

**The Feeding Ecology and Behaviour
of Whiting (*Merlangius merlangus* L.)**

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

by

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ABSTRACT
The Feeding Ecology and Behaviour
of Whiting (*Merlangius merlangus* L.)
by Iain J. Staniland

The development of multispecies fisheries models has led to a need for improved information on the diet composition and consumption rates of fish. This study was an attempt to investigate the feeding ecology of whiting, with an emphasis on how the fishes' behaviour might influence its diet.

Analysing the stomach contents of North Sea whiting, found that as whiting increased in size they switched from a crustacean, to a fish dominated diet, and the average size of prey eaten increased. Smaller trawl caught whiting were found to have a higher instance of regurgitation. The whiting appeared to be exploiting one prey species in an area. The majority of fish stomachs sampled at a station contained the same prey type.

Studies showed that sandeels were evacuated from the stomachs of whiting at a higher rate than prawns. When fed in combination the evacuation rate of sandeels increased, and the rate of prawns decreased. It was postulated that these evacuation rate changes could be because of stomach packing and/or the prawns' abrasive exoskeleton.

Video analysis of whiting feeding on shrimp studied the effects of changing the predator to prey size ratio, stomach fullness and experience. As the predator to prey size ratio increased the handling time decreased, and probability of successfully eating a shrimp increased. As the fish gut filled up the probability of a strike being successful decreased and handling time increased. With increasing experience the hunting sequence of the fish became simplified and the probability of a strike being successful increased.

Results from the video analysis were used to develop a stochastic dynamic program of whiting feeding. The program was used to model the optimal prey choices of whiting feeding on two sizes of shrimp. In the model the probability of success was found to be the most important factor in determining the optimal shrimp size. The time spent in handling the shrimp was also found to be important.

It was concluded that a more behavioural approach could help in understanding why fish eat what they do and aid investigations into the problems of fish species interactions.

For Mum and Dad

Acknowledgements

Thanks go to Dr. Paul Hart and Dr. Peter Bromley for setting up the project and guiding me through the dark labyrinth of post graduate research.

I would like to thank all the people at Lowestoft for the assistance they gave me from catching my fish to putting up with my dodgy jokes. On the fish side I thank Terry Watson for passing on his extensive knowledge of fish guts, Matt Harvey for his fish keeping and messenger service. On the computing and Maths side Richard Ayers, Phil Welsby and Laurence Kell were superb.

Socially there are so many who fed this starving student; Debbie and Andy "barbecues 'R' us", Kev and Jimmy "Reeves and Mortimer", Mark 'I haven't had my third wave yet' Scriven (+ all the little Scrivens) and last and certainly not least 'The love Buffalo'. And to everyone else in the most Easterly Place in England, have a Bustard on me and remember 'it is not the end of the world but you can see it from there'.

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CONTENTS

CHAPTER 1 : GENERAL INTRODUCTION

INTRODUCTION.....	2
The biology of the whiting.....	2
Multispecies fisheries management	5
The current study	6

CHAPTER 2 : FEEDING ECOLOGY

INTRODUCTION.....	9
MATERIALS AND METHODS.....	12
Data analysis.....	16
Stomach state.....	16
Diet	17
Prey Size.....	17
Feeding patterns.....	17
Foraging habitat.....	18
Continuous sampling.....	19
RESULTS	20
Importance in the Diet.....	22
The predator prey size relationship	26
Feeding patterns.....	28
Location of Feeding	32
Temporal changes in feeding.....	33
DISCUSSION	35
Regurgitation	35
Importance of prey.....	36
Prey size	38
Method of Feeding.....	39
Foraging Habitat	40
Feeding patterns.....	41

CHAPTER 3 : GASTRIC EVACUATION

INTRODUCTION.....	44
MATERIALS AND METHODS.....	49
Analysis.....	52
Individual lengths and weights.....	53
RESULTS	54
Gastric evacuation model	54
Prey type.....	56
Mixed vs Single diet.....	59
Individual Weights and Lengths	61
Single vs mixed diet.....	62
DISCUSSION	68
Mixed Diet	71

CHAPTER 4 : FEEDING BEHAVIOUR	
INTRODUCTION.....	74
MATERIALS AND METHODS.....	76
Experimental procedure.....	78
Analysis.....	81
Experiment one.....	83
Experiment two.....	84
DESCRIPTION OF BEHAVIOURS.....	85
The Fish.....	85
Novel behaviours.....	89
RESULTS.....	91
Experiment 1.....	91
Stomach Fullness.....	91
Fish Size.....	102
Experience and learning.....	103
Experiment 2.....	109
Shrimp Size.....	113
Fish Size.....	117
Discussion.....	119
Experiment 1.....	119
Stomach fullness.....	120
Fish Size.....	121
Experience and Learning.....	122
Experiment 2.....	119
Shrimp Size.....	124
Fish Size.....	126
CHAPTER 5 : FEEDING MODEL	
INTRODUCTION.....	129
THE MODEL.....	132
Forward iteration.....	136
Parameter Values.....	138
Interpolation.....	140
TESTING THE MODELS.....	142
Fish size models.....	142
The small fish model.....	142
The large fish model.....	144
Testing the effects of the handling and success functions.....	147
Probability of Success.....	147
The larger difference model.....	147
The fixed difference model.....	148
Handling Time.....	149
The linear handling model.....	150
The fixed handling model.....	150
Testing the Robustness of the Model.....	151
Analysis.....	152
RESULTS.....	155
Investigating the Influence of Fish Size.....	155
Small fish model.....	155
The small fish model with reduced stomach size.....	160
The large fish model.....	162
Investigating the Influence of the Probability of Success Function.....	166

The larger difference model.....	166
The fixed difference model	171
Investigating the Influence of the Handling Time Function.....	175
The linear handling model	175
The fixed handling model.....	179
Testing parameter values	183
DISCUSSION	184
The effects of energy and stomach state.....	184
The effect of fish Size	185
The small fish model	185
Large fish model	185
The Influence of the Probability of Success Function.....	186
The Influence of the Handling Time Function.....	187
The Robustness of the Model	187
Conclusions	188

CHAPTER 6 : GENERAL DISCUSSION

DISCUSSION	191
Search and Encounter	192
Attack and Strike.....	194
Handle and Swallow	194
Whiting to prey size ratio	196
Stomach fullness.....	198
Whiting interactions	200
Conclusion.....	201

APPENDIX I

APPENDIX II

BIBLIOGRAPHY

CHAPTER 1

GENERAL INTRODUCTION

"The truth is that those who have never entered upon scientific pursuits know not of the poetry by which they are surrounded"

Herbert Spencer

INTRODUCTION

The biology of the whiting

The whiting *Merlangius merlangus* (L.) (previously *Gadus merlangus*) belongs to the cod family, the Gadidae, of the order Anacanthini (Wheeler 1975). It is a typical round fish with the greatest girth at the shoulders and has a large mouth with a small barbel under the lower jaw (Plate 1.1). The median fins, three dorsal and two ventral are large. The pelvic fins are situated anterior to the pectorals, just posterior to the opercula. All the fins have soft rays, the first two of which are free at the distal end in the pelvic fin.

