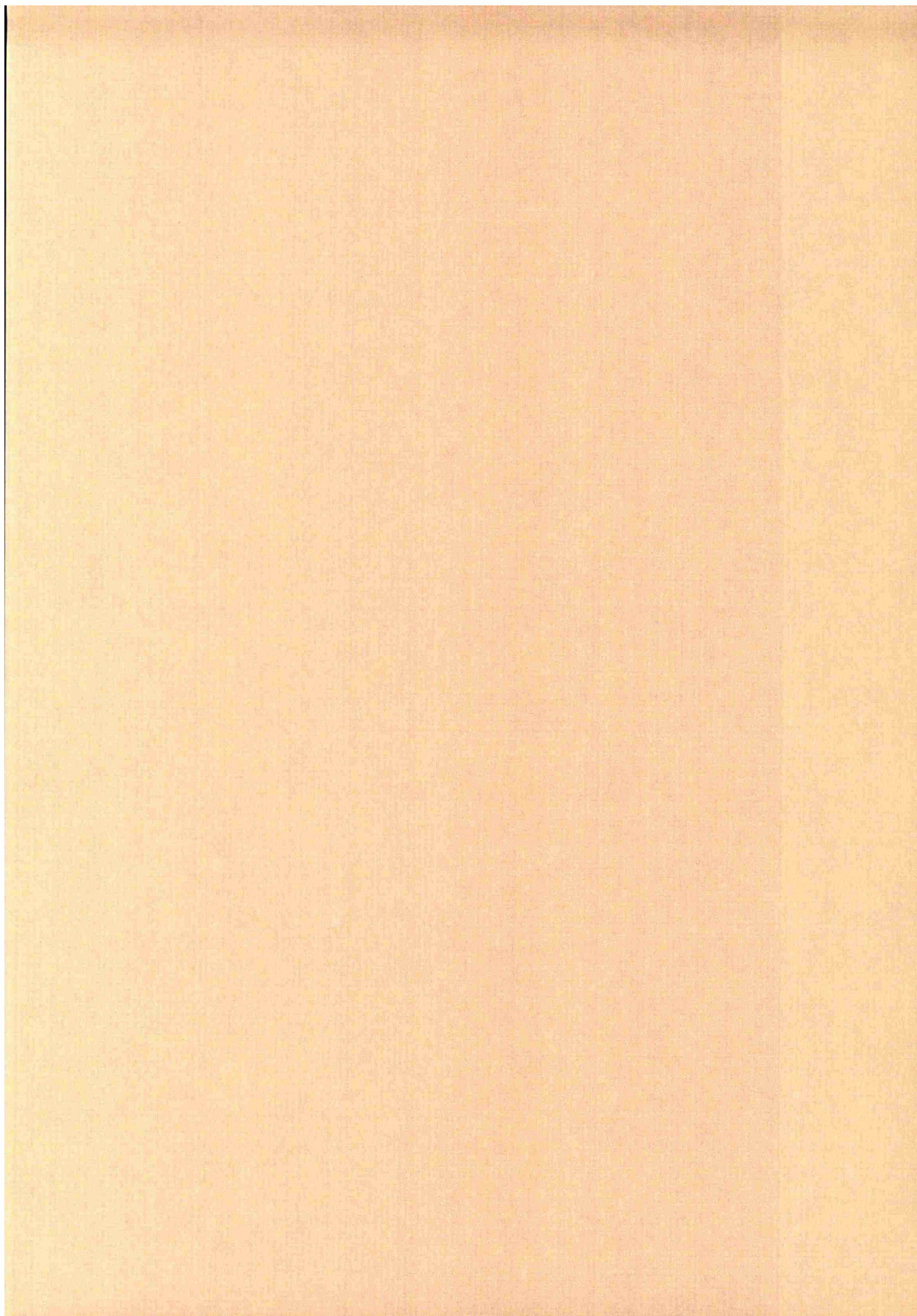
In order to determine the sex of the fish, to examine the stomach capacity and to check for parasites, the fish were killed with an overdose of soluble anaesthetic (3-amino-benzoic acid ethyl ester, synonym: MS222). No gut parasites were found in any of the fish. Also, the sticklebacks from the River Welland have been found to have a low incidence of eye flukes (Owen *et al*, in press).

As the study progressed I became aware of a morphological dimorphism in the head sizes of the male and female fish. I have determined that the male fish has a significantly larger head in relation to its body length than does the female. Mori (1984) reported a similar result for a single isolated population of sticklebacks in Japan. The relationship between the head and body length is being studied further with fish from

different habitats and geographic locations as it has great implications for future study into feeding differences in male and female stickleback.

Behavioural Analyses

The feeding sessions were filmed with a panasonic super-VHS video camera, which gives good definition at normal speed and in slow motion. With the aid of a video recorder, the feeding movements and behaviour of each fish could be followed with precision. Analysis of the video record was the major tool used in this study. Acceptance and rejection of prey were recorded on data sheets during each trial. The data sheets were used as a reference guide to the filmed feeding sequences. The results from the data sheets and the video were statistically and graphically analysed using S.A.S., Statview and Cricketgraph available on the VAX network and the Apple MacIntosh, the non-parametric package of Meddis (1984) on the BBC-B microcomputer, and with reference to Sokal & Rohlf (1981) and Siegel & Castellan (1988). The statistical tests used are specified where appropriate.





To eat or not to eat
that is the question?



CHAPTER 2

Constraints on prey size selection by the threespine stickleback: energy requirements and the capacity and fullness of the stomach.

ABSTRACT

This experiment was designed to study how stomach fullness and encounter with 5mm *Asellus aquaticus* influenced acceptance or rejection of less profitable 8mm *Asellus* by 45mm sticklebacks. Whenever a fish orientated to a prey the behaviours which followed were pursuit and manipulation, independent of prey size. The decision to accept or reject prey occurred after one manipulation, a criterion that was more variable for the larger prey. The fish were found to always accept 5mm prey whereas 8mm prey were accepted with an initial probability of about 0.9, this probability decreased as the stomach filled. Fish of differing sizes and sex had similar daily energy intakes per unit body size, however, the acceptance of 8mm prey was related to fish size. For one feeding session per day the total energy intake was almost constant despite the changing combination of prey sizes eaten. The fish ate prey with long handling times if the energetic contents of the stomach had not reached 450 Joules. Calculations were made of how many of each millimetre prey size group would satisfy the 450J demand and how long the estimated number would take to handle. This showed that the best option was to consume 5mm prey if given the choice.

INTRODUCTION

In natural surroundings a predator such as the threespine stickleback (*Gasterosteus aculeatus*, L.) has to choose from a range of prey types that vary in availability and abundance (Hynes, 1950; Maitland, 1965; Manzer, 1976). The varied diet of the stickleback in the wild has been demonstrated most thoroughly by the river study of Hynes (1950). He found that the crustaceans - cladocera, copepoda, ostracoda and *Asellus*; the insects - chironomid larvae and pupae; molluscs and oligochaetes were predominant in the diet throughout the year. Prey availability is influenced by a variety of factors including substrate (Ibrahim & Huntingford, 1989a), cover (Stein, 1977; Engel, 1985; Hargeby, 1990), season (Snyder, 1984; Engel, 1985), inter and intraspecific competition (Maitland, 1965; Werner, 1979; Thorman, 1983; Milinski, 1986) and abiotic factors (Thorman & Wielderholm, 1983). These variables not only affect the availability of different prey species but also affect the availability of size groups from within a prey species.

In this context, which factors are most important in determining the particular prey item that a stickleback takes? Larson (1976), Lavin & McPhail (1986) and McPhail (1993) have shown morphotype to be a causal factor in the food selection of the stickleback. Werner (1977) demonstrated that predator size and morphology account for the food sizes selected by three centrarchids. Decision rules for prey selection by threespine stickleback were analysed by Ibrahim and Huntingford (1989b) who found that colour, movement and shape were major influences. The changing density of a prey type affects the fishes choice (Visser 1982), mainly through its influence on prey profitability (Werner & Mittlebach, 1981). An equally important consideration is the physiological state of the fish at the time of decision. The hunger effect is well documented by Beukema (1968), Heller and Milinski (1979) and Thomas *et al* (1985) who studied stickleback feeding under the influence of varying degrees of starvation. Estimation of prey profitability by a fish may well be changed by hunger (Croy & Hughes, 1991b).

Hart & Ison (1991) found that sticklebacks choosing *Asellus aquaticus*, a freshwater isopod, from a sequence of different sizes tended to reject prey above a

threshold size which lay between 5 and 8mm for 40-50mm fish. The 5mm *Asellus* were mainly accepted whilst 8mm prey were mainly rejected. Analysis of the results showed that the acceptance probability of a prey was a function of the size of the prey, the encounter with the prey and the fish's state of satiation. It was hypothesised that a fish with an empty stomach would be more likely to choose an 8mm *Asellus* than fish that have first eaten a number of *Asellus*. To test this hypothesis an experiment was designed to investigate how stomach fullness and previous encounter with a more profitable prey (greater energy gain per unit handling time (E/H)) influenced acceptance or rejection of 8mm *Asellus*. A second experiment investigated the role of the fish's stomach capacity by examining the maximum number consumed of a range of prey sizes.

METHODS

Experiment 1

The experimental animals were six threespine stickleback, three male and three female, from the River Welland, with a mean fork length of 43.8 ± 1.2 (S.E.)mm. The prey, *Asellus aquaticus*, were obtained from the same river. Fish were first acclimatised to the experimental protocol for one month. Work began in December 1989 and ended February 1990.

The experimental aquarium is described in chapter 1. During the trials the fish were fed once a day between 09.00 and 12.00 hours. As this experiment was testing the influence of gut fullness on the choice of two distinct prey sizes the fish were only introduced to 5mm and 8mm *Asellus*. *Asellus* were measured to the nearest millimetre and only males or non-ovigerous females were used to keep down the variance of prey profitability. Each fish was presented with one of six sequences of 10 prey (Table 1).

Table 1. The six sequences of prey presented to the fish to study effect of stomach fullness on the acceptability of 8mm *Asellus*. The body of the table shows the prey sizes (mm) offered to the fish. Each fish received a different treatment per day, with the pattern repeated three times.

Treatment	Number in sequence									
	1	2	3	4	5	6	7	8	9	10
NIL	8	8	8	8	8	8	8	8	8	8
ONE	5	8	8	8	8	8	8	8	8	8
TWO	5	5	8	8	8	8	8	8	8	8
THREE	5	5	5	8	8	8	8	8	8	8
FOUR	5	5	5	5	8	8	8	8	8	8
FIVE	5	5	5	5	5	8	8	8	8	8

Three distinct behaviours were described from the video record:

Orientation - movement to directly face the prey, allowing both eyes to fixate

Pursuit - direct movement towards the prey

Manipulation - handling of the prey in the jaws, the prey were often spat out and regrasped giving multiple manipulations.

The numbers of prey eaten were divided by the numbers of prey presented for each number in the sequence, giving the proportion eaten. The arcsine transformation was applied to the results before analysing the proportion data. Proportions transformed in this way closely approximate the normal distribution (Sokal & Rohlf, 1981). For each prey presented the occurrence of the behaviours specified above were recorded from the video tapes. The number of manipulations was also recorded. These data were matched with the numbers and sequence of prey offered to show their probabilities of occurrence.

Experiment 2

A shorter experiment was undertaken to investigate the maximum number of different sized prey that a 45mm fish would eat. Six different sticklebacks of the leiurus morph with a mean fork length of 44.0 ± 0.5 (S.E.)mm were used. The fish were exposed to either a 3mm, 4mm or 5mm prey each day. Each prey size was offered to each fish three times. Prey larger than 5mm were not used as data was available from a different experiment. A fish was deemed to be satiated when it rejected four prey in a row. At the conclusion of this experiment the fish were investigated internally for stomach distension and the orientation of prey within the stomach.

Differences between treatments were tested for significance using the non-parametric tests given by Meddis (1984).

RESULTS

The Acceptance of 8mm Prey

The proportion of 5mm *Asellus* accepted was close to 1 for all treatments, confirming the results recorded by Hart & Ison (1991), (Figure 1). Figure 1 shows that the proportion of 8mm prey taken for each treatment varied between 0.15 and 0.3. Even when five profitable prey were offered and eaten there was still an appreciable number of large prey taken.

When the sequence of prey acceptances for each treatment was plotted separately (Figure 2) the change in acceptance probability over the prey sequence became clear. Treatment NIL showed that the fish took 8mm prey with a probability of about 0.9 when they were offered first in the prey sequence. The fish had empty stomachs at this point. 5mm prey were nearly always eaten when they were encountered regardless of the treatment (Figures 1 & 2). The acceptance of the first 8mm prey offered decreased as the number of 5mm prey already eaten increased. The probability of accepting an 8mm prey generally declined to a low level as its position in the sequence increased. Under some of the treatments the number of 8mm prey eaten increased again towards the end of the sequence. The treatment where all the 5mm prey had been eaten also showed this pattern.

Feeding Behaviours and Prey Acceptance

The results from the video analysis show a consistent feeding behaviour was used by all the fish. The fish always orientated towards the prey as soon as it was detected. A pursuit occurred if the fish then decided to investigate the prey further. If this pursuit ended with an attempt at handling the prey, the number of manipulations was recorded. The probabilities of occurrence of the three behaviours shown by the foraging stickleback are given in Table II.

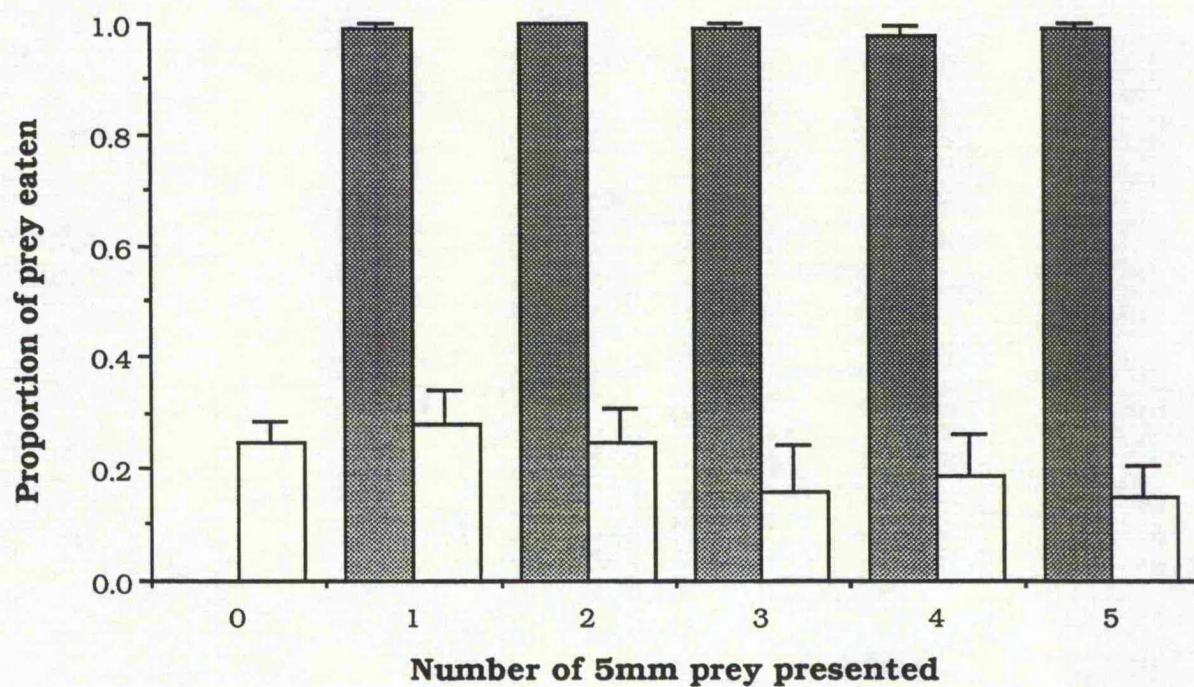


Figure 1. The proportion of prey consumed with respect to the total number of both prey sizes available. ■ : the proportion of 5mm prey eaten (+S.E.) in relation to the number of 5mm prey presented; □ : the number of 8mm prey eaten (+S.E.) as a function of 8mm prey available from each treatment. The proportions eaten and the associated errors correspond to arcsine transformed data (see text).

Figure 2. The pattern of acceptance for each different treatment. Each point indicates the proportion of prey taken (\pm S. E.) with respect to the position of the prey in the sequence. The proportions and the S. E. values correspond to arcsine transformed data (see text). \bullet - 5mm prey; \circ - 8mm prey.

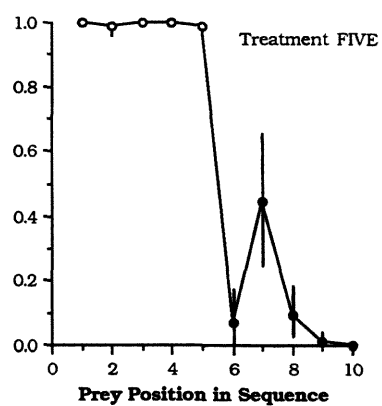
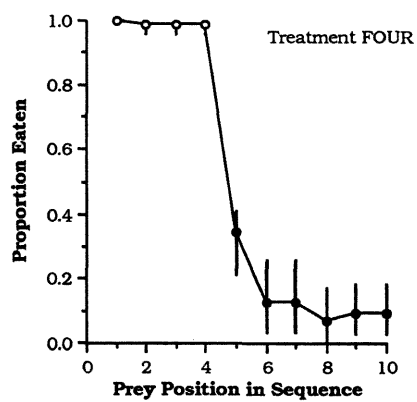
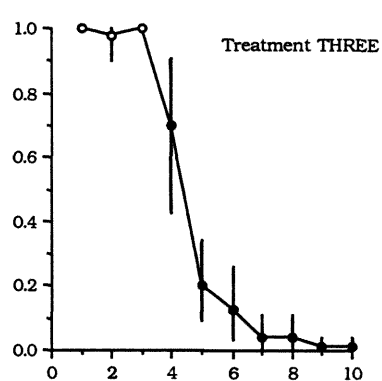
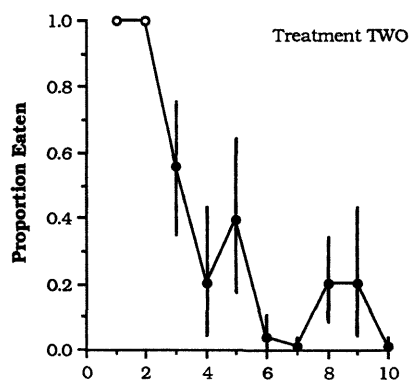
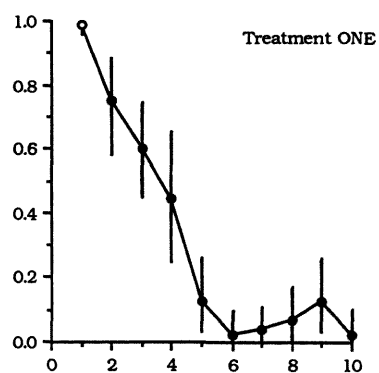
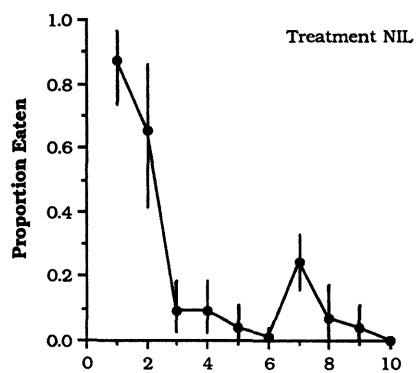


Table II. The probability of occurrence of the three stickleback foraging behaviours when 5mm and 8mm *Asellus* were offered.

Number of 5mm prey offered	Probability					
	Orientate		Pursuit		Manipulate	
	5mm	8mm	5mm	8mm	5mm	8mm
0	-	0.95	-	0.91	-	0.90
1	1.00	0.98	1.00	0.94	0.94	0.92
2	1.00	0.96	1.00	0.91	0.97	0.88
3	1.00	0.89	1.00	0.85	0.98	0.83
4	0.97	0.97	0.96	0.95	0.96	0.89
5	0.99	0.94	0.99	0.88	0.99	0.85

Presentation of an *Asellus* resulted in an orientation with a probability close to one. A fish that orientated to the prey then went on to complete all three behaviours with a high degree of probability, which was independent of prey size. There was no difference between the behaviour of individual fish and no difference in the fish behaviour for each treatment, (Orientate $H=6.87$, Pursuit $H=4.04$, Manipulate $H=4.79$, 5 df, $p>0.05$ for all three) where H is a measure of the variation amongst the sample rank means and is distributed as χ^2 .

The number of manipulations performed by the fish on each prey size with associated probabilities are shown in Figure 3. For 5mm *Asellus* there were insufficient rejections to make possible the separation of manipulations into those for prey consumption and those for prey rejection. 5mm prey were usually accepted after only one manipulation. The numbers of manipulations by fish handling 8mm prey were separated into those recorded during prey acceptance and those for prey rejection. Of the 8mm prey consumed the majority were accepted after less than five manipulations, this is significantly different from the 5mm results ($z=10.218$, $p<0.001$) where z is a standardised normal distribution. The majority of fish tended to reject 8mm prey after less than four manipulations, a significant difference from the number of manipulations associated with acceptance ($z=3.841$, $p<0.001$). For both prey sizes encountered the most probable outcome was for the fish to manipulate once.

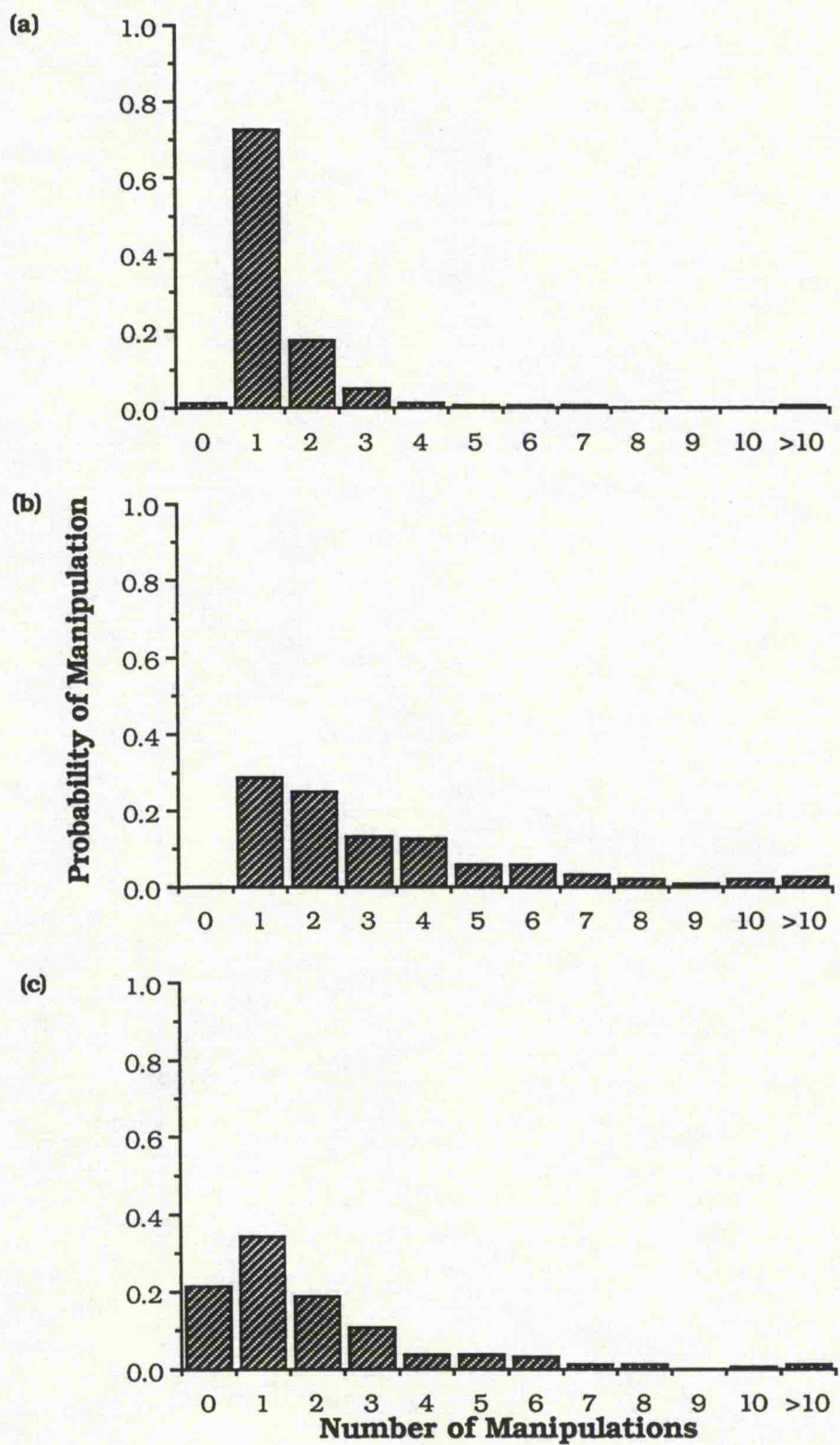


Figure 3. The probability of prey manipulation associated with eaten and rejected 5mm and 8mm prey. (a) 5mm prey; (b) 8mm prey accepted; (c) 8mm prey rejected.

Energy Intake and Prey Choice

The average energy contained in a 5mm *Asellus* is 58.6 Joules, whereas an 8mm prey contains an average of 171.7 Joules (Daoud 1984). The energy content in the gut of the fish could be estimated by multiplying these energy values by the mean number of prey eaten (Table III). The total energy consumed by the fish was similar despite the change in combination of the prey sizes consumed.

Table III. The mean number of *Asellus* taken for each treatment converted to energy to give an estimate of intake in relation to fish size. Estimated bomb calorific content of *Asellus* taken from Daoud (1984); 5mm=58.6 J; 8mm=171.7 J.

Number of 5mm Prey	Mean		Energy		Total Energy
	5mm	8mm	5mm	8mm	
0	-	2.44	-	418.95	418.95
1	0.94	2.67	55.32	456.72	511.74
2	2.00	2.06	117.20	352.84	470.04
3	2.88	1.55	168.77	266.14	434.91
4	3.83	1.33	224.61	228.36	452.97
5	4.88	0.83	285.97	143.03	429.00

The fish were not all the same size or sex so the influence of these factors was analysed. The numbers of 5mm prey eaten for each treatment did not vary between fish (ANOVA, $p>0.05$) but the numbers of 8mm prey eaten did (ANOVA, $p<0.01$, $F=5.906$, df 5, 25). Differences due to sex did not account for this variation. The acceptance of 8mm prey was found to be related to fish size; fish larger than 45mm consumed a significantly greater number than the smaller fish (ANOVA, $p<0.01$, $F=76.03$, df 1, 5).

A further consideration is that stomach capacity could have played a major role. The larger fish presumably had a larger stomach volume. The proportion of prey eaten by individual fish for each treatment is shown in Figure 4. Each fish could consume all 5mm prey offered up to the maximum of five (Figure 4a). The number of 8mm prey eaten for each treatment is shown in Figure 4b. This emphasises the difference between the fish and also shows the decreasing numbers of 8mm prey taken as the number of the

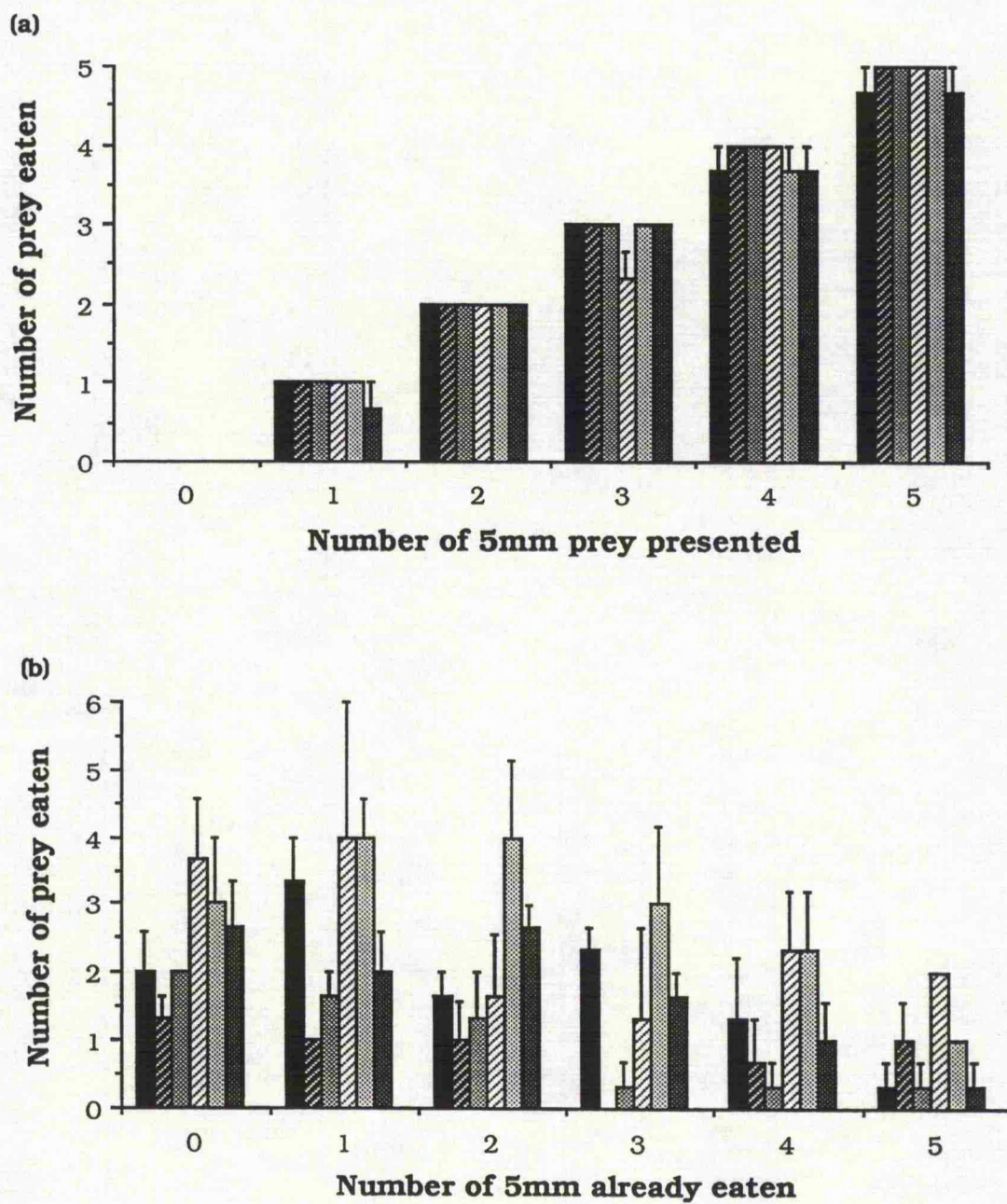


Figure 4. The mean number of prey consumed (+S.E.) by each of the fish. (a) The number of 5mm prey eaten. (b) The number of 8mm prey eaten. Each fish is represented by a specific bar pattern; ■ Fish1; ▨ Fish2; ▩ Fish3; ▪ Fish4; ▫ Fish5; ▬ Fish6.

smaller prey already eaten increased. The proportions in the histograms were converted to average weight eaten per day per fish (Table IV). The amount eaten daily, as a percentage of body weight, by each fish could then be determined (Table IV). The final column shows clearly that although these fish are different sizes and sexes they have similar daily intakes per unit of body size.

Table IV. Dry weight eaten per day by each fish averaged for all prey taken.

Fish	mg/day(\pm SD)	Fish weight(mg)	%body weight/day
C1	36.4(\pm 9.1)	774	4.7
C2	23.2(\pm 7.6)	547	4.2
C3	25.5(\pm 3.6)	628	4.1
C4	45.9(\pm 10.9)	1010	4.5
C5	52.0(\pm 9.7)	1200	4.3
C6	34.6(\pm 6.3)	764	4.5

Experiment 2

The mean number of 3,4 and 5mm prey consumed by the fish were 27.2 ± 5.1 ; 18.0 ± 1.4 and 7.8 ± 1.3 respectively (\pm S.E.). When the fish were examined internally the distended stomach occupied most of the body cavity. The liver and spleen were removed to reveal the full extent of distension (Figure 5). On opening the left lateral side of the fish's stomach, the prey were seen to be packed with their dorsal surfaces showing. Most of the prey were curled up and their long axes tended to be perpendicular to the longitudinal axis of the fish (Figure 6). This gave an impression of order within the stomach. Discernible prey nearest the pyloric sphincter were orientated head first towards the intestine.

Figure 5. The extent to which the body cavity was dominated by the distended stomach in a 45mm stickleback fed to satiation with 4mm *Asellus* prey.

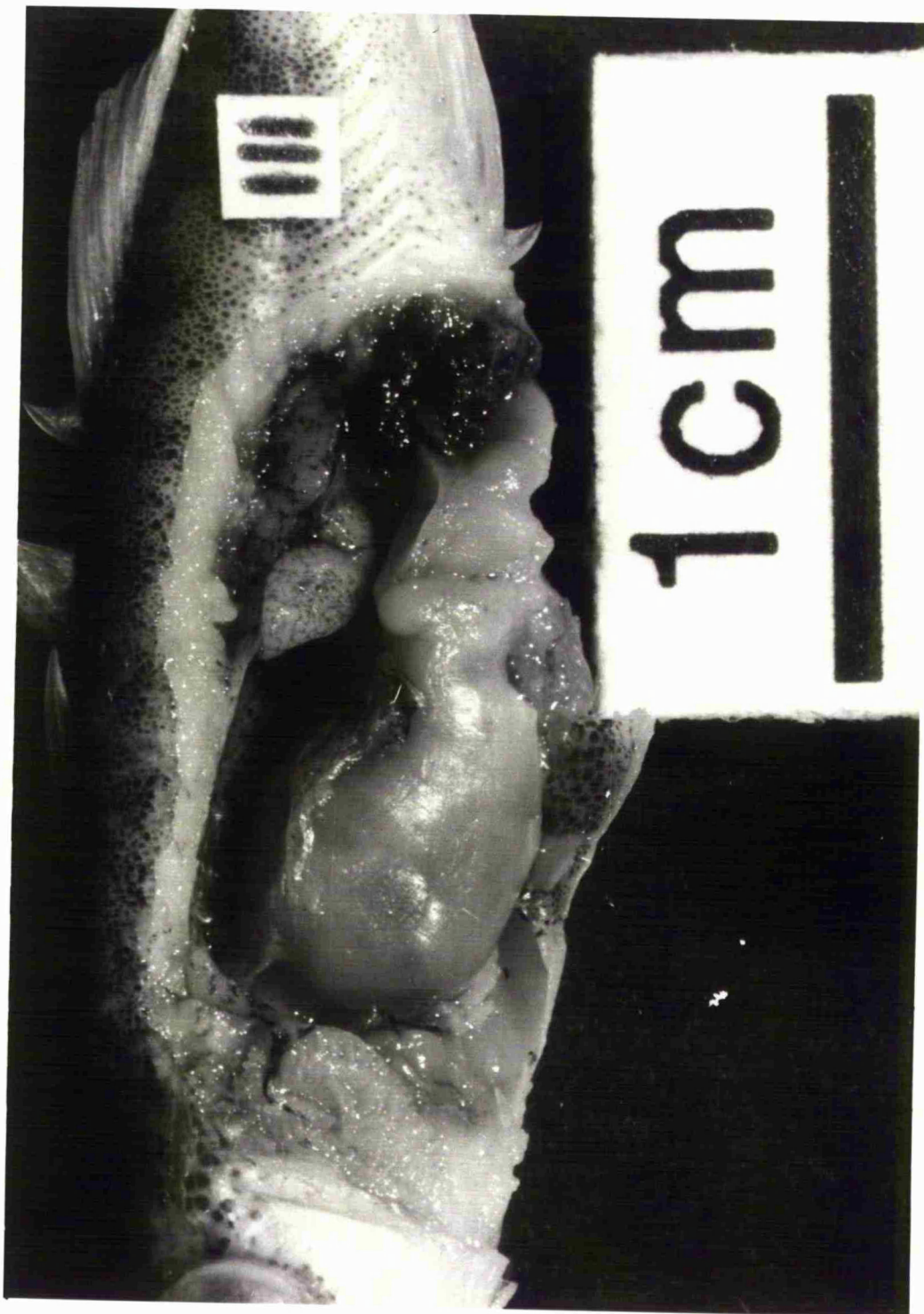


Figure 6. Orientation and packing of the Asellus within the stomach showing that the dorsal surfaces of the 4mm prey were against the stomach wall. the prey alignment is perpendicular to the longitudinal axis of the fish. The white bar is 5mm in length.



DISCUSSION

Feeding Behaviour

Although individual sticklebacks had significant differences in consumption, their feeding behaviour showed many similarities. The most profitable prey (Energy content/Handling time = E/H) available to the fish were always taken. The foraging behaviours of orientation followed by pursuit and then handling were consistent for all the fish. This pattern of behaviours began whenever a fish orientated to a prey. Similarly, Atlantic salmon (*Salmo salar*) alevins have been reported to attack virtually everything seen (Browman & Marcotte, 1986).

The complexity of the behavioural sequence was greater when the fish were attacking the bigger prey size. Larger prey had to be manipulated more than the small prey.

All the sticklebacks were able to consume a number of 8mm prey although their acceptance reduced with increasing gut fullness. Hart & Ison (1991) concluded from their experiment that fish with an empty stomach would accept any *Asellus* between 3 and 9 mm. This result was true also of the present study in which the 8mm prey were accepted 9 out of 10 times when the gut was empty. As the contents of the gut increased the fish become more selective. This has also been documented by Ivlev (1961), Kislalioglu & Gibson (1976), Heller & Milinski (1979), Visser (1982) and Godin (1990). The behavioural prey capture sequence did not change as the gut filled. Tactile stimulation was required for both the acceptance and rejection of a prey. This suggests that fish were not using vision alone to decide on acceptance or rejection. The fish need a touch to recognise the prey type (Hughes 1979). At this point taste may also play a part.

Prey Choice

The feeding decision process of a threespine stickleback proposed by Hart & Ison (1991) suggested that the fish would reject *Asellus* greater than 7mm when they had already consumed more than 400 Joules(J). For this experiment the gut was never filled to over 400 J by 5mm prey alone even for treatment F. The fish had to take 8mm prey to reach the energy threshold. The likelihood of acceptance of an 8mm *Asellus* for a fish that

has already consumed 200-299 J was estimated by Hart & Ison (1991) to be around 0.1. In the present experiment with five 5mm *Asellus* already consumed, giving the fish 200-299 J in the gut, the probability of taking an 8mm prey was about 0.15 (Figure 1). These results demonstrate that the fish will take prey with a long handling time if the energy in the stomach has not reached a critical point. Fish have been found to eat to meet an energy requirement (Bromley, 1980; Jobling, 1981). As energy comes in discrete packages a fish that has not quite reached its energy requirement may be forced to exceed it. This explains why in Figure 2 some of the graphs increase towards the end of the prey sequence offered. The fish were only fed once so no more food was available per day. It is also likely that due to the design of the experiment the fish learnt that once an 8mm prey was encountered it was only followed by more 8mm prey, so the fish could only get enough energy intake by eating a large prey. It has been previously shown that sticklebacks take about 7 days to learn about prey types (Ibrahim & Huntingford, 1989c). This experiment resets the criterion at 450 J which leads to a revised decision-making process for 45mm stickleback (Figure 7). Independent support for the 450 J criterion comes from Rajasilta (1980) and from Wootton *et al* (1980), who predicted a maximum voluntary consumption of 450 J for stickleback weighing 1g at 15°C feeding on *enchytraeid* worms. 450 J is the gross energy intake and does not take account of handling time and the other cost factors. The energy criterion is essentially the point where feeding motivation is suppressed.

Energetic Interpretation

Assuming that fish required an energetic intake of 450 J, calculations were made of how many of each millimetre size group of *Asellus* prey would satisfy the demand and how long the estimated number required would take to handle, assuming that the fish was feeding on them alone (Figure 8). The smallest number required with the shortest cumulative handling time would be derived from 5mm prey. Assuming a suitable encounter rate, a 'rational' fish could match its energy requirement quickest by selecting only 5mm *Asellus*. It may also be true that 5mm *Asellus* is the size that packs best into the stomach to give the greatest available energy per unit volume.

Handling times of prey smaller than 5mm are short and therefore the fish have lower opportunity costs, but the fish cannot pack enough prey of these sizes into the

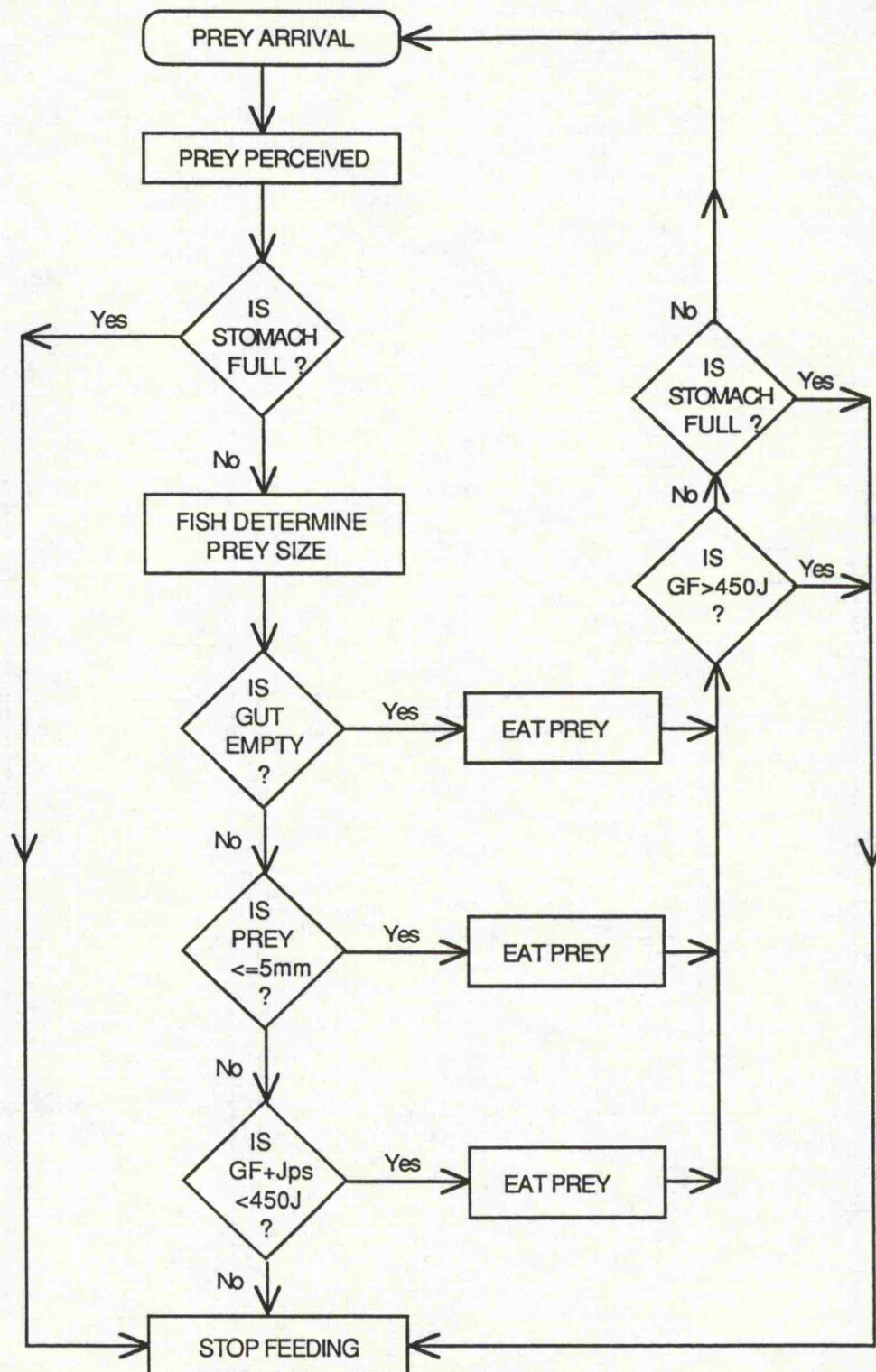


Figure 7. The feeding decision process for sequential encounter of prey, all of which is within the limits set by mouth morphology of the fish. The oval represents the start of the process, the rectangles represent perceptive tasks or events and the diamonds represent decisions by the fish. GF:- Energy content of prey in the gut. Jps:- Energy content of the prey under selection.

stomach to reach the 450 J requirement in one feeding session. Hart & Ison (1991) found that an encounter with a 3 or 4mm prey always resulted in consumption. By taking small prey the fish will be moving closer to the 450 J contour with little cost as handling times are small, reducing the probability of energetic shortfall. In addition, as small prey have little variance in value to the fish, they are more likely to be selected for as satiation increases. This result has been found for guppies (*Poecilia reticulata*) (Godin, 1990).

Stickleback require only small numbers of prey greater than 5mm to reach their required intake but the handling times and opportunity costs increase rapidly for each 1mm increment in length. Profitability values (E/H) for large prey have the widest variance (Hart & Ison, 1991). Large prey are of greater value to a hungry fish, this value decreasing markedly as the stomach of the fish fills.

The 5mm prey size appears to be at the critical point in the range of prey sizes offered to the fish. Anything below or equal to this size is eaten, whilst consumption of larger prey only occurs when the encounter rate with profitable prey is low and depends on the stomach fullness level. As the gut fills the amount of energy needed to reach the energy requirement will be reduced so stimulating the fish to select smaller prey. Only these prey will fit into the remaining space in the stomach. In short, when hungry a stickleback will give a higher value to a given sized prey than when satiated. McNamara (1990) has provided a theoretical interpretation of such a change in relative value of prey as energy reserves increase. At low energy reserves the probability of not meeting the daily energy requirement is high so any food is of great value. However, when the animal is say half full, the probability of reaching the requirement is better than when the stomach is empty, so the value of a prey of a similar size is less as rejecting it does not mean the difference between meeting the requirement or not.

As a fish gets larger, so its metabolic requirements increase (Peters, 1983). Sticklebacks larger than 45mm will presumably require more than 450 J so more of each prey will be needed to reach the criterion. The larger fish will have a larger jaw and stomach capacity for prey, therefore, the probability of acceptance of prey larger than 5mm should increase with fish size. Fish in this experiment ate more large 8mm

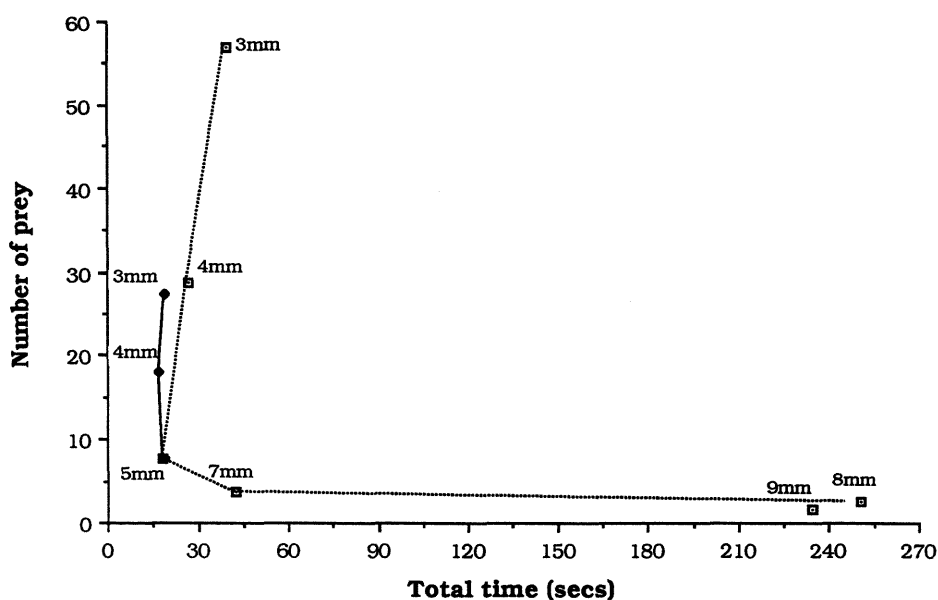


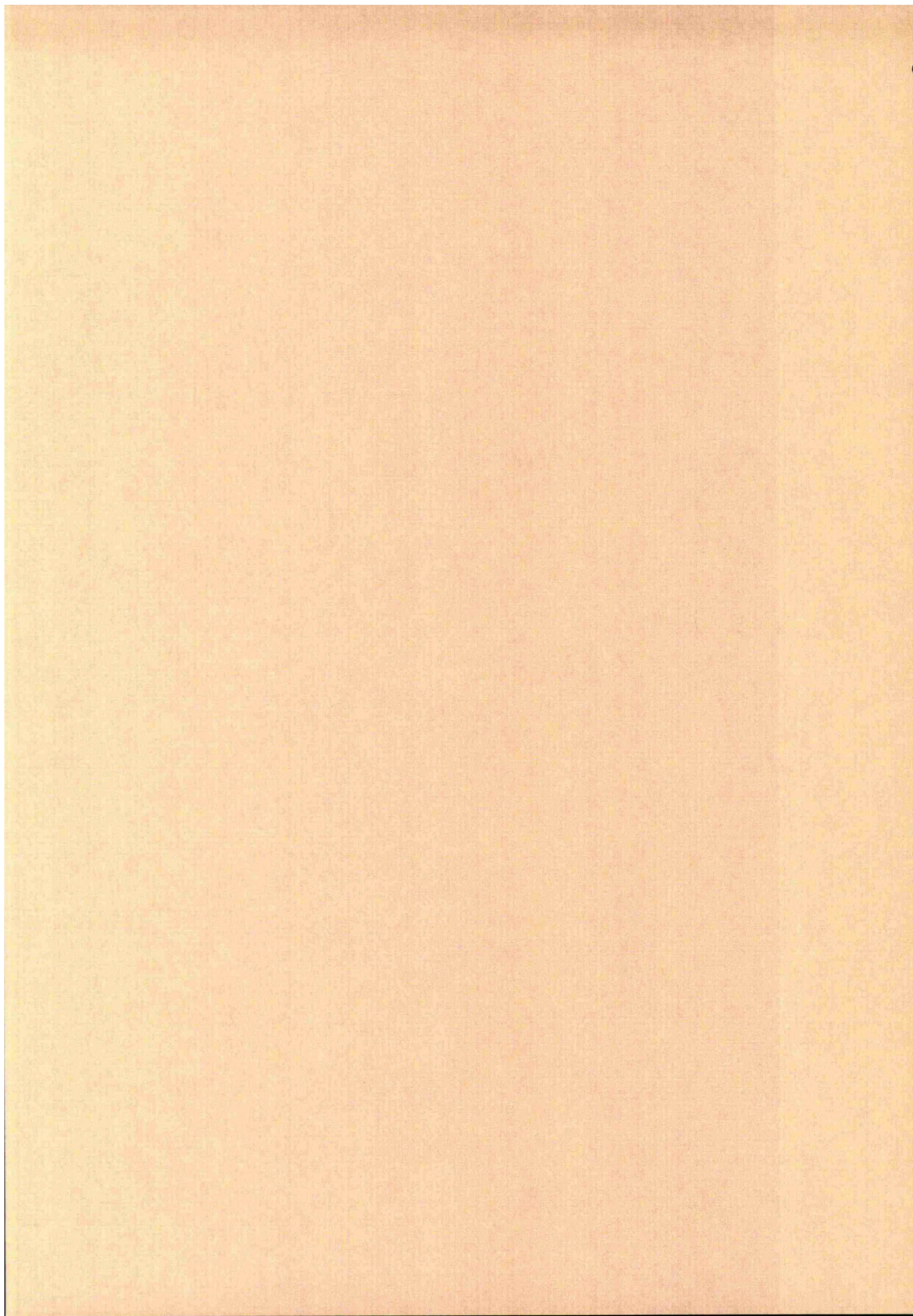
Figure 8. Energy contour. The broken line is the estimated contour of the number and time combinations per prey size which yield 450 J. The energetic values of the different sized *Asellus* (Daoud, 1984) were divided into the 450 J energy criterion, giving the numbers of prey that fish require to reach the criterion. This figure was then multiplied by the median handling time for each size of prey (Hart & Ison, 1991) to give a cost in terms of time. The continuous line shows the values of the maximum number of prey eaten for the 3, 4 and 5mm prey sizes. Estimates on this line came from the second experiment. The graph will be cut off at the greatest prey size that the fish can consume.

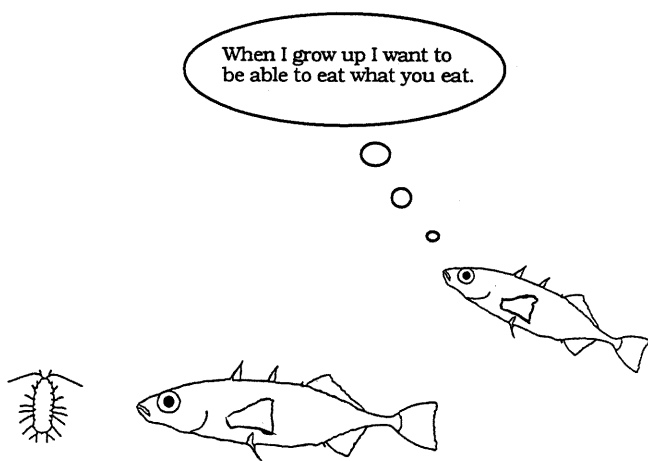
prey if they were larger in size (Figure 4b) which suggests that these fish have a correspondingly greater stomach capacity.

A possible prediction from Figure 8 is that, at a given encounter rate, as fish increase in size 3mm prey may be rejected. The numbers needed to reach an energetic criterion would be so large that the benefit to the predator would be negligible for each single prey consumed. An additional factor reducing the likelihood of these prey being in the diet is that as fish get larger the visual ability to detect small prey decreases (Hairston *et al*, 1982), so they are less likely to be encountered (Werner & Hall, 1974; Mittlebach, 1981; Eggers, 1982).

Conversely, fish smaller than 45mm will be more likely to include smaller prey in their diet as their energy criterion will be lower. Also, as fish size decreases the prey handling time increases (Kislalioglu & Gibson, 1976; Kaiser *et al*, 1992a), and jaw and stomach constraints will probably mean that larger prey are less likely to be selected.

(This study has been published in the Journal of Fish Biology 40: 205-218. Entitled- 'Constraints on prey size selection by the threespine stickleback: energy requirements and the capacity and fullness of the gut.)'





CHAPTER 3

Feeding behaviour and prey choice of the threespine stickleback: the interacting effects of prey size, fish size and stomach fullness.

ABSTRACT

This study investigated changes in the foraging behaviour of threespine stickleback of different body sizes, in response to increasing prey size and stomach fullness of the fish. Within the behavioural feeding sequence, a decision to attack and a decision to eat the prey were made by the fish. As fish became smaller, there was an increased likelihood of hanging during the attack and a greater need to manipulate the prey when handling. An increase in fish body size resulted in an increased probability of attacking and eating the prey. The probability of success, however, decreased as prey got larger. Success also decreased with increasing stomach fullness when prey larger than the prey width:mouth width (PW:MW) ratio of 0.6 were encountered. Regardless of fish or prey size, there was a constant handling time of approximately 3 seconds during which the fish made the decision to eat. The time taken to handle and eat a prey decreased as fish got larger and rose as prey size increased. Spitting frequency increased with prey size and spitting was always required for prey greater than the 0.6 PW:MW ratio. This corresponded to a preference for prey orientated head first and ventral side up. Prey closest to the 0.6 PW:MW ratio were the largest prey that could be eaten with little change in the time cost over all levels of stomach fullness. These prey, therefore, gave the fish the best energy return per unit cost, except when the stomach was empty, as larger prey represented a bigger energy return for the same time cost giving them a greater effective profitability. The morphological relationship between a predator and prey determines the resulting feeding behaviour and prey choice, although this choice also depends on the predator's need to acquire food.

INTRODUCTION

The ability of a predatory fish to consume a whole prey item is dependent on the morphological relationship between the prey and the mouth of the fish (Moore & Moore, 1976; Wankowski 1979, 1981) together with the associated processing ability of the jaw apparatus, the size of the visual reactive field (Wetterer, 1989) and experience with the prey (Croy & Hughes, 1991a). The limits set by these factors are likely to be influenced by the body size of the fish and further by the state of satiation which influences prey size selection (Chapter 2; Kislalioglu & Gibson, 1976; Hart & Ison, 1991; Hart & Gill, 1992).

A foraging stickleback (*Gasterosteus aculeatus*) utilises a basic repertoire of behaviours (see Chapter 2 and present study for details; Hart & Gill, 1992), the most obvious and arguably the most influential of which is handling behaviour. The time taken to handle a prey is a basic cost which is balanced against the energetic benefit of eating the prey (see Stephens & Krebs, 1986).

A basic definition of handling time is the amount of searching time lost when a prey has been captured (Werner, 1974; Hoyle & Keast, 1986). Handling time increases rapidly with increasing prey size (Werner, 1974; Kislalioglu & Gibson, 1976; Hoyle & Keast, 1986). Dunbrack and Dill (1983) divided the probability of successfully capturing a prey into the probability of attack and the probability of ingestion following attack. Prey handling time is one of the main variables determining these two probabilities. In a study into stochastic dynamic foraging models Hart & Gill(1993) proposed a more specific definition of handling time. Handling time only occurs when prey are physically attacked and can be separated into handling time associated with successful and failed prey capture. In general, the probability of successfully capturing a prey decreases with increasing prey size, which is moderated by predator size. It is demonstrated here that the time taken to decide whether or not to eat the prey, shown by the handling time for failed prey capture, is constant independent of predator body size and prey size. Conversely, when the prey has been attacked and eaten, handling time increases as prey become larger and fish get smaller. Fish body size is important when considering the handling time/unit energy return from different prey sizes. A

small fish presented with a slight increase in prey size would suffer a larger increase in the cost compared to a large fish, which would experience little change in the cost for a similar increase in prey size (Werner, 1974).

There have been many studies which relate the width of a prey to the mouth width of a fish (Werner, 1974; Kislalioglu & Gibson, 1976; Wankowski, 1979; Scott, 1987; Prejs *et al*, 1990). These studies have established that the prey which optimizes the energy intake, in terms of costs and benefits, has a width which is 0.6 times the width of the fish's mouth. Scott (1987) and Prejs *et al* (1990) also showed that this was the most preferred prey size.

This experiment set out to test the acceptance of a variety of prey sizes by different size groups of threespine stickleback and to demonstrate the effect of predator size on the handling time and the behaviours utilised when encountering each size class of prey with respect to the fullness of the predator's stomach.

METHODS

Threespine stickleback were caught from the River Welland. Four length groups of fish were chosen 25mm, 35mm, 45mm and 55mm fish. The width of the mouth at the point of articulation of the upper and lower jaw was measured with calipers. The fork length and mouth width measurements (\pm S.E.) of the four different size groups were: length=25.8 (\pm 0.56) mm, mouth=1.4 (\pm 0.17) mm; length=34.9 (\pm 0.53) mm, mouth=1.9 (\pm 0.16) mm; length=44.0 (\pm 0.45) mm, mouth=3.1 (\pm 0.16) mm and length=53.4 (\pm 0.49) mm, mouth=3.5 (\pm 0.16) mm. The experiments, between May and December 1990, tested one size group of fish at a time, starting with the 25mm fish and ending with the 55mm fish. All the fish groups were of mixed sex. The *Asellus* prey were sorted into millimetre size groups in the range 3mm-9mm body length. The 25mm fish were too small to be sexually mature which permitted experimentation during May and June, the normal breeding season of the sticklebacks.

Individual sticklebacks were offered the feeding regime outlined in Table I. Each fish encountered each of the prey sizes three times through the course of the experiment. Early in the 25mm fish experiment there was one fish fatality. It became apparent that the larger prey sizes being offered far exceeded the jaw dimensions of these fish. Therefore, the experiment continued with the remaining five fish and the 8mm prey size group was dropped from the test regime. The largest sized prey presented to the 55mm fish was altered to 9mm as the 8mm prey presented no test to the upper acceptance limit. As a result of this change the 3mm prey were dropped from the regime. From previous experiments (Chapters 2; Hart & Ison, 1991; Hart & Gill, 1992) it was expected that 3mm prey would be consumed with a high probability by the 55mm fish. The experimental apparatus is described in detail in chapter 1.

Table I. Prey presentations according to fish size group. The 35mm and 45mm length fish were subjected to the same prey sizes. The body of the table indicates the prey sizes (mm) offered on each day in a sequence of 10 prey. The sequences were replicated three times.

(a) 25mm fish.

Fish Number	Day				
	1	2	3	4	5
C1	3	7	6	5	4
C2	4	3	7	6	5
C3	5	4	3	7	6
C4	6	5	4	3	7
C5	7	6	5	4	3

(b) 35mm & 45mm fish

Fish Number	Day					
	1	2	3	4	5	6
C1	3	8	7	6	5	4
C2	4	3	8	7	6	5
C3	5	4	3	8	7	6
C4	6	5	4	3	8	7
C5	7	6	5	4	3	8
C6	8	7	6	5	4	3

(c) 55mm fish

Fish Number	Day					
	1	2	3	4	5	6
C1	4	9	8	7	6	5
C2	5	4	9	8	7	6
C3	6	5	4	9	8	7
C4	7	6	5	4	9	8
C5	8	7	6	5	4	9
C6	9	8	7	6	5	4

The video records were analysed for three prey captures and three prey rejections by each fish encountering each prey size. In each case the first record, the middle record and the last record were analysed. When there were less than three captures or rejections then all available records were analysed. For each prey presented the behaviours of the fish and the number of times each behaviour was performed were recorded. Behaviours studied were:

Approach:- this included orientation to the prey and movement towards the prey;

Hang:- any time that the fish stopped in midwater during the approach whilst still fixated on the prey;

Handle:- any physical contact with the prey;

Spit:- expulsion of the prey from the mouth during handling;

Eat or Reject.

Only six behaviours were defined in order to minimise ambiguity between analyses. Handling time was defined as the time from the first physical contact with the prey until the fish rejected the prey or the prey had been swallowed and the fish had begun searching again.

The behavioural sequences were analysed using transition matrices. This method uses a matrix to score the frequency with which each behaviour is followed by another. From these frequencies the probability that a behaviour occurs given that another behaviour has just occurred can be calculated. These resulting probabilities are known as conditional probabilities (Slater, 1973).

Data were analysed using Cricketgraph, the non-parametric statistical package of Meddis (1984), the Wilcoxon 2-sample test with a continuity correction of 0.5 and the Kruskal-Wallis test on SAS, which gives the test statistics as χ^2 approximations. The Kruskal-Wallis multiple comparison test was used to identify any group giving a significant result (Siegel & Castellan, 1988). Statistical results with $p \geq 0.05$ were regarded as non significant in order to reduce the possibility of making a type I error, which is conservative but pertinent due to the large number of statistical comparisons which would have increased the possibility of chance significant results.

RESULTS

Prey Acceptance

Figure 1 shows that the number of prey eaten decreased with increasing prey size. As fish became larger the numbers of all prey sizes eaten increased. The figure shows the maximum number of prey that each fish size ate when feeding on a single prey size. The constraint on prey numbers eaten was the stomach capacity of each fish size group. The curves join the values of maximum numbers eaten of each prey size and can be interpreted as stomach fullness contour lines, representing the limit to which the stomach can be filled by one prey size alone (Figure 1). It was found that the 45mm and 55mm fish were capable of eating more than 10 of the 3mm & 4mm prey and 4mm & 5mm prey respectively. The analysis which follows takes this into account.

Predator Mouth Constraints

A prey width/mouth width (PW:MW) ratio of 0.6 is critical for prey selection. The PW:MW relationship was investigated to predict better the change in prey preference with fish body size. A strong linear relationship between the prey width and the mouth width was found for all the fish sizes (Figure 2). For each fish size the critical prey sizes were: 35mm- 3mm; 45mm- 5mm; 55mm- 6mm, but for the 25mm fish the prey used all gave a value larger than the 0.6 ratio (Figure 2). Those PW:MW values >1 mean that the prey were wider than the mouth. This could be attributed to measurement error or jaw/prey plasticity or the angle which the prey were ingested.

Probability of Success (P_{si})

After physically attacking a prey a fish may go on to either eat or reject it. Combining the probability of attack (P_{att}) and the probability of eating (P_{eat}) gives the probability of a successful predatory event (P_{si}).

As fish became larger the probability with which prey were attacked and eaten increased, this probability however decreased as prey size increased (Fig. 3a-d, striped bars). As the probability of a successful attack decreased, the probability of an attack resulting in failure increased (Figure 3a-d, black bars).

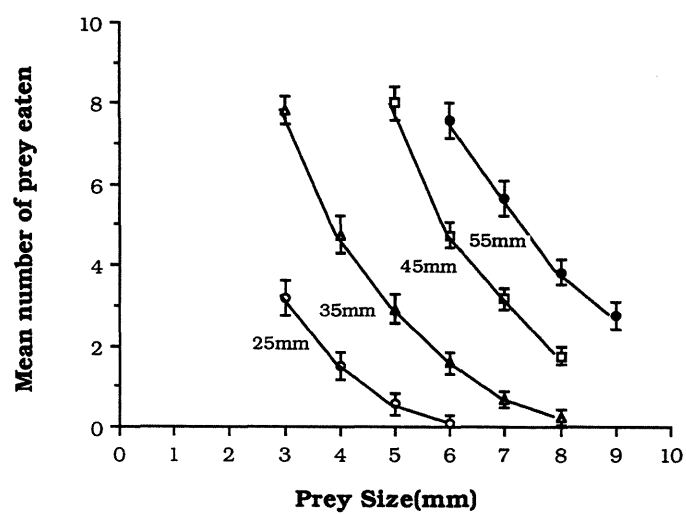


Figure 1. The mean number (\pm S.E.) of each prey size eaten by each fish size. The curves represent the stomach capacity of each fish feeding on one prey size.

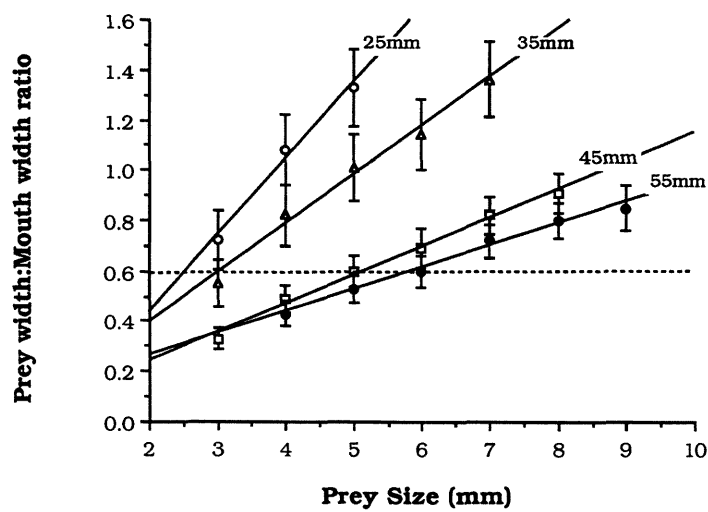


Figure 2. Prey Width: Mouth Width (\pm S.E.) relationship for each fish size. The dotted line indicates the ratio which predicts the most profitable and preferred prey size. Linear relationships :- 25mm: $y = -0.177 + 0.305x$, $R^2 = 0.989$; 35mm: $y = 0.006 + 0.194x$, $R^2 = 0.987$; 45mm: $y = 1.457 + 0.114x$, $R^2 = 0.993$; 55mm: $y = 0.092 + 0.087x$, $R^2 = 0.989$.

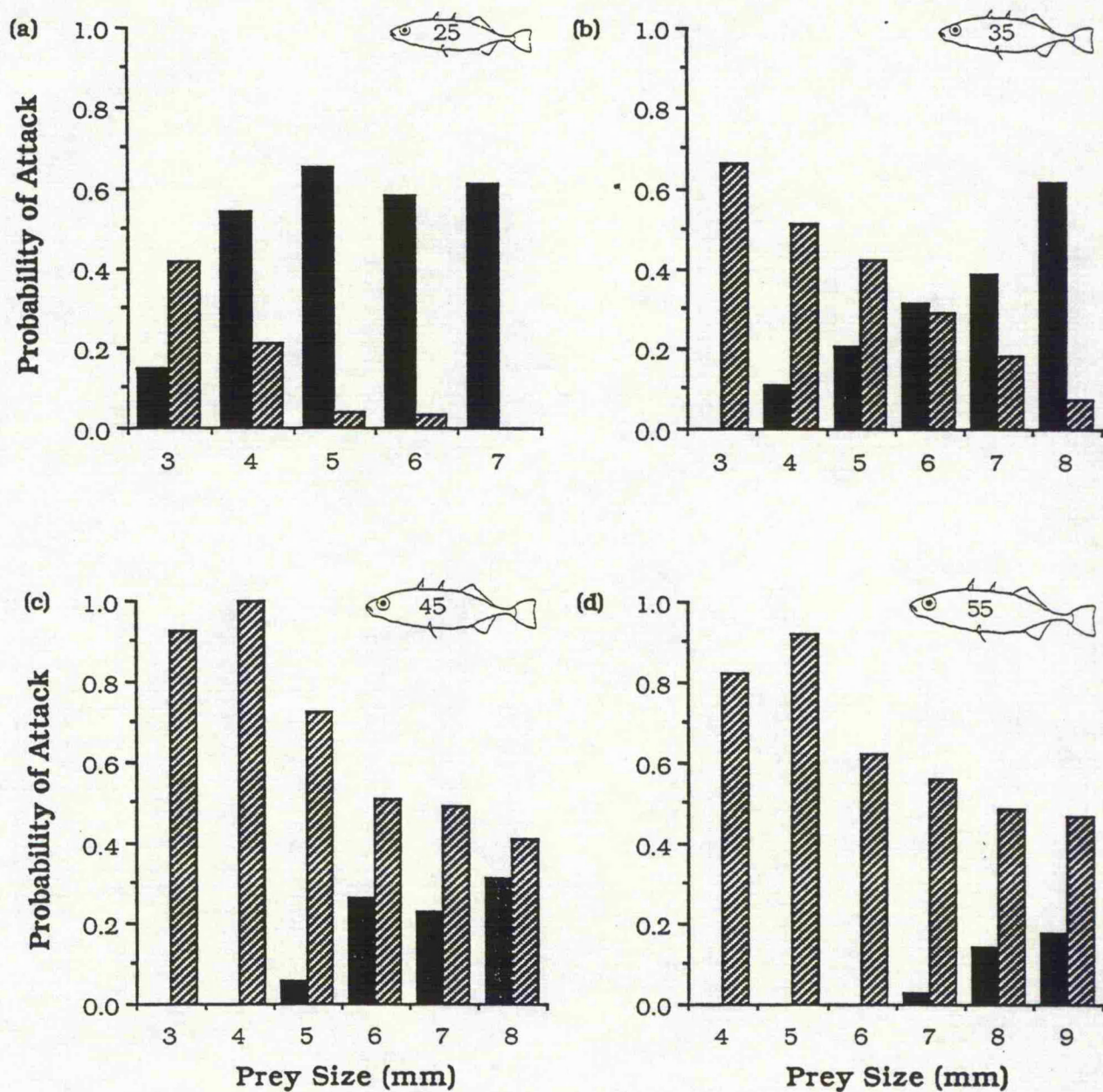


Figure 3. The probability of attacking (P_{att}) each different prey size with respect to fish size. The data were separated into those for successful prey capture (▨) and those for failed prey capture (■). (a) 25mm; (b) 35mm; (c) 45mm; (d) 55mm.

For any fish with an empty stomach the initial Peat was always the greatest, Peat the larger prey reduced as stomach fullness increased (Figure 4). For a given prey size the Peat decreased with decreasing fish body size. There was a limit, set by the stomach size of each individual fish, as to how many of each prey size could be eaten. If all the fish had the same stomach capacity then each shaded band in Figure 4 would be cut off at this upper limit. However, the bands gradually become thinner and some of the bands rise towards the end of a prey sequence showing the individual variation found in the numbers ingested. A few 5mm and 6mm prey were eaten by the 25mm fish when presented first in the sequence, but the Peatvalue of 0.01 was too small to show on the graphs.

Handling Time

Differences with stomach fullness

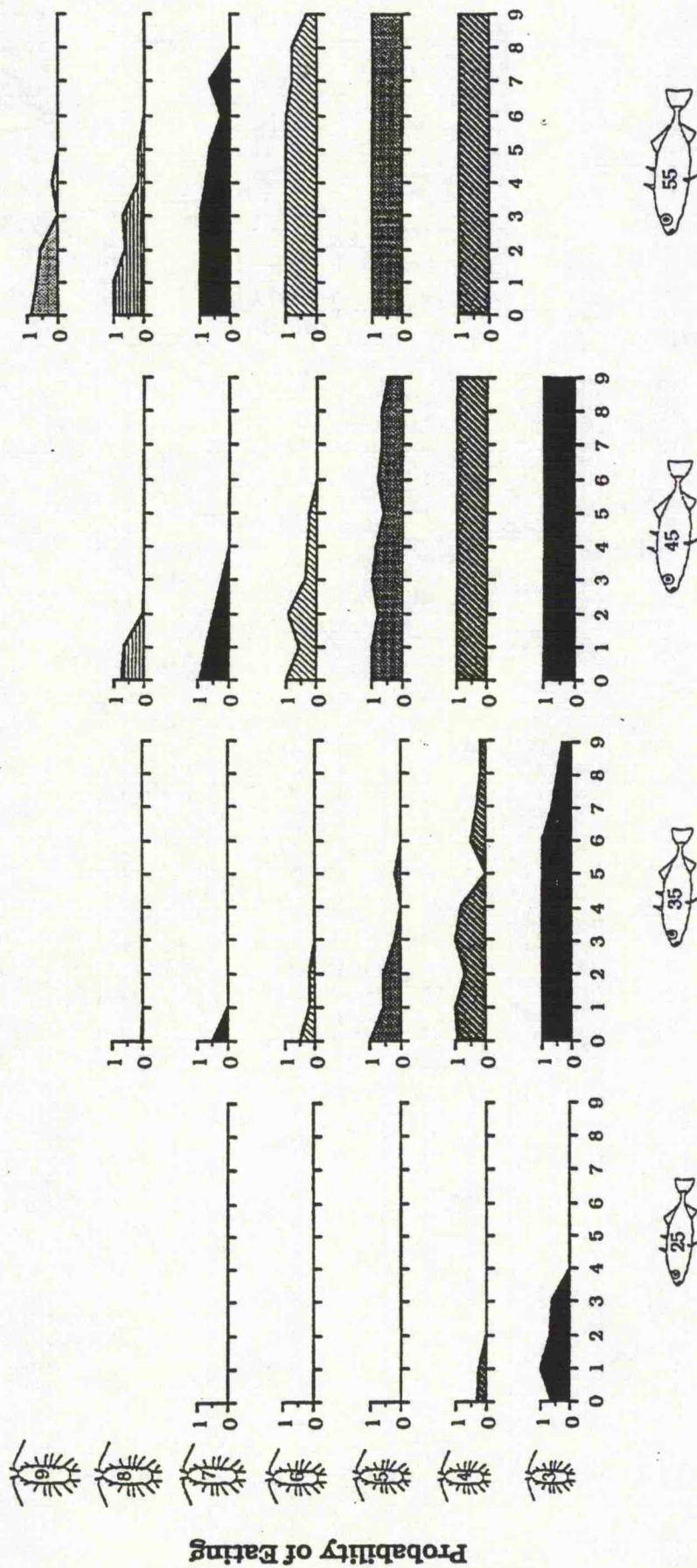
Stomach fullness had no significant effect on the handling time of any prey size by any fish size ($p > 0.09$ for all prey sizes whether capture was a success or failure, where p is the probability of obtaining a greater observed χ^2 value) except, one 55mm fish which had already eaten two prey. This fish took longer to handle and eat the 7mm prey ($\chi^2 = 14.79$, $df = 6$, $p < 0.05$) compared to the prey handling times for all the other levels of satiation.

When eating prey, all the fish sizes showed a significant difference in the handling time for each prey size when compared at similar levels of satiation (25mm: $\chi^2 = 7.91$, $df = 3$, $p < 0.05$; 35mm: $\chi^2 = 68.33$, $df = 5$, $p < 0.001$; 45mm: $\chi^2 = 124.93$, $df = 5$, $p < 0.001$; 55mm: $\chi^2 = 90.05$, $df = 5$, $p < 0.001$).

Successful and failed capture

The median handling time for ingesting prey increased exponentially with increasing prey size (Figure 5). The handling time for each prey size decreased as the fish became larger (3mm: $\chi^2 = 32.28$, $df = 2$; 4mm: $\chi^2 = 61.57$, $df = 3$; 5mm: $\chi^2 = 36.37$, $df = 2$; 6mm: $\chi^2 = 27.60$, $df = 2$; 7mm: $\chi^2 = 19.51$, $df = 2$; 8mm: $\chi^2 = 18.51$, $df = 2$; all prey sizes $p < 0.001$).

Figure 4. The change in the probability of eating prey (P_{eat}) with the degree of satiation of the fish as a function of fish size and prey size. Along the horizontal axis, each prey size graph has the same shading pattern allowing the P_{eat} of each fish size to be compared. The pictorial representations of fish size (abscissa) and prey size (ordinate) assist in interpreting all the graphs.



Number of Prey Consumed

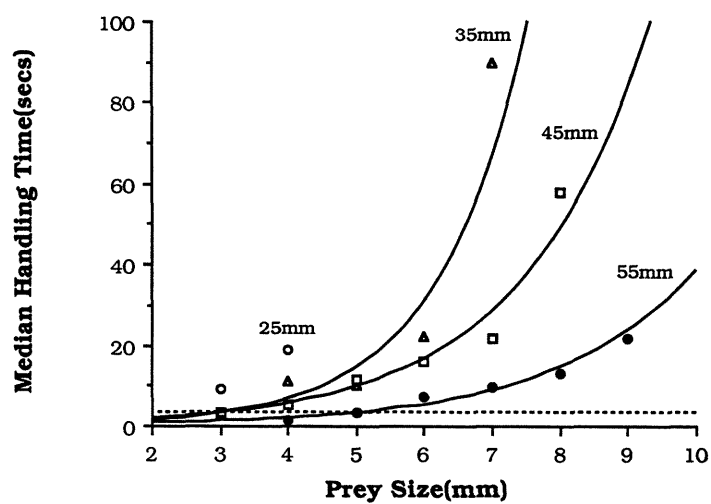


Figure 5. Effect of prey size and fish size on the median prey handling time of prey successfully captured. The broken line shows the time taken in failed prey capture by all fish sizes for all prey sizes. Relationships for the curves:- 35mm: $y=0.318 \cdot 10^{(0.331x)}$, $R^2=0.905$; 45mm: $y=0.668 \cdot 10^{(0.233x)}$, $R^2=0.972$; 55mm: $y=0.282 \cdot 10^{(0.214x)}$, $R^2=0.967$.

Table II. A statistical test of the difference in handling times for successful and failed prey capture. The data were tested using the Wilcoxon 2-sample test with a 0.5 continuity correction. S = smallest sum of the rank scores; z= ratio of (S-expected)/Std.Dev.:—approximately normally distributed; p= the probability of a greater observed z value. ('*' : significant; '-' : no record; 'x' : all eaten; '+' : none or insignificant number eaten).

Prey Size(mm)	Statistic	Fish Size			
		25	35	45	55
3	S	28.0	x	x	-
	z	-3.85	x	x	-
	p	<0.0001*	x	x	-
4	S	137.0	60.0	x	x
	z	2.75	-2.95	x	x
	p	<0.006*	<0.003*	x	x
5	S	+	148.0	39.0	x
	z	+	-2.01	-1.13	x
	p	+	<0.044*	>0.259	x
6	S	+	360.0	266.0	x
	z	+	4.72	-4.05	x
	p	+	<0.0001*	<0.0001*	x
7	S	-	179.0	163.0	28.0
	z	-	3.84	-4.49	-0.69
	p	-	<0.0005*	<0.0001*	>0.49
8	S	-	75.0	161.0	98.0
	z	-	2.51	-4.37	-3.54
	p	-	<0.012*	<0.0001*	<0.0004*
9	S	-	-	-	123.5
	z	-	-	-	-3.08
	p	-	-	-	<0.002*

When a fish ingested a prey with a PW:MW ratio >0.6, the handling time was significantly longer than the handling time of failed prey capture (see Table II). There was no difference in the handling times when fish attacked smaller prey as none of these were handled and then rejected (Table II). A comparison between the handling times could only be made when a enough prey were both eaten and rejected, this varied with fish size (Table II). Although 7mm prey have a PW:MW ratio >0.6 for the 55mm fish (see Figure 2), these prey were handled for a similar amount of time whether capture

was a success or a failure ($z=-0.69$, $p>0.49$). Failure to capture prey ≤ 0.6 PW:MW was unlikely (see Figure 4).

A constant handling time was used by all the fish when failing to capture each prey size, (4mm: $S=68.5$, $z=-1.33$, $p>0.18$; 5mm: $\chi^2=0.5$, d.f.=2, $p>0.78$; 6mm: $\chi^2=2.19$, d.f.=2, $p>0.33$; 7mm: $\chi^2=0.96$, d.f.=3, $p>0.81$; 8mm: $\chi^2=0.41$, d.f.=2, $p>0.81$). Only the 25mm fish failed to capture some of the 3mm prey. Handling time for failed capture stayed the same for each fish size regardless of the size of the prey (25mm: $\chi^2=0.78$, d.f.=4, $p>0.94$; 35mm: $\chi^2=4.47$, d.f.=4, $p>0.35$; 45mm: $\chi^2=1.29$, d.f.=3, $p>0.73$; 55mm: $\chi^2=4.08$, d.f.=2, $p>0.13$). Thus, the median handling time of any fish failing to capture any prey was 3.3 seconds (Figure 5; the 10th and 90th percentiles were 0.5 and 14.4 respectively).

Visual comparison between fish sizes shows that differences in the handling times increased as the prey got larger (see Figure 5). When small prey sizes were eaten the handling times for the different sizes of fish became similar, as in the case of the 35mm and 45mm fish handling 3mm prey. The few records of 25mm fish eating 5mm and 6mm prey showed that handling times were greatly increased, but as these data were limited they were omitted from Figure 5.

Behaviours

Two distinct decision points were defined within the behavioural sequence of a foraging stickleback. The first occurred when a fish encountered a prey, defined as the decision to attack. The second decision was whether or not to eat the prey, this occurred whilst handling the prey.

The resulting outcome of the first decision was either to reject or attack the prey. The likelihood of a fish rejecting the prey without attacking decreased as fish size increased (Table III). Consequently, the larger fish were more likely to attack and then handle the prey (Table III).

Table III. How fish size affects the decision to attack prey, shown as probabilities.

Fish Size	Decision	
	Reject	Attack
25	0.34	0.66
35	0.25	0.75
45	0.15	0.85
55	0.15	0.85

For the analyses of the behavioural sequence resulting from a decision to attack, the probability of transition from one behaviour to the next was examined. Subsequent to this the factors affecting the frequency of occurrence of the behaviours following both decisions were analysed.

Transitions between behaviours

No temporal change in the behavioural sequence was found (see next section) so stationarity was assumed. A stationary sequence is one in which there is no change in the probabilistic structure with time, simplifying analysis and interpretation of the transition matrices (Slater, 1973).

Figure 6 shows that for a given prey size, the probability that a hang followed an approach decreased as fish size increased ($L=796.0$, $z=3.48$, $p<0.0005$), where L measures the agreement between the sample rank means and the coefficients predicting the ordering of these means and z is a standardized normal distribution. If the fish did hang then an approach always followed, after which the prey was handled (Figure 6). The successful capture of a prey was more likely if the hang behaviour was used and was of greater importance as fish became smaller (Proportion of hangs (P_{hg}) used in successful prey captures : 25mm $P_{hg}=0.86$; 35mm $P_{hg}=0.82$; 45mm $P_{hg}=0.71$; 55mm $P_{hg}=0.65$).