The colour of the whiting's dorsal surface, varies from sandy brown to dark blue, but the sides are always silvery with faint golden brown longitudinal stripes, and the belly is white. Whiting have a well developed muscular stomach that can distend to accommodate prey (Plate 1.2). Few whiting in the North Sea grow larger than 50cm (Wheeler 1975). Being a shallow-water species whiting are found inside the 200m contour on the north European, west Mediterranean, and Atlantic coasts. Young fish (up to 52mm) remain inshore in the nursery grounds for up to 1 year (Nagabhushanam 1964) and are often associated with the jellyfish *Cyanea lamarckii* and *Rhizostoma pulmo*.

Few of the whiting breeding grounds in the North Sea are known (Figure 1.1). The spawning season extends from February to June, but peaks later with increasing latitude. Pawson (1974) observed that, fish spawning in the laboratory holding tanks usually spawned in May and June. The single spawning season period is about ten weeks and each female produces between 1-3 million pelagic eggs of about 1.22 to 1.12mm in diameter (the number is dependant on the size of the female) (Hislop 1975).

Whiting are closely related to cod (*Gadus morhua*) (Wheeler 1975) and generally found in the same habitats. In the North Sea their food consists mainly of fish, crustacea, and some polychaetes. It has been estimated by Hislop *et al* (1991) that North Sea whiting ate a total of 730 000t of fish in 1981 making it one of the most important piscivorous fish. The large



Plate 1.1: A whiting, *Merlangius merlangus*.
(The measuring board is graduated in millimetres)

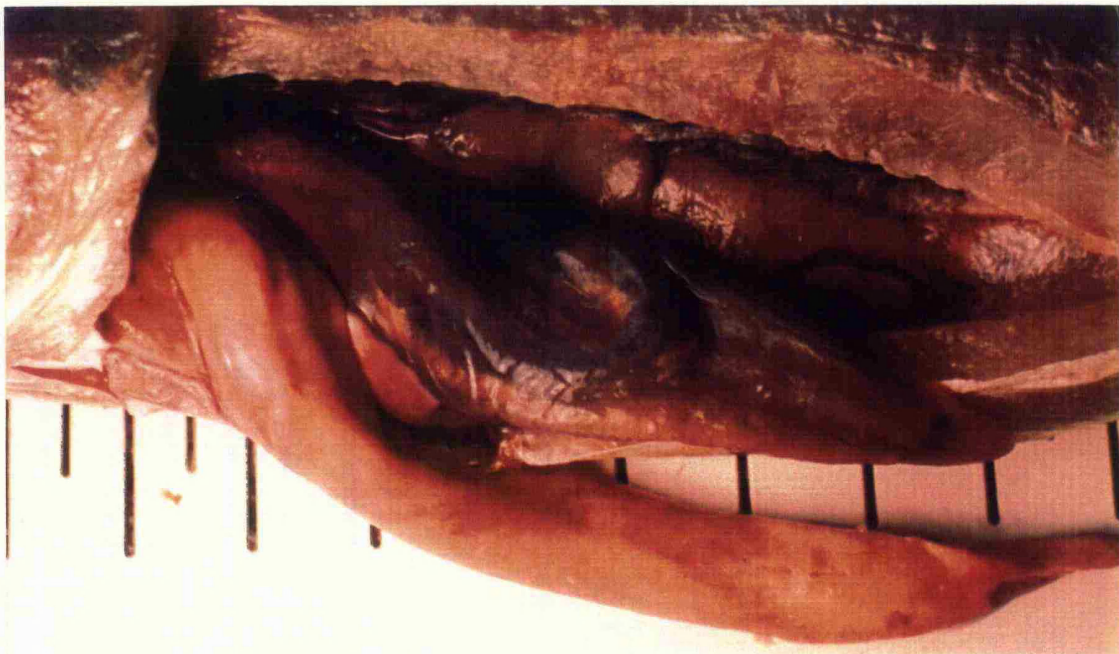
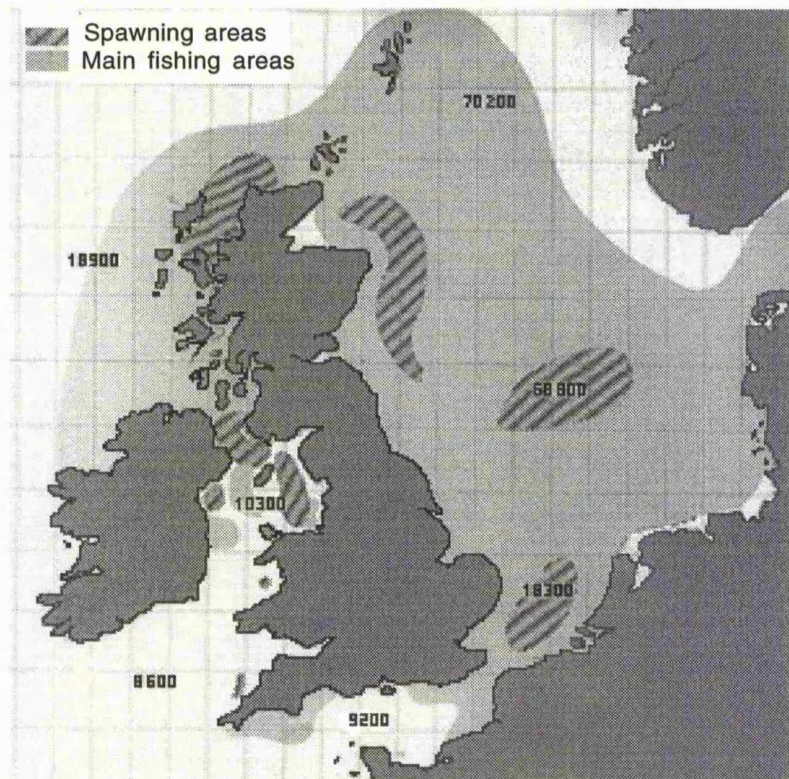


Plate 1.2: The dissected body cavity of a maturing male whiting with a distended stomach full of sandeels. The testes are visible at the top of the cavity and the liver has been laid out of the cavity at the bottom of the plate. (N.B. The large graduations are 1cm apart)

weight of fish eaten by whiting is attributable partly to their diet, which includes a high proportion of fish, and partly because they are very abundant throughout the North Sea.