For each of the fish sizes, the probability of transition to hang or handle behaviour after approach was independent of prey size (25mm: $\chi^2=2.52$, $df=4$, $0.5<p<0.7$;

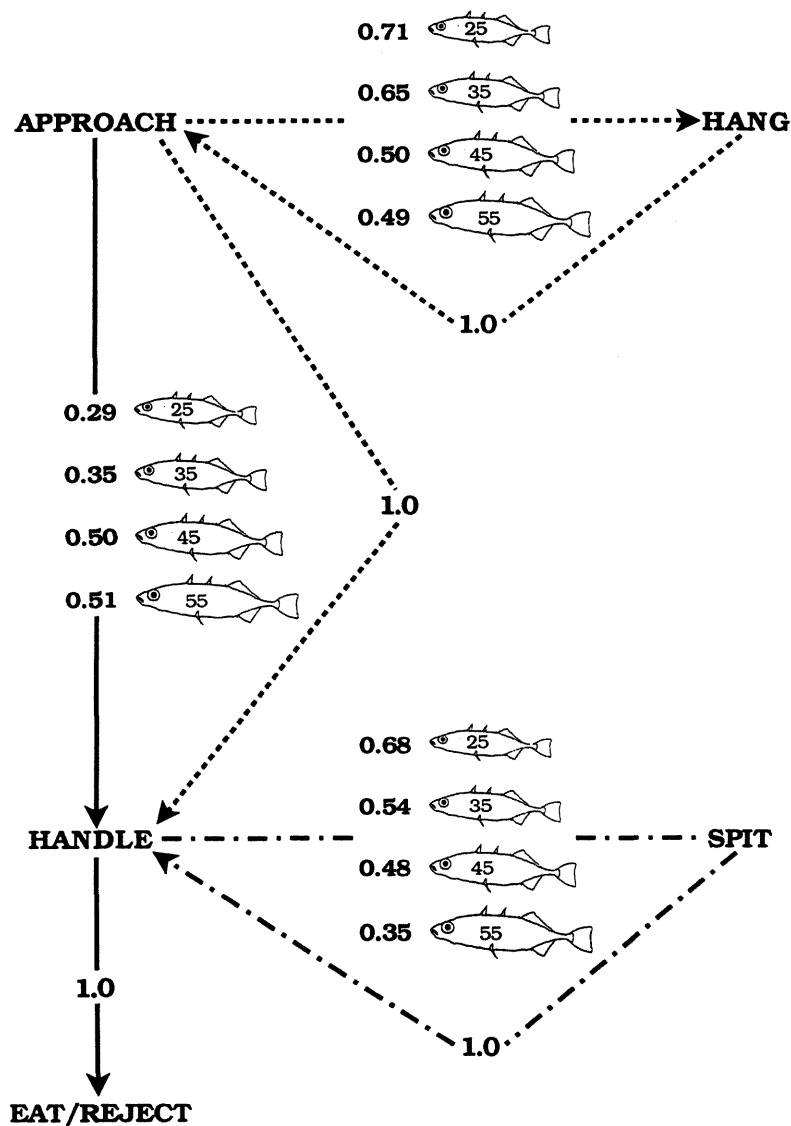


Figure 6. The probability of one behaviour being followed by another (the transitional probabilities) and how these probabilities changed with fish size when prey were attacked. Where there is only one number, the probability was similar for all the fish sizes (see text).

35mm: $\chi^2=2.24$, df=5, $0.8 < p < 0.9$; 45mm: $\chi^2=4.42$, df=5, $0.3 < p < 0.5$; 55mm: $\chi^2=3.98$, df=5, $0.5 < p < 0.7$).

Larger fish were more likely to handle the prey immediately after the initial approach ($L=817.0$, $z=3.06$, $p=0.001$; Figure 6). Smaller fish were more likely to spit the prey after the handle ($L=752.5$, $z=2.26$, $p=0.012$; Figure 6).

After any sequence of behaviours the final behavioural transition was always to either eat or reject the prey, the result depended on the prey size, fish size and stomach fullness of the fish.

Frequency of Behaviours

Any changes in the frequency of behaviour were likely to follow the decisions made by the fish, therefore the behaviours immediately subsequent to the two decision points were analysed. If the fish decided to attack the prey, the behaviour which followed was the approach. The decision to eat occurred whilst the fish was handling the prey, the following behaviour was a spit unless the prey was eaten without the need for manipulation.

Differences with stomach contents

The number of behaviours used did not change significantly with respect to the energy in the gut, regardless of whether the prey was rejected, captured unsuccessfully or captured successfully ($p > 0.05$ for all prey sizes and all fish sizes). This means there was no temporal change in behaviours. One exception was 7mm prey eaten by 55mm fish (spit: $\chi^2=13.60$, df=6, $p < 0.035$). This increase in spitting frequency was not correlated with increasing gut fullness, it probably resulted from lack of replicates at some stomach fullness levels.

Behavioural changes with prey size

The frequency of approach behaviour did not change with respect to the prey sizes rejected or attacked for any fish size ($p > 0.05$ for all fish sizes).

The amount of spitting behaviour subsequent to the prey being handled, only changed when prey were eaten. An increase in prey size lead to a highly significant increase in the number of spits used by the 35mm, 45mm and 55mm fish (35mm: spit $\chi^2=34.04$; 45mm: spit $\chi^2=65.38$; 55mm: spit $\chi^2=43.265$; $df=5$, $p<0.0001$ for these fish sizes), as shown in Figure 7. The 25mm fish had a high spit frequency for all prey attacked and eaten, this did not change with prey size ($S=111.5$, $z=0.743$, $p>0.46$). Figure 7 also shows that an increase in fish size lead to a reduction in the probability of spitting. The prey sizes at which the fish began to be unsuccessful at capturing is shown. These were the prey sizes which were on or above the 0.6 PW:MW ratio. The frequency of spitting was low at prey sizes less than the PW:MW ratio of 0.6.

Behavioural changes with fish size

Comparing the frequency of approach behaviour used, there was no difference with fish size nor was there any difference with prey size encountered when prey were rejected or attacked ($p>0.05$ for all prey sizes and fish sizes). There were however two exceptions. The 25mm fish used more approaches when 7mm prey were rejected (approach: $\chi^2=9.46$, $df=3$, $p<0.024$), this was the largest prey these fish encountered. 55mm fish used fewer approaches when attacking 4mm prey (Approach: $\chi^2=9.46$, $df=3$, $p<0.024$), the smallest prey they encountered.

All fish sizes showed no change in the frequency of spitting when prey were unsuccessfully captured ($p>0.05$ for all prey sizes).

When eating prey, the spitting behaviour decreased significantly as fish size increased (3mm: $\chi^2=40.9$, $df=2$, $p<0.0001$; 4mm: $\chi^2=34.05$, $df=3$, $p<0.0001$; 5mm: $\chi^2=15.58$, $df=3$, $p<0.001$; 6mm: $\chi^2=9.81$, $df=3$, $p<0.02$; 8mm: $\chi^2=19.35$, $df=2$, $p<0.0001$) except for 7mm prey eaten ($p>0.22$). The data for spitting 7mm prey was very similar between 35mm and 45mm fish and both fish sizes spat more compared to the 55mm fish, however the difference was not statistically significant.

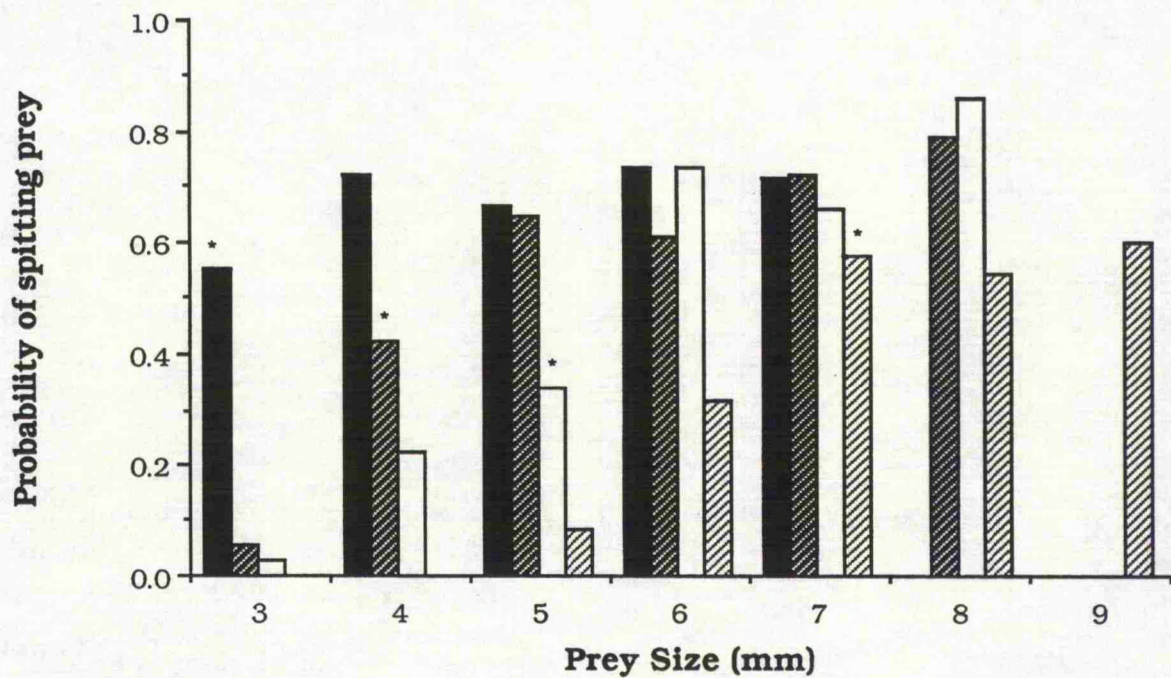


Figure 7. How the probability of spitting changed with prey size for successful prey captures. '*': indicates the prey sizes at which each fish size began failing to capture prey.

■ :25mm; ▨ :35mm; □ :45mm; ▩ :55mm.

Prey Orientation

Once handled the orientation of the prey became important, 79% of the attacks were directed at the head of the prey. Prey were preferentially eaten head first ($\chi^2=121.49$, d.f.=2, $p<0.001$) and also with the ventral surface facing upwards ($\chi^2=5.64$, d.f.=1, $p<0.02$). In order to orientate the prey the fish used spitting behaviour. An increase in prey size lead to a significant increase in the number of spits used by the 35mm, 45mm and 55mm fish (35mm: spit $\chi^2=34.04$; 45mm: spit $\chi^2=65.38$; 55mm: spit $\chi^2=43.27$; d.f.=5 and $p<0.0001$ for these fish sizes). The 25mm fish had a high spit frequency for all successful prey captures regardless of prey size ($z=0.74$, $p>0.46$).

Preferred orientation of the prey was dependent on fish size (Table IV). Increasing fish size reduced the importance of prey orientation (Table IV) and therefore less spitting behaviour was used for a greater range of prey sizes. Preference for a particular prey orientation and an increase in the spitting frequency coincided with the probability of a failure.

Table IV. The preference probability for head first ingestion of prey shown by each fish size group. '+' : insufficient data; '-' : no record.

Fish Size(mm)	Prey Size						
	3	4	5	6	7	8	9
25	0.83	1.0	+	+	-	-	-
35	+	+	0.57	0.75	0.83	+	-
45	0.2	+	0.48	0.86	0.88	0.93	-
55	-	0.13	0.25	0.44	0.73	0.77	0.83

DISCUSSION

When a predator encounters a food item the decision to eat must take account of the physical properties of the prey under selection relative to its own. It has been shown here that the size of both prey and predator and the stomach fullness of the predator interact to affect the choice and range of prey eaten.

A summary decision sequence for a foraging fish is shown in Figure 8. A searching fish encounters a prey and decides whether or not to attack. The decision is based on prey colour, movement, size and shape (Holmes & Gibson, 1986; Ibrahim & Huntingford, 1989b; Croy & Hughes, 1991c). If the fish decides to attack, the prey is approached, during which the fish may stop and hang. This appears to allow time to identify the head of the prey which increases the chance the fish has of successfully attacking the prey (Kaiser *et al.*, 1992a) and also makes swallowing easier. The fish then handles the prey and decides whether to accept the prey or not within a certain period of time, in the case here about 3 seconds. This decision and whether a fish is successful in consuming the prey is dependent on the interaction between prey size, fish size and stomach fullness.

Success or Failure

The capacity of the stomach is a controlling factor in stickleback prey choice (Chapter 2; Hart & Gill, 1992). Stomach capacity sets the upper limit on consumption for each fish size (Figure 1). At some point there will be no more room for another prey of a particular size. If a fish, near this limit, had a selection from different prey sizes there should be space in the stomach for a smaller prey. Sticklebacks eat a wide range of prey types (Hynes, 1950), so the gap in the stomach could also be filled by alternative prey.

The predicted preferred prey sizes were those nearest to the 0.6 PW:MW (Figure 2). The 25mm fish were not presented with prey of the preferred size, which could explain their reluctance to feed.

The factor which is important to consider for all fish sizes is the success of an attempted capture. This is reflected in the probabilities associated with attacking and

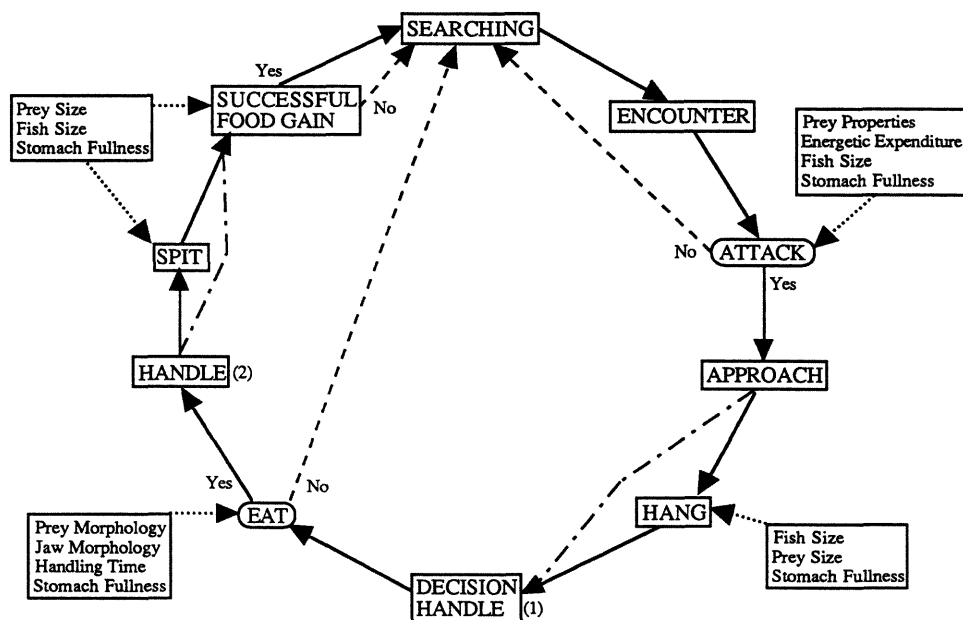


Figure 8. The cyclical foraging sequence of the threespine stickleback. The rectangles show the observed behaviours and the ovals represent the active decisions of the fish. The influential factors on behaviour are shown in the boxes. (1) Handling of the prey on which the decision to eat is based. (2) This handling is the actual attempted consumption of the prey.

consuming a prey. This probability of success (P_{si}) is based on the physical attributes of both the predator and prey. It is predicted that for any size of fish, the prey size which is preferred has a prey width:mouth width (PW:MW) ratio at which the prey can be attacked and eaten with high probability at all levels of stomach fullness. This requires the predator to coordinate swimming velocity and the judgement of distance to the prey (Nyberg, 1971). The suggested preferred prey sizes (see previous paragraph) for each fish size matched those prey sizes which the fish had a high probability of successfully capturing (P_{si}) for all levels of satiation. Prey with a PW:MW ratio <0.6 were also successfully captured with high probability, suggesting that preference for prey 0.6 of the mouth width is linked to energy return (see energetics section).

For all fish sizes, it was found that the P_{si} fell as prey size increased and also fell as the number of large prey already in the gut increased. An increase in prey size gave a cost/benefit trade-off between the handling time, the number of prey needed to fill the gut and the corresponding decrease in the probability of successful capture.

Not only does the P_{si} reduce as the prey size increases, but it has been suggested that it will also reduce at very small prey sizes (Wilson, 1975; Dunbrack & Dill, 1983). The range of prey sizes available varies according to the size of the fish. If very small and very large prey, relative to the size of the fish, are not captured with great success, then there will be a plateau between these two extremes where the probability of prey capture is high. The extent of this plateau on the prey size axis will depend on fish size, with large fish having a wide plateau and small fish having a narrow one. This study deals mainly with the large end of the scale. Whether there is an effect of stomach fullness on the P_{si} at small prey sizes is not known but as small prey contribute very little to stomach fullness, the effect of satiation would only become apparent if the fish ate a large number of prey.

Feeding Behaviour

Across all fish sizes an initiated approach was most likely to lead to attack and then handling of the prey (see also Chapter 2; Hart & Gill, 1992). During approach the fish showed a high probability of hanging, this reduced as fish size increased. O'Brien *et al*

(1990) have shown that a fish needs to stop to search, this is known as saltatory searching. In the case here a stop, or hang, probably gave the fish an opportunity to consider the orientation of the prey, enabling the fish to aim the attack so increasing the chance of success. With the size range of prey offered to the fish, the smaller fish had to use the hang behaviour more to successfully capture the prey, this may be a function of the size of the prey in comparison to the fishes mouth.

As in other studies, handling time increased rapidly with increasing prey size (Werner, 1974; Hoyle & Keast, 1986) and was also a function of the size of the fish (Kislalioglu & Gibson, 1976; Kaiser *et al*, 1992a). Handling success depends on the morphology of the prey being handled and the mouth morphology of the fish (present study; Croy & Hughes, 1991a). Handling times of prey which the fish captured and failed to capture were different only when there was a probability of failure, which corresponds with a PW:MW ratio of 0.6 or more. Handling prey with a PW:MW ratio ≤ 0.6 nearly always resulted in consumption. Hence the predicted preferred prey sizes are likely, over all states of satiation, to be consumed once attacked.

If the prey was attacked it was handled for about 3 seconds presumably enabling the fish to gain tactile information, allowing an assessment on the possibility of gaining energy. During these first few seconds the fish made a choice whether or not to eat the prey which is likely to be based on the physical and possibly chemical properties of the prey and on stomach fullness. The handling decision time stayed constant for all prey and fish sizes. This may be a common phenomenon, shore crabs also have constant short decision times when confronted with a range of prey (Elner & Hughes, 1978)

After the fish decided to eat, prey >0.6 PW:MW were preferentially ingested head first and ventral side up. Fifteen spine stickleback (*Spinachia spinachia*) eat *Gammarus* more easily head first, modifying their behaviour so that they direct attacks at the head of the prey (Croy & Hughes, 1991a). Attacking the head also decreases the chance of the fish missing the prey (Kaiser *et al*, 1992a). The sticklebacks employed spitting behaviour to get the prey into the desired orientation. An increase in fish size meant that the prey could be eaten without the preferred orientation, resulting in fewer

spits. This infers that a large fish would have an advantage over a smaller fish if they simultaneously encountered a prey.

Energetic Considerations

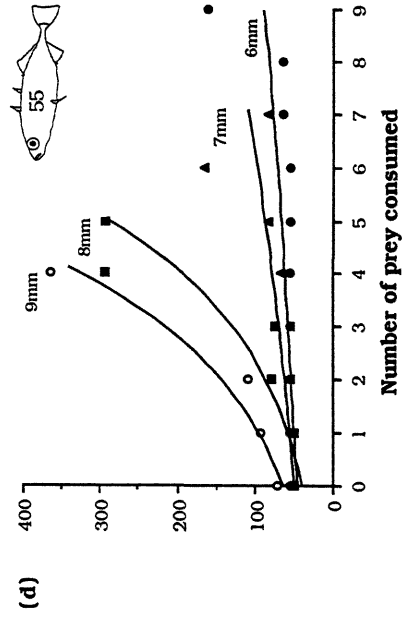
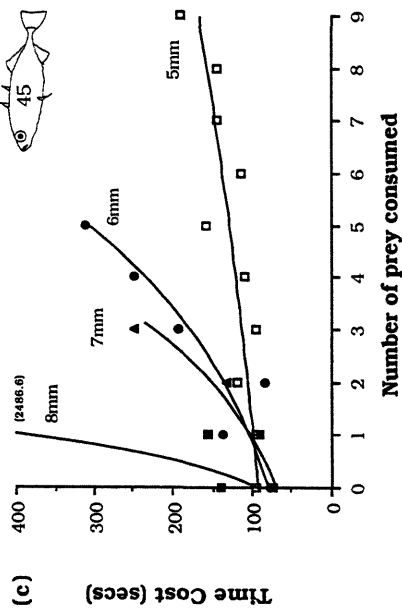
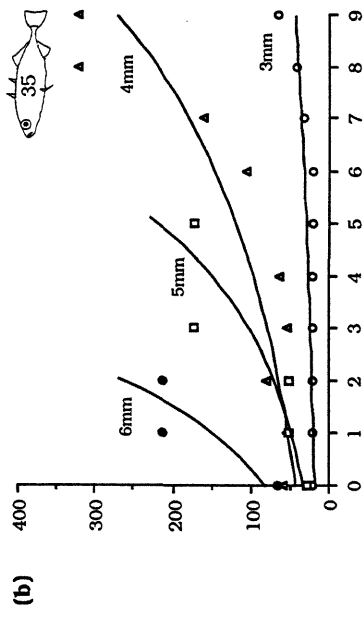
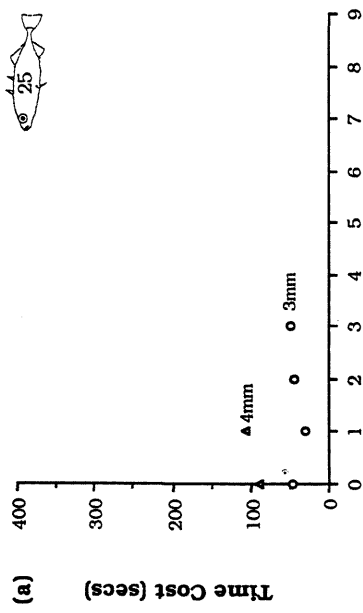
The experimental conditions presented the fish with a situation in which they either gained some energy or gained nothing. A fish never chose the latter option when hungry. In the previous chapter (Chapter 2; Hart & Gill, 1992) it was shown that sticklebacks feed to reach a daily energetic requirement. This requirement should increase with an increase in body size (Peters, 1983).

When a prey is eaten the cost is immediate whereas the benefit is delayed until digestion takes place. Dietary preferences have been shown to be based on the pre-digestive aspects of feeding and not on the long term energetic benefits (Kaiser *et al* , 1992b). In the stickleback, the choice to eat prey appeared dependent on handling time and the motivational state of the fish relative to the prey and fish size.

The costs and benefits involved in acquiring prey upto the limit of the stomach have been summarised in Figure 9a-d, where the cost is defined in terms of time. As the fish was never far from the prey, the swimming cost of attack is assumed negligible. Each prey size has a constant energy value so the energetic benefit was constant while motivational state changed. Prey sizes not included in Figure 9 were those which were either not eaten in significant numbers or were not presented in enough numbers to fill the stomach.

When hungry, the fish attacked prey which were larger than the prey regarded as the most preferred, as the time cost was similar but the energetic return greater. This is due to the larger prey containing more energy, as stated in the legend of Figure 9. As the stomach fullness increased, the cost associated with larger prey increased faster than the cost associated with smaller prey (Figure 9a-d), due to the probability of success decreasing at a greater rate for larger prey sizes. Smaller prey, including the predicted preferred prey size, probably became more attractive due to the lower cost. Hence partially sated fish became more selective choosing prey which could be successfully captured. Over all levels of satiation, prey with a width 0.6 or less times the mouth

Figure 9. An energetic interpretation of the experimental results. The number of prey consumed represents increasing stomach fullness. The time cost shown was the estimated immediate cost to the fish calculated as the product of handling time (H_t) and the maximum number of that prey size eaten (N_{max}). This scaled each prey size for direct comparison with one another. $H_t * N_{max}$ was then divided by the P_{eat} (see Fig. 4) giving an estimate of the change in cost with stomach fullness. The energetic content of each prey size are 3mm=7.9J; 4mm=15.7J; 5mm=58.6J; 6mm=80.0J; 7mm=122.4J; 8mm=171.7J and 9mm=264.5J, these values were taken from Daoud (1984). The graphs are truncated at N_{max} . (a) 25mm, (b) 35mm, (c) 45mm and (d) 55mm.

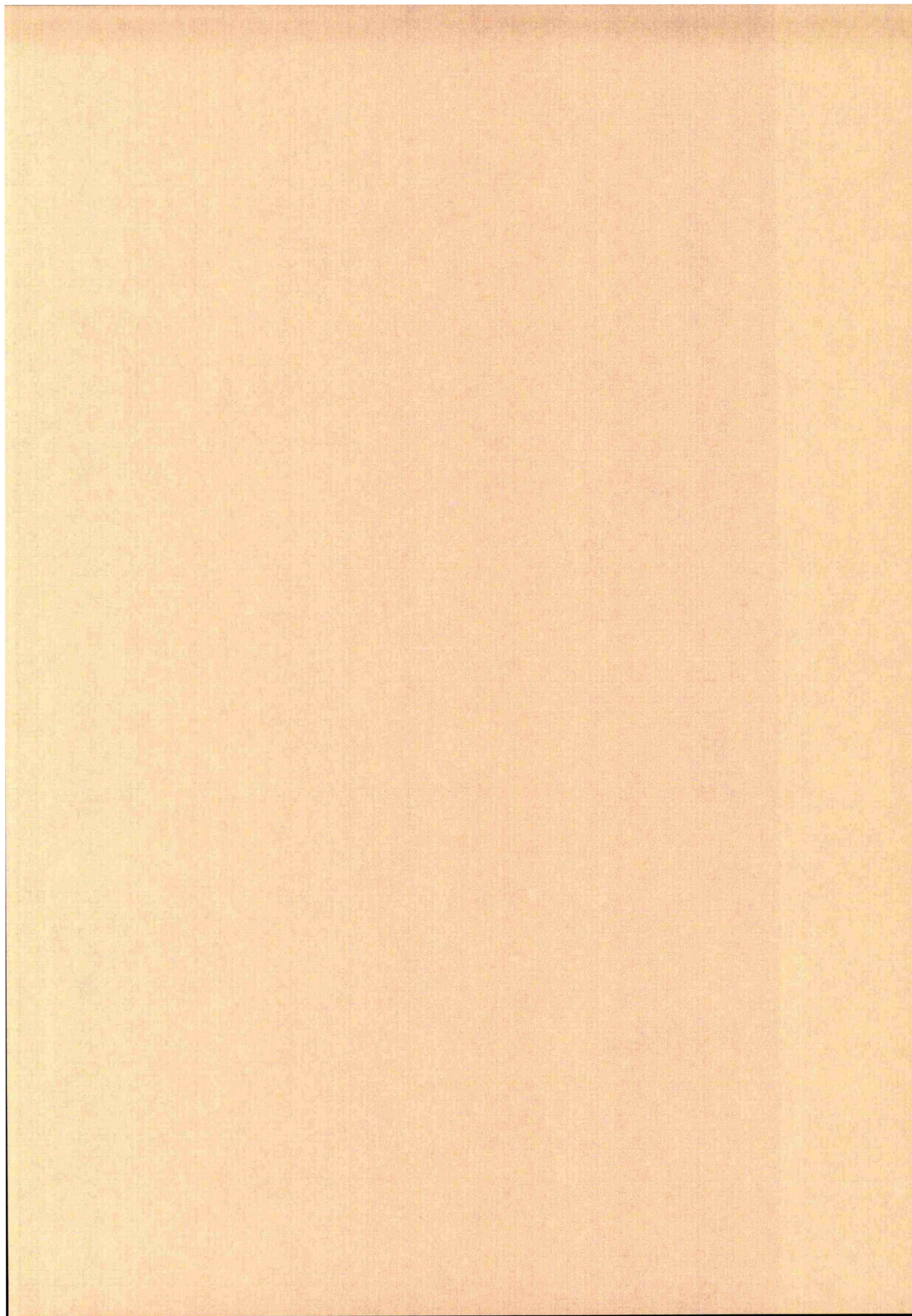


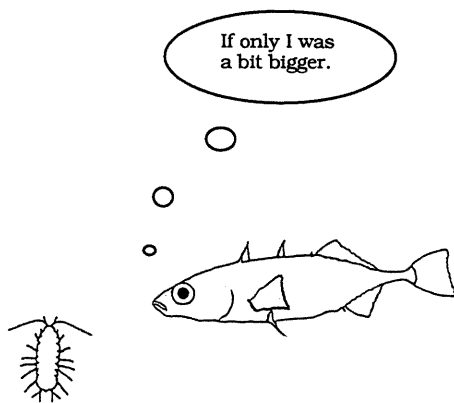
width of the fish were captured with the greatest success (see Figure 4) and had the lowest cost (Figure 9). Although prey <0.6 PW:MW had a low time cost, eating small prey is costly in terms of total time taken to reach an energy requirement (Chapter 2; Hart & Gill, 1992). Prey nearest to the critical 0.6 PW:MW ratio are the largest that can be eaten with little change in the time costs over the full range of stomach fullnesses. Therefore these prey give the best energy return per unit time cost.

Predators which eat prey whole are able to take relatively large prey, but when prey capture is not guaranteed it is more beneficial and less risky to choose prey which can be caught with certainty. For hungry predators this choice of certain prey capture is overridden by the necessity to acquire energy in some form as the potential energetic reward is much greater. Large prey have a greater profitability than the prey which are certain to be captured when fish approach low energy reserves. Stomach fullness levels of the predator dynamically change the effective profitability of each prey size encountered (present study; Croy & Hughes, 1991b; Gill & Hart, in press). For prey choice, the importance of this dynamic change in effective probability is greater as the prey become large in size compared to the size of the predator.

Diet choices are thus based on constraints imposed by the morphology of both predators and prey. In the long term these factors will alter through ontogeny (Galis, 1990). In the short term the amount of food in the stomach continually modifies potential prey profitability. Hence foraging decisions need to be continually upgraded (Kaiser *et al*, 1992b), which requires the predator to learn from encounters with prey in relation to its own morphological and physiological status (Hughes *et al*, 1992).

(This study is to be published in the journal Animal Behaviour).





CHAPTER 4

How the feeding energetics and prey size selection are altered by a small increase in the body size of the threespine stickleback.

ABSTRACT

Changes in the foraging behaviour due to variation in the body size of the fish were investigated. All fish sizes had a high probability of attacking prey whenever encountered. The probability of eating the prey, though, increased with the size of the fish, as the larger fish had larger jaws and a greater stomach capacity. Therefore, as fish increased in size there was an increase in the probability of successful prey capture. The frequency of spitting the prey increased for all fish sizes with prey size when the prey were eaten, but stayed constant when the prey were rejected. Being a larger fish meant that the frequency of spitting prey was lower, hence the prey were handled quicker. The level of satiation did not have an effect on the prey handling time contrary to other studies. The discrepancy appeared to be a result of the large prey sizes encountered by the fish. The physical size of the prey meant that the handling times were long regardless of the motivational level of the fish. The larger fish took in more energy and at a faster rate, however, the time to reach satiation was similar for all fish sizes. Thus, the advantage that large fish appear to have in the success of gaining large prey is negated by their greater metabolic requirement.

INTRODUCTION

It is a well documented fact that as predators become larger in size there is an increase in the amount of food ingested (Peters, 1983). This relationship is expected as larger predators tend to have a larger capacity for food intake. The studies summarised by Peters (1983) deal with a comparison of predators which differ in size by orders of magnitude. It has been noted though that with threespine stickleback similar in size, there are also differences in the numbers of prey that are eaten (see Chapter 2; Hart & Gill, 1992). This variation appears to be related to individual phenotypic differences of the fish, which consequently causes variation in the probability of successfully capturing a prey (see Chapter 3; Gill & Hart, in press). The variable results noted in these chapters were investigated further to study what consequences to food choice a small difference in body size has for a feeding stickleback.

As a fish increases in body length so the jaw width increases. This is important for fish prey choice, in terms of the prey width in relation to the jaw width of the fish, known as the Prey Width:Mouth Width (PW:MW) ratio (Chapter 3; Werner, 1974; Kislalioglu & Gibson, 1976; Moore & Moore, 1976; Wankowski, 1979; Gill & Hart, in press). Even though many prey sizes are within their feeding capabilities, the fish tend to prefer to eat prey which are about 0.6 of their jaw width (Scott, 1987; Prejs *et al.*, 1990). Prey which have a width >0.6 of the fish's jaw width are taken with decreasing success as the stomach fills (Chapter 3; Gill & Hart, in press). Here we see if this has any bearing on an individual fish's feeding performance when comparing similarly sized stickleback which may be found together socially.

Many fish species, including sticklebacks, choose to join with conspecifics forming a shoal (see Pitcher & Parrish, 1993). It has been shown that sticklebacks show a preference for being with others of a similar body size, known as size assortative shoaling (Ranta & Lindström, 1990). One function of shoaling is the increased probability of find food patches (Pitcher & Parrish, 1993). Once a group has found a patch of food then the competition between individual fish will be a critical factor in food acquisition. Fish which do assort by size will have slight morphological differences, which will translate into individual differences in competitive ability

(Milinski, 1986). The competitive ability of individuals within the shoal has been shown to increase with body size (Ranta & Lindström, 1993). So, being slightly larger than your shoaling partners may have benefits in terms of gaining the food. When a stickleback handles a prey, the time taken before ingestion decreases as body size increases (Chapter 3; Gill & Hart, in press).

As the number of prey ingested increases, then the need for the stickleback to acquire food will wane. It would therefore be expected that as hunger declines then the time taken to deal with prey would take longer. It has been shown for other fish species that handling time does increase with increasing amount of food in the stomach (Ware, 1972; Werner, 1974; Kislalioglu & Gibson, 1976). For stickleback feeding on *Asellus*, however, there was no increase in prey handling time with declining hunger (see Chapter 3; Gill & Hart, in press). It may be that the large prey sizes offered an obstacle to the stickleback, in terms of physical size and awkwardness. Therefore, the handling time to overcome natural prey with various appendages and protrusions may mask the effect that hunger has on the handling time.

How long a fish takes to handle and eat a prey puts a limit on the rate of energy intake. The shorter the prey handling time, the quicker the energy can be taken in. Ranta & Lindström (1990) showed that the rate of sticklebacks feeding on *Daphnia*, increased with an increase in the size of the fish. This increase in feeding rate with fish size, has to be balanced against the energetic needs of a fish which is bigger. The question of whether this increased rate of food intake has any benefit to the larger fish is addressed here.

METHODS

The majority of fish used throughout this thesis were chosen to be around 45mm in fork length. As the study progressed, variations were noticed in the results obtained when fish were offered large prey. This appeared to be caused by the phenotypic variates of the individual fish. Therefore, the variation around this size was used to choose the sizes for this study. I decided an acceptable error would be $\pm 1\text{mm}$. Thus, the fish size groups of approximately 42mm, 45mm and 48mm fork length, were chosen so as not to overlap in size. Eighteen fish were used with mean lengths ($\pm\text{S.E.}$) : $6 \times 41.7 \pm 0.22\text{mm}$, $6 \times 44.0 \pm 0.44$ and $6 \times 47.3 \pm 0.19\text{mm}$, obtained from the River Welland. It was shown in Chapter 3 that prey >0.6 of the fishes jaw width were taken with less success as the gut filled compared to those prey ≤ 0.6 of the jaw width. 6, 7 and 8mm *Asellus* were all >0.6 of the jaw width. It was expected that when encountering these large prey, the phenotypic differences of each fish would result in differential feeding success. The prey were presented individually to the fish in a sequence until 4 prey in a row were rejected (Table I). The prey presentations were filmed and analysed later where the behavioural response of each fish, the result of each prey presentation and the handling times were recorded.

Table I. The sequence of prey sizes (mm) offered to the fish. The prey were offered until the fish rejected four prey in a row. The schedule was repeated for two more sets of fish, giving six replicates for each fish size.

Fish	Fish Length	Day								
		1	2	3	4	5	6	7	8	9
1	42mm	6	8	7	8	7	6	7	6	8
2	45mm	7	6	8	6	8	7	8	7	6
3	48mm	8	7	6	7	6	8	6	8	7
4	42mm	6	8	7	8	7	6	7	6	8
5	45mm	7	6	8	6	8	7	8	7	6
6	48mm	8	7	6	7	6	8	6	8	7

The same experimental apparatus as shown in Figure 3 of chapter 1 was used, with the experiment being conducted during April -May 1991 and November 1991. The last set of fish were not studied until November due to the effects of the breeding season in the intervening period.

The results were analysed with the Statview and Cricketgraph packages on the Apple Macintosh computer and with reference to Siegel & Castellan (1988) and Sokal & Rohlf (1981).

RESULTS

Fish Morphometrics

A small increase in the body length of the fish lead to an increase in the jaw width and the body mass (Table II).

Table II. Morphometrics of the three fish size groups, mean values (\pm S.E.).

Measurement	Fish Length(mm)		
	42	45	48
Wet Weight(mg)	635.17 (\pm 35.89)	742.78 (\pm 45.99)	1013.80 (\pm 65.47)
Jaw Width(mm)	2.45 (\pm 0.12)	2.48 (\pm 0.16)	2.72 (\pm 0.12)

Number of Prey Eaten

Figure 1 shows the mean (\pm S.E.) number of each prey size eaten by the fish. A small increase in body length lead to a significant increase in the mean number of prey eaten (ANOVA: 6mm: $F=10.57$, d.f.=2, $p=0.0001$; 7mm: $F=13.13$, d.f.=2, $p=0.0001$; 8mm: $F=12.73$, d.f.=2, $p=0.0001$). Pairwise comparisons showed that the difference in number of prey eaten was between the 42mm and 48mm and the 45mm and 48mm fish (Scheffe's F-test $p<0.05$). There was no difference between the 42mm and 45mm fish (Scheffe's F-test $p>0.05$). All the fish sizes ate less prey as prey size increased.

Following a predatory attack by the fish, the proportion of prey which were rejected increased as fish size decreased and as prey became larger (see Table III). This means that the larger the fish the more likely the fish was at successfully gaining the food encountered.

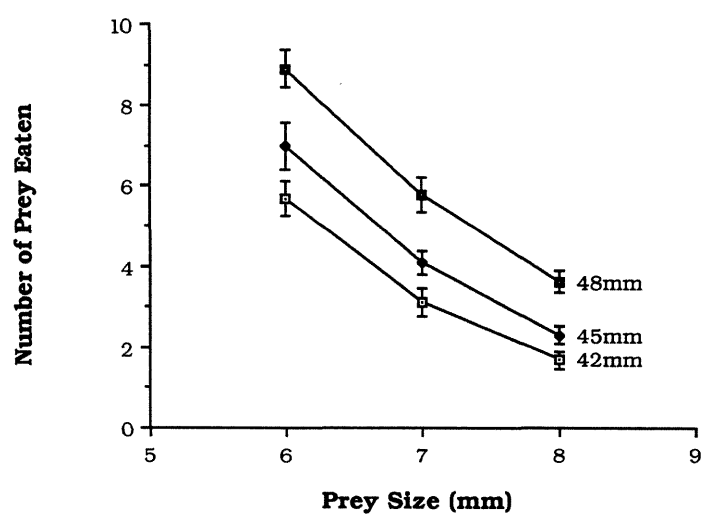


Figure 1. The mean (\pm S.E.) number of each prey size eaten by the three fish size groups.

Table III. The mean proportion (\pm S.E.) of prey eaten and rejected after attack, as a function of fish size and prey size.

Fish Size (mm)	Prey Size (mm)					
	6		7		8	
	Eat	Reject	Eat	Reject	Eat	Reject
42	0.67 (± 0.05)	0.33	0.43 (± 0.05)	0.57	0.25 (± 0.03)	0.75
45	0.72 (± 0.04)	0.28	0.59 (± 0.05)	0.41	0.37 (± 0.04)	0.63
48	0.88 (± 0.03)	0.12	0.67 (± 0.05)	0.33	0.59 (± 0.06)	0.41

The Probability of Success (P_{si})

As can be seen from Figure 2, the P_{si} was greatest when the stomach was empty. Thereafter, the P_{si} reduced with increased stomach fullness, this was also shown in chapter 3 (Gill & Hart, in press). This reduction was faster as fish size decreased and prey size increased.

The probability of attacking the prey (P_{att}) multiplied by the probability of eating the prey (P_{eat}) gives the probability of success (P_{si}) (see Chapter 3; Dunbrack & Dill, 1983; Gill & Hart, in press). Any changes in the P_{si} , shown in Figure 2, can be associated with either changes in the P_{att} or the P_{eat} . Table IV shows a statistical comparison between the fish, of the P_{att} and the P_{eat} , at the different levels of stomach fullness.

Figure 2. The probability of successfully capturing a prey as a function of stomach fullness of each of the three size groups of fish. '*' : the point after which the data comes from a decreasing sample size, as some fish were more successful than others at higher levels of stomach fullness. ■: 42mm; ▨: 45mm; ▩: 48mm fish.

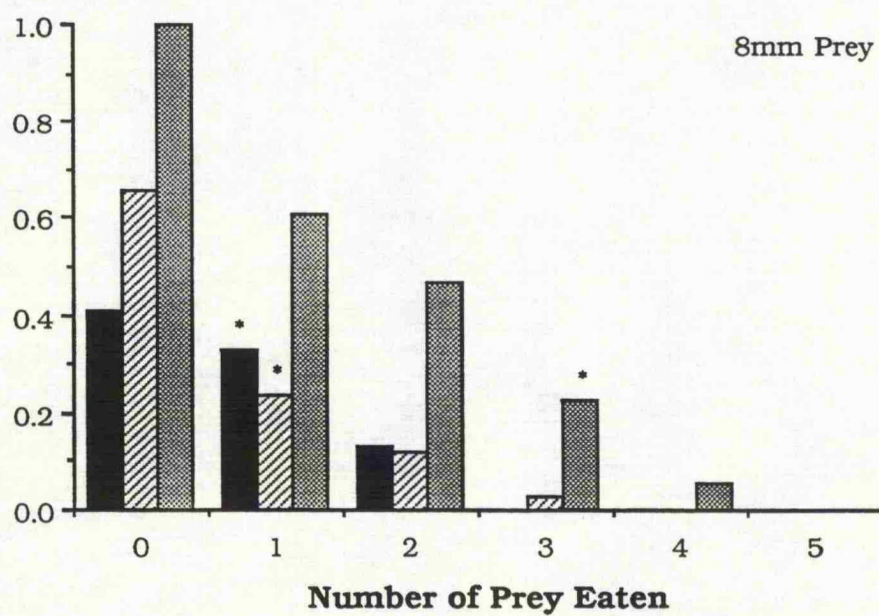
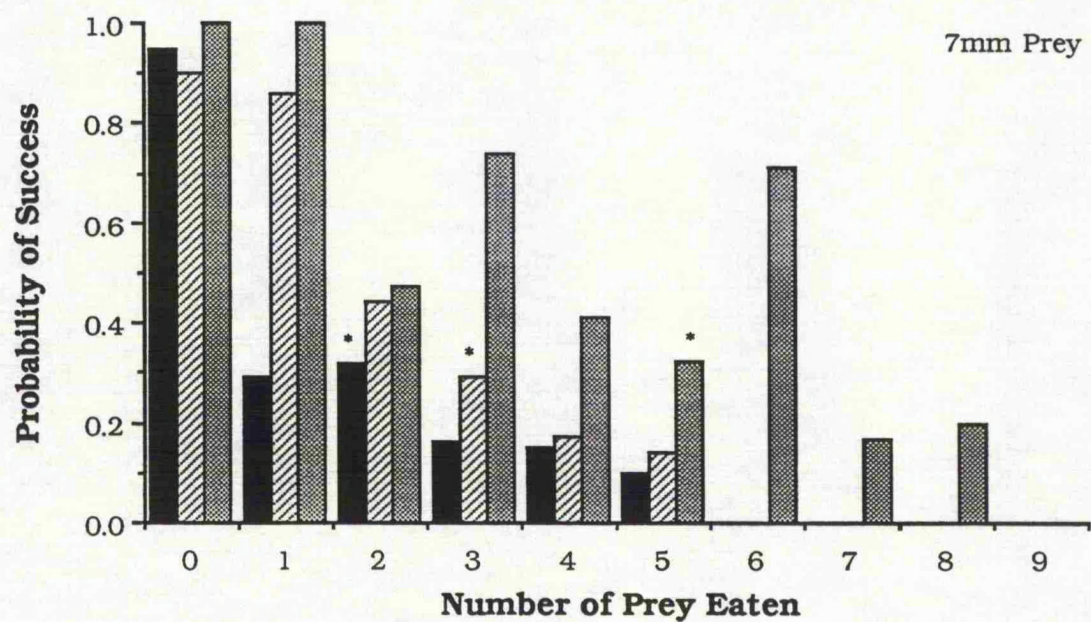
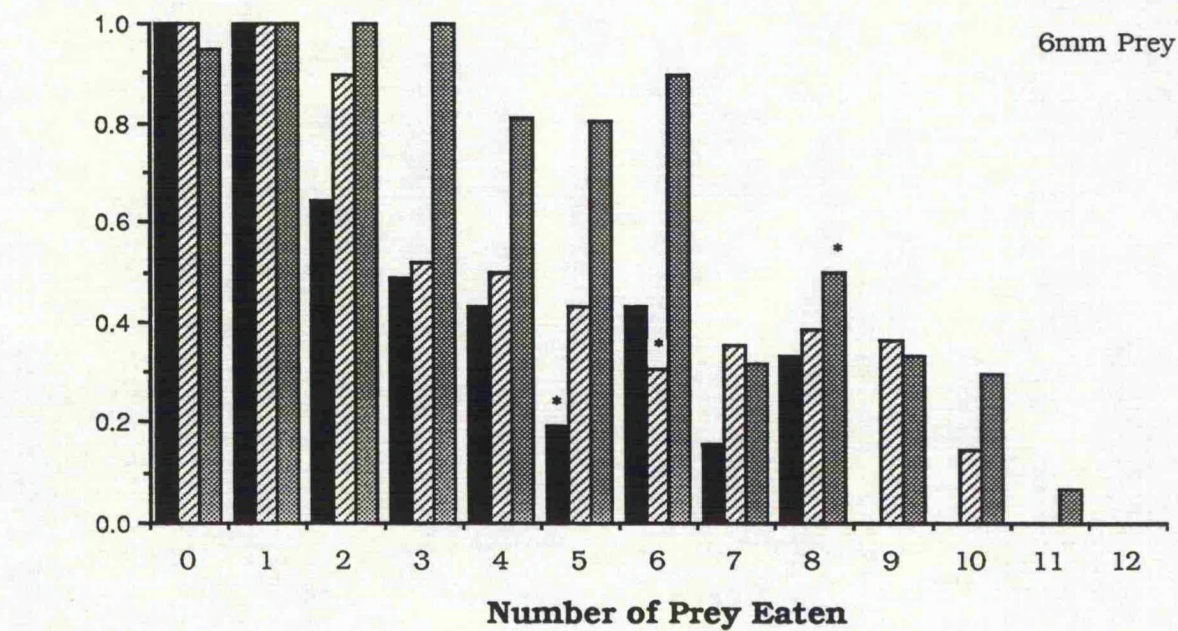


Table IV. A statistical analysis of how the Peat prey changed with fish size as stomach fullness increased. Fish sizes shown are those which had probabilities significantly greater or less than the other fish sizes ($p < 0.05^*$), as indicated ('†': less; '‡': greater). The differences were identified by breaking down the contingency table analysis (see Siegel & Castellan, 1988). '+': sample size too small, more than 20% of the expecteds were <5; '*': statistically significant result.

Number of prey eaten	Prob.	6mm			7mm			8mm		
		χ^2	p	sig. diff. fish size	χ^2	p	sig. diff. fish size	χ^2	p	sig. diff. fish size
0	Att Eat	1.88 0	0.39	None None	0 1.99	0.37	None None	0 18.33	0.0001* 0.0001*	None 48mm‡
1	Att Eat	0 0		None None	4.15 32.96	0.13 0.0001*	None 42mm†	0.22 13.08	0.90 0.0001*	None 48mm‡
2	Att Eat	4.74 6.84	0.09 0.03*	None 42mm†	1.64 3.07	0.44 0.22	None None	22.41 8.60	0.0001* 0.01*	45mm† 48mm‡
3	Att Eat	5.19 8.41	0.08 0.02*	None 48mm‡	9.40 22.91	0.01* 0.0001*	45mm† All	4.56 6.81	0.10 0.03*	None 48mm‡
4	Att Eat	2.81 13.43	0.25 0.001*	None 48mm‡	0.68 6.77	0.71 0.03*	None 48mm‡	+ +	+ +	+ +
5	Att Eat	4.65 15.70	0.10 0.0004*	None 42mm†	7.74 +	0.02* +	48mm‡ +			
6	Att Eat	7.66 7.86	0.02* 0.02*	48mm‡ 48mm‡	+ +	+ +	+ +			
7	Att Eat	1.70 1.02	0.43 0.60	None None	+ +	+ +	+ +			
8-12	Att Eat	+ +	+ +	+ +						

The 48mm fish were the most likely to successfully capture the prey encountered over all states of satiation due to a greater *Peat* the prey (Table IV). The difference in success was most prominent when the fish were presented with the largest prey (8mm). All the fish had a similar *Peat* the 6mm and 7mm prey when their stomach's were empty. However, with an increasing number of these prey eaten, the smaller fish had a lower *Peat* the prey compared to the large fish (Table IV).

Spitting Behaviour

In chapter 3 the frequency of spitting behaviour exhibited by the fish, increased with an increase in prey size and decreased as the fish became larger in size. It was therefore predicted in this study, that each fish size would spit prey more often if the prey size increased and that prey size would be a more influential factor as fish size decreased, due to the need for prey orientation (see Chapter 3; Gill & Hart, in press).

Prey size

Figure 3 shows how the spitting behaviour changed for each fish size handling each prey size. Looking at the effect of prey size on the number of spits used by each size group of fish when eating prey, the 42mm fish only showed significantly fewer spits of the 6mm prey than the 8mm prey (Table V). The 45mm fish spat the prey more often before consumption, as the prey size increased (Table V). The 48mm fish used a lower number of spits when eating 6mm prey compared to spitting the other two prey sizes, as shown in Table V.

The 42mm and 45mm fish used more spits when rejecting 8mm prey compared to spitting and rejecting the 6mm and 7mm prey (Table V). 48mm fish used the same number of spits when rejecting any of the prey sizes (Table V).

Figure 3. Frequency distributions showing the number of spits used by each fish size when eating and rejecting each prey size. ■: Eat; ■: Reject.

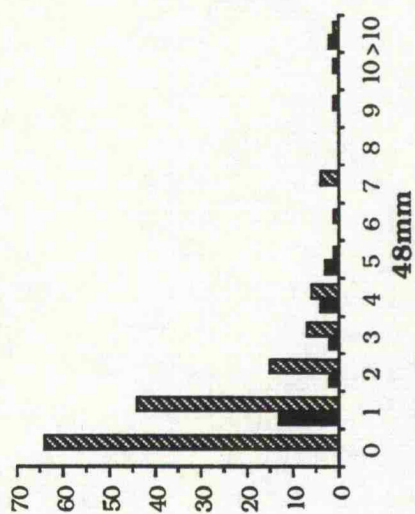
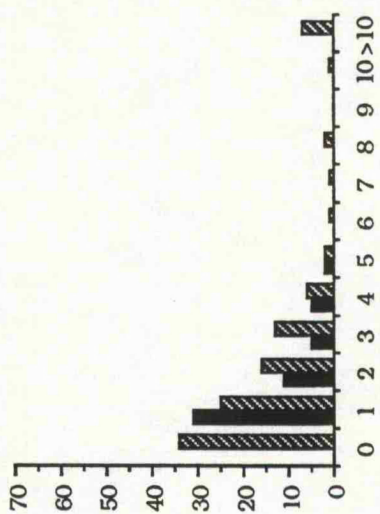
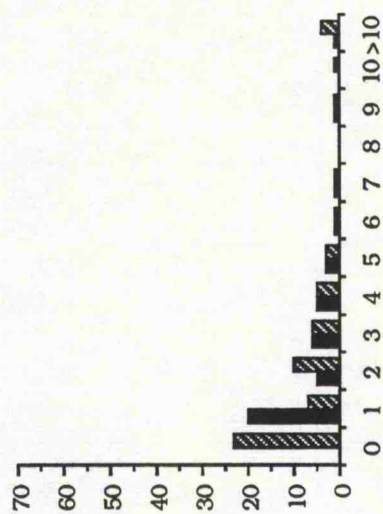
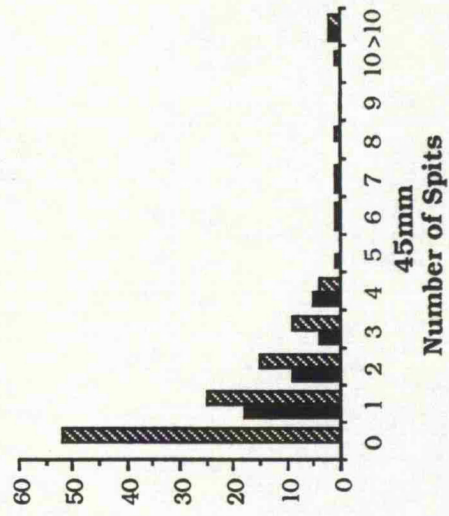
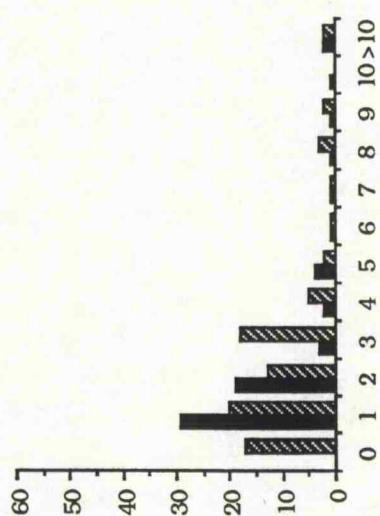
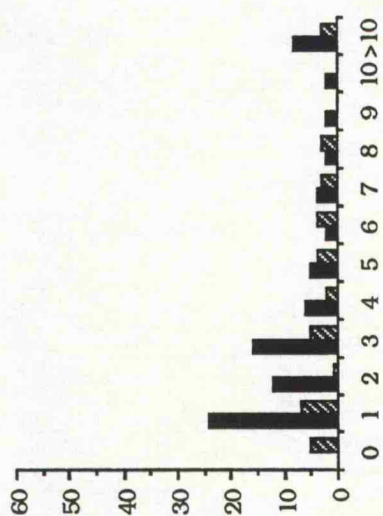
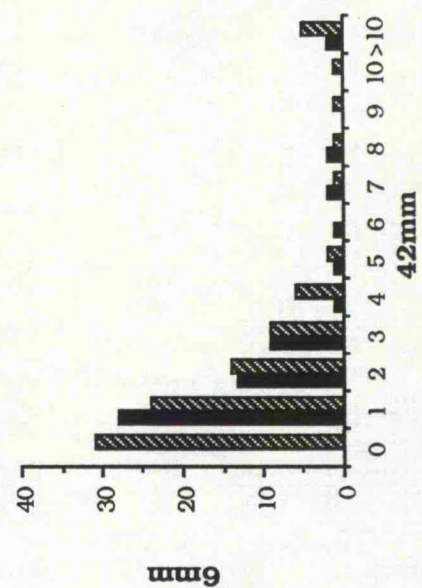
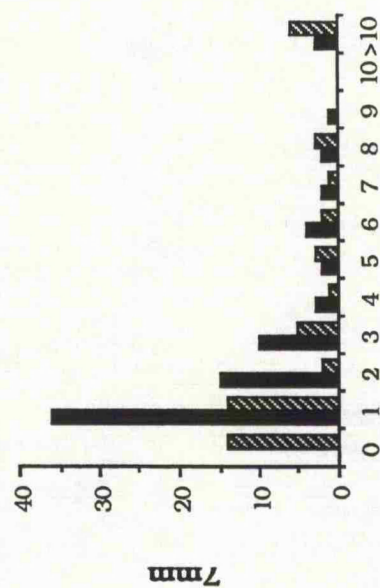
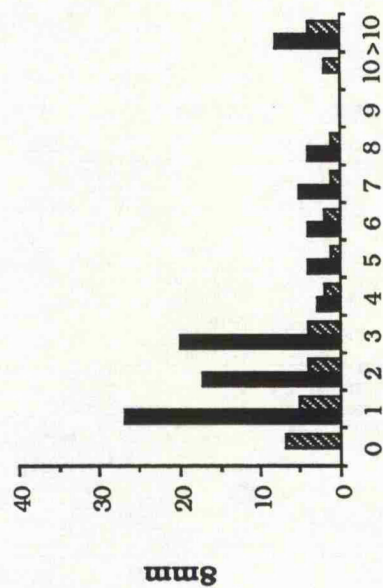


Table V. A comparison between prey sizes of the frequency of spitting behaviour used by each fish size when eating or rejecting prey. The table shows the results of a Mann-Whitney U-test (one-tailed). '*': statistically significant.

Fish Size(mm)	Prey sizes(mm) compared	Eating prey		Rejecting prey	
		z	p	z	p
42	6 v 8	-2.277	<0.025*	-2.597	<0.005*
	6 v 7	-1.086	>0.1	-0.391	>0.1
	7 v 8	-1.103	>0.1	-2.281	<0.025*
45	6 v 8	-4.933	<0.000005*	-2.239	<0.01*
	6 v 7	-4.099	<0.000005*	-0.319	>0.1
	7 v 8	-2.647	<0.005*	-2.913	<0.005*
48	6 v 8	-2.384	<0.01*	-0.031	>0.1
	6 v 7	-2.837	<0.005*	-1.605	>0.05
	7 v 8	-0.259	>0.1	-1.299	>0.05

Fish size

It was hypothesised that the larger fish would be able to eat prey with fewer spits than the fish smaller than themselves. Figure 3 shows the number of spits used had a frequency distribution which became wider as the fish got smaller, hence smaller fish were more likely to spit the prey and spit more often.

When eating the 6mm prey, the 45mm and 48mm fish used a similar number of spits, however, the 42mm fish spat the 6mm prey more often (Table VI). Eating the 7mm prey lead to no differences in the amount of spitting by each fish size (Table VI). 8mm prey were eaten with less spits needed by the 48mm fish as compared to the 42mm and 45mm fish, these two smaller fish sizes used a similar number of spits when eating 8mm prey (Table VI).

When rejecting the prey there was only a difference in the number of spits used when 8mm prey were encountered, the 48mm fish rejected 8mm prey with less spitting

than the other two fish size groups (Table VI).

Table VI. A comparison between fish sizes of the frequency of spitting used when eating or rejecting each prey size. The table shows the results of a Mann-Whitney U-test (one-tailed). '*': statistically significant.

Prey Size(mm)	Fish sizes(mm) compared	Eating prey		Rejecting prey	
		z	p	z	p
6	42 v 45	-2.206	<0.025*	-0.417	>0.1
	42 v 48	-2.352	<0.01*	-0.434	>0.1
	45 v 48	-0.54	>0.1	-0.161	>0.1
7	42 v 45	-0.207	>0.1	-0.336	>0.1
	42 v 48	-0.832	>0.1	-1.606	>0.05
	45 v 48	-1.469	>0.05	-1.283	>0.05
8	42 v 45	-0.764	>0.1	-0.578	>0.1
	42 v 48	-1.676	<0.05*	-1.646	<0.05*
	45 v 48	-2.792	<0.005*	-2.004	<0.025*

Handling Time

Working under the hypothesis that the larger the fish the shorter the prey handling times, it was found that the 42mm and 45mm fish took a similar time to handle the prey, regardless of prey size (Table VII). The 48mm fish, however, were able to handle the 6mm and 7mm prey in a quicker time than the other two fish size groups (Table VII).

Table VII. A comparison of the prey handling times of the fish. The table shows the results of a Mann-Whitney U-test (one-tailed). '*': statistically significant.

Fish sizes (mm) compared	Statistic	Prey Size (mm)		
		6	7	8
42 v 45	z	-1.515	-0.235	-0.224
	p	>0.05	>0.1	>0.1
42 v 48	z	-2.861	-1.665	-1.106
	p	<0.005*	<0.05*	>0.1
45 v 48	z	-1.954	-2.154	-1.099
	p	<0.025*	<0.025*	>0.1

The time taken by a fish to handle and eat a prey has been shown to increase with increasing stomach content for other fish species (see Introduction). However in an earlier study (Chapter 3; Gill & Hart, in press), no change was found in the handling times with increasing satiation level. As the present experiment followed the response of the fish to every prey encountered, it was decided to investigate this discrepancy in handling time further.

Testing the full data set statistically gave results similar to the earlier study (Chapter 3; Gill & Hart, in press). There was no significant effect of hunger on the prey handling times of the fish ($p > 0.1$ for all comparisons), except for 45mm fish feeding on the 6mm prey (Kruskal Wallis: $H = 17.647$, d.f.=9, $p < 0.05$).

The prey presentation order was standardised for all the sequences by dividing the place in the sequence (n) by the total number of prey eaten for the sequence (N_i), (Werner, 1974). The handling time of the prey under selection was then taken and divided by the handling time of the first prey eaten (H_n/H_1). This is because if the theory is to be supported, then the handling time of the first prey should be the shortest and the ratio (H_n/H_1) should increase and become > 1 when comparing all other handling times with

the first. Werner (1974) used the mean of the first two handling times, this was inappropriate in this study due to the small total number of prey that were eaten.

Figure 4 shows the results of the experiment with handling times and the effect of stomach fullness. There was greater variability in handling times as stomach content increased. The majority of the plotted points on the graph are close to the H_N/H_1 ratio of 1. This means that a lot of the handling times did not change with hunger, hence the best fit regression line shows a poor relationship between increasing handling time and stomach content. It should be noted that a large proportion of the data is actual below the ratio of 1, these handling times for partially sated fish were less than the handling time to eat the first prey. This interesting point is attended to in the discussion.

Energy Intake

The mean (\pm S.E.) total intake of energy (Joules) increased as fish size increased (Figure 5). A significant reduction in the total energy intake of the 42mm fish was found, as prey size increased ($H=8.004$, d.f.=2, $p<0.02$). There was no apparent reduction in overall energy consumed by the 45mm and the 48mm fish (45mm: $H=5.626$, d.f.=2, $p>0.05$; 48mm: $H=2.15$, d.f.=2, $p>0.30$).

The temporal energy intake and the cumulative time needed for this intake are shown in Figure 6. Generally, the larger the fish the greater was the rate of energy intake. The slightly bigger fish took in energy more quickly than smaller fish, resulting in the slope of the curve being steeper. The three fish sizes had a similar energy intake to begin with but the rate decreased as the gut filled. This difference was demonstrated when comparing the rate of energy intake by the 42mm and the 48mm fish (see Table VIII). When encountering the 6mm and the 7mm prey, the 42mm and 45mm fish had similar energy intake rates and the 45mm fish took energy in slower than the 48mm fish. The 45mm and the 48mm fish encountering the 8mm prey did not differ in energy intake rate, but the samples sizes were small.

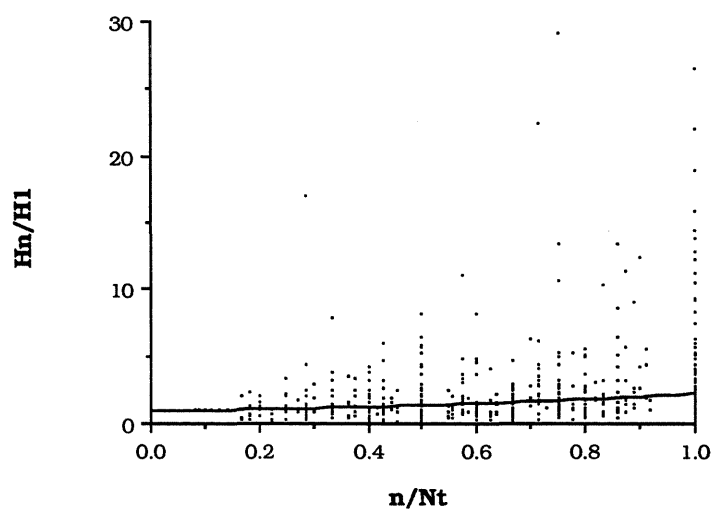


Figure 4. The effect of stomach fullness on the prey handling time of the fish. Stomach fullness of the fish was standardised by dividing the numerical position in the sequence of each prey eaten (n) by the total number of prey eaten in that sequence (N). The handling time was standardised by dividing the handling time of the prey under selection (H_n) by the handling time of the first prey eaten (H_1). The equation of the curve is $y=0.804 \cdot 10^{(0.422x)}$, $R^2=0.103$.

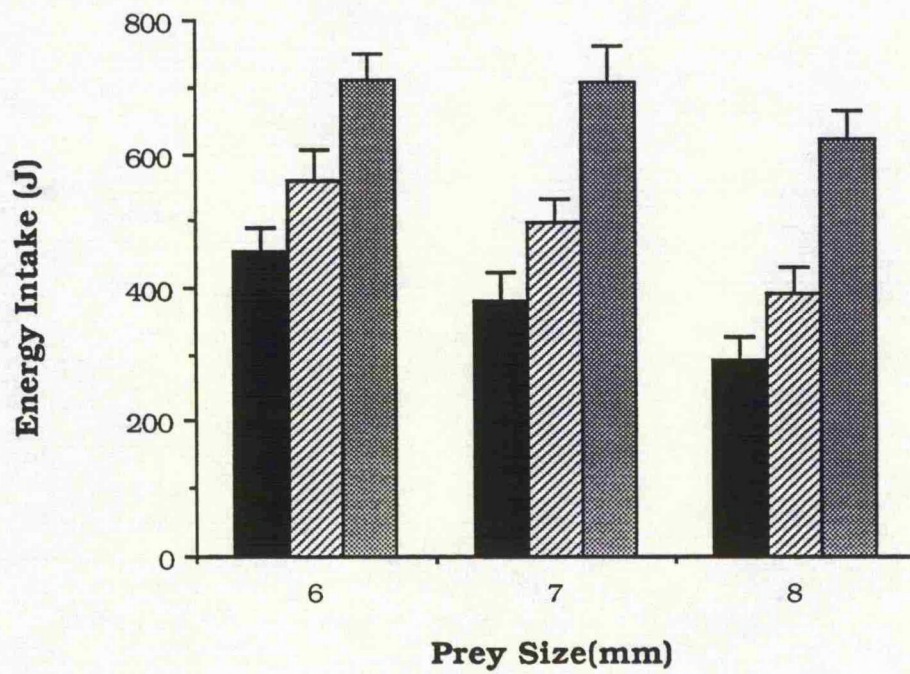


Figure 5. The mean(\pm S.E.) energy intake (Joules) of each fish size feeding to satiation on each prey size. ■ : 42mm; ▨ : 45mm; ▩ : 48mm fish.

Figure 6. The rate of energy intake by the fish. The dotted lines from the y-axis show the mean energetic intake of each fish size. Where the dotted line crosses the x-axis, indicates the length of time it took the fish to reach their respective energy requirements.

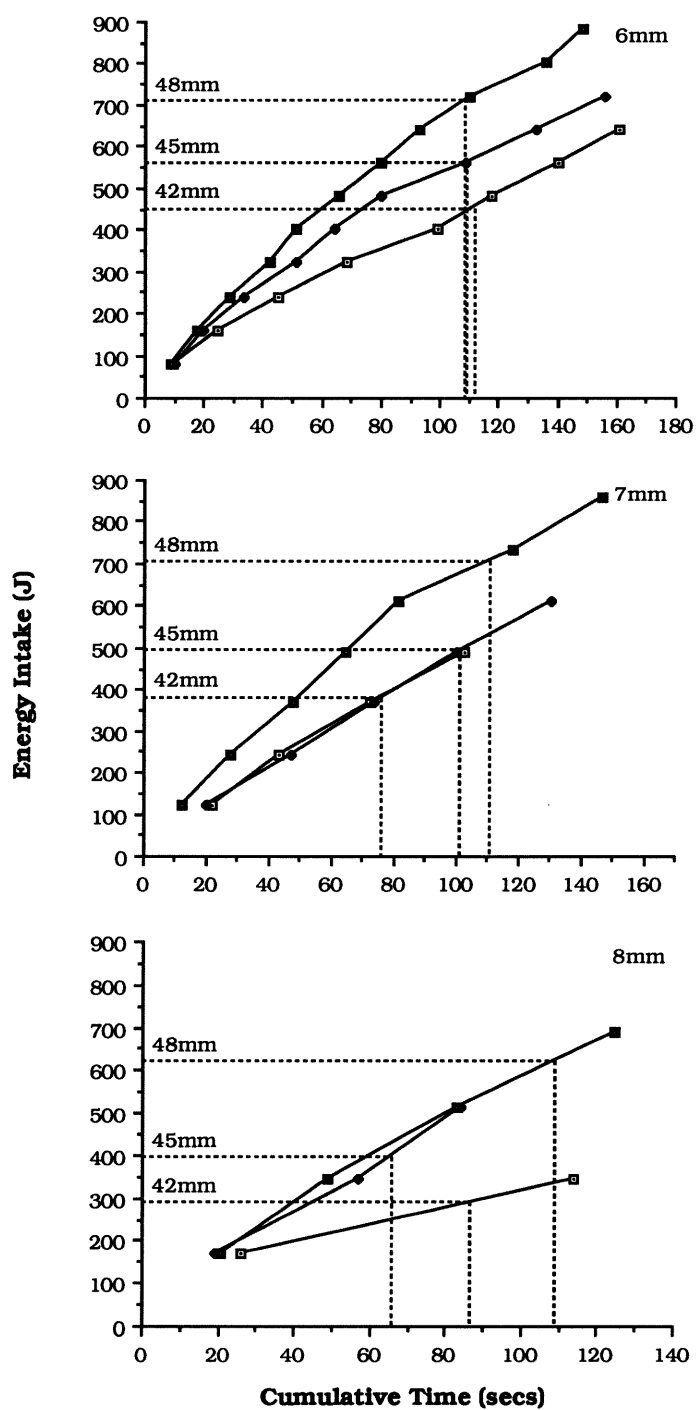


Table VIII. A statistical comparison of the energy intake rates of the fish size groups using the Kolmogorov Smirnov test. A significant result indicates that the larger of the two fish sizes had a faster rate of energy intake. The values in the table show the test statistic of $m.n.D_{m,n}$ where m =the size of the first sample; n =the size of the second sample; $D_{m,n}$ =the maximum difference between the two cumulative frequency distributions of the two samples. '*' : statistically significant value; '-' : too few sample intervals.

Fish Pair	Prey Size (mm)		
	6	7	8
42mmv48mm	60.98 $p \leq 0.025^*$	28.01 $p \leq 0.05^*$	-
42mmv45mm	30.02 $p > 0.1$	6 $p > 0.1$	-
45mmv48mm	37.03 $p > 0.1$	35 $p \leq 0.05^*$	5 $p > 0.1$

When feeding on the 6mm prey all the fish took a similar amount of time to reach the mean satiation level (Figure 6). This was shown by the broken lines, representing the mean energy intake, extrapolated to the time axis. So although the larger fish took in energy quicker, the amount of energy needed to reach satiation was greater, as shown in Figure 5. In Figure 6, the points plotted above the mean energy intake value show that some individual fish took in more energy than the average.

As noted in Figure 5, there was no significant reduction in the total energy intake of the 48mm fish. This is reflected in Figure 6 by the amount of time taken to reach the mean satiation level being similar, around 110 seconds, regardless of prey size. For the 42mm and 45mm fish, the amount of cumulative time to reach stomach fullness

reduced (see Figure 6) as the mean amount of energy taken in decreased (see Figure 5), although this was only statistically significant for the 42mm fish.

DISCUSSION

Prey Selection

A small increase in the body length of the fish lead to an increase in jaw width and body weight. There are two effects which can be predicted from these morphological increases of the fish. First, an increase in jaw width would suggest a greater facility for dealing with prey, thus leading to greater success with a given prey size. This would also allow a wider range of prey sizes to be included in the diet of the fish. Second, a larger body weight and jaw size of the fish is only gained at the cost of greater metabolic need due to the standard metabolic rate increasing with body size (Peters, 1983; Schmidt-Neilsen, 1990). There would therefore be an expected increase in the amount of food consumed to satisfy the requirements of the fish. Larger stickleback have been found to eat a greater amount of food per day (Chapter 3; Cole 1978; Gill & Hart, in press). These two studies dealt with substantial differences in stickleback size. In the study discussed here, there was also an increase in the number of prey eaten, with a small increase in fish size. The 48mm fish were able to eat more of all the available prey compared to the two smaller fish size groups. The number of prey eaten decreased with an increase in prey size, a relationship expected if we refer to chapter 3 (Gill & Hart, in press). Stomach capacity is a major constraining factor.

Prey rejection was more probable with an increase in prey size and a decrease in fish size. This increase in the likelihood of prey rejection was expected because as fish size decreases the amount of food needed to satisfy energetic requirements also reduces (see Peters, 1983).

If a feeding fish has reached its energy requirement level, then a reduction in the probability of attacking (P_{att}) and the probability of eating (P_{eat}) prey would be expected (see Chapter 3; Ivlev, 1961; Walkey & Meakins, 1970; Gill & Hart, in press). The P_{att} , however, did not differ between fish sizes, indicating that the fish were still motivated to feed. The probability of success (P_{si}) showed that an increase in fish size lead to greater success of prey capture at all levels of stomach fullness. The difference between the success of the fish size groups became more prominent as prey size

increased. The major factor causing this change in P_{si} was the fish size groups having different probabilities of eating (P_{eat}) the prey. The increased P_{eat} as fish size increased can be related to the larger jaw sizes of the bigger fish, which would have allowed easier prey ingestion. The smaller fish did attack the prey but the combined constraints of their jaw size and probably also stomach capacity reduced the P_{eat} , which in turn devalued the P_{si} .

Spitting Behaviour

The constraint of fish jaw size was aptly demonstrated by the frequency of spitting behaviour utilised by the fish. All the fish were more likely to spit the prey with an increase in prey size. Suggesting that as prey increase in size so they become more awkward to handle and ingest, thus the need for prey orientation becomes greater (see Chapter 3; Gill & Hart, in press).

We can consider minimising the spitting behaviour as an advantage to the fish, as it means that the prey can be dealt with quicker so reducing the time costs to the fish, regardless of whether the prey is actually eaten or rejected. When comparing the spitting behaviour of the three fish sizes, the 42mm fish were at a disadvantage when eating the 6mm prey, as they needed to use more spitting behaviour than the two larger fish size groups. The 48mm fish were able to deal with the 8mm prey with less spitting than the other fish, a factor which can be partly attributed to the larger jaws.

The fact that the 42mm and 45mm fish used more spitting behaviour than the 48mm fish did, only when they handled the largest prey (8mm), may be reflecting the food requirements of these fish sizes. The 42mm and 45mm fish may have been motivated to obtain food, so the 8mm prey were attacked and handled, however, these fish probably did not have enough space in the stomach to fit in these large prey. Both the 42mm and 45mm fish size groups may have been caught in a dilemma of wanting and needing to eat the prey but not having the required stomach capacity. If smaller prey had been available, then it would be predicted that these prey would have been consumed to fill the gap in the gut.

Handling Time

Handling time is regarded as a basic foraging cost. For small fish the handling cost is relatively greater than for large fish when handling and eating the 6mm and 7mm prey. Times to handle and eat the 8mm prey were found to be similar for all the fish. There was, therefore, no advantage to the 48mm fish when handling and eating 8mm prey in terms of the handling costs. The consequence of small fish having longer prey handling times was that the rate of intake of prey was lower than for the fish which were larger. The handling times of the 42mm and the 45mm fish were similar regardless of prey size. This may be expected as the jaw widths of these fish were very close in size (see Table II).

There was no relationship found between the amount of food eaten by the fish and the prey handling time, which is in contrast to other studies (Werner, 1974; Kislalioglu & Gibson, 1976; Croy & Hughes, 1991b). This discrepancy may be a function of the initial motivation of the fish and the morphological properties of the prey. A fish with an empty stomach, regarded as being maximally motivated, was seen to handle and attempt to ingest any prey as quickly as possible. As prey size increases handling time is known to increase (this study, Chapter 3, Werner, 1974; Hoyle & Keast, 1986; Gill & Hart, in press), the P_{si} decreases (this study, Chapter 3; Gill & Hart, in press) and the fish have an increasing need to orientate the prey (Chapter 3; Gill & Hart, in press). These three factors all counter the attempts of the fish to eat prey as quickly as possible. Additionally, the *Asellus* prey which were used have major protruding appendages which hamper quick ingestion by the fish. The fish often appeared to get large prey stuck in their mouth (pers. obs.). Prey morphology is known to have a large effect on prey handling by a fish predator (Hoyle & Keast, 1986). Therefore, the high motivation to obtain energy quickly is actually counter productive to the fish.

In the earlier studies of handling time, the prey were either small in comparison to the fish predator or the prey had a morphology which did not present a great barrier to ingestion by the fish. The results in Figure 4, show a greater variation in prey handling times by the fish as stomach content increased, so there may be an underlying trend in the data which matches the findings in other studies but it is masked by the combined effects of the fishes motivation to acquire food and the prey morphology.

Prey defence may also play a role. The principal result is that as the motivation of the fish decreases the fish are less impulsive, which allows them time to assess the properties of the prey and whether or not to choose to eat the prey.

Energy Intake

With the fish feeding on one prey size at a time, the total energy intake of the 45mm and 48mm fish was constant. The 42mm fish, however, had a significantly decreased energy intake as the prey got larger. In chapter 2 we saw that the energy requirement for fish approximately 45mm in length was estimated at 450 Joules (Hart & Gill, 1992). The results gained here show that the energy requirement rises considerably for a slight increase in fish body size.

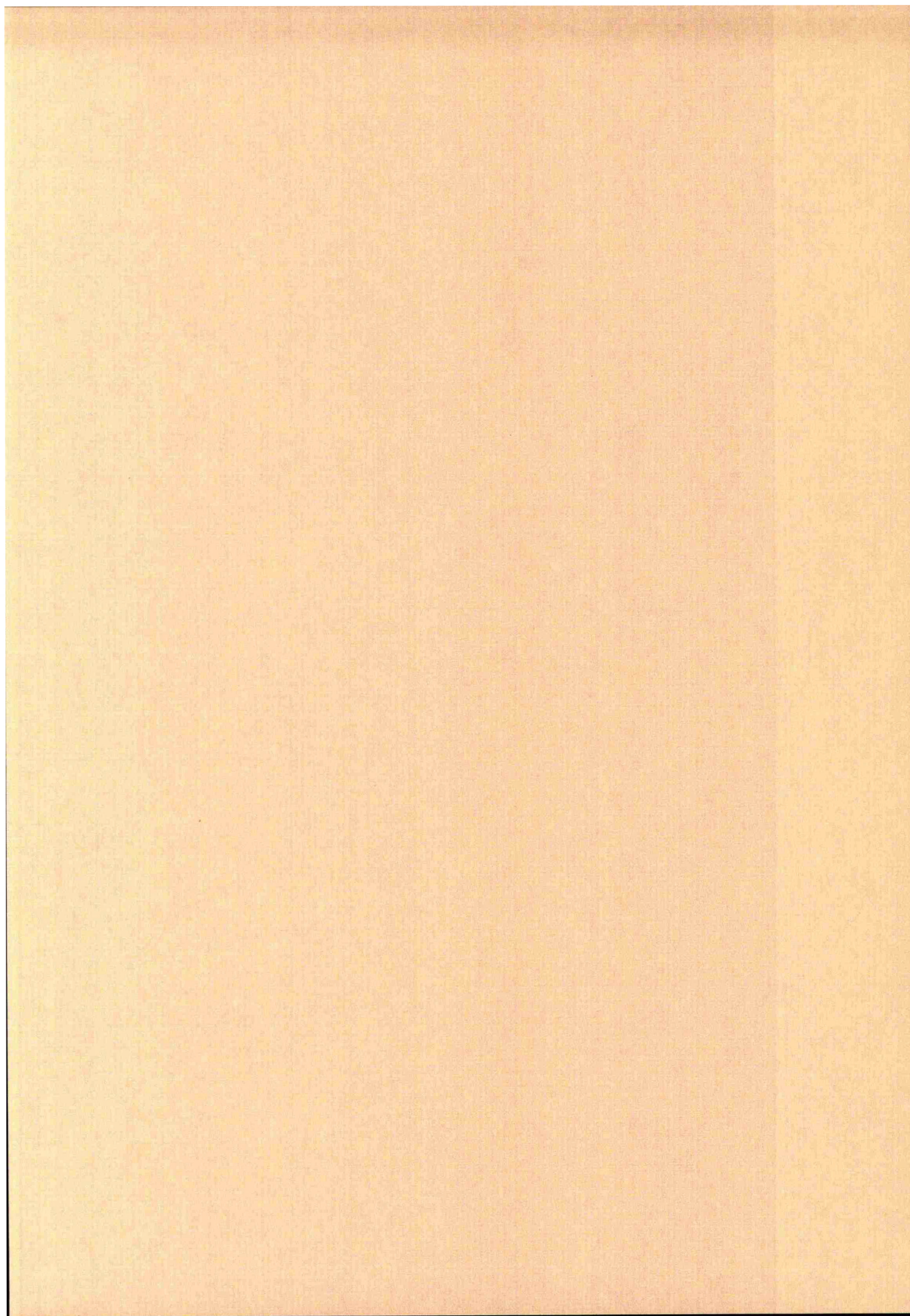
Prey with widths close to 0.6 of the fish jaw width are preferred as they give the best cost/benefit trade-off (Chapter 3; Scott, 1988; Prejs *et al*, 1990; Gill & Hart, in press). In this study the 6mm prey were the nearest available prey to this ratio, thus the amount of 6mm prey eaten was most likely to give a good estimate of the energy requirement of each of the fish sizes. Figure 6 shows that the time taken to ingest the estimated mean energy requirement was similar for each fish size. In essence the larger fish had to be able to eat the prey quicker than the other fish in order to reach the increased energy requirement in the same time. This was found to be true in the handling time analysis of this experiment. Although being a larger fish means that the success with a large prey is greater, it could be a reflection of the greater energetic needs of the larger fish. These fish may be motivated for longer than smaller fish, to acquire the food. Here we find another trade-off, fish becoming larger in size are able to handle prey quicker and easier, due to larger jaws, but the standard metabolic rate will rise with an increase in fish size, due to the rate of respiration being a function of the body weight of the stickleback (Wootton, 1984). The larger fish need to consume more food to fuel this increased need.

The increase in prey size lead to the smaller fish having a reduced overall energy intake. This may be attributed to two constraints, 1- the morphological constraint of jaw size and 2- the physical capacity of the stomach of the fish. The former leads to a reduction in the probability of successful capture of the prey. The latter may not be

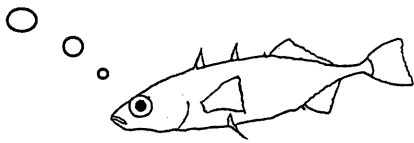
great enough for the required number of prey, as would be estimated from the energy contour analysis in chapter 2 (Figure 8 of Chapter 2; Hart & Gill, 1992). Fish which have this stomach capacity constraint would be better to eat smaller prey as the stomach should be able to accept the required number to satisfy needs. Eating smaller prey also means that the capture success will be greater (Chapter 3; Gill & Hart, in press) due to the mouth constraint being reduced. There is however, a constraint on how small the prey can become. The energy contour analysis (Chapter 2; Hart & Gill, 1992) with 3mm and 4mm *Asellus*, showed that a fish feeding only on these small prey could not eat enough of them to reach the criterion in one feeding period. The fish in this case would need to feed for a longer time to obtain the daily requirement. Also as prey become smaller they become more difficult for the fish to detect (Werner & Hall, 1974; Eggers, 1982; Hairston *et al.*, 1982; Mittlebach, 1983).

These findings taken together would suggest that the only diet combinations which would satisfy the energy requirements of a stickleback, would be a narrow diet of preferred prey, around the 0.6 PW:MW ratio, or a wide prey size diet which would encompass the less desirable prey also.