Figure 1.1: The main spawning and fishing areas for whiting in the North Sea (The numbers are the average annual catch in tonnes for the period 1973 - 77) (after Anon 1981)



The North Sea can be divided into a northern and a southern area on the basis of water temperature and depth (Anon 1981). As whiting increase in size there is a gradual shift in diet composition, from crustaceans to fish, this trend is much more significant and complete in the northern area. Molluscs and polychaetes represent a relatively constant component of the whiting diet throughout the size range in the North Sea though the proportion is generally insignificant in the north (Casey *et al* 1986). The smaller maximum size which whiting achieve compared to cod means that most of the commercially exploited fish that whiting eat are in age classes 0+ and 1+.

Seasonal variation in the food of whiting has been linked to changes in prey abundance. As prey species become seasonally more important so they also increase in importance in the diet of whiting. Hislop *et al* (1991)

found there was no difference in the incidence of empty stomachs throughout the year though there was a higher incidence of regurgitation in the first two quarters of the year.

The specific areas in which whiting feed are highly variable and depend on factors such as; time of year, water temperature, time of day and food abundance (Pawson 1974).

Multispecies fisheries management

The management of fish stocks like whiting, has in the past been done using single species models. Parameters such as, growth, mortality and reproduction have been used to predict population size and the maximum sustainable yield (Pitcher and Hart 1982). Single species models that have been developed include; surplus yield or Schaefer models (Graham 1935, Schaefer 1954), virtual population analysis (Fry 1949, Gulland 1965) and cohort analysis (Pope 1972). A major problem with single species assessments is that they ignore the affect fish species have on each other through competition and predation. When these models were first developed a smaller number of species were commercially harvested and the interaction between species was not a significant factor. As the number of species that are commercially exploited has increased so has the influence of inter-specific interactions e.g. predation and competition for food. The collapse of the North Sea herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) was thought to have caused a subsequent increase in the number of gadoids (Cushing 1980). Jones and Richards (1976) postulated that this increase in the gadoid numbers was mainly because of a decrease in the competition for food. There were less herring and mackerel feeding and so more food was available for other species.

The problems of single-species' assessments lead to the development of multispecies models that take a more ecological approach (Andersen and Ursin 1977, Pope 1979, Sparre 1980). These models are related to the Beverton and Holt dynamic pool model and Gulland's single species virtual population analysis, but account for changes in natural mortality that are due to predation. This extra component of natural mortality is estimated for each age of each species included in the model. For this

estimate to be accurate an extensive knowledge of the diet composition of component species and their consumption rates is required.

The composition of the diet is usually quantified through sampling fish stomach contents at sea. In the North Sea a large international stomach sampling project (Anon 1980) was carried out in 1981 to assess the diet of whiting (Hislop *et al* 1991), cod (Daan 1983), saithe (*Pollachius virens*) (Gislason 1983) mackerel (*Scomber scombrus*) (Mehl and Westgård 1983) and haddock (*Melanogrammus aeglefinus*) (De la Villemarqué, 1985). Estimating the consumption of fish species has been done through stomach content data gathered in the field or through the measurement of evacuation rates. The basic reasoning behind the evacuation studies is that the digestion rate of the food is proportional to the ingestion rate, i.e. input equals output (Tyler 1970, Talbot 1985, Bromley 1994). Different models have been used to estimate the rate of consumption of different fish species (Table 1.1).

Table 1.1: Examples of three different models used to estimate the consumption rates of fish species.

Name	Equation	Author
Linear Model	$R = \frac{2 \times S}{D}$	Daan (1983)
Exponential Model	$R = c1 \times S$	Elliot & Persson (1978)
General Model	$R = \frac{(2 - c2) \times S}{(1 - c2) \times D}$	Jobling (1981)

Where R = ration

S = average stomach content weight

D = digestion time

$c1$ and $c2$ = constants

The current study

A problem with many of the studies used to investigate the interactions of fish stocks is that they tend to isolate one aspect of the feeding and ignore others. The investigations are usually concerned with sampling in the

field, or with laboratory experiments measuring evacuation rates. They also tend to concentrate on the commercially exploited sizes of fish and their consumption of other commercially important species. Singh-Renton (1990) in a previous study at the Fisheries Laboratory Lowestoft investigated the gastric evacuation of small whiting and cod and sampled their stomach contents in the southern North Sea. The Singh-Renton (1990) work concentrated on the common invertebrate prey species as food items. The intention of the study reported here was to continue on from the previous work but also to bring in other aspects of the feeding ecology of whiting. It was hoped that the use of behavioural analysis could provide a more specific picture of whiting feeding and lead to new ways of approaching the problem of species interaction. As well as quantifying what whiting predate upon in the North Sea the aim was to gain an insight into why they choose what they do.

The thesis is arranged into six chapters. Chapter 2 deals with the feeding ecology of small whiting in the North Sea with particular reference to the northern area. Chapter 3 details experiments on the gastric evacuation of two types of prey sandeels (*Ammodytes spp.*) and prawns (*Pandalus spp.*). This chapter also investigates the affect of using more than one prey type in a test meal. The fourth chapter is concerned with the hunting and handling behaviours used by the whiting to capture their prey. The experiments described used the brown shrimp (*Crangon crangon*) to look at the affects of learning, and prey size on the whiting's feeding behaviour. Chapter 5 describes the development and testing of a computer program designed to model the choices of whiting in relation to two different sizes of prey. The final chapter is a general discussion synthesising the findings of the current study in the context of previous work.