The results of this study can be considered in the context of social behaviour (see Pitcher & Parrish, 1993). Being slightly smaller than conspecifics in the group means that individual successful acquisition of large prey is reduced and handling costs increase, but the overall food requirement is lower. Larger fish have to take in more food and so spend a similar total time feeding as their smaller conspecifics do. This gives evidence for Persson's (1985) contention that larger animals tend not to be competitively superior in terms of their increased capacity to feed. The time costs of a foraging fish to reach an energetic requirement may be the same regardless of body size, as shown with the sticklebacks here. Whether the energy expenditure in handling prey by the different sized fish is the same is not known. The possible advantage in terms of food acquisition to be gained from being larger in a social group may be linked to the competitive ability of the individual fish. Being a good competitor will give a fish a greater chance of monopolizing resources and therefore increase feeding success, this however is a function of resource distribution in time (Grant & Kramer, 1992).



I'll need a turbo fitted
to beat this fella!



CHAPTER 5

Changes in the foraging behaviour of the threespine stickleback due to intraspecific competition.

ABSTRACT

Competition between pairs of sticklebacks was studied to investigate the effects of fish size, prey size and the level of stomach fullness on the behaviour and competitive ability of the fish when prey were encountered sequentially. All of the fish attacked the prey with high probability. The first fish to handle the 5mm prey was likely to eat it. The likelihood was less when fish encountered the 8mm prey. Each fish attempted to capture the 8mm prey more than if it was a 5mm prey. This was due to the larger prey being visible longer as the fish had to manipulate them before swallowing. Even when a prey was out of sight the unsuccessful competitor stayed near to the other fish for about 7 seconds. This time increased if the prey was seen in the mouth of the successful fish. Prey handling times were no different to those found previously for solitary fish handling the same prey sizes. The probability of eating any prey was dependent on the phenotypic properties of the individual fish, and dependent on stomach fullness when the prey was an 8mm. Competitive ability was a function of the fishes reaction time, the ability to reach the prey first and the capability of the jaw apparatus to ingest the prey. A fish which had these properties reached its daily energy requirement regardless of the prey size encountered.

INTRODUCTION

Competition for food can be defined as any interference between individuals which causes a reduction in foraging success to one or the other. The term 'scramble competition' has been used to describe individuals that simultaneously encounter a single prey item and compete in a non-aggressive manner for the resource (Milinski & Parker, 1991). In this case the prey is a discrete package of energy, which means only the fastest reacting individual can successfully obtain it at the expense of the other competitors. The successful individual is said to have a greater competitive ability.

For a fish, this competitive ability requires quick reaction times, fast swimming capability and a high degree of capture success. Milinski (1982) indicated that, for threespine sticklebacks (*Gasterosteus aculeatus*) feeding on *Daphnia*, the fastest swimmer and hence the first to the prey had the greatest competitive ability, as they always ate the prey. The important point to note when considering the capture success is the relative size between the prey and the predator. In Milinski's experiment the prey were relatively small in comparison to the jaw size of the fish, so any fish which reached the prey first consumed it. Planktivorous fish have a capture success of approximately 100% for most prey sizes handled (Griffiths, 1980). Solitary stickleback, however, feeding on relatively large prey (*Asellus aquaticus*) have a capture success which is dependent on the morphological relationship between the prey and the fish jaws and the motivational state of the fish (Chapter 3; Gill & Hart, in press). So the competitive ability may change with prey size for a fish with a diet consisting of a wide range of prey. Here it is shown what effect the motivation to acquire food has on the competitive interactions between pairs of fish in terms of foraging success, set within the morphological constraints of each individual fish.

In a competitive interaction, the fish which is unsuccessful incurs a cost in terms of wasted time and energy. Chapter 3 (Gill & Hart, in press) showed that a single fish, regardless of size, decided whether or not to eat a prey in the first few seconds of handling it. The decision to reject the prey became increasingly more likely as prey size increased and motivation decreased. Depending on the motivation of the fish handling the prey, a competitor could have the opportunity to intercept a rejected prey. An

interesting question is, how much time will the unsuccessful competitor commit to waiting for a prey that might be rejected?

METHODS

Six sticklebacks, with a mean fork length of 45.8 ± 0.4 (S.E.), were obtained from the River Welland. The experimental apparatus used is described in chapter 1, Figure 3.

Asellus prey of the required size, measured to the nearest millimetre, and number were loaded into separate tubes fixed to a carousel above the aquarium. One prey at a time was entered into the feeding arena containing two fish. The prey was either eaten by one fish or rejected by both. Rejected prey sank into a funnel in the arena floor and were collected in a net under the aquarium. In this way, the fish were exposed to only one prey at a time.

Each individual fish was identified by unique characteristics such as fin shape, spine size and number, head and eye size and relative colouring. The fish were then assigned a home tank which kept the fish separated and away from the feeding arena when not being experimented on. During the trials, the pairs of fish were fed once a day. If, during the trials, a fish did not obtain the required daily energy intake of about 450 Joules (see Chapter 2; Hart & Gill, 1992), extra prey were given in the home tank ensuring each fish was at a similar hunger level by the next day.

Acceptance and rejection of prey were recorded as they happened, onto data sheets and the feeding sessions were also filmed with a S-VHS camera. This allowed the feeding behaviour of each fish to be analysed precisely for each prey encountered.

Each single prey which the fish encountered was from sequences of 5mm and 8mm *Asellus* in a ratio of either 1:3, 1:1 or 3:1 (5mm:8mm). Each fish was paired with every other fish and each pair encountered the sequences shown in Table I.

Table I. The three prey size sequences offered to all possible pairings of six fish. The ratio of 5mm : 8mm prey encountered for each sequence is indicated.

Sequence	Prey Number											
	1	2	3	4	5	6	7	8	9	10	11	12
A (1:3)	8	5	8	8	8	5	8	8	8	5	8	8
B (1:1)	8	5	8	5	8	5	8	5	8	5	8	5
C (3:1)	5	8	5	5	5	8	5	5	5	8	5	5

The prey ratios in this experiment were used to investigate what the effect was on the energy intake of competing fish when the availability of prey with different profitabilities (E/H) was changed, where E is the energetic content (Joules) of the prey and H is the handling time of that prey. Hart & Ison (1991) demonstrated that for feeding sticklebacks the 5mm prey had a greater profitability than 8mm prey. It was expected that a good competitor would take the 5mm prey, due to greater profitability, when this prey was available. In the 1:3 and 1:1 ratios where availability of 5mm prey was reduced a good competitor was expected to consume both prey sizes in order to reach the daily energy requirement. The 8mm prey were likely to be taken early in the prey sequence, due to high motivation of the fish (see Chapters 2 & 3; Hart & Gill, 1992; Gill & Hart, in press). In the 3:1 ratio, one fish could reach its daily energetic requirement by selecting only the 5mm prey.

The results were analysed using the Statview package and with reference to Siegel & Castellan (1988)

RESULTS

Morphometrics

The morphometrics of the predator and the prey, shown in Table II, were required to correlate with the competitive ability of each of the fish. It has been shown that sticklebacks have competitive strategies conditional upon their phenotype (Milinski, 1986).

Table II. The morphometrics of predator and prey.

Measurements	Fish					
	1	2	3	4	5	6
Fork Length(mm)	46.0	44.7	46.0	47.2	45.0	45.7
Jaw Width(mm)	2.7	2.8	2.6	2.5	2.6	2.6

Prey Measurements	
Length(mm)	5 8
Width(mm)	1.9 2.8

Probability of Attack

Table III shows that there was a high probability that each fish would attack any of the prey presented. After prey detection, the attack involved initial orientation and pursuit as described in chapter 2 (Hart & Gill, 1992). Attack only included manipulation if the fish reached the prey first or intercepted prey which had been spat out by the other fish.

Initially, one would expect that the most successful fish was the one most likely to attack the prey, fish 4 in this case. But as indicated in the introduction, success will also be influenced by the size of the prey in relation to the jaw size of the fish.

Table III. The mean (\pm S.E.) probability of each fish attacking the prey encountered.

Prey Size	Fish					
	1	2	3	4	5	6
5mm	0.79 (\pm 0.05)	0.69 (\pm 0.04)	0.71 (\pm 0.11)	0.97 (\pm 0.02)	0.76 (\pm 0.11)	0.71 (\pm 0.08)
8mm	0.97 (\pm 0.02)	0.92 (\pm 0.04)	0.77 (\pm 0.06)	0.95 (\pm 0.03)	0.84 (\pm 0.06)	0.80 (\pm 0.07)

Fish that were first to handle the 5mm prey were likely to eat it (Table IV). The likelihood of eating was less for fish that were first to handle 8mm prey. The probability of a fish first to handle then eat 8mm prey when encountering sequence A was considerably lower than for sequences B and C. This was a consequence of the greater number of 8mm prey encountered in sequence A. Of the nine 8mm prey presented in sequence A, only a few were likely to be eaten as the maximum number of 8mm prey that a stickleback will consume is approximately three (see Chapter 2; Hart & Gill, 1992). Even if both sticklebacks ignored the 5mm prey and ate 8mm prey, there would have been at least three 8mm prey encountered and not eaten in sequence A. This had the effect of reducing the overall probability of eating. The situation of just eating 8mm prey never arose during the experiments as the 5mm prey were always more likely to be eaten (see Table IV).

Table IV. Probability that the first fish to handle the prey eats it.

Prey Size	Sequence	Probability
5mm	A	0.96
	B	0.89
	C	0.91
8mm	A	0.38
	B	0.71
	C	0.65

Number of Attempts

As shown in the previous section, there was a high probability that a fish would attack a prey when encountered. Following the attack, the number of attempts made by each of the paired fish to capture the prey was recorded. Figures 1a and 1b show the frequency distributions of attempts made by the fish for successful and failed capture of each prey size. This figure only records those attempts by the fish to capture the prey. There were some occasions where the unsuccessful competitor was late in detecting the prey so did not initiate an attack as the prey had already been captured, this occurred more frequently when 5mm prey were presented to the fish.

A fish which successfully captured a 5mm prey attempted capture more often than when it failed to capture this prey size, as shown in Figure 1 (Mann-Whitney U-test: $z = -2.679$, $p < 0.004$; where z approximates a normal distribution). The number of attempts made during successful or failed capture of 8mm prey did not differ (Mann-Whitney U-test: $z = -1.479$, $p = 0.14$). Figure 1b shows that the spread of the data is similar for both. This figure also shows that upto 3 attempts were the most likely outcome when a fish encountered an 8mm prey. The fish made more attempts to capture the 8mm prey than the 5mm prey, regardless of whether prey capture was a success or failure, as shown in Figure 1a and 1b (Mann-Whitney U-test: Success :- $z = -5.544$; Failure :- $z = -7.798$; $p < 0.00001$ for both). This was also demonstrated by the range of attempts used by the fish being greater for the 8mm prey (5mm: 1-14 attempts and 8mm: 1-32 attempts).

Prey Abandoning Time (P.A.T.)

The prey abandoning time occurred when one fish was handling a prey and the other fish was waiting close by for an opportunity to intercept, or when both fish rejected the prey after some time spent handling it. It is, therefore, the time that a fish spent on an unsuccessful outcome.

Figure 2 shows the median length of time it took for a fish to abandon a prey in each of the three sequences. If the fish encountered an 8mm prey first in the sequence, as in sequences A and B, then the median P.A.T. of this prey was 17.8 seconds. This time was greater than the P.A.T.'s for the rest of the prey encountered in the sequence (Kruskal-Wallis:- A: $H = 26.543$, $df = 11$, $0.01 < p < 0.001$; B: $H = 24.163$, $df = 11$, $0.02 < p < 0.01$),

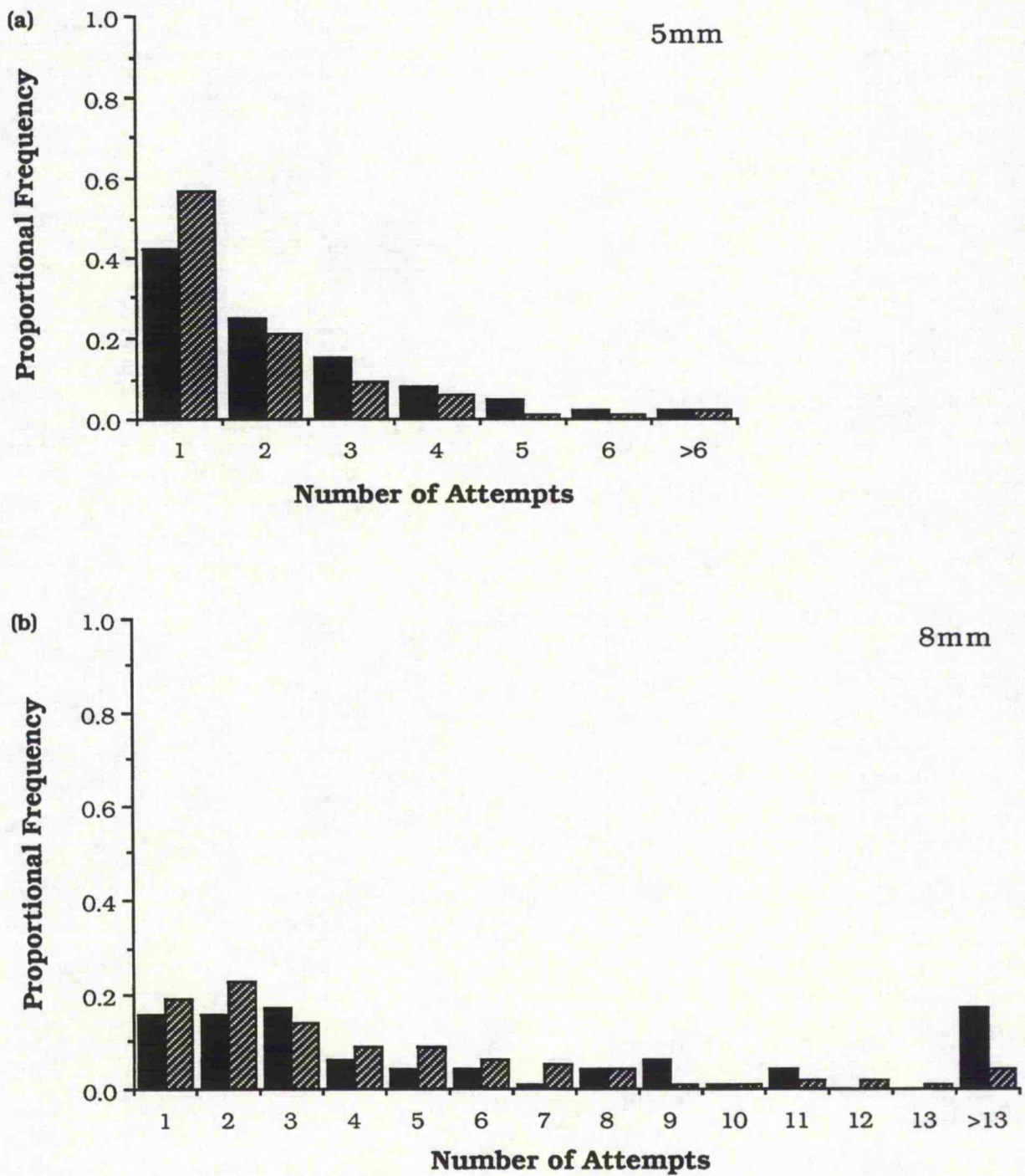


Figure 1. The frequency of attempts made by the fish to gain each prey size. (a) 5mm; (b) 8mm; ■ : success; ▨ : failure.

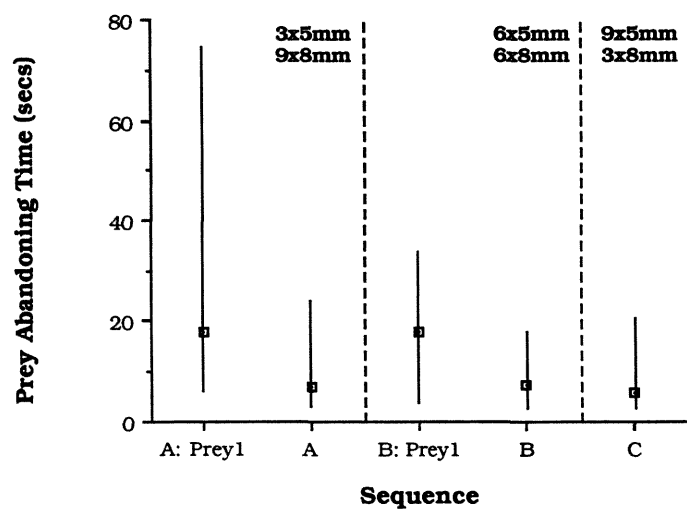


Figure 2. The median Prey Abandoning Time (P.A.T.) for each prey sequence. For the sequences where an 8mm prey was offered first (Sequences A and B) the first P.A.T. and the median P.A.T. for the rest of the prey encountered in the sequence are shown separately. The error bars show the 10th and 90th percentiles.

and the P.A.T. was more variable, as shown by the error bars in Figure 2. The median P.A.T. for all the other prey encountered was about 7 seconds as there was no difference in the P.A.T. between these prey sizes encountered (Mann-Whitney U-test:- A: $z=-0.548$, $p>0.58$; B: $z=-1.883$, $p>0.06$; C: $z=-1.217$, $p>0.22$). There was also no difference between the sequences (Kruskal-Wallis:- $H=2.891$, $df=2$, $0.3<p<0.2$). Stomach fullness had no effect on the P.A.T. when the fish encountered either prey (Kruskal-Wallis:- 5mm: $H=12.53$, $df=8$, $p>0.1$; 8mm: $H=13.44$, $df=9$, $p>0.1$)

The P.A.T. values were normalised by transformation to logarithms. As the number of attempts made to capture the prey increased the P.A.T. correspondingly increased (Figure 3). An increase in the P.A.T. of an unsuccessful competitor was expected as a consequence of an increased number of attempts as the prey was visible for longer, and therefore still available for capture by the competing fish. This was most likely for fish encountering 8mm prey and more likely when these prey were presented first in a sequence, as shown by the greater P.A.T. in Figure 2.

Handling Time

A major cost to a feeding fish is the length of time spent handling the prey. The time spent by the fish handling the 5mm prey did not change with the availability of this prey size (Kruskal-Wallis 5mm: $H=2.763$, $df=2$, $0.5<p<0.3$). Similarly, the changing 8mm prey availability made no difference to the time the fish took to handle prey of this size (Kruskal-Wallis 8mm: $H=2.844$, $df=2$, $0.3<p<0.2$).

The handling times for fish eating the two prey sizes were analysed to compare the handling times shown by single fish and fish in pairs. Solitary sticklebacks feeding to satiation on a single prey size have a median handling time of 11.8 seconds for 5mm prey and 58.0 seconds for 8mm prey (Chapter 3; Gill & Hart, in press). The handling times of the solitary fish and fish in pairs did not differ (Mann-Whitney U-test 5mm: $z=-1.374$, $p>0.17$; 8mm: $z=-0.56$, $p>0.57$).

Probability of Eating

Once the prey was attacked, the probability of eating it was dependent on the individual fish. Figure 4 shows the probability that each fish had of eating the prey as a function of

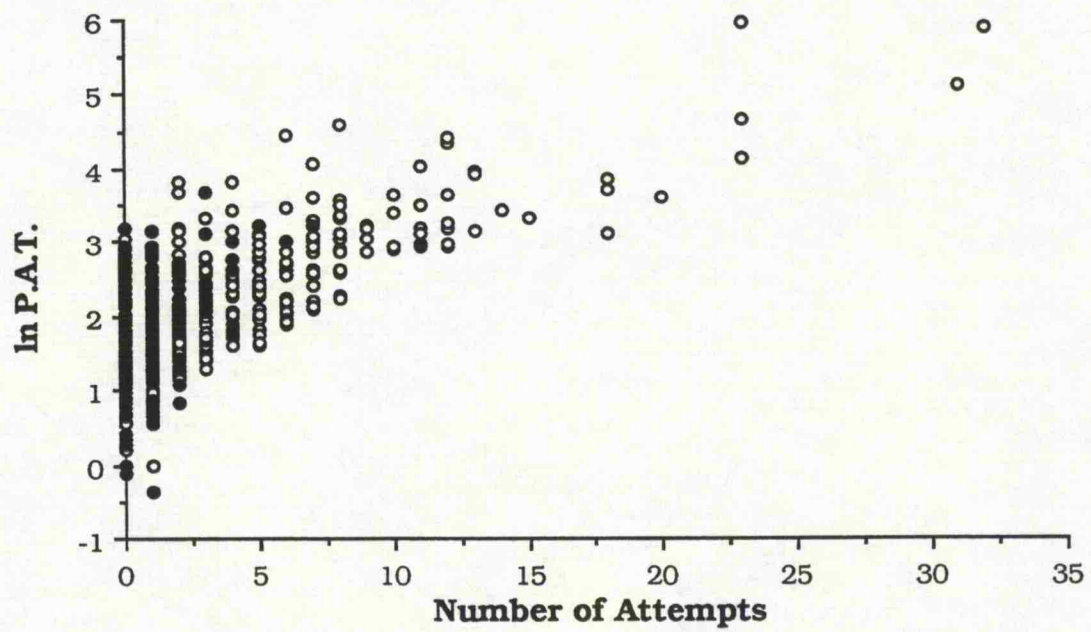
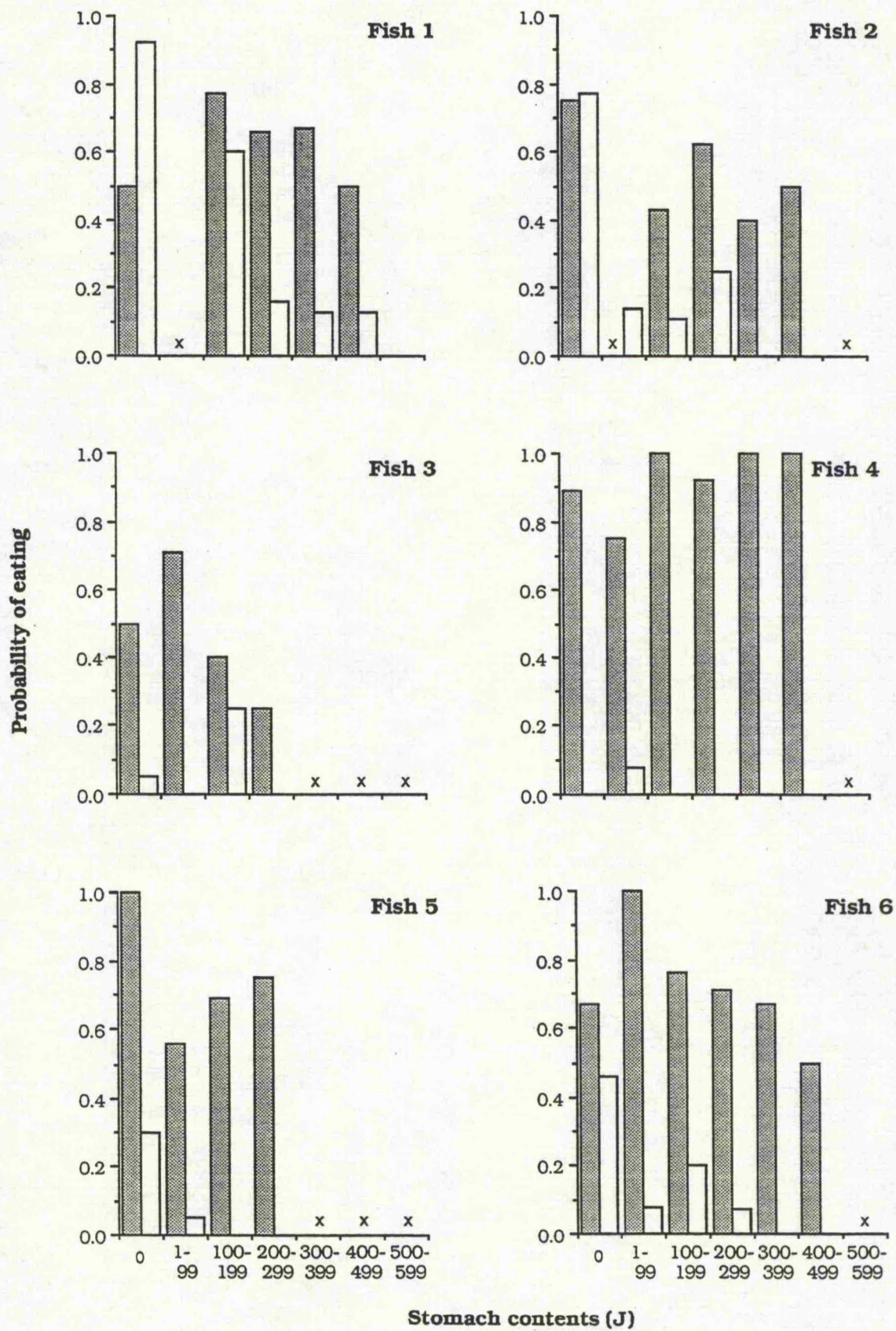


Figure 3. The relationship between the number of attempts at prey capture and the logarithm of the P.A.T. ●:5mm; ○:8mm.

Figure 4. Probability of prey ingestion by each individual fish when competing for a single prey with another fish, as a function of stomach fullness. ■:5mm; □:8mm; 'x': no data.



the energy already consumed. All of the fish were more likely to eat the 5mm prey. The probability that the 8mm prey would be eaten depended on the individual fish and the contents of the stomach (Figure 4). Of the few fish that ate the 8mm prey the probability of eating decreased as the stomach content increased. Consumption of the 5mm prey was again dependent on the individual fish. Table V compares the probability distributions of eating the prey resulting from the competition experiment and the experiment using solitary fish (Chapter 2; Hart & Gill, 1992) using the Kolmogorov-Smirnov test. Under competition, fish 4 and fish 5 had a relatively constant probability of eating 5mm prey similar to that found with solitary fishes feeding on this prey size. Fish 1 and fish 2 showed a similarity to solitary fishes consuming 8mm prey with the probability being a function of gut fullness. Fish 1 was the most likely to eat both prey. Fish 4 was the fish most likely to eat the 5mm prey.

Table V. The Kolmogorov-Smirnov test comparing the probability distributions of eating 5mm and 8mm prey for fish in pairs and solitary fishes. Non significant values indicate a similarity in the distributions of prey eaten by fish in the two situations. m=average sample size for 6 solitary fish; n=sample size for each fish in pairs; D=the Kolmogorov-Smirnov statistic; mnDmn=the product of the 3 variables, which is compared to values in a Kolmogorov-Smirnov statistical table. '*': non significant; '+': low sample size from competition experiment

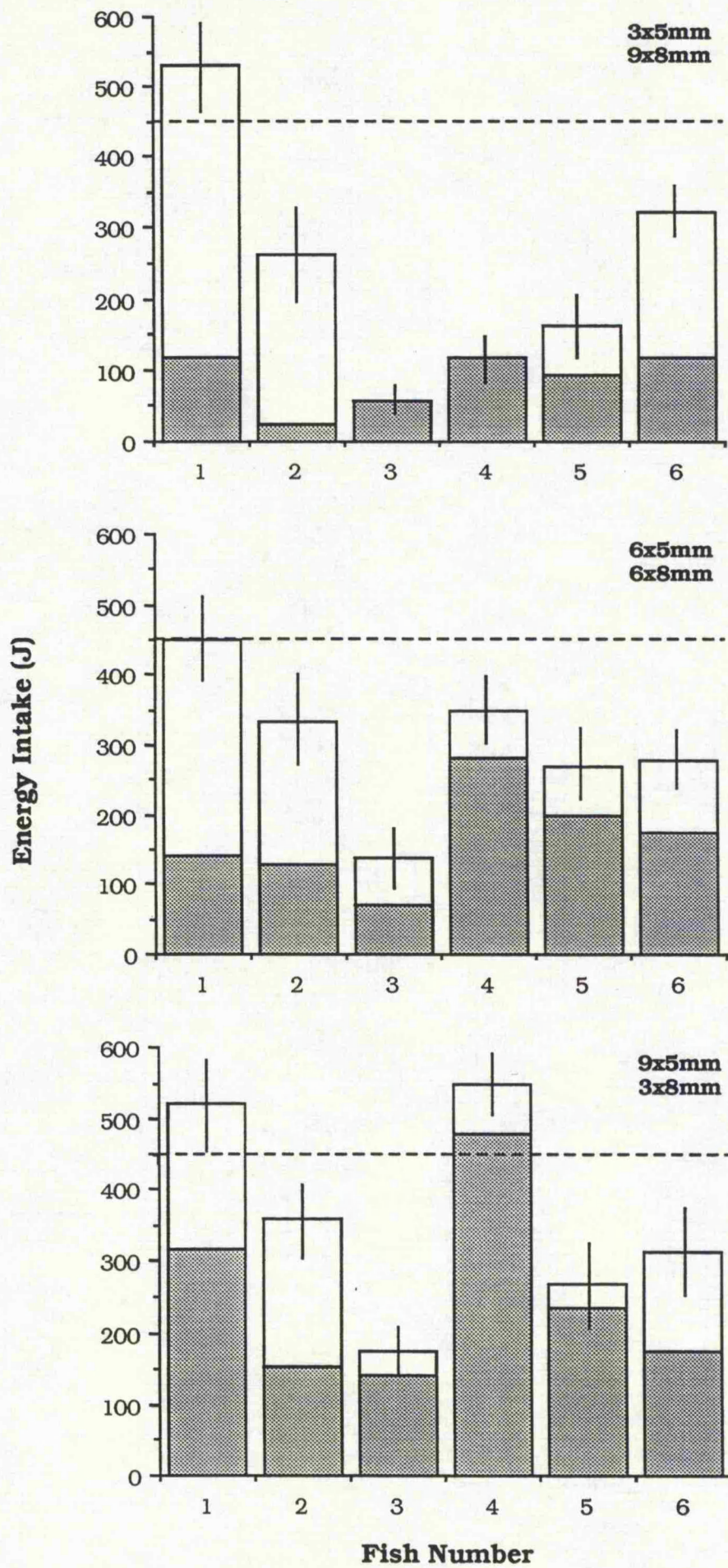
Fish	Prey Size(mm)	m	n	D	mnDmn	probability
1	5	4	6	1	24	0.01
2	5	4	5	1	20	0.05
3	5	4	4	1	16	0.05
4	5	4	6	0.5	12	>0.1*
5	5	4	4	0.75	12	>0.1*
6	5	4	6	0.83	20	0.05
1	8	8	5	0.35	14	>0.1*
2	8	8	5	0.55	22	>0.1*
3	8	8	4	0.75	24	0.1+
4	8	8	6	1	48	<0.01
5	8	8	4	0.75	24	0.1+
6	8	8	6	0.67	32	<0.1

Competitive Ability

The average energy intake was used as a measure of the competitive ability of each fish. This made it possible to rank the fish for each interaction. Daoud (1984) found that 5mm and 8mm *Asellus* contained 58.6J and 171.7J of energy respectively. Calculations of the average energy intake of each fish for each sequence of prey were made by multiplying the average number of each prey eaten by the appropriate prey energy value and then adding these values together.

In chapter 2 (Hart & Gill, 1992), it was shown that solitary fishes feeding on *Asellus* had an energy intake of around 450 J regardless of the numbers of 5mm and 8mm prey encountered. In this study, the total average energy intake of each fish increased as the abundance of 5mm prey increased, except for fish 1 (Figure 5). The changing energy intakes, shown in Figure 5, were a result of competition. The greatest competitive ability was assigned to fish 1 as it always reached its daily energy requirement. The ability of this fish to obtain the required amount of energy was due to its high likelihood of attacking both prey sizes (see 'Probability of Attack' above) and its success at eating those prey attacked (see 'Probability of Eating' above).

Figure 5. Average energetic intake (Joules \pm S.E.) of each fish for each prey sequence encountered. The broken line indicates the daily energy requirement for sticklebacks of 45mm fork length. ■:5mm; □ :8mm.



DISCUSSION

Determinants of Competitive Ability

To be the fish with the best overall competitive ability required a combination of a high probability of attacking the prey (P_{att}), a high probability of handling the prey first and a morphology to cope with the prey offered. An individual with these properties would have its food intake constrained only by the space available in the stomach. Space in the stomach is most important when the fish are attacking large prey (Chapters 2, 3 & 4; Hart & Gill, 1992; Gill & Hart, in press).

When in pairs, all the fish were likely to attack the prey encountered. For solitary fish an initiated attack usually leads to the prey being handled (Chapters 2 & 3; Hart & Gill, 1992; Gill & Hart, in press). When two fish were competing, both attacked and attempted to handle the prey, but only one fish was able to handle the prey at any one time. The first fish to handle the prey was likely to eat it, this likelihood being greater when 5mm prey were encountered. This suggests that a quick reacting and fast swimming fish is able to get to the prey faster than competing fish, giving it a competitive advantage.

There is, however, a major constraint on a fish capturing a prey item, which is the size of the prey in relation to the jaw morphology of the fish (Werner, 1974; Wankowski, 1979). Chapters 3 & 4 (Gill & Hart, in press) showed that the probability of a stickleback successfully capturing a prey is a function of the ratio of the prey width to the fishes mouth width (PW:MW). The results from the present study indicate that this PW:MW relationship has an influence on the competitive ability of the fish. The probability of eating (P_{eat}) the 8mm prey was greatest for those fish with the widest jaws and hence a lower PW:MW ratio (Table II & Figure 4). Ingestion was also more likely as the motivational state of the fish increased. A fish with an empty stomach was most likely to eat the 8mm prey (see Figure 4), as has been shown previously for solitary fish (Chapters 2, 3 & 4; Hart & Gill, 1992; Gill & Hart, in press).

Fish 1 was the best competitor as it attacked the prey with high probability (P_{att}),

had a high probability of handling the prey and had the morphology to cope with and ingest the prey presented. Being the best competitor meant fish 1 gained the required amount of energy, for each of the three prey sequences encountered, and had a similar probability of eating 5mm and 8mm prey as a solitary fish does. Fish 2 had a similar pattern of intake to fish 1 although its energetic gain was reduced due to a lower competitive ability resulting from a low P_{att} . Fish 3 being the poorest competitor, had the lowest energetic intake and would probably have starved if its diet had not been supplemented after each trial. Although being the best at attacking the prey, fish 4 would have been deprived of food due to its small jaws, unless the encounter with the more profitable 5mm prey was relatively high. Fish 5 was similar to fish 4 in intake pattern but its low P_{att} meant that its prey intake and hence its competitive ability was lowered. Fish 6 had an intake of both prey sizes which was consistent for each sequence encountered suggesting that this fish was not limited by its feeding morphology, but was let down by its low P_{att} .

As already mentioned the probability of attacking a prey in a competitive situation is dependent on the reaction and swimming capability of the fish involved. If a fish is not the best at this then it is likely that its performance is related to the performance of the competitor. A mediocre performer is only likely to gain access to the food against a poorer competitor. In the case here, the poorest competitor was fish 3, any other fish in an interaction with this fish was likely to capture the food. Having a greater competitive ability meant the fish were more likely to get an energy return.

The performance of each individual fish in the experimental conditions suggests what may happen in the fishes natural environment. If we consider the situation of single prey drifting down a river, the most competitive fish is likely to gain each prey encountered. Coates (1980) has demonstrated that reef fish with a high competitive rank are first to the prey as they maintain the best feeding positions in a current. The most competitive fish therefore gets the daily energy needed in the shortest time. This leaves more time for other activities. The fish of lower competitive ability would have to increase their foraging time in order to reach the daily energetic requirement, thus reducing the time available for other activities and also increasing the risk of exposure

to predation. As this experiment limited the feeding time, the fish did not have the chance to increase energy intake by increasing foraging time so some fish did not reach their daily requirement.

This experiment was designed to give both fish the required energy intake. It was found, however, that most of the fish did not reach their energy requirement. In comparison to the feeding of solitary stickleback (see Chapter 2; Hart & Gill, 1992), the presence of a competitor reduced the intake of food. This reduction in food intake is brought about by interference between the competing fish (Milinski & Parker, 1991).

Milinski(1982) has shown how competition changes the relative profitability of the prey for each individual predator, dependent on competitive ability. Less successful competitors should include the less profitable prey in their diet with increasing probability. As success in capturing the profitable prey decreases these predators should adopt a generalist feeding strategy. In this study, the fish which was able to generalise in the prey sizes eaten was the most competitive. This apparent contradiction to the suggestion of Milinski (1982) can be resolved if the size of the prey is taken account of. The prey offered to Milinski's sticklebacks were *Daphnia* (1.1 -1.7mm) which were relatively small compared to the size of the fish (approximately 48mm in length) and easily eaten by all the competing fish. The *Daphnia* had an increase in profitability with prey size. Ranta & Lindström (1990) have also reported that sticklebacks prefer large to small *Daphnia*. As prey get larger there comes a point where the profitability reduces, as the cost of handling time increases exponentially with prey size (Chapter 3; Werner, 1974; Kislalioglu & Gibson, 1976; Hoyle & Keast, 1986; Gill & Hart, in press). The 8mm *Asellus* offered to the sticklebacks (approximately 46mm in length) in this study are known to have a lower profitability than the 5mm *Asellus* (Hart & Ison, 1991). The total amount of energy ingested was used to judge the competitive ability of the fish used in this experiment. The ability of fish 1 to generalise in prey selection made it the most competitive. It must however be noticed that as the proportion of the more profitable 5mm prey increased then the competitive ranking of fish 4 increased. This indicates that the encounter rate with the prey sizes offered was a determinant in the competitive ability of the fish.

Diet theory predicts that the prey encounter rate has a bearing on the feeding strategy of the predator (see Stephens and Krebs 1986). If the encounter with profitable prey is low or variable then a fish will only gain enough energy if it is able to broaden the range of food selected, hence generalising. As the encounter with profitable prey increases the predator can become more specialised in the choice of prey. In this experiment the fish had to eat both prey types in order to gain the required amount of energy. This, however, was found to be dependent on the fishes success at eating the prey. Being able to successfully capture a wide range of prey is a better policy for a fish if prey encounter is variable and limited. A fish which has a high success within a narrow range of prey will need to find a habitat that will give a high enough encounter rate with the right prey.

From this analysis it can be predicted that the competitive ranking of a fish will change with the encounter rate of prey and will also be dependent on the size of the prey encountered.

Prey Abandoning Time (P.A.T.)

Although handling time is regarded as a major cost to a predator, the time used in an unsuccessful encounter must be another significant cost in terms of wasted time, energy and opportunity (Milinski & Parker, 1991). It has been demonstrated in this study that an important cost component of the foraging behaviour of a fish under competition is the length of time committed to the prey encounter before it is abandoned. This is the Prey Abandoning Time (P.A.T.), as defined earlier.

A parallel can be drawn between the P.A.T. and the Giving Up Time (G.U.T.) as defined by Croze (1970). He took G.U.T. as an expression of the amount of effort a predator allots to pursuing a particular prey, which he regarded as a measure of the persistence of the predator. The P.A.T. can be thought of as a timing of the persistence of an unsuccessful competitor. The stickleback is known to spit prey out for reorientation depending on prey size (see Chapters 2, 3 & 4; Hart & Gill, 1992; Gill & Hart, in press), so it was worthwhile for the initially unsuccessful fish to stay for a short time in order to take advantage of a further chance at prey capture. It would appear to be a particularly pertinent strategy for the experimental situation encountered here, as there was only

one prey available at a time.

As the number of attempts to capture the prey increased the P.A.T. increased correspondingly. When eating an 8mm prey there is a high likelihood of the fish using multiple spits before swallowing (Chapter 2 & 4; Hart & Gill, 1992), so the P.A.T. of the unsuccessful competitor would be expected to increase. The probability of eating an 8mm prey was at its highest at the beginning of a sequence of prey, the only time that both of the fish had an empty stomach. The probability of a stickleback eating an 8mm prey decreases as stomach fullness increases (Chapters 2, 3 & 4; Hart & Gill, 1992; Gill & Hart, in press). Both fish would have been at their highest level of motivational to capture the prey, therefore the level of interference between the fish was probably at a maximum, giving an increase in the P.A.T.

Foraging Theory Considerations

The literature on foraging theory has defined two different model situations that a forager may be found in, dependent on the encounter with prey (see Stephens & Krebs, 1986). The essential difference between these two situations is the decisions which the models analyse. The first foraging situation is sequential encounter with single prey, with the forager deciding whether to attack or reject the prey. The second situation is when the forager encounters a patch of food, where the decision is how long to stay in the patch before giving up and searching for another patch.

This experiment suggests an extension to the sequential encounter model to include two foragers competing for a single prey. There are two decisions which a forager needs to make, the decision to attack or reject the prey and additionally how long to commit to each prey encounter if the competing fish is first to handle the prey. The latter decision is the P.A.T.

A theoretical interpretation of the P.A.T. results is shown in Figure 6. This interpretation was developed from the patch Giving Up Time (G.U.T.) rule of McNamara (1982). Figure 6 shows the probability of success from the point of view of the unsuccessful competitor. When a prey is seen both fish decide to attack, it is assumed that the fish expect to capture the whole prey if they attack, hence the $P_{si}=1$. As the

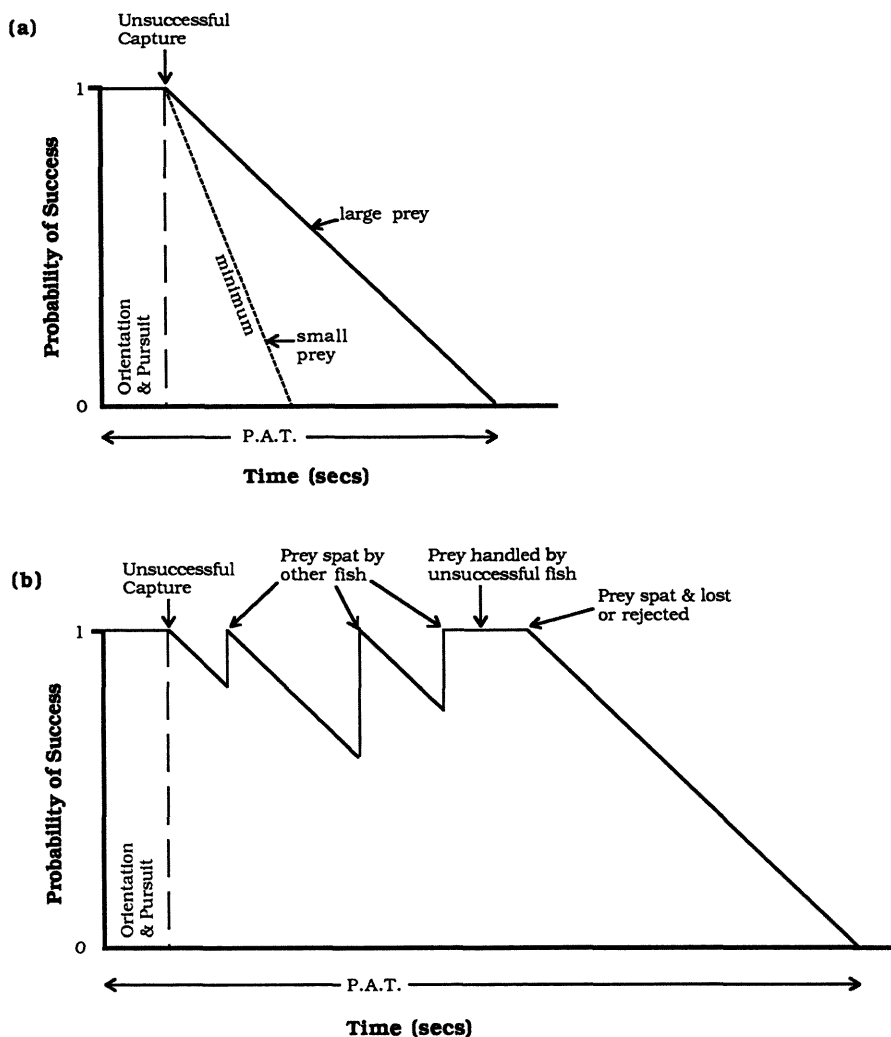


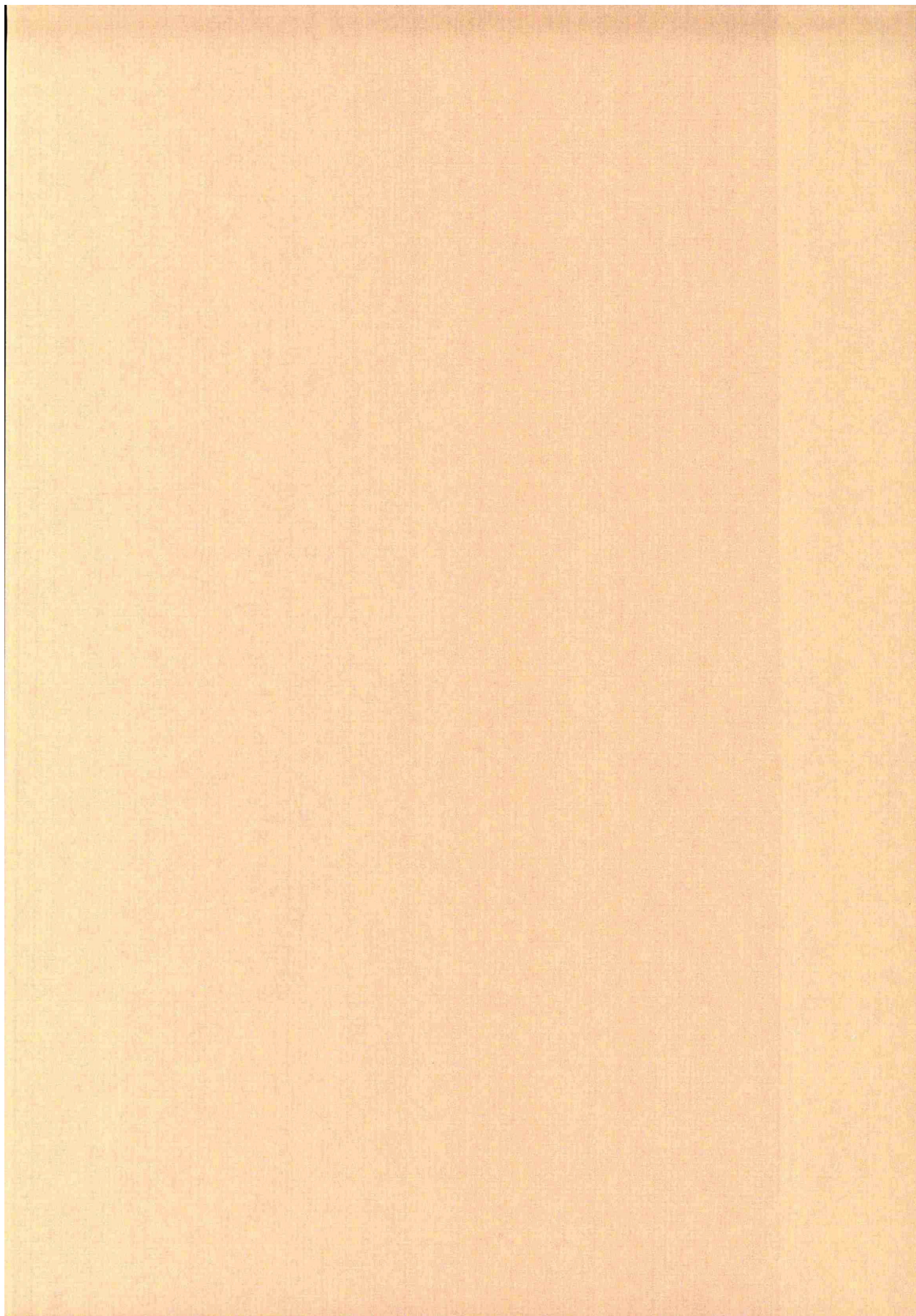
Figure 6. A theoretical interpretation of the Prey Abandoning Time (P.A.T.) of an unsuccessful competitor (see text for details). (a) The case when the prey is seen to be eaten without being spat out. There is assumed to be a minimum level which corresponds to the time it takes for the fish which is handling the prey to decide whether or not to eat it. (b) The case when the prey is spat out for reorientation by the successful fish, showing how the probability of success (P_{si}) is reset to 1 when the prey is available for capture. If the unsuccessful fish manages to handle the prey the P_{si} remains high.

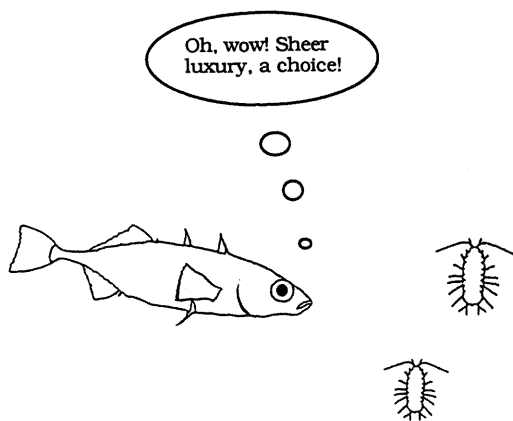
experiments showed that the fish never abandoned the prey encounter immediately if the competitor caught the prey, the P_{SI} became a declining function of time. The simplest case for an unsuccessful fish is when the competitor handles the prey first and eats it without spitting it out (Figure 6a). The unsuccessful competitor remains to cover the possibility of the prey being spat out. It is hypothesised that the rate of P_{SI} decline will be more rapid as the prey become smaller in size as the probability of spitting prey reduces with prey size (Chapters 2, 3 & 4; Hart & Gill, 1992; Gill & Hart, in press). The declining rate of the P_{SI} will likely reach a minimum level which may correspond to the length of time that it takes for a fish to decide to reject a prey, found to be about 3.3 seconds for the stickleback (Chapter 3; Gill & Hart, in press). If the prey are spat out, then the P_{SI} of the unsuccessful competitor is assumed to be reset to 1 as the food is again available for capture (Figure 6b). The P.A.T. was found to increase if the initial stimulation of seeing the prey was reinforced by it periodically becoming available.

The apparent rule of thumb that the unsuccessful fish is using is 'stay near to the other fish for a certain amount of time, dependent on the size of the prey, before abandoning the encounter'. Presumably the fish is maximising the energetic costs and benefits in some way. If the fish stays for some time then it may get a chance at capturing the prey, this is more likely as prey get larger. In the experiment here, there was no benefit to be gained from giving up straight away to look for food elsewhere. It could be hypothesised that if the encounter rate with the prey was increased then the P.A.T. for a competing fish would be shorter as there would be alternative prey available. Milinski (1982) reported that in a simultaneous two prey situation, if both fish went for the same prey, the competitor which was unsuccessful would then divert attention to the other prey.

It has been found that good competitors suffer a lower loss of food, from an increase in competitor density, than do poorer competitors (Coates, 1980; Rubenstein, 1981). It has been shown here that a competitor has the effect of decreasing the success of prey capture by a fish. This decrease in success is also a function of the fishes competitive ability. A poor competitor not only has a lower rate of food intake than those competitively better than itself, but also incurs an increase in foraging costs in

terms of lost time and energy. This interpretation needs to be balanced against the costs associated with being competitively better. When foraging, good competitors are more dependent on their individual phenotypic limitations and motivational state rather than on the presence of competing fish.





CHAPTER 6

Simultaneous v sequential prey encounter: consequences to the foraging behaviour of the threespine stickleback.

ABSTRACT

As sticklebacks encounter prey both sequentially and simultaneously in their native habitat, this chapter deals with a comparative study of the effect of changing encounter type on the fish foraging behaviour. The fish were more likely to include hanging behaviour in the attack when prey were encountered together, and this hang was longer compared to sequentially encountered prey, allowing the fish to decide between the two prey presented. Prey nearest to the fish were the first to be handled except when the relative size difference between the prey was large. In this case the smallest prey was eaten. In general, the first prey handled was the prey which was eaten, except in the case of the largest difference in prey size, where the larger prey was often rejected in favour of the smaller one. This became more likely as stomach fullness increased. All the fish had a similar energetic intake regardless of the prey sizes encountered and eaten. If a prey was eaten and the other prey was still available, the fish were opportunistic and ate the second prey. The available space in the stomach was found to be the main constraint on whether prey were eaten or not. Fish fed on one prey size to satiation did not eat further prey if they were larger than those already eaten. If however the prey were smaller, then they were eaten with a likelihood which increased as prey size decreased. Within the stomach, prey were positioned according to the order in which they were eaten. The results of this study show that the fish have changes in selectivity of prey which are due to the physical constraint of stomach capacity.

INTRODUCTION

Throughout the past 4 chapters, the emphasis has been on how a stickleback responds to a single prey presentation, monitored through the effect on prey choice and the feeding behaviour.

Although it is fair to expect that fish in a river do come across prey singly in the drift (Waters, 1972) or appearing on the periphery of the vegetation (Johannes & Larkin, 1961), the fish is also likely to come across prey simultaneously in swarms or patches. Many prey are found closely associated with certain types of substrate (Engel, 1985) or adjust their lifestyle and aggregate as a form of anti-predator behaviour (Sih, 1987). The *Asellus* prey used throughout this study were often found in aggregations of mixed body sizes (pers. obs.)

Optimal foraging theory predicts how an animal should feed most efficiently if for example there are two prey available that differ in profitability (potential energy gain per unit handling time, E/H) and are found in varying numbers in the environment. The animal should concentrate only on the more profitable type if abundance is above a certain threshold, otherwise it should feed unselectively upon both prey types (MacArthur & Pianka, 1966). Dynamic changes in state also play a role in whether the fish should be unselective (Chapters 2 & 3; Godin, 1990; Hart & Gill, 1992; Gill & Hart, in press). Within this unselective feeding state, how does the animal choose between two prey encountered at the same time?

The simplest case, tested in this experiment, is when the fish is presented with two prey at the same time. That is to say the two prey are close together so that the effects of distance are negated, as food separated by a distance can give one food a bias in terms of profitability (Waddington & Holden, 1979). The aquarium was not very large (see Chapter 1, General Materials and Methods) so any prey seen together would be close to each other when the fish detected them. This reduced the possibility of an apparent size effect (O'Brien *et al.*, 1976).

With two prey, the fish will have to make a decision as to which prey to attack and then which prey to eat. From chapter 3 (Gill & Hart, in press), it is known that there are two decisions made by the fish, the decision to attack and the decision to eat. It was suggested that the decision to attack may be on a gross scale i.e. is the item food or not. Fish use basic visual rules of thumb to make this decision (Holmes & Gibson, 1986; Ibrahim & Huntingford, 1989b; Croy & Hughes, 1991c). The decision to eat is a finer judgement, providing the fish with information on aspects of the prey properties. The study reported in this chapter analyses the decisions with respect to simultaneous encounter with prey.

The initial decision to attack may have been influenced if more than one prey was available. It has previously been suggested (Chapter 3; Gill & Hart, in press) that a hang behaviour may indicate that the fish is considering the orientation of the prey. In the two prey case of this study, it was hypothesised that a hang may be a point where the fish can decide which prey to attack. As this requires looking at both prey and considering orientation (Chapter 3; Gill & Hart, in press), it was expected that the hang times would be longer and that the probability of hanging would be greater.

Attacking and eating a prey incurs a cost in terms of handling time (Werner, 1974; Hoyle & Keast, 1986; Stephens & Krebs, 1986). The length of time that both prey are available for capture must be important. If the prey are drifting in the water column or are active and can escape, then the predator must take account of this and modify its behaviour accordingly (Kaiser *et al*, 1992a). How long the second prey is available may influence which prey is attacked first. The response of the fish to the availability of a second prey is investigated in this chapter.

It is expected that a fish will preferentially attack the larger prey because they are detected at a greater distance and therefore are more likely to be encountered (Werner & Hall, 1974; Mittlebach, 1981; Eggers, 1982). For prey that differ only in size, the distance at which a prey can be detected, known as the reactive distance (Ware, 1972), is proportional to the length of the prey (Hairston *et al*, 1982). The influence of factors already studied in this thesis must also be taken into account. The size of the prey offered and the difference between the prey sizes may be used to judge which prey to

attack. This will be moderated by the level of stomach fullness (Chapter 2; Hart & Gill, 1992). Space in the stomach will be important, as if one prey is eaten then other prey can only be eaten if there is room. It is expected that there will be changes in the fishes selectivity of the prey as the stomach fullness increases.

In energetic terms, the fish are expected to select those prey which give the highest rate of energy return. The success of prey capture needs to be balanced against the potential energy gain (Chapters 3, 4 & 5; Gill & Hart, in press). As prey get larger the handling time increases (Chapter 3; Werner, 1974; Kislalioglu & Gibson, 1976; Hoyle & Keast 1986; Gill & Hart, in press) and also the probability of success drops (Chapters 3, 4 & 5; Gill & Hart, in press). Stickleback encountering prey simultaneously have been found to preferentially feed on those prey which they could catch successfully (Visser, 1982). Largemouth bass (*Salmoides micropterus*) choose to eat prey which are easier to eat (Savitz & Jansson, 1982). Hart & Hamrin (1988) found that pike (*Esox lucius*) preferred small over large rudd (*Scardinius erythrophthalmus*) as they were easier to capture due to slower escape and smaller size compared to the mouth of the pike. The relationship between the prey size and the mouth size is important for stickleback choosing prey (Chapters 3, 4 & 5; Gill & Hart, in press). It is predicted that the fish will have changes in the selection of prey with respect to the energy deficit, as the deficit reduces the fish are predicted to choose prey which can be captured with success whenever encountered.

METHODS

Five sticklebacks, with a mean (\pm S.E.) fork length of 46.3 (\pm 1.24)mm and jaw width of 3.2 (\pm 0.11), were obtained from the River Welland. Six fish were chosen initially but one of the fish was not a consistent feeder initially so it was not used in the experiment which was filmed. It was used later for the second experiment investigating gut fullness. The experiments took place during March and April 1992.

Experiment 1

The experimental apparatus (see Chapter 1) was adapted to enable two prey to be presented at a time. A tube was connected to a funnel with a constant stream of water running down it. The end of the tube was always beneath the surface film of the water so that prey dropped through the water column and did not get trapped at the surface. A mirror was attached at an angle of 45° above the tank, allowing the prey presentations to be viewed from the side and above simultaneously. This meant that the prey nearest the fish could be estimated in 3-dimensions. The prey were sorted into 3, 5 and 7 millimetre size groups.

As 5mm *Asellus* prey have been shown to be the most profitable to a stickleback (Hart & Ison, 1991) they were the focal prey size around which the experiment was designed. The 3 and 7mm prey were chosen as it has been shown that a stickleback feeding on either of these prey sizes would get a similar energy return for a set time feeding on them (see Chapter 2, Figure 8; Hart & Gill, 1992). For all three prey sizes the main differences are the energy contained in each prey (Daoud, 1984) and the time it takes the fish to handle the prey if ingested (Chapter 3; Gill & Hart, in press). Pairs of these prey were presented to the fish, as shown in Table I.

Table I. The pairs of prey sizes(mm) presented simultaneously to the fish. The presentations were repeated four times giving a total of 16 days of experiments.

Day	Fish				
	1	3	4	5	6
1	5/7	5/5	3/5	3/7	5/7
2	3/7	5/7	5/5	3/5	3/7
3	3/5	3/7	5/7	5/5	3/5
4	5/5	3/5	3/7	5/7	5/5

5mm prey were presented in a pair to act as a control. The prey were sorted into their appropriate pairs and were introduced into the funnel where they were washed down by the stream of water. The two prey then sank through the water column and were either eaten or rejected. Those prey rejected sank away through the funnel set in the arena floor and were collected in the net beneath the tank. Prey were offered until three pairs in a row were rejected.

Occasionally, the prey arrived at different times due to one of the prey gaining purchase on the inside of the tube. This meant that some of the presentations of the second prey were delayed. This problem was taken advantage of as it allowed a comparative study of the reaction of the fish to a single prey and the reaction to simultaneous prey, under the same conditions.

Experiment 2

At the conclusion of the first experiment, a test of how a full stomach affects the choice of eating further prey was carried out. This experiment was not recorded on film.

The fish were fed either a 5mm or 7mm prey until no more were eaten and three prey in a row were rejected. The fish were then offered an alternative prey size either larger or smaller. Each fish was presented with a 5mm first then a 7mm alternative, a 7mm first then a 3mm alternative and 7mm first then a 5mm alternative, with the presentations being replicated three times. There was no pattern offering 3mm first

then a 7mm alternative as it was expected that the fish would not be able to fit a prey so large into the full stomach, a result predicted due to the findings of offering 7mm prey after the 5mm prey had been eaten first.

On the final day of this experiment the prey were marked with a mixture of correction fluid and waterproof paint on the telson to identify the individual prey. A record was kept of where these prey came in the feeding sequence presented to the fish. This was to see if the prey were ordered in the stomach according to the order in which they were eaten. If so would this leave stomach space for smaller prey after a sequence of prey eaten, as suggested in Chapter 4?

The results were analysed statistically with the Statview package and with reference to Siegel & Castellan (1988)

RESULTS

The results compare the response by a fish to two simultaneous prey and to a prey on its own.

Behaviour

The probability of hanging (P_{hg}) when a fish was presented with a single prey was 0.83, whereas the P_{hg} for two prey was 0.97. The fish were more likely to hang when encountering more than one prey. This increase in hanging was demonstrated by the fish having longer pursuit times when two prey were encountered (Mann Whitney U-test $z=-11.289$, $p<0.00001$). The median time of pursuing single prey was 1.3 secs (10th percentile=0.9; 90th percentile=2) whereas for two prey it was 2.1 seconds (10th percentile=1.2; 90th percentile=4.8).

Attacking Two Prey

The relationship between the prey nearest to the fish and the prey first handled was investigated to see if there was a choice made between prey sizes or if the fish just chose to attack the nearest prey. The prey which was nearest was handled first for all the prey pairs encountered except the 3mm/7mm pair, as shown in Figure 1. This shows that for the control, the 3/5mm and the 5/7mm pairs the fish always handled the nearest prey (control: $\chi^2=0$; 3/5mm: 3mm & 5mm $\chi^2=0.19$, $p>0.5$; 5/7mm: 5mm $\chi^2=0.09$, 7mm $\chi^2=0.10$, both $p>0.7$). Figure 1d shows that although the 7mm prey were most often the nearest prey (a random result), the fish were more likely to handle the 3mm prey (3/7: 3mm $\chi^2=6.40$, $p<0.02$; 7mm $\chi^2=3.88$, $p<0.05$). If the prey nearest was the first to be handled then the bars would be at a similar level, as in Figures 1a-c. The 3mm prey were not the nearest very often but they were the most often handled first, indicating that the fish chose not to handle the 7mm prey.

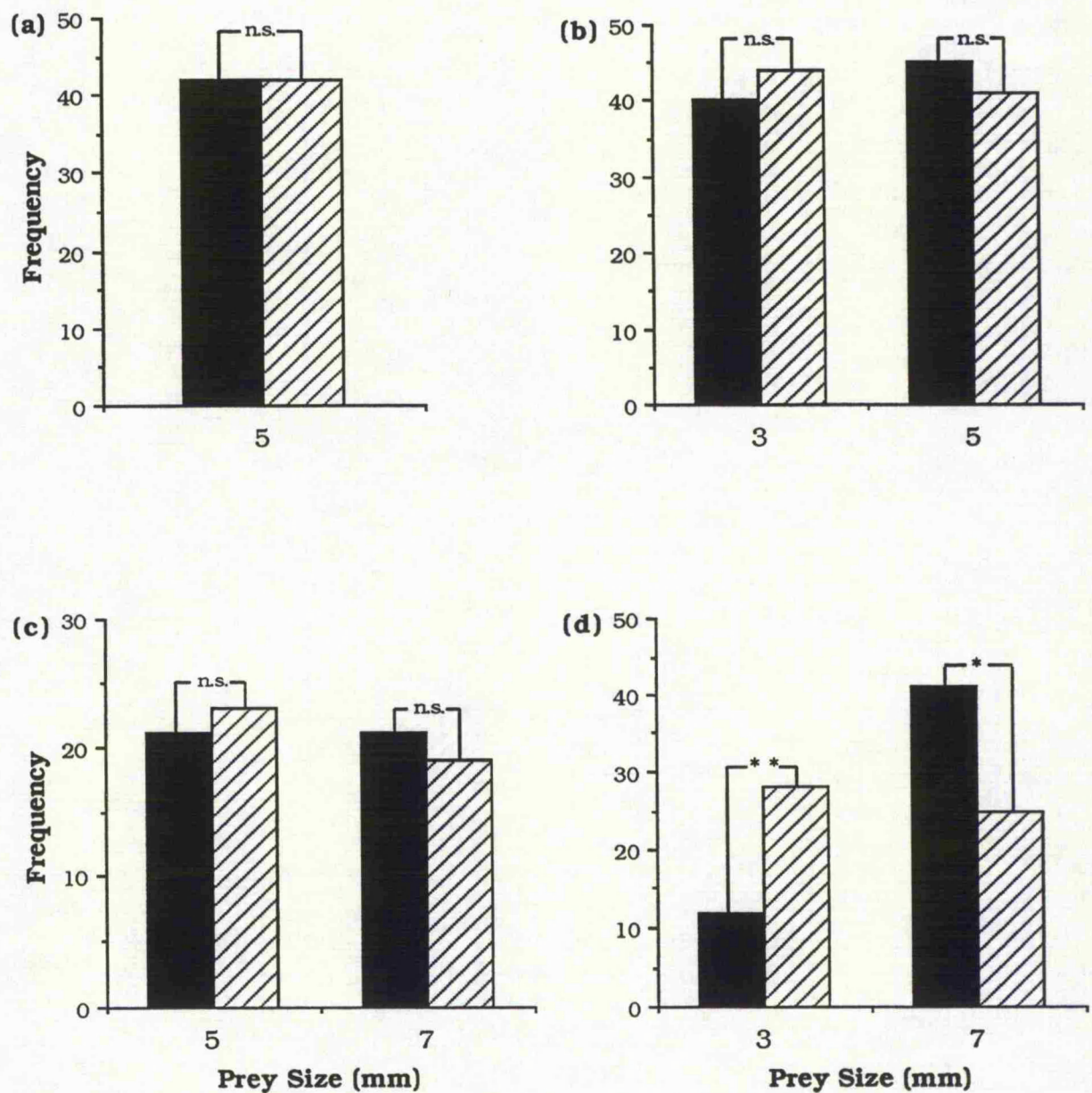


Figure 1. The relationship between the nearest prey to the fish and the first prey handled for each prey pair presented to the fish - (a) 5mm/5mm; (b) 3mm/5mm; (c) 5mm/7mm; (d) 3mm/7mm. ■ : nearest prey, ▨ : prey first handled. *: $p < 0.05$; **: $p < 0.02$; 'n.s.': non-significant.

Eating Two Prey

Numbers eaten

Table II shows the mean (\pm S.E.) number of prey eaten and an estimate of the energetic intake of the fish feeding on two prey simultaneously. There was no difference in the level of energetic intake regardless of prey pairing (Kruskal-Wallis: $H=3.001$, d.f.=3, $p>0.3$).

Table II. Mean number of each prey size eaten and an estimate of total energy intake from the pairs of prey presented.

Data	Prey Pair(mm)					
	5	7	3	7	3	5
Sample size	18	18	19	19	19	18
Mean No. Eaten (\pm S.E.)	4.5 (0.52)	2.3 (0.30)	7.1 (1.28)	3.2 (0.41)	8.5 (1.24)	7.3 (0.84)
Total Intake (J)	549.3 \pm 48.9		442.7 \pm 51.0		493.0 \pm 58.1	
					533.9 \pm 70.3	

Availability of prey

The time that the prey were in view was thought to be influential in the decision of which prey to go for. Therefore, sinking times of each prey size were recorded and compared. The sinking time was recorded as the time from when the prey entered the arena to the time it sank away out of sight of the camera and down the funnel. The median time for the prey to sink was 7 seconds (10th percentile=5; 90th percentile=10) there being no differences in the sinking times of the three different prey sizes offered (Kruskal-Wallis: $H=3.11$, df=2, $0.3<p<0.2$).

With prey being available for about 7 seconds it could be predicted that the fish should go first for the prey with a short handling time thus allowing the larger prey to also be tackled. If the fish goes for the large prey, then during the time spent handling it,

the smaller prey is likely to have sunk away and is therefore not available. It must be noted that the time to pursue the prey must also be accounted for. The prediction would be that the fish should go for the 3mm prey, if available, as this has the shortest handling time of approximately 3.4 seconds (Chapter 3; Gill & Hart, in press). This would mean that the fish would gain some energy quickly and still be able to tackle the other prey presented.

It was therefore decided to study what was the probability of eating (P_{eat}) the first prey handled. Table III shows how the P_{eat} changed with stomach fullness.

Table III. The P_{eat} the first prey handled for each prey size in a pair with respect to the level of satiation. P_{eat} was found by dividing the number of prey eaten by the number of prey first handled, for each prey size. The sample sizes were between $n=4$ and $n=25$, some data has been omitted due to low sample sizes. '+': insufficient data.

Energy in Stomach(J)	Prey Pair						
	5	7	3	7	3	5	5
0-99	+	0.75	+	1.0	1.0	1.0	1.0
100-199	0.6	+	+	0	1.0	0.75	1.0
200-299	+	+	1.06	0.09	0.75	0.5	1.0
300-399	+	+	1.2	+	0.86	0.63	+
400-499	0.22	0.33	1.2	+	1.5	0.33	0.86
500+	0.67	0	+	0.29	0.79	0.42	0.56

A change in P_{eat} with stomach content was expected from previous results in

chapters 2, 3, 4 and 5 (Hart & Gill, 1992; Gill & Hart, in press). When hungry, Peat the first prey handled was very high regardless of prey size. As stomach fullness and prey size increased Peat the first prey handled decreased.

There are some Peat which are greater than 1, due to the number of 3mm prey handled first being less than the number of these prey eaten first. This appears to have occurred due to the decisions made by the fish. As noted earlier for the 3/7mm pair (Figure 1d), there was a choice made by the fish while hanging to preferentially attack the 3mm prey. There also appeared to be a decision made once the fish had handled the prey. If the 7mm prey was handled the fish often decided to reject it and go and eat the 3mm, hence the Peat value was greater than 1. This was more probable as the stomach content increased. It was also recorded, but to a lesser extent, for the 3/5mm pair when the fish were close to satiation i.e. 400-499 J in stomach.

Handling Time

As suggested earlier, if the handling time was short enough for the first prey handled then the fish could attack the other prey of the pair. With a median sinking time of 7 seconds and a median pursuit time of 2.1 seconds, the critical handling time of the first prey handled in order to allow a chance at the second prey can be found from:

$$\text{Handling Time of 1st prey(secs)} + \text{Pursuit Time(secs)} \leq \text{Sinking Time(secs)}$$

$$\therefore \text{Handling Time (1st)} + 2.1 \leq 7 \text{ seconds}$$

$$\therefore \text{Handling Time (1st)} \leq 7 - 2.1 \text{ seconds}$$

$$\therefore \text{Handling Time (1st)} \leq 4.9 \text{ seconds}$$

The handling time of the first prey eaten and the probability of attacking (Patt) and eating (Peat) the second prey in the same presentation were calculated. Table IV shows those handling times which were above and below or equal to the critical handling time of 4.9 seconds.

Table IV. The probability of attacking and eating the second prey of a pair with reference to the critical handling time.

2nd Prey Handling Time	Number of 1st Prey Eaten	Number of 2nd Prey Attacked	Number of 2nd Prey Eaten	Patt	Peat
≤4.9 secs	26	19	15	0.73	0.79
>4.9 secs	136	6	4	0.04	0.67

Most of the times recorded for the first prey handled and eaten were too long to give the fish an opportunity to attack the second prey. But those prey encounters which did allow the fish to tackle the second prey showed a high probability of success (P_{SI}). The fish were restricted by the long handling times of the first prey eaten. The time of 4.9 seconds assumes that the fish saw the prey immediately. If this was not the case then the critical handling time would be reduced and hence the chance to get both prey lowered. Those six records of the second prey being attacked after the critical handling time were very close (5 - 8.5 seconds inclusive). This was expected due to experimental variation in the sinking times and the pursuit times. A longer sinking time and a shorter pursuit time would mean the prey were visible longer, so the fish had a better chance of getting to the prey.

Experiment 2

Fullness of the gut

As mentioned earlier, the space in the gut appears to be an important factor limiting the size of prey a fish can eat. The size of prey presented may have put constraints on the fish in terms of how much space each of the prey sizes takes up in the stomach, especially when full. It would be expected that as a fish approaches satiation there may be room in the stomach for small prey but not the large prey. Table V shows that when fed on 5mm prey until no more were eaten, the fish were unlikely to attack and eat a

7mm prey. But when offered 7mm prey until no more were taken, the 5mm and 3mm prey were likely to be attacked and eaten. This was more probable if the prey presented was a 3mm. So although a fish could not eat any more 7mm prey there was still room in the stomach for the smaller prey. For this available space to exist, there must have been a space between the prey already in the gut which was large enough for a smaller prey. The prey filling the space was expected to be near to the oesophageal opening to the stomach as this was the last prey eaten.

Table V. The probability of attacking and eating a second prey size after being fed to fullness with a different prey size. '+' : number of records too small.

1st Prey Size(mm)	2nd Prey Size(mm)	P(att)	P(eat)
5	7	0.11	+
7	5	0.72	0.62
7	3	0.61	1.0

It has already been shown that ingested *Asellus* prey are ordered and lie perpendicular to the long axis of the fish in the stomach of a stickleback (Chapter 2; Hart & Gill, 1992). Figure 2 shows the top and side view of the stomachs of the fish with the sequence number of the prey noted. Again, the prey were perpendicular to the long axis of the fish with the dorsal surface facing the stomach wall and the first prey eaten was nearest to the pyloric sphincter. The prey lay in the stomach in the order they were eaten, so the last prey eaten was nearest to the oesophagus. Those fish which were offered the 7mm prey to satiation and then the 3mm prey as the alternative had room in their stomachs to fit in the smaller prey (Figure 2).

Figure 2. Sequential packing of prey into the stomach. The view of the stomach from the side and above showing the number order in which the prey were eaten. The gap nearest the head represents the oesophageal opening and the gap nearest the tail indicates the pyloric sphincter. The dorsal view is needed to show the prey which cannot be seen from the dissected side of the fish stomach. Those prey shown in brackets were found in the middle of the prey around them. The size of prey which the fish were fed on to satiation (1) and the second prey offered (2) are indicated for each fish. H=Head; T=Tail; D=Dorsal; V=Ventral.

STOMACH CONTENT

FISH	SIDE VIEW	DORSAL VIEW
1 (1) 7mm prey (2) 5mm prey		
2 (1) 5mm prey (2) 7mm prey		
3 (1) 5mm prey (2) 7mm prey		
4 (1) 7mm prey (2) 5mm prey		
5 (1) 7mm prey (2) 3mm prey		
6 (1) 7mm prey (2) 3mm prey		

DISCUSSION

Behaviour

Within the behavioural feeding sequence of orientating to the prey through to handling, the occurrence of hanging behaviour is frequent (Chapter 3, O'Brien *et al.* 1990; Gill & Hart, in press). This has been attributed to a point in the sequence where the fish considers the orientation of the prey (Chapter 3; Kaiser *et al.* 1992; Gill & Hart, in press). The probability of hanging increased when two prey were encountered together compared to a single prey encounter. It has been shown here that the hang behaviour in the two prey situation can be a decision point. If this hang is a decision point then we would expect the fish to spend longer hanging, as the time to assess two prey and decide between them must be longer than considering the orientation of a single prey. The fish have to pay attention to each prey in turn, as assessing two prey at the same time is extremely difficult (see Ohguchi, 1981). The amount of information that needs to be transmitted to the brain will also be greater. When two prey were encountered, the fish took nearly a second longer in pursuit than for a single prey encounter. This difference in pursuit times is quite large if we consider the size of the tank (see Chapter 1). The fish were never very far from the prey so differences in swimming speed were probably small. The increase in time appears to be due to an increase in time spent hanging.

In general, attacking the prey appeared to be based on the rule of thumb, attack whichever prey is the nearest. Two reasons can be put forward in explanation. The nearest prey was probably the first to be seen or the nearest prey was the more profitable. The latter option was controlled for as much as possible by presenting the prey close together, so actual prey size was the only indicator of profitability. Only in the case where there was an obvious difference in size, did the fish sometimes choose not to attack the large prey although it was the nearest (3mm/7mm pairing). The other pairings may not have offered a large enough visual difference in prey size. Although the 5mm prey were the most profitable (Hart & Ison 1991) there was no active choice to preferentially attack them. The proportional difference between the prey sizes may not have been large enough to make a visual choice. These results suggest that comparison between prey sizes is probably proportional. The fishes reaction to the prey pairings was to attack the nearest unless the size difference was large and obvious, then go for

the smaller of the two. It must be remembered that we are here dealing with prey which are relatively large, so the larger prey tend to be less profitable as the time costs involved in capture are high (Chapter 3; Gill & Hart, in press). We are looking at the opposite end of the prey size spectrum to planktivorous prey, where the profitability tends to increase with prey size (Milinski, 1982; Ranta & Lindström, 1990).

When presented with two prey, the fish must base its decision to attack on which prey is the nearest, and its decision to eat on how long the prey will take to handle and what is the benefit from choosing that prey. The decision to eat appears to be on a finer level than the attack decision, as discrimination of prey size appears to take place. The fish handle the prey possibly to get an idea of size and other prey properties, which are important in terms of the relationship between the size of the prey and the mouth width of the fish, and the possibility of gaining energy (Chapters 3, 4 & 5; Gill & Hart, in press). It appears that the fish cannot achieve the judgement by just looking at the prey.

Eating Prey

Regardless of the prey pairings, the energetic intake was the same and this intake matches the earlier estimates for a single fish feeding on sequentially encountered prey (Chapter 2; Hart & Gill, 1992). Beukema (1968) found that sticklebacks fed to a similar satiation level whether one or two prey types were available. Sticklebacks in experimental surroundings appear to feed to stomach fullness independent of prey type or size, which is also true of wild sticklebacks feeding on natural prey items (Manzer, 1976).

Eating the prey depended on how full the stomach was and the size of the prey. This result was expected from the results found in chapters 2, 3 and 4. Hungry fish ate whatever prey they handled first. As the stomach filled so the fish chose not to eat the larger 7mm prey and preferentially fed on the 3mm prey. The fish actively rejected the 7mm prey after handling, knowing that the smaller prey was available. The process which the fish appear to be using is, eat whatever prey comes along but as the stomach fills choose to eat smaller prey. The fish could be choosing to eat the prey which is more profitable; as the stomach fills the larger prey become less profitable (Chapter 3; Gill & Hart, in press). Godin (1990) found that guppies (*Poecilia reticulata*) dropped the larger,

less profitable prey from the diet as the fish approached satiation. The fish maybe judging the decision to eat on the gastric sensation of the stomach filling combined with the information gained when handling the prey. As the fish were not naïve to these prey, they would have experience of the handling time and physical awkwardness of each prey size.

The fish could have maximised energy gain by concentrating on eating the 3mm prey first then attacking the other prey, because the fish had about 5 seconds to deal with the first prey and the time to handle a 3mm prey is less than this (Chapter 3; Gill & Hart, in press). However, the fish did not use this strategy. The need to acquire energy in the short term overrides any long term energetic considerations. If, however, a prey was eaten quickly, the other prey was attacked if still available. The fish does not appear to budget for this situation, but if the opportunity arises it is taken advantage of. A foraging strategy like this is particularly good if the prey have the capability to escape, as the prey which is not attacked may take the opportunity to get out of the vicinity. There is no energetic or time benefit in taking a small prey then hoping that the other more energetically beneficial prey will still be around. Pike attacking rudd have to choose one individual to attack as the other prey fish will burst swim away from danger (Hart & Hamrin, 1988). Escape responses of prey are very important as fish need to adopt appropriate feeding modes to increase the chances of prey capture (Persson, 1985; reviewed by Helfman, 1990; Kaiser *et al*, 1992a).

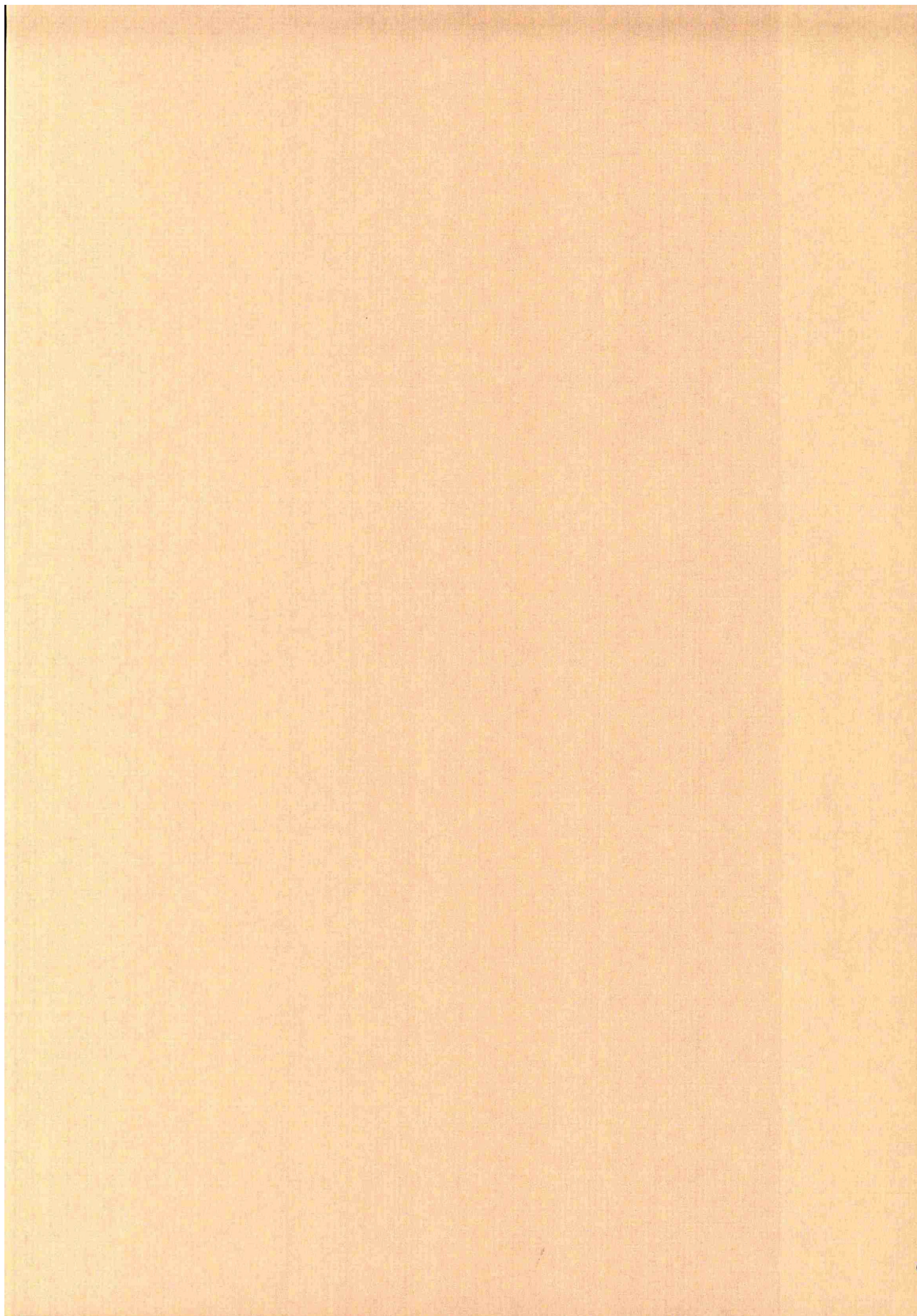
Fullness of the Gut

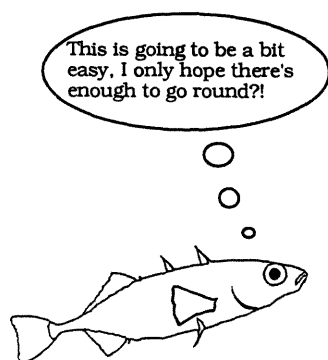
The idea that the space in the stomach is a limiting factor in prey choice was supported. A fish feeding on one prey size to what appeared to be satiation was not necessarily totally full (this was suggested in Chapter 4). The fish may have been full on one prey size but smaller prey could still be eaten. The experiment here showed that the smaller the prey the more likely it would be eaten if the fish was apparently sated.