CHAPTER 2
FEEDING ECOLOGY

“The most incomprehensible thing about the world is that it is
comprehensible”

Albert Einstein

INTRODUCTION

To complement laboratory and theoretical studies of whiting feeding ecology, the diet and feeding patterns of whiting in the wild were investigated. Direct observation of fish feeding in their natural habitat is very difficult in most situations, especially marine fish. Stomach content analysis is the practical alternative as it is relatively cheap and easy, but there are problems. Some fish masticate their food and consequently their stomach contents are hard to separate and identify (Kennedy 1969). Prey items that are digested quickly leave little or no identifiable remains in the stomach. This can cause their contribution to the diet to be underestimated. The relative abundances of food items in the stomach may not reflect the proportions in which they were ingested (Macdonald *et al* 1982).

The analysis of stomach contents can be done either qualitatively or quantitatively. Qualitative analysis such as recording the number of stomachs in which a prey item occurs in can be useful in determining the breadth of the diet. In whiting this has already been studied for many areas e.g. The North Sea (Jones 1954), Manx coastal waters (Nagabhushanam 1964). The contribution of prey items to the diet can be assessed using quantitative methods. There are three main ways of doing this; numerical, gravimetric and volumetric (Hyslop 1980). Numerical analysis involves counting the number of individuals of each food type (Frost 1954, Cranmer 1986). This technique is useful when the food items can be easily identified and separated into individuals. If food in the stomach does not separate into discrete individuals, or the individuals are very small, numerical analysis can be difficult. In gravimetric analysis food items are divided into taxonomic groups and weighed, using either wet or dry weight (Daan 1981). Unlike numerical analysis individuals do not need to be separated and so non discrete items and micro-organisms can be measured easily. There are two methods of volumetric analysis; direct and indirect (Hyslop 1980). Both techniques are similar in methodology to gravimetric in that taxonomic groups are measured. In direct analysis the volume of food groups is measured by displacement (Ricker 1941) and in indirect analysis they are compared against blocks of known volume (Starostka and Applegate 1970).

An important part of feeding is the type of food taken and any patterns in feeding intensity throughout the day. These patterns can be driven by light intensity or availability of prey items due to migrations. Diurnal patterns can be investigated by sampling sequentially at short time intervals over the same area. The presence or absence of empty stomachs can give a picture of feeding intensity. Periods of feeding intensity can also be detected by the presence of fresh (showing little or no signs of digestion) food items in the stomach.

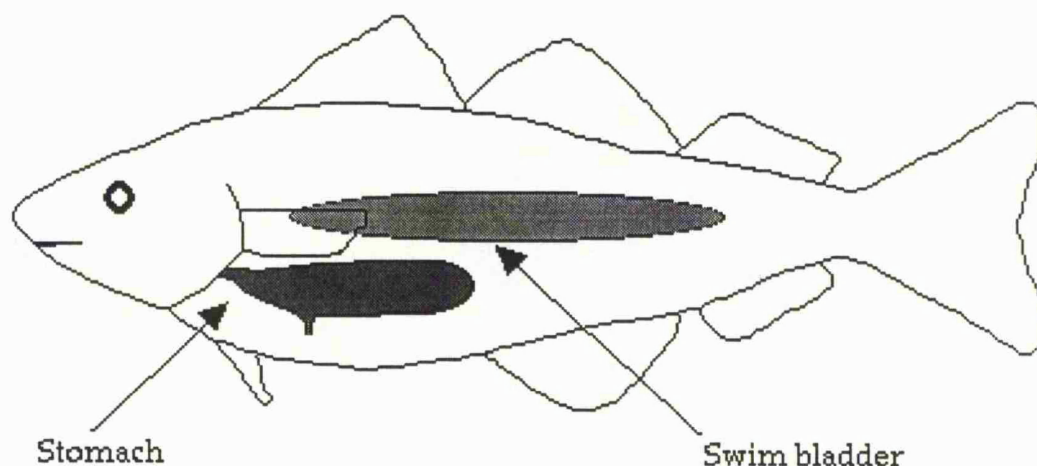
In the collection of fish for stomach sampling a number of methods have been used including, rod and line, passive and active netting. Using rod and line, full or nearly full fish are under sampled as they are less likely to be feeding. Biased sampling of fish is also a consequence of passive netting, as feeding and active fish have a greater chance of being caught in the nets. There is also the problem of continued digestion of stomach contents after the fish has been caught in the net which can lead to underestimation of stomach fullness (Hayward *et al* 1989). Trawling is an active method of sampling fish and does not have the drawbacks of continued digestion or bias sampling, though some size bias does occur. Sampling by trawling also has problems, as prey can be consumed in the trawl (Bromley 1990). With all of these sampling techniques regurgitation of stomach contents can occur. This regurgitation if undetected or ignored can bias subsequent calculations of consumption rates, diurnal feeding patterns and the importance of food items in the diet.

The main cause of regurgitation by fish sampled with a trawl is the effect of the pressure difference when fish are brought to the surface (Bowman 1986). Expansion of gas in the swim bladder as the external pressure decreases enlarges the bladder. The swim bladder is located above and behind the stomach (Figure 2.1) and so as it expands it pushes on the stomach forcing the food towards the oesophagus.

Piscivorous fish which eat large prey have a distensible oesophagus and regurgitate more frequently than fishes which feed on small prey (Bowen 1983). Whiting being physoclistous and having a digestive tract adapted to eating large prey (Hislop *et al* 1991) are often found to be in a regurgitated state when trawled from depth. The effects of pressure can cause the extremes of total inversion of the stomach and/or rupture of the swim bladder. The weight of fish caught in the trawl can also cause regurgitation

as the body cavity is crushed and the stomach contents are forced out. Fuller stomachs are affected to a much greater extent by these two situations where the stomach is crushed. Ignoring stomachs in a total or partial state of regurgitation can lead to underestimation of feeding rates.

Figure 2.1: A diagram to show the position of the whiting stomach in relation to its swim bladder



Stressing fish is also known to cause the expulsion of food from the stomach especially recently eaten items. Whiting caught in the laboratory have been observed to occasionally regurgitate when caught in hand nets or when removed from the water (pers. obs.). Rates of regurgitation can be affected by such factors as, temperature, time of day and time of year (Bowman 1986).