The first prey eaten was against the pyloric sphincter and therefore would be the first into the intestine and subjected to digestion. Feeding on one prey size to satiation gives signals to the fish via stretch receptors in the stomach, to control feeding (Hamilton 1965). Although sticklebacks have the ability to considerably distend the

stomach (Chapter 2; Hale 1965; Hart & Gill, 1992), there comes a point where distension competes for space with the other organs in the body cavity. The fish cannot eat a further prey which would require further stomach expansion, but a small prey can be squeezed in between the prey already in the stomach without further distension. This supports the suggestion made in Chapter 4 for the smaller fish still attacking prey after being fed on one prey size, their stomachs were probably not completely full with one prey size. The amount that the stomach contains plays a major role in prey choice. As stomach fullness increases it becomes less likely that large prey can fit into the stomach. This could be a confounding reason in addition to the increased handling cost, for the increase in prey selectivity which is shown by many feeding studies (Ivlev, 1961; Holling, 1966; Kislalioglu & Gibson, 1976; Bence & Murdoch, 1986).

The results of this experiment show that the fish take advantage of whatever food is available when hungry, but as stomach fullness increases choices begin to be made which could be regarded as saving time and energy. Larger expensive prey are rejected in favour of smaller easily eaten prey which are likely to be successfully captured. Nearing satiation the fish become more selective. This appears to be a combination of the fish choosing to minimise costs in terms of handling time and failure to capture the prey, and a physical constraint imposed on the fish by its own stomach.





7

CHAPTER 7

Feeding on a different prey type: the effect on the behavioural response of the threespine stickleback.

ABSTRACT

As sticklebacks are catholic in their diet, the effect of a different prey type on the behavioural response of the fish was studied to relate and compare to the previous chapters. When *Daphnia* sp. were presented both sequentially and simultaneously to the fish, there was a high likelihood of them being eaten. The number of prey eaten by the fish did not differ with the way in which they were encountered. The percentage body weight of *Daphnia* eaten was similar to the amount of *Asellus* eaten in previous chapters. All of the fish spent a similar time feeding to satiation, however, the time spent handling was longer when the prey were encountered sequentially. As satiation increased the prey handling time increased. This increase was more marked for prey encountered simultaneously. Very few prey were rejected, but those that were occurred as the fish approached satiation. The probability of rejection was greater when the fish encountered the prey together. The time taken to decide to reject the prey was constant regardless of satiation. As stomach fullness increased, the time between prey captures increased for simultaneous prey encounter, which meant that the rate of prey capture was greatest when the fish were hungry. An increase in stomach fullness also lead to the behavioural sequence becoming more complex. Generally, the fish did not need to spit the prey out but as satiation increased the probability of spitting increased as did the probability of the fish hanging prior to the final attack. With the constraint of prey size relaxed, this experiment showed that the encounter rate with prey and the stomach fullness of the fish were the main determinants of the behavioural response of the fish.

INTRODUCTION

All the preceding chapters in this thesis were concerned with studying aspects affecting the feeding behaviour and prey choice of the stickleback encountering a relatively large prey type, *Asellus aquaticus*. In order to relate the importance of these results to a stickleback in its natural environment and to generate general fish foraging principles, it was relevant to investigate the effect of a completely different prey type and size on the feeding behaviour of the fish. As the *Asellus* were large, benthic prey the obvious alternative prey was a small planktonic species such as *Daphnia*.

There are numerous studies of fish feeding on planktonic prey in the foraging behaviour literature (e.g. Werner & Hall, 1974; Confer & Blades, 1975; Zaret & Kerfoot, 1975; Werner, 1977; Eggers, 1982; Mittlebach, 1983; Wetterer, 1989; see O'Brien *et al.*, 1990). More specifically, the stickleback-*Daphnia*, predator-prey relationship has been at the crux of feeding studies on this fish species (Gibson, 1980; Rajasilta, 1980; Ohguchi, 1981; Milinski, 1982 & 1986; Visser, 1982).

Planktonic prey present different problems to the fish. Gone are the constraints of prey size in relation to mouth size, found to be so important in the previous experiments. The handling times of planktonic prey are much reduced (Werner, 1974). This means that the larger planktonic prey are more energetically favourable than the smaller prey, the opposite to the situation with *Asellus*. One major problem that the fish face is that of detecting the prey. As the prey get smaller in size detection by the fish is less likely (Werner & Hall, 1974; Mittlebach, 1981; Eggers, 1982), and the reactive distance of the fish decreases (Ware, 1972). How visible the prey is has been shown to be an important determinant in planktonic prey choice of fish (Zaret & Kerfoot, 1975).

A major constraint which affected the feeding behaviour of the sticklebacks when encountering the large, *Asellus* prey, was the stomach fullness of the fish. Eating just one *Asellus* changed the stomach fullness quite considerably, dependent on the size of the prey eaten. With small, planktonic prey, changes in the stomach fullness are more gradual. This differential effect in the scale of satiation has been shown to be very important for the application of foraging models to predicting prey choice by fish (Hart

& Gill, 1993).

The gradual increase in satiation of a fish eating relatively small prey has been shown to increase the prey handling time near to satiation (Werner, 1974; Kislalioglu & Gibson, 1976; Croy & Hughes, 1991b), whereas a fish eating large prey has high handling times independent of satiation (Chapters 3 & 4; Gill & Hart, in press). To examine this paradox further it was decided to investigate this relationship for myself to test the suggestion given in chapter 4, that the physical size and awkwardness of the large prey means the handling time is independent of satiation level.

Capture success changes with satiation for sticklebacks presented with large prey (Chapters 2, 3, 4, 5 & 6; Hart & Gill, 1992; Gill & Hart, in press), whereas planktivorous fish have a high overall prey capture success rate (Confer & Blades, 1975; Kettle & O'Brien, 1978). High capture success has also been found for stickleback feeding on *Daphnia* (Visser, 1982).

The majority of fish foraging behaviour studies have concentrated on fish exposed to multiple prey, thus changing the fishes encounter rate with the prey (e.g. Werner & Hall, 1974; Milinski, 1977). As most of my preceding work revolved around sequential encounter with prey, it was decided to study the response of the fish to both single planktonic prey and an abundance, in order for a comparison to be made between the two prey presentation types and also with the previous sequential and simultaneous Asellus work.

METHODS

Initially, six sticklebacks with a mean (\pm S.E.) fork length of 45.3 (\pm 0.86) and jaw width of 2.7 (\pm 0.11), were used in this experiment. However, one of the six fish was extremely timid and did not train properly, a common phenomenon found throughout this study. This fish was left out of the experiment. The time required to train a new fish with the novel prey and the imminent onset of the breeding season meant that the experiment continued with the five remaining fish.

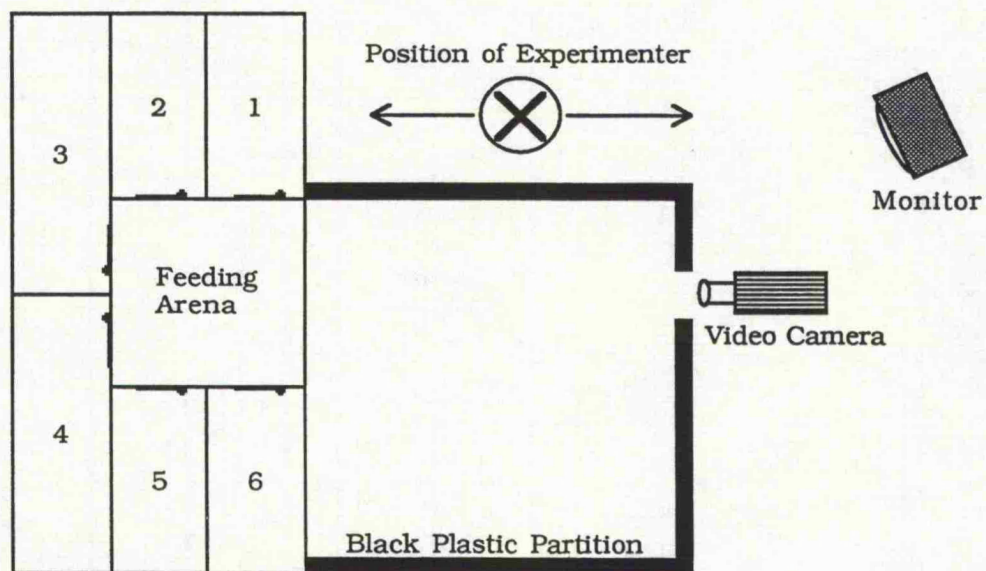
A plan view of the experimental apparatus is shown in Figure 1a. The aquarium used in the previous studies (see Chapter 1) was adapted for the purposes of this experiment. The funnel at the base of the aquarium, was blocked off with a sheet of perspex which was covered with gravel, giving the feeding arena a complete bottom. Each fish was assigned to an individual holding tank (Numbers 1-6 in Figure 1a) and trained to enter the feeding arena where *Daphnia* prey were presented (Figure 1a). As these fish were from a flowing stream it was assumed that *Daphnia* would be a novel prey item, so the fish were exposed to these prey for over two weeks prior to the experiment to minimise learning effects. The experiments took place during May 1992.

For the simultaneous prey experiment, about 300 *Daphnia*, sorted through a 2mm and retained by a 1.5mm mesh, were placed into the middle of the arena with a hand net. The fish were then allowed into the arena and the resulting feeding behaviour was recorded with the video camera (Figure 1a). The experimenter was able to freely move between the tank and the camera behind the partition without disturbing the fish (Figure 1a). The trial was ended when the fish had ceased eating the prey. This was regarded as the point where the fish was sated. After the fish had been returned to its own holding tank, a further amount of *Daphnia* was put into the arena equivalent to the recorded number of prey that had just been eaten. The next fish then entered the arena to replicate the experiment. Each fish was presented with the prey once per day over four days.

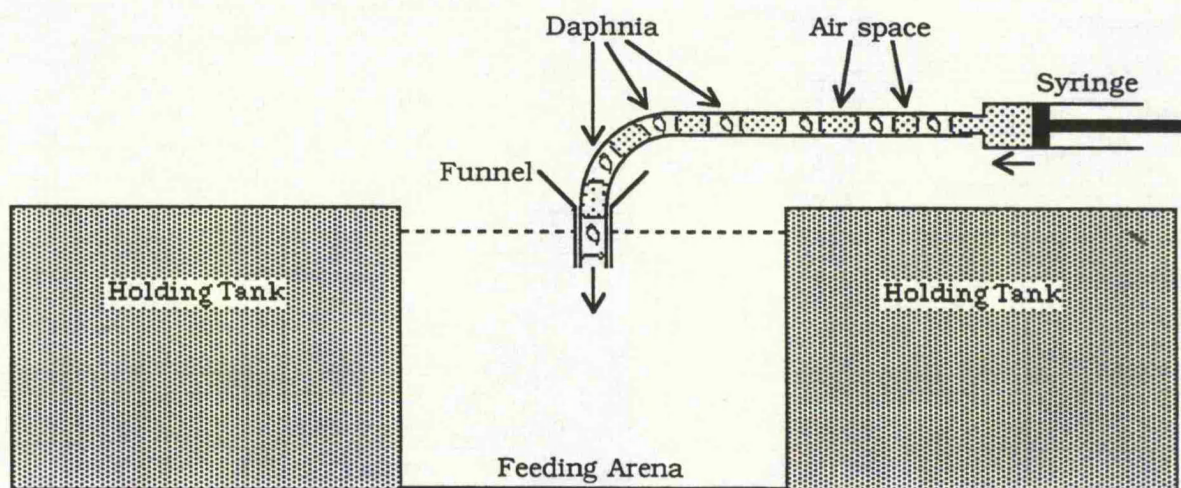
In the sequential encounter experiment, individual *Daphnia* were presented sequentially to the fish at the front, centre of the arena via a tube and syringe apparatus

Figure 1. The experimental apparatus. (a) The plan view of the apparatus showing the aquarium with feeding arena and fish holding tanks (numbered) with doorways, which were opened and closed with attached wires pulled by the experimenter from behind the plastic partition. The experimenter was able to move freely between the aquarium and the video camera without being seen by the fish. The behaviour of the fish could be seen on the monitor regardless of where the experimenter was positioned. (b) The view seen from the level of the camera during the sequential encounter experiment. The prey were kept separated by sucking in a small amount of air between the prey. It was possible to push the syringe plunger with one hand and focus the camera with the other.

(a) Plan view



(b) Side view



(Figure 1b). Single prey were sucked up into the tube, then a small amount of air was taken in before the next *Daphnia* was sucked up. Thus the tube was filled with alternating prey in a bubble of water and a pocket of air (Figure 1b). Everytime the tube was empty it was removed from the fixed retaining funnel and reloaded, it was then replaced into the funnel and the trial continued until the fish ate no more prey. Any prey remaining in the tank were removed before the next fish entered the arena. Again, each fish encountered the sequence of prey once a day for four days.

The prey handling times were calculated by superimposing a timer accurate to 25 frames per second onto the video record. Handling time was defined from the moment the prey was physically handled to the resumption of searching by the fish. The behavioural sequences were analysed by using transition matrices (see Chapter 3 for details of this technique).

RESULTS

Prey Eaten

There was a high probability that the fish ate any prey encountered in both prey sequences (Simultaneous: $P_{eat}=0.90$; Sequential: $P_{eat}=0.94$).

Table I. The mean (\pm S.E.) number of prey eaten by each fish encountering prey simultaneously and sequentially. This table includes a statistical comparison between the mean numbers eaten by each fish for the two prey sequences encountered.

Fish	Prey Encounter		Statistics
	Simultaneous	Sequential	Simultaneous v Sequential
1	51.5 (± 3.52)	50.8 (± 5.74)	$z=-0.577$ $p>0.56$
2	55.0 (± 4.42)	50.0 (± 4.88)	$z=-0.866$ $p>0.38$
3	67.3 (± 4.85)	47.5 (± 12.36)	$z=-1.155$ $p>0.24$
4	78.5 (± 8.03)	80.3 (± 7.12)	$z=-0.289$ $p>0.78$
5	55.8 (± 4.25)	47.8 (± 1.03)	$z=-1.155$ $p>0.24$

There was no difference in the number of prey eaten by each fish when encountering prey either simultaneously or sequentially (Table I). There also was no significant difference between the fish in the numbers of prey eaten (Kruskal-Wallis: simultaneous $H=8.69$, d.f.=4, $p>0.05$; sequential $H=7.55$ d.f.=4, $p>0.1$). Therefore in general, the mean (\pm S.E.) number of prey eaten when encountered simultaneously was $61.6 (\pm 3.10)$ and sequentially was $55.2 (\pm 4.08)$.

An estimate of the percentage body weight eaten by each fish was found by taking the wet weight of the fish and dividing this value into the wet weight of prey removed

from the stomach on the last day of the experiments. While removing the stomachs it was noted that they were considerably distended. The results in Table II show that there was a similar amount eaten per milligram body weight of the fish, but the sex of the fish suggests that male fish ate more in proportion to their body size. The male fish were no bigger than the females.

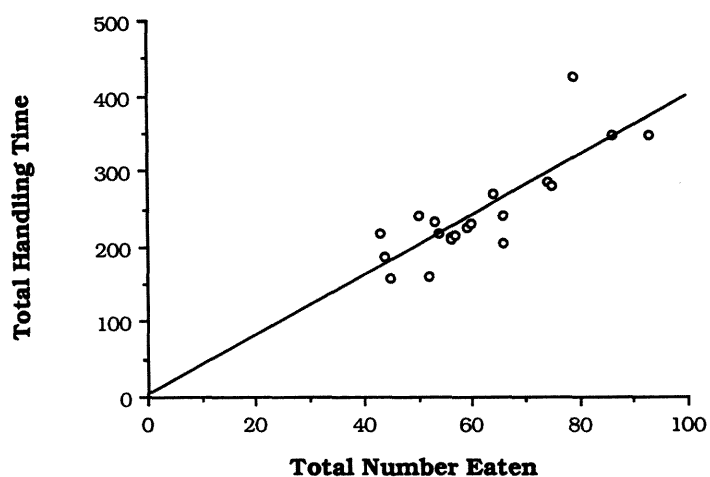
Table II. The percentage body weight of prey eaten.

Fish	Sex	% Body Weight
1	female	3.4
2	female	3.2
3	female	3.7
4	male	5.7
5	male	6.9

Handling Time

The total amount of time taken in handling all the prey eaten was positively correlated with the total number of prey eaten, as shown in Figure 2 (Spearman rank correlation coefficient one-tailed test: simultaneous $N=20$, $Rho=0.737$, $p<0.0005$; sequential $N=20$, $Rho=0.745$, $p<0.0005$). The resulting two relationships show that each fish spent a similar amount of time feeding to satiation for the two prey encounter types. There was however, a significant difference between the total handling times of the fish due to the way the prey were encountered (ANCOVA: $F_{s(1, 37)}=5.744$, $p<0.025$). Prior to this statistical test the data was log transformed to correct for the data being skewed to the right.

(a) Simultaneous Encounter with Daphnia



(b) Sequential Encounter with Daphnia

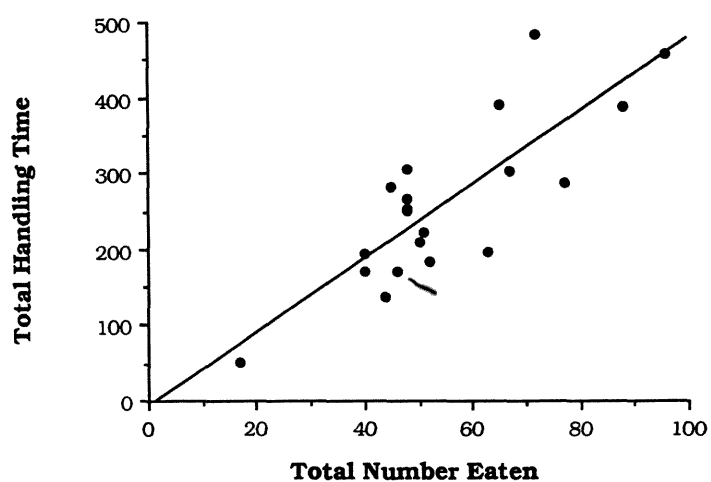


Figure 2. The relationship between the total amount of time taken handling the prey and the total number of prey eaten. The equations of the lines are (a) Simultaneous encounter: $y=2.138+3.951x$, $R^2=0.694$; (b) Sequential encounter: $y=-8.459+4.876x$, $R^2=0.677$.

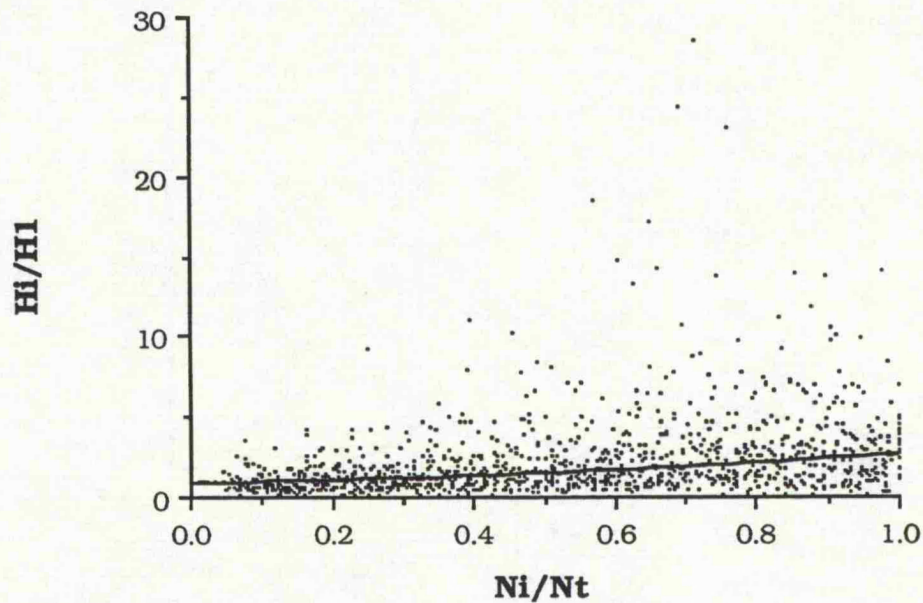
Satiation

The relationship found above however, does not indicate any temporal changes in the handling time with increasing stomach fullness. As mentioned in the introduction, this relationship has been found to be important for a feeding fish. To investigate the effects of satiation on the handling time, the data were standardised to a common scale (see Werner, 1974). For the x-axis, the prey number in the sequence was divided by the total number of prey eaten in that sequence. For the y-axis, the mean of the first three prey handling times was found and divided into all the other prey handling times (Figure 3). The relationships found indicate that the handling time rose as the stomach approached fullness, but the best fitting curve, found to be exponential, gave a low coefficient of determination (R^2) for both the simultaneous ($n=1153$) and sequential ($n=980$) prey encounter. However, a close inspection of the graphs suggested that the handling time increased close to the N_i/N_t value of 1, this represents a nearly full stomach.

To investigate this further, the first, middle and last three prey handling times of each behavioural response by the fish, representing a fish with an empty, half full and full stomach, were found and compared statistically. For either prey presentation, the handling times were not significantly different between the fish when compared at each level of satiation (Friedman two-way ANOVA by ranks: simultaneous $\chi^2=3.16$, d.f.=4, $p>0.5$; sequential $\chi^2=8.79$, d.f.=4, $p>0.05$).

There was a significant increase in the prey handling time with increased satiation (Kruskal-Wallis: simultaneous $H=46.03$, d.f.=2, $p<0.001$; sequential $H=41.56$, d.f.=2, $p<0.001$). Using the multiple comparison between treatments procedure (Siegel & Castellan, 1988) the handling times which were different were identified. For fish encountering prey simultaneously, the increase in handling time was significant at all levels of satiation. Fish encountering prey sequentially only showed an increased handling time for those prey eaten when the stomach was close to being full.

(a) Simultaneous Encounter with Daphnia



(b) Sequential Encounter with Daphnia

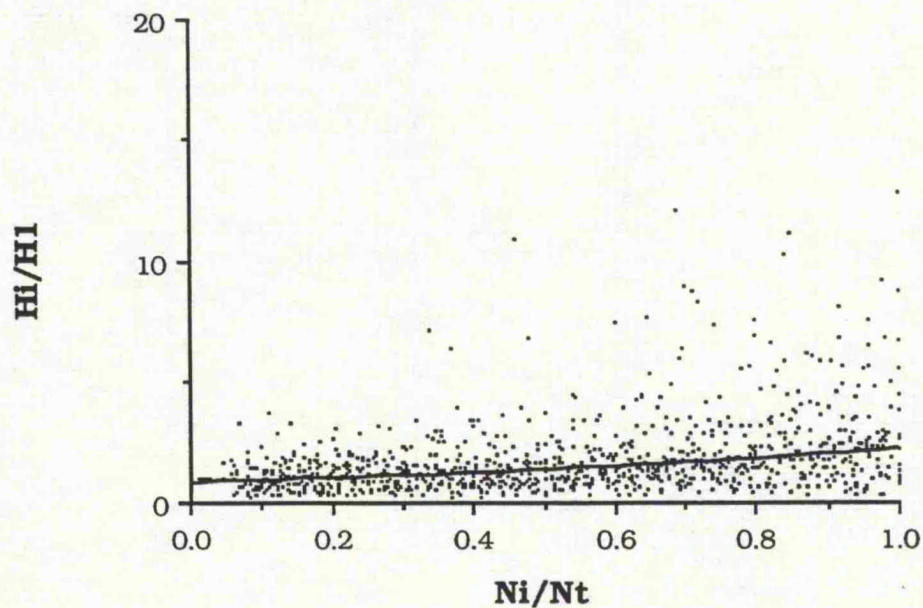


Figure 3. The relationship between the degree of satiation (N_i/N_t), represented by the prey number in the sequence (N_i) divided by the total number of prey eaten in that sequence (N_t), and the prey handling time (H_i/H_1) represented by the mean of the first three handling times (H_1) divided into all the other handling times (H_i) in the sequence.

(a) Simultaneous encounter: $y=0.784 \cdot 10^{(0.531x)}$, $R^2=0.152$; (b) Sequential encounter: $y=0.797 \cdot 10^{(0.426x)}$, $R^2=0.155$.

Simultaneous v Sequential

It was hypothesised that the fish would take longer to handle prey when they were encountered sequentially, as the stimulus of other available prey was not present. Using the data for the first, middle and last prey handling times, a significant difference was found between the prey presentations, with the handling times being greater when fish were eating prey encountered sequentially (Wilcoxon signed rank test, one-tailed: $z=-4.81$, $p<0.000005$).

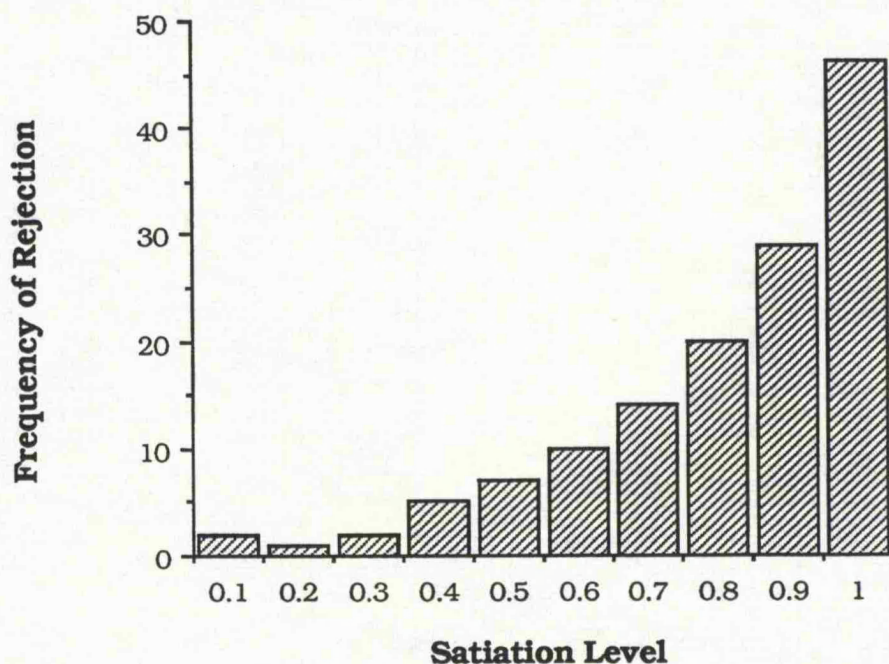
Prey Rejection

Although the general outcome of a prey encounter resulted in the fish consuming the prey, there was a percentage of prey rejected (simultaneous=9.9%; sequential=5.7%).

It was expected that these rejections would occur as the fish reached stomach fullness. Figure 4 shows the frequency of prey rejection as an increasing function of satiation level. The majority of rejections occurred when the stomach of the fish was full, thus indicating that the continuous rejection of prey was a reliable indicator of a replete fish. The histograms show that the probability of rejection was greater for a fish encountering prey simultaneously and was more likely at lower levels of stomach fullness compared to sequential prey encounter (Kolmogorov-Smirnov: simultaneous cases=136, sequential cases=67, $D_{max}=0.369$, $p<0.001$).

The times the fish took to reject prey were tested to see if this handling time was a function of satiation level. The data were grouped into 11 satiation class intervals to give a larger data set per interval. There was no increase in the time taken to reject the prey as the amount of food in the stomach increased for prey presented simultaneously (Kruskal-Wallis: $H=10.23$, $d.f.=10$, $p>0.3$) or sequentially (Kruskal-Wallis: $H=2.13$, $d.f.=5$, $p>0.8$). There also was no difference between the rejection handling times for the two treatments (Mann-Whitney U-test: $z=-0.953$, $p>0.34$). Therefore, the median handling time taken to reject any prey was 1.12 seconds (10th percentile=0.24, 90th percentile=6.80).

(a) Simultaneous



(b) Sequential

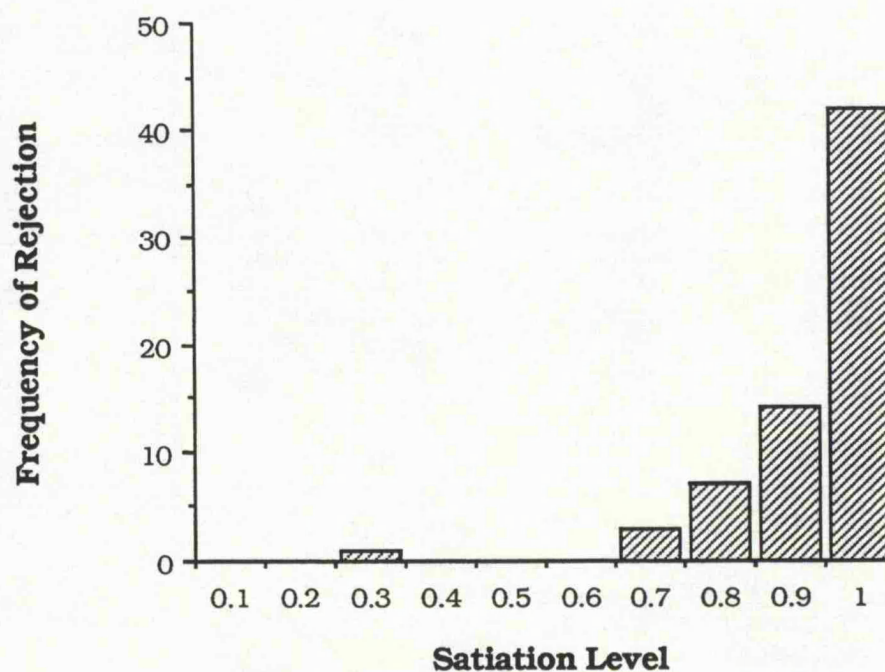


Figure 4. The frequency of rejecting prey in relation to the level of satiation. (a) Simultaneous prey encounter; (b) Sequential prey encounter. The satiation levels represent the upper inclusive limit of each class interval (0-0.1; 0.11-0.2; ; 0.91-1.0).

Interprey Catch Time

The time between prey being handled was recorded for fish presented with prey simultaneously, to give an indication of the fishes motivation to feed as the stomach filled. Unfortunately, this time could not be recorded for the prey presented sequentially as I had to continually reload the prey presentation tube and syringe, so delaying the fish.

Figure 5 shows how the interprey catch time increased and became more variable as stomach fullness increased. This means that the fish had short times between prey captures when hungry, but as feeding motivation declined the time spent not handling prey increased. The rate of prey capture was therefore greatest when the fish were hungry and gradually decreased as the stomach filled.

Behaviour

In order to analyse the sequence of behaviours elicited by the fish as they fed, transition matrices were formed separately for both the simultaneous and sequential prey presentations, and for the first, middle and last three behavioural records.

Figure 6 shows that as the stomach filled the behavioural sequence became more complex as more behaviours were employed by the fish regardless of how the prey were encountered. The probabilities of each behaviour following another are shown in this figure.

A statistical comparison between the first, middle and last behavioural sequences showed that when prey were encountered simultaneously there was an increase in the probability of a fish hanging, spitting and rejecting the prey after handling as the level of satiation rose (Table III). When prey were encountered sequentially there was an increased probability of hanging, rejection without handling the prey, spitting and rejection after handling as satiation increased (Table III).

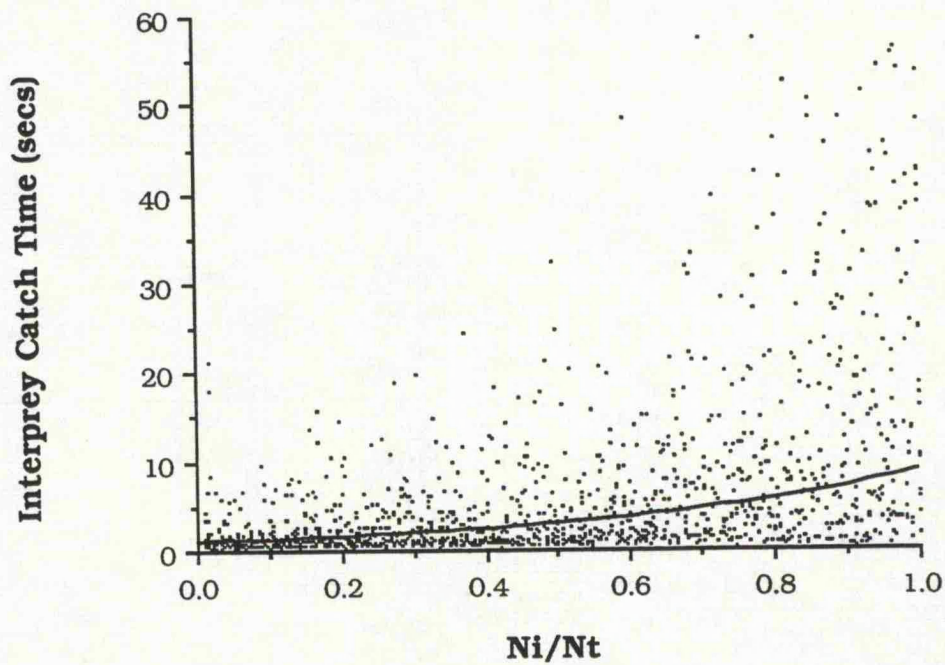
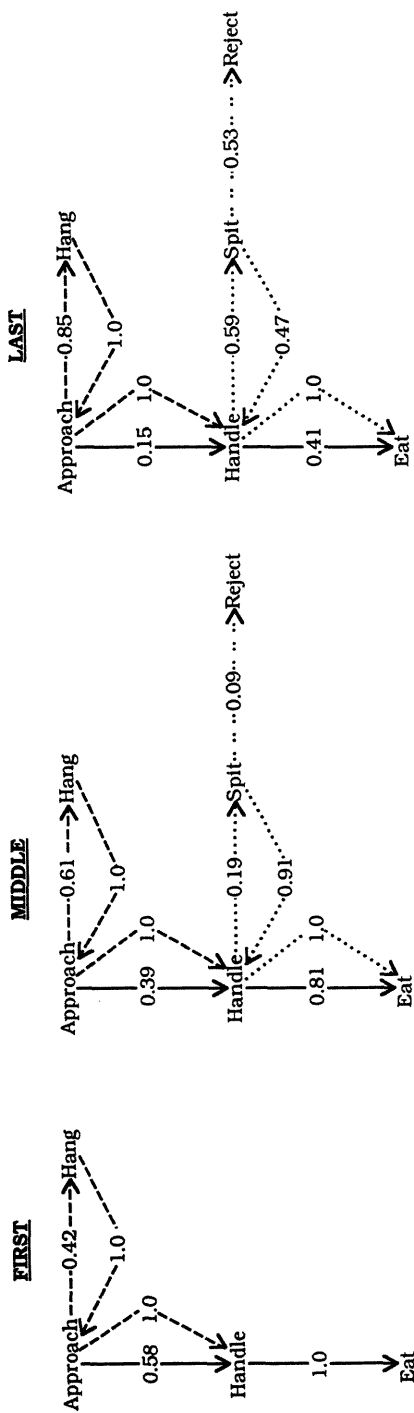


Figure 5. The interprey catch time as a function of satiation, when prey were encountered simultaneously ($y=0.989 \cdot 10^{(0.944x)}$, $R^2=0.268$). One interprey catch time of 180 seconds is not shown on the graph.

Figure 6. The sequences of feeding behaviour found for both prey presentations, (a) simultaneous and (b) sequential encounter. The first, middle and last behavioural records indicate how the feeding sequence became more complex as the stomach filled. The probabilities of transition between each behaviour are shown.

(a) Simultaneous



(b) Sequential

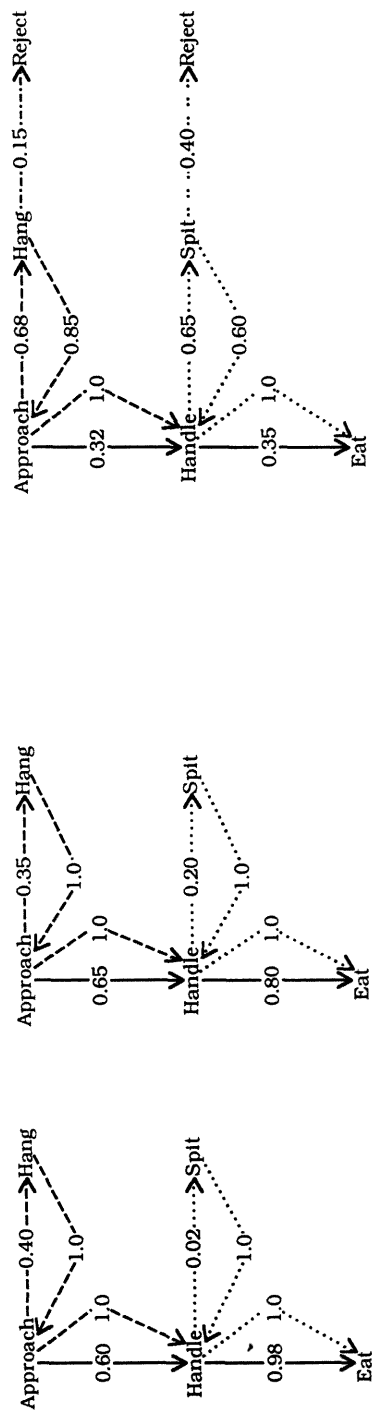


Table III. A comparison between the first, middle and last three behavioural sequences when encountering prey. After each behaviour there were two possible behaviours which followed. A significant result shows that there was a difference between the transitional probabilities of the first, middle and last three sequences. '*' : significant result.

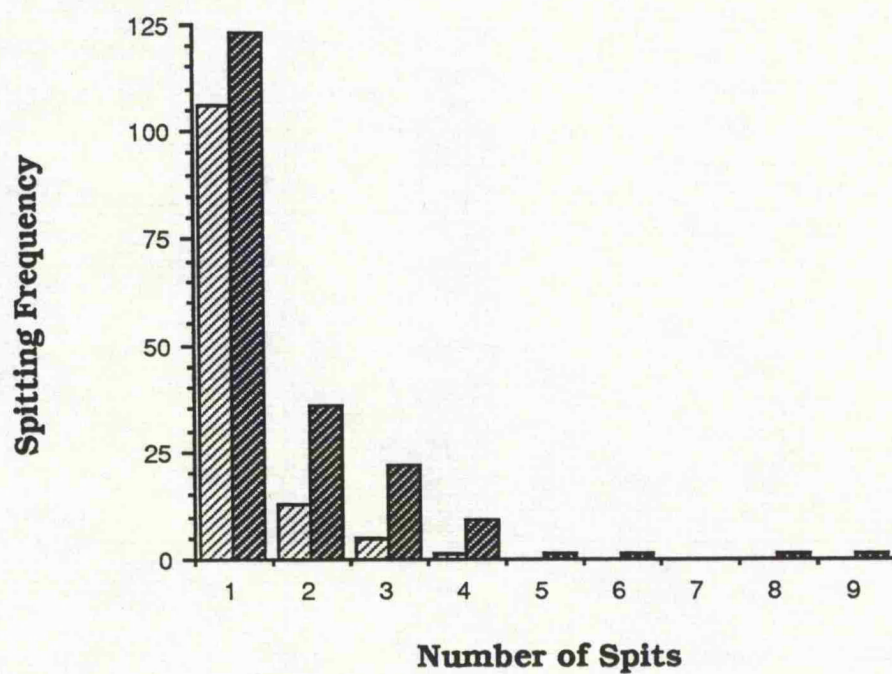
Behavioural Transition	Prey Encounter	
	Simultaneous	Sequential
Approach → Hang or Approach → Handle	$\chi^2=22.76$ d.f.=2 p<0.001*	$\chi^2=14.56$ d.f.=2 p<0.001*
Hang → Reject or Hang → Approach	$\chi^2=0$ n.s.	$\chi^2=6.9$ d.f.=2 p<0.05*
Handle → Spit or Handle → Eat	$\chi^2=51.06$ d.f.=2 p<0.001*	$\chi^2=57.35$ d.f.=2 p<0.001*
Spit → Reject or Spit → Handle	$\chi^2=28.91$ d.f.=2 p<0.001*	$\chi^2=7.35$ d.f.=2 p<0.05*

In Chapter 5, when a fish encountered large prey simultaneously there was a greater probability that hanging behaviour was used. Comparing the two prey presentations in the present experiment, showed that when the fish were hungry there was no significant increase in the probability of hanging ($\chi^2=0.04$, $p>0.8$). As the stomach filled however, the fish were more likely to use the hanging behaviour when the *Daphnia* were encountered simultaneously (middle: $\chi^2=7.99$, $p<0.01$; last: $\chi^2=4.7$, $p<0.05$).

Spitting

The most frequent number of spits used by the fish was one, regardless of whether the prey was eaten or rejected (Figure 7). From the above behavioural data it can be seen that the use of spitting behaviour was more likely as the fish approached satiation. The fish were able to eat the prey most of the time without the need to spit. Comparing the two presentation types, there was no difference in the number of spits used by the fish (Kolmogorov-Smirnov: simultaneous cases=9, sequential cases=9, d.f.=2, Eat $D_{\max}=0.222$, Reject $D_{\max}=0.333$, $p>0.1$ for both), but the frequency of spitting was markedly less when rejecting prey which were encountered sequentially (Figure 7).

(a) Simultaneous



(b) Sequential

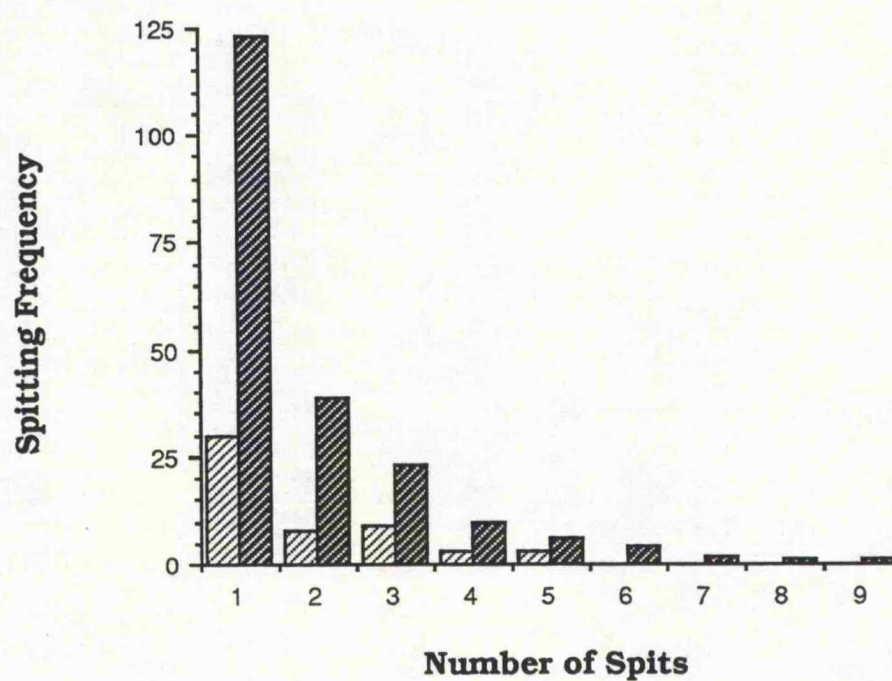


Figure 7. The frequency of spitting behaviour found for simultaneous (a) and sequential (b) prey encounter. ▨: prey rejected; ▤:prey eaten.

DISCUSSION

By using a different prey type and analysing the resulting feeding behaviour in the same way as the previous experiments, it is possible to draw comparisons between the studies.

The fish ate prey until they could eat no more, a case found previously using *Asellus* and also for other studies of stickleback feeding (Tugendhat, 1960; Beukema, 1968). This lends weight to the notion that sticklebacks feeding on natural prey items eat to fill their stomachs. Eating to fill the stomach appears to be a common feeding strategy in many fish (Ishiwata, 1968; Brett, 1971). It made no difference to the number of prey eaten by the fish if the prey were encountered simultaneously or sequentially. The percentage body weight eaten was comparable with the values found in chapter 2 for sticklebacks feeding on *Asellus*, and is also similar to the estimates of Manzer (1976) and Rajasilta (1980) found for sticklebacks feeding in the wild at a comparable temperature.

The encounter rate with the prey did however have a bearing on the amount of time taken to feed to satiation. The fish took longer overall to handle and eat the prey when they were encountered sequentially. This would appear to be related to the availability of other prey. When the fish encountered prey simultaneously, it had the chance to locate the next prey very quickly. The fish were often seen fixating on the next prey whilst finishing handling the present prey (pers. obs.).

It was expected from previous fish feeding studies, that the rate of food intake for a fish presented with multiple prey would be a decreasing function of satiation level (Tugendhat, 1960; Beukema, 1968; Ishiwata, 1968; Brett, 1971; Ware, 1972). The interprey catch time increased as satiation increased which meant that the fish gradually took longer between handling each prey. Although there may have been an effect of the prey becoming more dispersed as the experiment proceeded, the fish were still seen to take longer to begin swimming to the next prey as the stomach filled. Hence the fish had greater interprey catch times, which suggests a temporal decrease in the motivation to feed. Taking longer between prey handling has the effect of reducing the number of prey eaten in a set period of time and so reduces the intake rate.

Although the handling times were different between the two prey presentations, there was a similar increase in handling time with a rise in stomach fullness. This relationship has been found in a variety of studies of fish using prey which were readily eaten by the fish species under investigation (Beukema, 1968; Werner, 1974; Kislalioglu & Gibson, 1976; Croy & Hughes, 1991b). For sequential prey encounter, this increase in handling time was only apparent close to satiation, giving evidence that the stomach fullness level is an important factor in fish feeding. For the simultaneous encounter, the increase in handling time occurred even when the stomach was only half full. This may be related to the fact that initially the fish were hungry when they were presented with an abundance of prey, so they tried to eat as quickly as possible to reduce the hunger level. This was demonstrated by the short interprey catch times which gave a high rate of food intake. But as the stomach was gradually filled the urge to eat was curtailed and the handling times became longer. Multiple prey encounter rate appeared to elicit a behavioural response by the fish to gain food as quickly as possible. Foraging in this manner means that the hunger level will be reduced quickly and therefore the fish will be less likely to take a risk (Godin & Sproul, 1988; Godin, 1990), which reduces the exposure to predation and also increases the time available for other activities. Heller & Milinski (1979) have shown that sticklebacks feed on the densest part of a swarm of *Daphnia* when hungry, but as the stomach fills, the fish will concentrate on the prey nearer to the edge of the swarm. This feeding strategy has the effect of reducing the confusion effect to the fish and therefore reduce the risk of predation (Milinski & Heller, 1978).

The increase in handling times as the stomach filled contradicted the results found for sticklebacks feeding on the *Asellus* prey. It appears, as proposed in chapter 4, that the physical attributes of the prey have an effect on how the handling time changes with satiation level. The *Daphnia* were easily consumed as their size did not appear to test the physical limits of the fish jaws. Without the morphological constraint of prey size, the effect of satiation was able to be expressed. It should be noted however, that the graphs plotted for the handling times (Figure 3) did not give a good overall relationship, unlike those found by Werner (1974) & Kislalioglu & Gibson (1976). This may be reflecting the variation in the handling times of the different sizes of *Daphnia* (1.5 -

<2mm). Also, my recording of handling time may be different to that found in the other studies, as the method of slow motion video playback is likely to be more precise than using a stopwatch. Video has the advantage over a stopwatch of checking results by replaying the sequence and also is not biased by the reaction time of the operator.

As the prey were readily eaten when encountered, it was expected that the rejection of prey would be due to high levels of satiation. This was found to be true. There was a difference between the prey presentation treatments with the probability of rejection being greater when prey were encountered simultaneously. This response of the fish can be explained if we consider the foraging situation that the fish were in. When feeding on prey encountered one at a time, the fish either gains the food or gets nothing, whereas if the prey are encountered at the same time, then the fish may decide that the prey which it can see is better in terms of energy gain than the prey being handled. This could result in the fish rejecting the prey which it is handling and attacking another. In essence, the fish can make a behavioural choice between the prey when encountered simultaneously. This cannot be done when prey are encountered sequentially.

It was found that the fish took a constant time to decide to reject the *Daphnia*. In chapter 3 (Gill & Hart, in press), sticklebacks also had a constant decision handling time when feeding on *Asellus*. The time taken to reject a *Daphnia* however, was shorter. It may be that as the *Asellus* are larger and potentially far more rewarding in terms of energy gain than the *Daphnia*, the stickleback has to take longer to decide. Also the physical size and the numerous appendages of the *Asellus* mean that the fish has to take in a relatively large amount of information. The appearance of a constant decision handling time for both prey types gives support to the contention in chapter 3 that the decision to eat the prey does not occur until the prey has been handled.

The behavioural sequences shown by the fish were similar to that studied in the previous chapters. The two stage decision process, deciding to attack and then eat, is common to a feeding stickleback. After the decision to attack has been made, the fish have been found to have a certain probability of hanging before the prey is handled (Chapters 3 & 6, present study; Gill & Hart, in press). This may be a point where the fish can assess the prey in order to direct the attack (Chapter 3; Kaiser *et al*, 1992a; Gill &

Hart, in press). As the *Daphnia* had the ability to move about, the fish would have needed to direct the attack at the anticipated point of interception (Kaiser *et al*, 1992a).

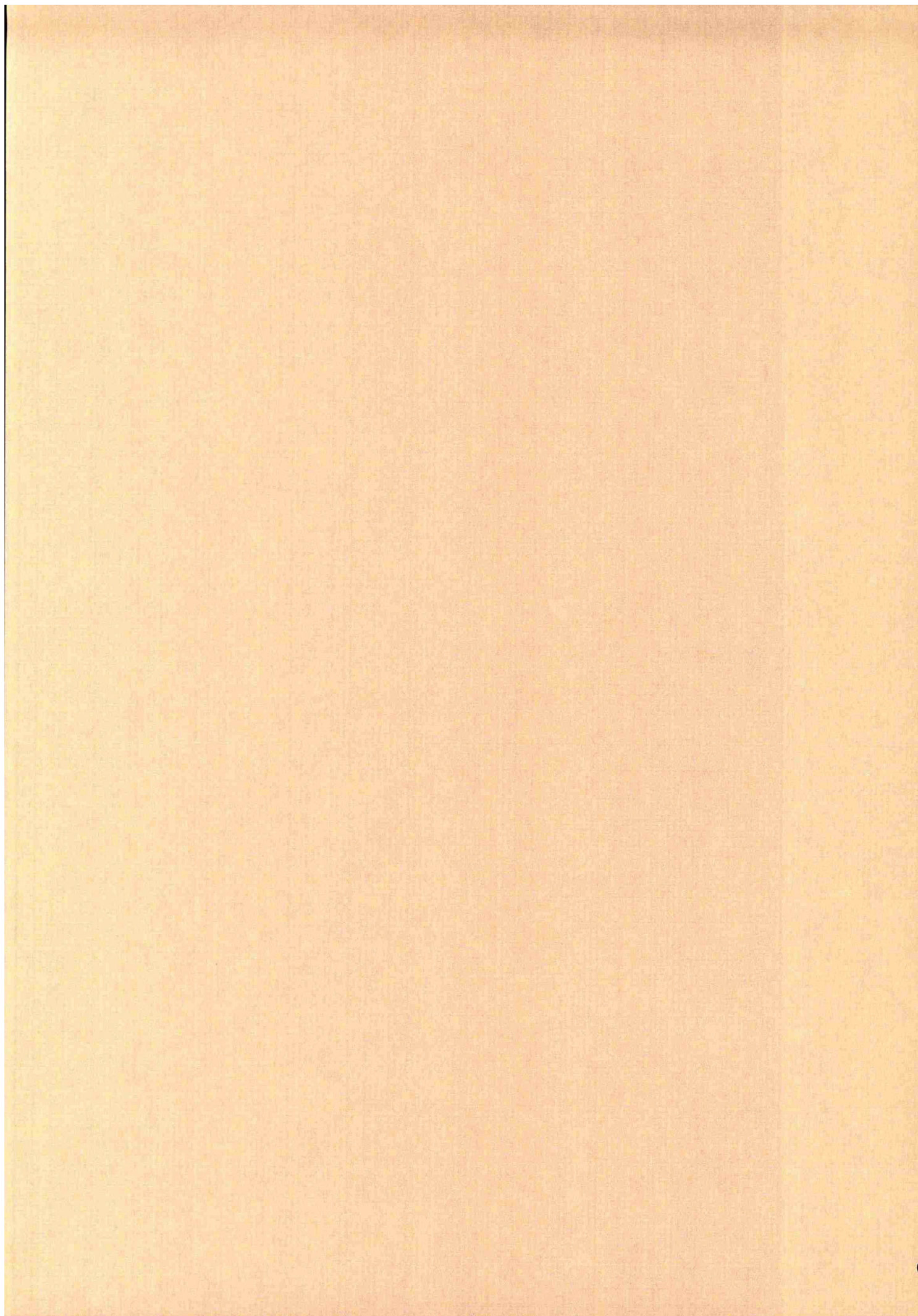
The fishes repertoire of behaviour, when encountering *Daphnia*, was dependent on the satiation level of the fish and the manner in which the prey were encountered. As the stomach filled so the behavioural sequence became more complex, involving more behavioural components. An increase in behavioural complexity due to an increase in satiation has also been shown for fifteen spine stickleback (Croy & Hughes, 1991b). When hungry, the fish were likely to complete the shortest sequence and always eat the prey. As the stomach filled so the probability of spitting increased and the probability of rejecting the prey was also greater (also shown earlier). An increase in spitting behaviour resulted in the prey being handled for longer, so the handling time correspondingly increased. With an increase in the handling time and a greater probability of rejecting the prey, the predatory efficiency of the fish will decrease. Croy & Hughes (1991) found a decrease in the handling efficiency of fifteen spine stickleback as satiation increased.

In the previous experiments with *Asellus*, the behavioural sequences of the fish were constant with satiation but became increasingly more complex as the prey increased in size. These fish had to depend on their handling and spitting skills for successful food gain. This is further evidence that the size of the prey can mask the effect of stomach fullness.

From the results here and from the experiment reported in chapter 6, the encounter rate with prey is important for the resulting behavioural feeding sequence. With the *Daphnia* presented simultaneously, the probability of the fish hanging was higher than when presented sequentially, except when the fish was hungry. This suggests that when the fish had an empty stomach any prey were taken. These were most likely to be the nearest prey to the fish, as shown in chapter 6. However, as the urgency to feed declined so the fish was able to become selective if alternative prey were available. A decrease in prey selectivity of fish as hunger increases has been found before (Chapter 6; Ivlev, 1961; Visser, 1982). When a stickleback is being selective and choosing between prey, the probability of hanging increases (Chapter 6). This suggests

that when the fish were feeding on *Daphnia* they were only choosing between prey when the stomach had some food in it. As the fish were only able to choose between prey when they were encountered simultaneously, the probability of spitting and of rejection of prey was higher than when prey were presented sequentially. The most frequent number of spits recorded was one, which was expected from chapters 2 and 4 as the need to spit decreases with prey size.

This comparative study shows that the key variables identified in the other experiments are still important for the behaviour of fish feeding on other prey types, but the precise effects can be different. In the case here the constraint of prey size which tested the upper acceptance limits of the fish feeding on *Asellus*, was relaxed which resulted in a greater probability of the fish capturing the prey. Without this constraint the encounter rate and satiation level were the main influences on the behavioural feeding response of the fish.



CHAPTER 8

SYNTHESIS

Feeding is such a universal and commonplace business that we are inclined to forget its importance. The primary driving force of all animals is the necessity of finding the right type of food and enough of it'

Charles Elton (1927)

As obtaining food is of such critical importance to an animal (see quote by Elton), the directive of the research in this thesis was to gain a greater insight into and understanding of the constraints on foraging behaviour, with particular reference to fish and specifically the threespine stickleback.

With so much known about the threespine stickleback (see Wootton, 1976, 1984; Bell & Foster, 1993), the study was able to concentrate specifically on the foraging constraints without the need to additionally investigate unknown aspects of the basic biology of this fish. Any study which attempts to address a specific question about an organism must be conscious of the overall biology of the species and be aware of external and internal influences which may be crucial to the interpretation of the study.

The overlying theme of all the experiments was how the size of a prey in relation to the size and the stomach fullness of the fish affected the predatory foraging behaviour. This theme was studied with reference to a number of situations in which the fish may find itself in its natural habitat.

Constraints on Foraging Behaviour

The causation of any behavioural response of an animal involves three steps, the initiation, the sustenance and finally the termination (Halliday, 1983). Behavioural regulation requires motivated and directed behaviour to achieve a necessary end (Teitelbaum, 1966). The behavioural response is a function of the animal's motivation. When considering motivation the role of internal and external causal mechanisms is of prime importance (Halliday, 1983). Throughout the studies in this thesis, the level of stomach fullness of the fish was regarded as an indicator of the internal mechanism regulating the motivation to feed.

When a stickleback encountered a prey item the sequence of behaviours which followed was found to be dependent on a number of factors which were influential at different stages of the behavioural response (summarised in Figure 1).

Attacking the prey

Once the prey had been detected the fish orientated towards it (shown in Chapter 2, observed in all other Chapters). The probability of an attack following the orientation was found to be dependent on the size of the prey encountered. As prey size increased the probability of attack reduced (Chapters 3 & 4). Conversely, the likelihood of the fish attacking the prey increased with fish size (Chapters 3 & 4). Combined with these two related constraints, an increase in the stomach fullness of the fish lead to a reduction in the probability of attack (Chapters 2, 6 & 7). The constraints of prey size, fish size and satiation were functions of both the increased need for larger fish to eat more prey and the fact that these fish had greater morphological capabilities for prey capture (Chapters 2, 3 & 4).

The ability to react fast to the prey was important if the fish was in competition for it. The fish which was first to attack was likely to capture the prey. This likelihood, however, decreased with an increase in prey size (Chapter 5). When large prey were encountered, the unsuccessful competitor was more likely to initiate an attack as well, as the chances of the prey becoming available for capture were greater, due to the need to spit these prey to orientate them before swallowing (Chapters 3 & 5).

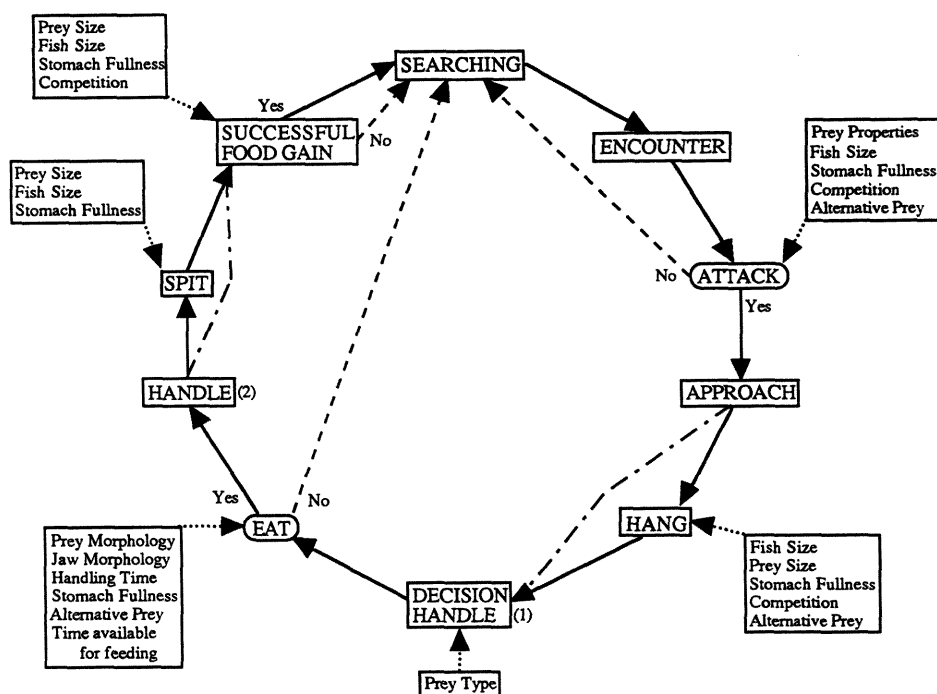


Figure 1. The array of factors found from the studies in this thesis, which influence the foraging behaviour of the threespine stickleback. The cyclical nature of the sequence shows how there is a dynamic change in the behaviour of the fish on each prey encounter. Within the foraging sequence the rectangles represent the observed behaviours and the ovals represent the decisions of the fish. The boxes outside the sequence show the factors which affect the feeding behaviour and the diet choice. (1) Prey handling on which the decision to eat is based; (2) The actual handling of the prey after the fish has decided to eat the prey.

During the attack, the fish would often use hanging behaviour (Figure 1). A hang was a point in the approach to the prey where the fish stopped a relatively short distance away. In the case of a stickleback encountering a single prey, the occurrence of this hang behaviour was defined as a point where the fish could consider the orientation of the prey (Chapter 3). For simultaneous prey encounter, the hang was also a decision point allowing the fish to choose between the prey, which resulted in the time spent hanging being longer than when prey were encountered sequentially (Chapters 6 & 7).

As the size of the prey increased in relation to fish size, the hang behaviour was more likely to occur (Chapter 3). This increased likelihood appeared to be related to a greater need to assess the physical properties and orientation of the prey, as large prey were required to be swallowed head first and ventral side up (Chapter 3). It has been demonstrated elsewhere that fifteen spine stickleback hover a short distance away from the prey in order to increase capture success by directing the attack at the head (Kaiser *et al.*, 1992a). In the case of the threespine stickleback, it was found that including a hang in the behavioural sequence resulted in a greater probability of successful prey capture (Chapter 3). This was an increasing function of fish size and prey size. The constraint of prey size in relation to the jaw size of the fish was therefore one determinant of the fishes behavioural response. The orientation of relatively small prey was of low importance to the fish, hence hanging was less frequently observed, although hanging did occur more often as the stomach fullness increased, which resulted in the feeding sequence becoming more complex (Chapter 7). This may have been an expression of doubt on the part of the near satiated fish as to whether to attack these prey or not, related to the need to acquire food.

The occurrence of the hang behaviour was therefore a function of the size of the prey and the body size and stomach fullness of the fish. Whether the hang is a common component of the predatory behavioural feeding response of fish has yet to be demonstrated.

The decision to eat

Regardless of whether a hang was used during the approach, as shown in Figure 1, the fish went on to handle the prey (Chapters 2, 3, 4, 6 & 7). The initial handling component was determined to be a point where the fish could receive information on the properties of the prey such as for example morphology and taste (Chapter 3). This would have allowed the fish to judge the possibility of gaining energy and thus make a decision to eat or reject the prey. The time taken to make this decision was constant regardless of stomach fullness or fish size, but was dependent on prey type (Chapters 3 & 7). The combination of the size and morphology of the prey appeared to be influential, as sticklebacks took less time to handle *Daphnia* compared to the *Asellus*, which had more appendages and spines (Chapter 3 & 7).

The fish ate to satiation regardless of their body size, size of prey and type of encounter (All Chapters). The critical factors in the choice of prey eaten were, the size of the prey and the size of the fish, in particular the relationship between the prey width and the mouth width of the fish (the PW:MW ratio), and the stomach fullness of the fish.

Costs and Benefits

In order for the fish to be selective in prey choice, it must have had a judgement criterion. This judgement was assumed to have been based on the time costs of handling and ingesting the prey a function of morphological constraints, and the energetic benefit contained within the prey.

If the fish had an empty stomach, any prey size encountered which was within the upper limits of the jaw, was consumed (All Chapters). Prey >0.6 PW:MW were the most beneficial energetically, although the handling time costs associated with them were large (Chapter 3). Prey handling time was found to increase exponentially with an increase in prey size (Chapter 3; also shown by Werner, 1974; Kislalioglu & Gibson, 1976; Hoyle & Keast, 1986; Gill & Hart, in press), which resulted in the larger prey being less attractive due to high time costs. The reason for the increase in handling time appeared to be a function of the size of the prey in relation to the jaw apparatus of the fish. The fish needed to utilise spitting behaviour in order to correctly orientate the prey to ease swallowing (Chapters 2, 3, 4, 5 & 6). This requirement was greater as fish

size decreased, prey size increased and stomach fullness increased (Chapter 3, 4 & 5). It also would have been dependent on how wide the oesophagus of the fish distended.

When encountering prey >0.6 of the fish's jaw width, the probability of successful prey capture decreased as stomach fullness increased. As the probability of success is based on the probability of attacking and the probability of eating the prey (Chapter 3, Dunbrack & Dill, 1988; Gill & Hart, in press), the reduction in success was found to be due to a decrease in the probability of eating these prey. A prey >0.6 of the jaw width was within the consumption capabilities of the fish, but reducing motivation through increased stomach fullness resulted in the fish becoming selective, being less likely to try and eat prey of this size (Chapters 3, 4, 5 & 6).

Prey ≤ 0.6 of the jaw width were eaten with a high probability regardless of stomach fullness (Chapters 2, 3, 5, 6 & 7). This high degree of success appears to be related to there being no need to orientate the prey before swallowing (Chapter 3 & 7). Of the prey ≤ 0.6 of the fish's jaw width, those nearest to the PW:MW ratio of 0.6 gave the best energy return per unit time cost over all levels of stomach fullness (Chapter 3) and allowed the fish to reach the energy requirement in the shortest time (Chapter 2). Nearing satiation, the fish would have received signals via the stretch receptors in the stomach, not to eat any more prey which would have distended the stomach further, therefore only small prey, <0.6 of the fish's jaw width, were able to be fitted in (suggested in Chapter 2 & 4, shown in Chapter 6). This physical constraint meant that the fish had to become very selective, rejecting the prey which were near to the 0.6 PW:MW ratio. There was a dynamic change in the value of each prey size to the fish based on stomach fullness, which was an indicator of the fish's motivation to feed.

Deciding to eat a prey was also a function of the availability of other prey. If another prey was detected whilst the fish was already handling one, the fish had the opportunity to decide to eat the one being handled or go for the other. This decision was dependent on the fullness of the stomach and the size of the other prey (Chapter 6). Simultaneous encounter with prey also affected the handling time. Coming across more than one prey lead the fish to eat more quickly (Chapter 7). This was dependent on satiation, as handling time increased with satiation for small prey (Chapter 7). Fish

have been found to feed at a faster rate when there is an abundance of prey and the fish are hungry (Heller & Milinski, 1979).

The time taken to handle large prey did not change with satiation (Chapter 3 & 4), but it increased when fish handled small prey (Chapter 7). Large prey therefore, had a high time cost associated with them whenever encountered. As the fish got less motivated the time spent consuming a large prey was probably not worth it in terms of risk. Fish are less likely to take risks when they are not hungry (Milinski & Heller, 1978; Godin, 1990). The handling time also became more variable with stomach fullness (Chapters 3, 4 & 7) and this variation has been found to increase with prey size (Hart & Ison, 1991), so the risk that the fish took in trying to eat the large prey would have become increasingly more difficult to determine. With increasing stomach fullness, feeding on smaller prey would have reduced the variability in handling time, resulting in the expectation of the fish becoming risk averse. Risk determination was likely to have been easier when prey handling times were less variable.

Although prey >0.6 of the fish's jaw had a high associated time cost (Chapter 3), when there were no other prey were available and the end of the experimental sequence of prey approached, they were eaten by the fish if there was space in the stomach (Chapter 2). It is hypothesised that a fish will take more of a risk and accept prey >0.6 of the jaw width, if the time left for foraging is short and the daily energy requirement has not been met. This hypothesis is strengthened by the two prey model produced by Lucas (1983), which predicts a broadening of the diet, to include lower quality prey, as foraging time begins to run out.

Feeding on medium to large sizes of *Asellus* meant that the fish gained the required daily amount of energy (Joules) in one feeding session (see Chapter 2 ; Beukema 1968; Rajasilta, 1980; Wootton *et al*, 1980). With small *Asellus* and *Daphnia*, the stomach was filled to its limits but the fish may not have received the daily energetic requirement in one feeding bout (see Figure 8, Chapter 2). This meant that the fish would have needed to forage longer to reach the requirement.

It was found that it took the fish about twice as long to feed to satiation on

Daphnia than on the large *Asellus*, which were >0.6 of the fish's jaw width (Chapters 4 & 7). Hart & Connellan (1984) reported that Pike (*Esox lucius*) ate for longer when feeding on small prey. It has been found that rainbow trout (*Salmo gairdneri*) will increase the size of their meals and the frequency of feeding to maintain daily intake (Grove *et al.*, 1978). The amount of digestible energy available is also dependent on prey type (Kaiser *et al.*, 1992b). Fish have been found to eat more and process what is in the stomach faster if the diet is low energy (Holmgren *et al.*, 1983). As the sticklebacks were constrained by their stomach capacity, they were not able to forage all of the time. Only after some prey had passed into the intestine would the fish have been able to feed again. The overall trade-off was that eating small prey was easy, shown by the high probability of success in Chapter 7, but the fish needed to spend longer feeding in order to reach the daily requirement. Therefore, the time available for alternative activities was reduced and the exposure to possible predation would have been greater.

For all the experimental situations that the fish encountered their response was to feed to achieve a full stomach. The prey which were the best to choose in order to fill the stomach, in terms of time and energy costs and benefits, were those nearest to the 0.6 prey width:mouth width ratio, although the satiation level was the overriding factor which controlled the fishes decision.

Success of prey capture

Even if the fish had made an initial choice to eat the prey, the success of this decision was again dependent on the interaction between prey size, fish size and stomach fullness. Increasing prey size and decreasing fish size meant that the physical mouth constraints of the fish were tested. Although the fish may have wanted to consume these prey, the physical size of the prey may have been too great (Chapters 3 & 4).

The presence of a competitor always increased the chances of the prey being stolen, hence the probability of successful consumption was lowered (Chapter 5). The relationship between the size of the prey and the fish was again found to be influential. With prey increasing in size, the fish were more likely to spit them out for reorientation (Chapters 2, 3, 4, 5 & 6), hence the chances of the prey being stolen were greater (Chapter 5). Depending on competitive ability, some fish did not feed to satiation although they

were offered sufficient prey to meet the criterion (Chapter 5). Due to the interference apparent between the two competitors the energy intake rate was reduced (Chapter 5). The expectation was that the poorer competitors would have fed to stomach fullness over a longer period of time if they had been presented with the opportunity. It is therefore suggested that the fish had a delayed energy intake due to the superior competitor monopolising the immediate food resource.

After the prey had either been eaten, rejected or was no longer available, the fish reverted back to the behavioural searching mode unless the stomach was full and no more prey could be eaten (Chapters 3 & 7). If searching was reverted to, the cyclical sequence of behaviour began anew but as the process was dynamic the effects of the variables at the stages shown in Figure 1 were often different in the ways already outlined. The behavioural response of the fish needed to be examined anew due to the dynamic changes related to the level of satiation.

Relation to Foraging Theory

To relate the findings of this study to general predictions for fish foraging, the results can be interpreted in the context of optimal foraging theory.

The changing value of prey

The results in this thesis clearly show the need to apply dynamism to any foraging situation.

To understand prey choice, we assume that the predator will rank the prey in accordance with the energetic and time costs and benefits of each prey. By taking the energetic content of the prey and dividing by the handling time we obtain a measure by which the prey can be ranked, this is the profitability measurement (E/H) (see Stephens & Krebs, 1986 for details). The energy content of a given prey does not alter over time, however the prey handling time has been found to increase with satiation (Chapter 7; Werner, 1974; Kislalioglu & Gibson, 1976; Croy & Hughes, 1991b). This increase only occurs near to satiation (Chapter 7; Werner, 1974), and is a function of prey size (Chapters 4, 7). The predicted profitability values will therefore remain the same until just prior to satiation.

The results throughout this thesis indicate however, that the profitability measurement of prey (E/H) is too simplistic as it does not take account of changes in satiation of the fish. It appears from the studies within this thesis that, when the fish had an empty stomach the most valuable prey was the largest upto the limits of the jaw width (Chapter 3). Large prey were valuable because of the immediate need to acquire food to reduce the energy deficit. The bigger the prey the greater the energy return upto the physical limits of the feeding apparatus. After eating a large prey the fish were less likely to suffer an energetic shortfall, so with the immediate need to reduce the energy deficit suppressed, the fish were able to concentrate on reducing time costs and risk, by choosing prey which were ≤ 0.6 of the jaw width. These prey would have been more appealing to the fish as they did not need to be orientated and the handling time was relatively short (Chapter 3) and less variable compared to the larger prey (Hart & Ison, 1991). The actual mechanism reducing motivation was probably physiological, perhaps being the sensation of the gut filling or the release of digestive chemicals or enzymes. Tugendhat (1960) found that the first few consummatory responses of the stickleback have a disproportionately large effect in reducing the motivation.

Approaching stomach fullness, the most profitable prey was unlikely to be able to fit into the stomach (Chapter 6). Therefore the most valuable prey to the fish at this stage would have been the small prey, as these were able to fit into the remaining space (Chapter 6).

This thesis therefore indicates that the calculation E/H is not a reliable measure of prey profitability. The calculation should be modified by some factor which is a function of the stomach fullness of the fish, to better represent the value of the prey to the fish.

It is hypothesised that due to food requirements and stomach capacity constraints of the fish, selectivity of the prey changes as motivation wanes, with larger prey being selected against as stomach fullness increases. An interpretation of this dynamic change in the value of the prey to a fish is shown in Figure 2. This interpretation follows an individual fish feeding to stomach fullness in order to reach a daily energy

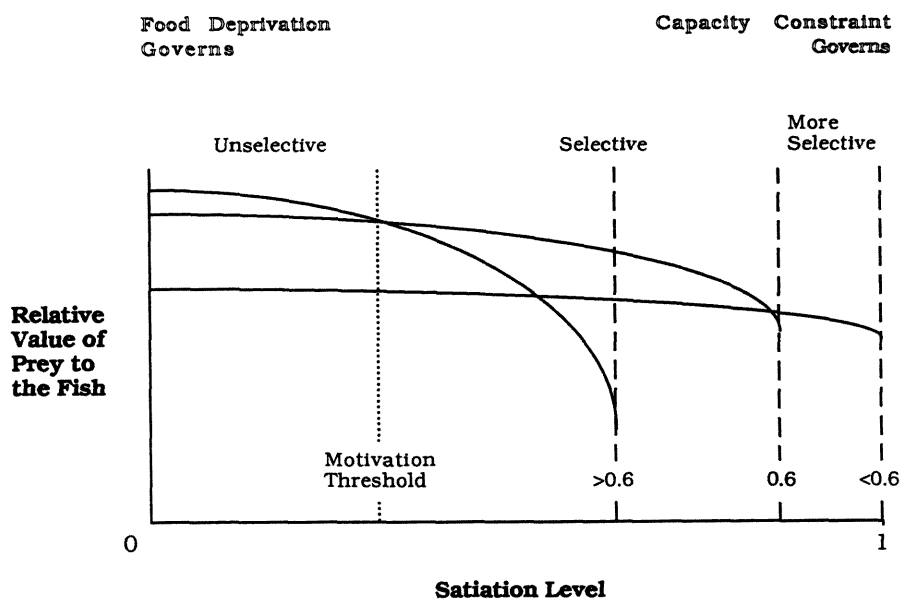


Figure 2. The dynamic change in the value of the prey to the fish, estimated to be based on the energetic and time costs and benefits and the fish's motivation to feed. The dotted line shows the arbitrary point where the amount of food eaten reduces the motivation sufficiently for the fish to become selective. The variable points where the fish have changes in selectivity are shown. Broken lines represent the capacity constraints of prey at the three prey width:mouth width ratios. A satiation level of 0 represents an empty stomach, a level of 1 a full stomach.

requirement. The prey which are 0.6 of the jaw width of the fish are regarded as the best average rate maximising prey. The values of all the prey are dependent on their respective energy benefits and handling time costs and the motivational state of the fish.

It can be seen from Figure 2, that when the fish has to make up a food deficit, which is when motivation is highest, the prey >0.6 of the jaw width of the fish are of the greatest value (Chapter 3). These prey give the greatest energy return regardless of the handling time cost. At this stage the fish is constrained by the demand for food. As there is a high variability in the handling times of these prey, we would expect the fish to be risk prone in order to gain them. The fish is expected to be unselective and accept any prey which it comes across, as shown in Chapter 6. Being risk prone when hungry is a common feature of a foraging animal (Milinski & Heller, 1978; Caraco, 1980, 1981, 1983; Barnard & Brown, 1985; Godin, 1990).

As the urge to acquire food reduces, represented by the arbitrary dotted line in Figure 2, the fish are able to be more economical in prey choice and so become selective. The large prey lose value quickly as they are costly in terms of the time spent dealing with them, so are less likely to be selected. The fish is expected to have a preference for those prey which can be obtained successfully and which give the best return for the amount of effort, the size of these prey are 0.6 of the jaw width of a fish which feeds on whole prey. Preference for prey of this size has been shown in other species of fish by Scott (1987) and Prejs *et al* (1990).

The stomach of the fish imposes a limit on the number of each prey size that can be eaten. This capacity constraint is reached earlier for larger prey. As the stomach fills the requirement for sustenance becomes less, which means that the value of all prey reduces, but the rate of reduction is a function of the size of the prey. It can be seen that the smaller the prey the less variable their value to the fish over all levels of satiation, as they have a short handling time and can be eaten without the need for orientation whenever encountered (Chapter 3). At some point the stomach will not be able to take anymore of the most preferred prey. The constraint of stomach capacity means that the fish will only be able to select prey <0.6 of the jaw width. At some further point, the fish

will not be able to take any more of these prey and the stomach will be full.

Predicting prey choice

Obviously, the dynamic nature of prey choice imposed due to changing satiation has consequences for any prediction of prey choice (Hart & Gill, 1992; Godin, 1990). Predictions from models need to account for the changes in satiation level of the predator and in particular the degree to which the prey fills the stomach. A large prey changes the stomach fullness dramatically, hence predicting the changes in prey choice needs to use stochastic dynamic programming methods (S.D.P) (Mangel & Clark, 1988; Hart & Gill, 1992). Using static models does not successfully predict the diet choice when there is large change in the satiation level (Hart & Ison, 1991).

As the stomach of a fish fills, the amount the stomach stretches will be related to the size of the prey. A number of small prey will need to be eaten to stretch the stomach to a degree comparable to one large prey. Therefore for small prey, the changes in prey choice due to satiation are likely to be gradual over a long period of time. Predicting prey choice in this case can be approximated with static models (Werner & Hall, 1974; Hart & Gill, 1992). When small prey are being considered their profitability tends to increase with prey size (Chapter 1; Milinski, 1982; Ranta & Lindström, 1990). In terms of Figure 2, the curves for the value of these prey will not drop off very quickly and the more profitable prey will have a greater value than the smaller prey until the capacity constraint of the larger prey is met. The selective zone, in Figure 2, will be wide which means that the total feeding period will be longer than for large prey, with the prey most likely to be eaten being the most profitable.

When predicting prey choice, the size of the prey is an extremely important variable as it affects the prey handling times and the level of satiation. Predictions of choice are more likely to be successful and easier when the prey sizes used are small, as the morphological constraints of the predator and prey are minimised. The only constraints are the motivational state of the predator, in terms of whether or not it needs to avoid an energetic shortfall, and the capacity constraint of the predator's stomach. To use the simple profitability judgement of E/H to predict prey choice, a level of stomach fullness should be chosen which represents a level of motivation at which

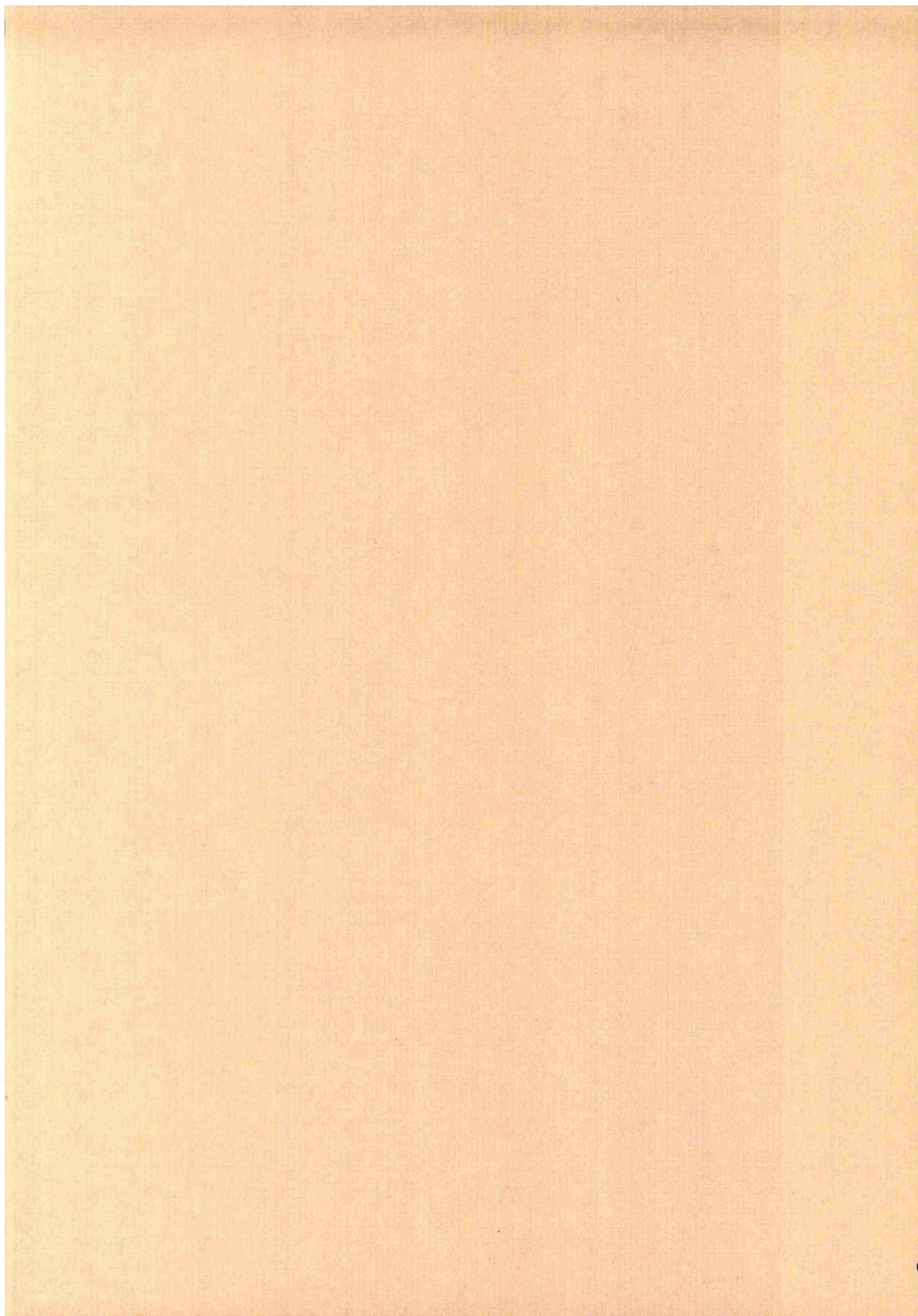
the fish can be genuinely selective and not influenced by the two extreme constraints.

Most models of diet choice deal with a single predator (Stephens & Krebs, 1986). This however, is only applicable to solitary species, whereas many fish are found together and nearly all fish are likely to suffer from competition whether inter or intra specific. Predicting the diet choice of a feeding fish in the wild needs an awareness of the fish's competitive ability, which is a function of its swimming ability, reaction time and jaw size in relation to the prey.

In terms of the fish encountering more than one prey at a time, again the motivational level will be a determinant in whether prey are eaten or not. The prediction from this study is that the optimal sized prey will not be preferentially chosen unless the stomach fullness is greater than the degree of fullness which leads to a deficit. After this the fish is likely to be selective until the stomach approaches satiation, with the fish then becoming even more selective. How increasing the prey encounter rate effects the selection of simultaneously encountered prey with changing stomach fullness is unknown? The studies here would still suggest that the prey eaten will be the nearest to the fish when the stomach is empty, however the size of the prey may be important.

Conclusion

The process of obtaining food is a fundamental necessity of any animal in order to reach a daily energetic intake and to grow and reproduce. This study has shown, just from the point of view of the predatory fish, that the behavioural responses required to obtain food and the choice of which prey is eaten are dynamic and dependent on the interaction of external factors relating to the prey and competitors in relation to the fish itself, and internal factors based on motivational state and energetics.



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