Feeding by predators in the trawl can affect stomach contents and subsequent analysis (Bromley 1990). Prey that would ordinarily not be available to the fish may be ingested when they come into contact in the net. Diurnal periods of feeding intensity may be masked as fresh prey are found in stomachs when the fish would not normally be feeding. Where the fish are feeding may also be obscured as benthic prey could be found in stomachs of pelagic feeding fish and vice versa. The size of the problem is species and size dependant (Lancroft and Robinson 1979). Whiting are prone to feeding in the trawl though it is less prevalent in smaller fish as their prey are generally too small to be caught in the trawl.

MATERIALS AND METHODS

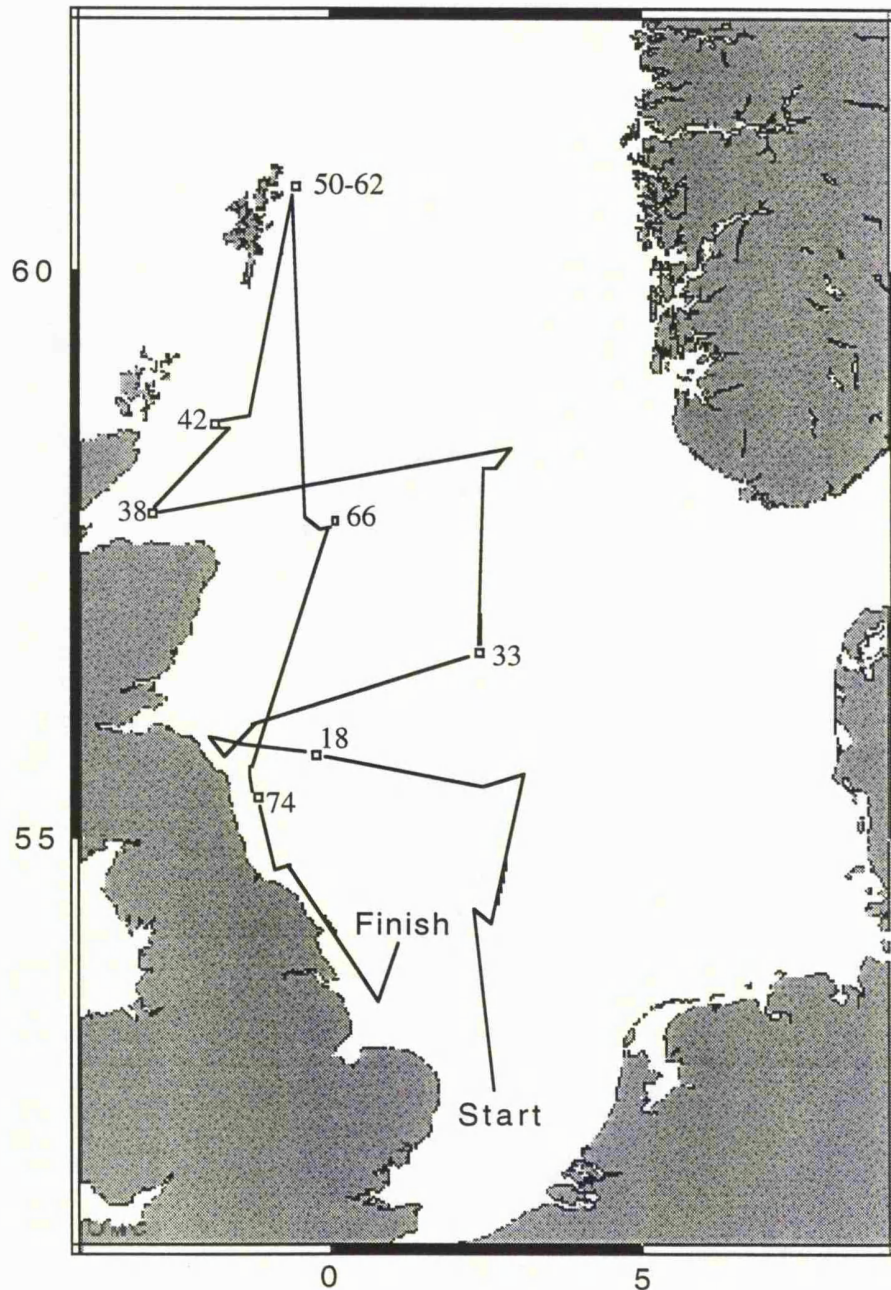
Samples of whiting were collected on a cruise of the *R.V. Cirolana* between 19 February and 10 March 1991. The fish were caught using a Portuguese High Headline trawl rigged for rough ground with 20cm rubber bobbins running the length of the footrope and with 16m of chain along each wing. The cod end was lined with 20mm mesh. Standard daylight trawls of two hours were used, shot over rough and smooth grounds. The first station of the cruise was at Smiths Knoll (52.73°N 2.38°E) from where the ship worked northwards with the most northerly station off the north-east coast of the Shetland Isles (Figure 2.2, Table 2.1).

Samples were collected as whole fish under 35cm as opposed to just stomachs because time did not allow for dissection on board. These fish were collected after the MAFF staff had taken their samples, but only when a sufficient number of fish were left (>10). The fish samples were placed in wax boxes and immediately blast frozen for later analysis in the laboratory.

Table 2.1: The dates and details of the trawls at each of the stations where whiting samples were taken. (N.B. The depths are given in meters)

station no.	date	shot time	haul time	shot depth	haul depth	shot latitude	shot longitude	haul latitude	haul longitude
18	22/2/92	11:32	13:03	72	82	55.84	1.76	55.76	1.65
33	25/2/92	17:02	18:33	80	79	56.66	-2.22	56.75	-2.23
38	27/2/92	14:24	15:34	78	78	58.03	2.35	57.99	2.5
42	28/2/92	11:15	12:45	99	110	58.71	1.72	58.76	1.56
50	1/3/92	18:14	20:14	113	103	60.85	0.46	60.73	0.54
51	1/3/92	22:15	24:00	107	113	60.73	0.52	60.83	0.44
52	2/3/92	02:02	03:42	108	106	60.82	0.45	60.73	0.53
53	2/3/92	06:02	08:02	105	114	60.72	0.53	60.83	0.45
54	2/3/92	10:09	11:48	106	110	60.74	0.54	60.83	0.45
55	2/3/92	14:02	15:57	107	101	60.82	0.47	60.72	0.55
56	2/3/92	18:08	20:02	104	115	60.73	0.54	60.84	0.45
57	2/3/92	21:59	24:00	104	115	60.73	0.54	60.84	0.45
58	3/3/92	02:00	04:00	107	103	60.82	0.46	60.72	0.54
59	3/3/92	06:07	08:00	100	111	60.73	0.55	60.83	0.46
62	3/3/92	16:16	17:34	105	110	60.82	0.48	60.88	0.59
66	4/3/92	16:51	18:23	115	106	57.85	-0.01	57.79	-0.1
68	4/3/92	10:38	12:38	100	97	55.53	1.15	55.43	1.06
74	6/3/92	06:02	07:59	100	100	55.43	1.04	55.52	1.15

Figure 2.2: Map of the North Sea showing the Cruise track of the R.V. Cirolana.
The locations of the stations where fish samples were taken are shown by the
open squares and numbers. Stations 50-62 were along the same trawl line and
were used for the continuous sampling.



Continuous sampling

Off the Northeast coast of the Shetland Isles there was a large group of predacious gadoids, including whiting feeding mainly on sandeels (*Ammodytes spp.*) (60.85°N 0.46°E). At this location one thirty-six hour survey was undertaken to look at the diurnal feeding patterns of the whiting (stations 50-56, Table 2.1). The survey consisted of six, two hour tows at four hour intervals. Each trawl was shot at the same point on a standard transect line. The fish samples were frozen and handled as previously described.

Laboratory analysis

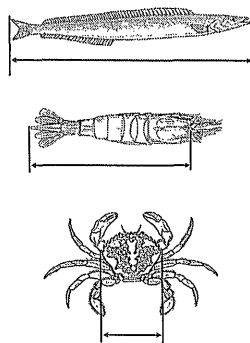
At the end of the cruise the boxed samples were removed and stored at the Laboratory at -24°C until analysis. After overnight defrosting the fish were weighed and measured and were checked for signs of regurgitation. This was easiest when there has been a total or partial inversion of the stomach. These fish were labelled as 'Regurgitated'. The other regurgitated stomachs were divided into two groups those with no food present in the stomach labelled 'Regurgitated' as before, and those with some food remaining labelled 'Part Regurgitated'. These stomach conditions can be distinguished from the two other stomach states i.e. 'empty' and 'food present' by the state of the stomach wall. The stomach is muscular in structure and contracts around the food bolus to provide the mechanical element of digestion (Plate 1.2). When food is regurgitated from the stomach the walls do not contract immediately leaving the stomach in a flaccid state, particularly around the top where it joins the oesophagus (Bowman 1986). Fish with digested matter present in the mouth were assumed to have undergone some measure of regurgitation and this was always associated with slackness in the stomach. Blast freezing the specimens means that the stomach is preserved in the state in which it was caught so that these signs can be detected. Food items collected from 'part-regurgitated' stomachs were recorded as such so that they could be separated from the other food items in the analysis.

The problem of feeding in the trawl was overcome by rejecting fish with fresh prey items in the buccal cavity, often found protruding from the mouth. Prey found in the stomach in pristine condition with no obvious

signs of digestion were examined closely. Any of these prey which were not mixed in with the stomach mucus were judged as having been taken in the trawl and also rejected. There was a concern that these prey items may have been eaten just before capture in the trawl but rejected fish were rare, so the effect of false rejection was minimal.

Food dissected from the stomach was weighed and then separated into individual items as far as was possible. Food items were weighed (to the nearest 10 mg), and the length measured (to the nearest mm). Length was recorded for fish prey from the tip of the jaw to the tip of the tail. With crustaceans such as shrimps and prawns the length was taken from the base of the eye socket to the end of the telson. Crabs were measured across the maximum width of the carapace (Figure 2.3).

Figure 2.3: The method of length measurement used for the major prey types. The lines show the points on the animals from which the length measurements were taken.



Individuals were then classified by their state of digestion. The digestion stage is based on six states for fish prey and four for crustaceans (Table 2.2).

The polychaete and molluscan prey were not allocated a digestion stage as their occurrence was low and most individuals were incomplete. Prey were identified to taxonomic group and then to species level if possible, depending on the state of the specimen.

Table 2.2: The digestion stages and their descriptions for fish and crustacean prey items.

Fish	
Digestion stage	Description
1	intact, no obvious signs of digestion
2	signs of digestion, abrasion of skin, frayed fins
3	stomach wall eroded, fins eroded, most of skin gone, can still be measured
4	heavy digestion, head/tail missing, very hard to measure
5	50:50 ratio of flesh and bones
6	remains, bones and otoliths

Crustacean	
Digestion stage	Description
1	intact no obvious signs of digestion
2	appendages breaking up, carapace softening
3	becoming fragmented but still recognisable
4	remains

Data analysis

Stomach state

The fish sizes were split into 1cm divisions between 11-35cm. The number of fish in each category of stomach state was then expressed as a percentage of the number in the size division. To test these percentages for trends, regressions of percentage of stomachs in each state against fish size were calculated. Size categories with less than 10 fish in were not used as with such a small sample size only differences of more than 44% can be detected with 90% confidence (Sokal and Rohlf 1981). Percentages can have distributions which do not approximate to a normal distribution so the data were transformed with the arcsine transformation recommended by Sokal and Rohlf (1981) (Appendix I).

Diet

To analyse the makeup of the diet, two methods of comparison were used; weight of prey items and numbers of prey items. In the diet analysis the fish were placed into five cm length classes. To look at general patterns, the prey items were placed into one of three groups: fish, crustacean and other prey. Other prey contained prey types such as polychaetes and molluscs. Both weight and numbers were expressed as a percentage of the total so that fish of different size groups could be compared. The same fish size groups were used to look at the prey items at the species level.

Prey Size

To compare the relationship between prey size and predator size, the same 5 cm fish length groupings were used as with the analysis of the general patterns. Prey size was determined by length. The mean prey length for each fish size category was calculated and then tested against each other using single classification analysis of variance (ANOVA). The differences between the means were then tested in a stepwise manner using the Student-Newman-Keuls (SNK) procedure for unequal sample sizes (Sokal and Rohlf 1981).

Feeding patterns

The number was recorded of different prey types in each non-regurgitated stomach containing food. This was performed for the major groups (fish, crustacean and other) and at the species level. At the species level the stomachs which contained unidentified fish or crustacean prey were rejected as these contents could not be compared to the other prey items.

The number of non-regurgitated stomachs at each station containing each prey type was calculated. These totals were then expressed as a percentage of the number of non-regurgitated stomachs at that station. The means of these percentages were calculated for each prey type. The mean number of each prey type found in the non-regurgitated stomachs was also calculated.

Foraging habitat

The location in the water column where the fish were feeding was investigated by the analysis of stomach contents. Prey types were placed into three categories depending on their habitat, determined from Wheeler (1975) and Barnes (1987) (Table 2.3). The indeterminate group contains prey items that could not be confidently placed into either the benthic or pelagic categories. The lack of a label was either because the prey was not identified to a high enough level or because the prey species migrates between the benthic and pelagic habitats. These indeterminate prey types were not used to indicate position of feeding in the water column. Stomachs were recorded as a benthic or pelagic feeding type if they contained a prey from one of these categories. Stomachs which contained both benthic and pelagic prey were labelled as such and the prey types within these stomachs were recorded. The numbers in each category were calculated at each station and summed for the cruise. Stations were then recorded as benthic or pelagic if a majority of stomachs were recorded in one of the two categories.

Table 2.3: The location category assigned to the prey groups

Benthic	Pelagic	Indeterminate
<i>Eurydice pulchra</i>	<i>Clupea</i> spp.	<i>Ammodytes</i> spp.
<i>Liocarcinus marmoratus</i>	Hyperiid	<i>Gadoid</i> spp.
	amphipods	
<i>Ophiuroidea</i> spp.	<i>Pleurobrachia pileus</i>	Unidentified fish
<i>Pectinaria</i> spp.	Euphausiid shrimps	<i>Gammaridae</i> spp.
<i>Polychaeta</i> spp.		<i>Idotea</i> spp.
		Unidentified Crustaceans
		<i>Loligo</i> spp.

Continuous sampling

The stations that were part of the continuous sampling procedure (nos. 50-59) were used to look at diurnal feeding patterns. Numbers of sandeels in fresh condition (digestion stages 1 and 2) were recorded at each sampling time and the occurrence of these sandeels was expressed in two ways. Firstly the number of stomachs which contained fresh sandeels was expressed as a percentage of the total number of stomachs. The mean number of fresh sandeels per stomach was then recorded. In both cases the partly or totally regurgitated stomachs were not used so that any bias in the regurgitation of freshly ingested food would not affect any patterns.

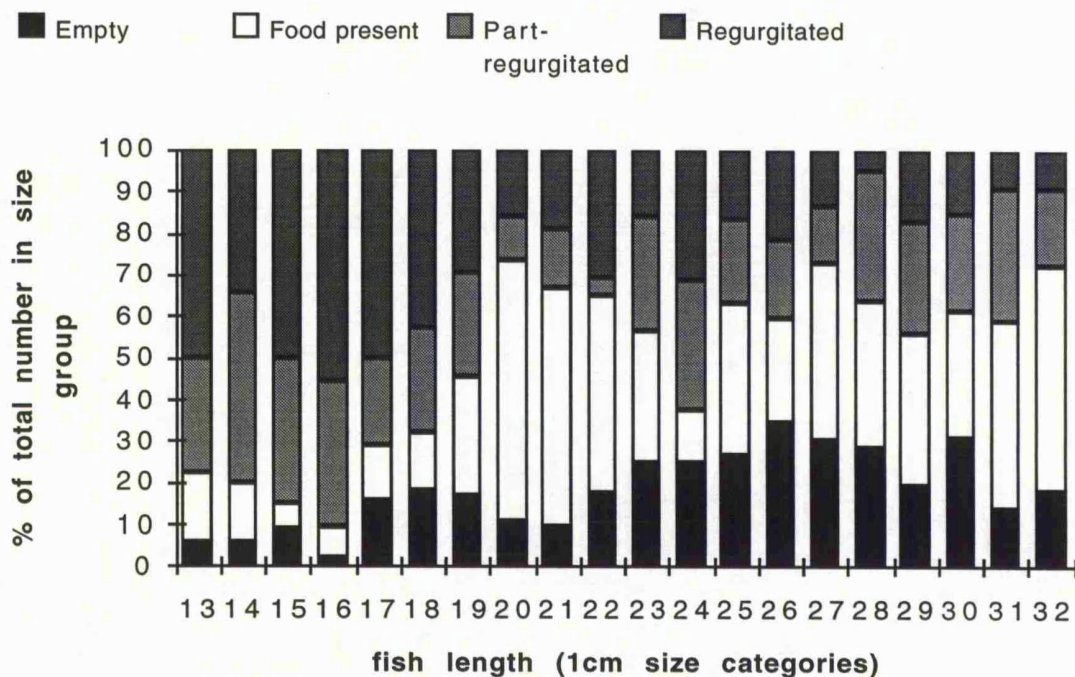
The percentage of all stomachs that were empty was calculated for each station. In this analysis, regurgitated stomachs were recorded as an indication of feeding

Throughout the chapter statistical significance was taken at the 0.05 probability level.

RESULTS

A total of 705 stomachs was sampled, the smallest fish sampled was 11cm and the largest 35cm. The percentage of stomachs in each state is shown in Figure 2.4.

Figure 2.4: The percentage of stomachs recorded in each state in each 1cm fish size category (only categories with n>10 are shown)



Regressions of the percentage of stomachs in each state against fish size, are shown in Table 2.4. There is a positive relationship between the percentage of empty stomachs and fish size. The positive relationship between food present in stomachs and fish size is also significant. There is a very strong negative relationship between the percentage of regurgitated stomachs and fish size.

Part regurgitation is the only stomach state that is not significantly affected by fish size. When the stomach states are combined 'no regurgitation' has a significant positive relationship, and combined regurgitation has an opposite negative relationship.

Table 2.4: The summary statistics of simple linear regression analysis of stomach state against fish size. Results are shown from non-transformed data and data transformed using an arcsine transformation

H₀: There is no relationship between stomach state and fish size.

H₁: There is a relationship between stomach state and fish size.

No Transformation				
Stomach state	Slope	Intercept	R ²	Probability
Empty	1.077	-6.161	0.468	<0.05
Feeding	1.661	-6.29	0.325	<0.05
Regurgitated	-2.269	77.623	0.722	<0.05
Part Regurgitation	-0.469	34.833	0.083	>0.05
No Regurgitation	0.738	-12.451	0.572	<0.05
Combined Regurgitation	-2.738	112.456	0.572	<0.05
Using Arcsine Transformation				
Stomach State	Slope	Intercept	R ²	Probability
Empty	0.888	0.575	0.490	<0.05
Feeding	1.144	1.571	0.355	<0.05
Regurgitated	-1.517	81.087	0.732	<0.05
Part Regurgitation	-0.291	33.818	0.062	>0.05
No Regurgitation	1.677	1.258	0.587	<0.05
Combined Regurgitation	-1.677	98.743	0.588	<0.05

When the data are transformed the results are similar though the slope of each line is flatter and the fit of the line is improved. If the stomach state categories 'combined regurgitation' or 'no regurgitation' are used then the variation in fish size accounts for over 57% of the variation in stomach state.

Importance in the Diet

When the stomach contents are compared in terms of weight the diet is dominated by fish prey (Figure 2.5). Only in the smallest fish (10-14cm size class) do crustaceans make up the largest percentage of the diet (60%). By the time the fish reach 20cm the diet is 90% fish. The other dietary items are mainly molluscs which contribute about 15% to the diet of the smallest fish size but then appear very little in the larger sizes.

The domination of the diet by fish is less obvious when the contents are expressed by numbers (Figure 2.6). The diet of the smaller fish sizes is mainly made up of crustacean prey with fish becoming the main food item around the 20-24cm size group. The fish component of the diet does not exceed 90% until the 25-29cm age group. Other prey items do not feature significantly in the stomach contents at any size.

In the smallest fish, sandeels were the only fish prey. They are the single most important food group in terms of weight (25.3%) (Figure 2.7). The rest of the diet is made up mainly of unidentified crustaceans (20.5%), Hyperiid amphipods (16.24%), *Pandalus spp.* (11.24%) and polychaete worms (18.0%). The diet of the remaining fish size groups is dominated by more than 77% sandeels with a few other fish (e.g. *Trisopterus esmarkii*) and crustacean species (e.g. Euphausiid shrimps and *Crangon crangon*).

The diet in terms of numbers had a slightly different emphasis (Figure 2.8). Only 1.3% of the diet of 10-14cm fish was of sandeels. The most important prey type was Euphausiid shrimps (48%) followed by unidentified crustaceans (31.1%) and Hyperiid amphipods (14.8%). The single most important food item in the 15-19cm group was sandeels (36.39%). The rest of the diet was mainly made up of unidentified crustaceans (22.8%), Euphausiid shrimps (20.6%), *Pandalus spp.* (8%) and Hyperiid amphipods (7.7%). The 20-24cm size group was dominated by sandeels (67.5%). The only crustacean prey to be represented in this size group were Euphausiid shrimps (19.67%) and unidentified crustaceans (9.8%). The stomach contents of the largest two fish size groups were both dominated by sandeels (>90%).

Figure 2.5: Comparison of fish and crustacean prey in terms of weight

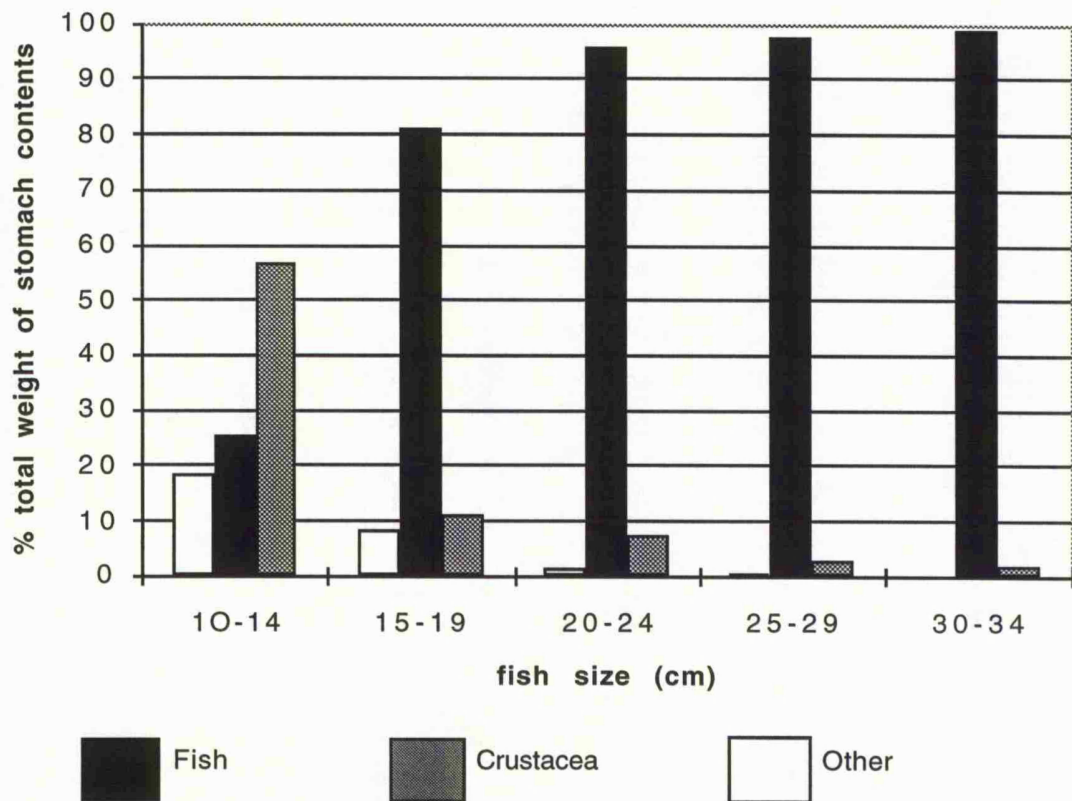


Figure 2.6: Comparison of fish and crustacean prey in terms of numbers

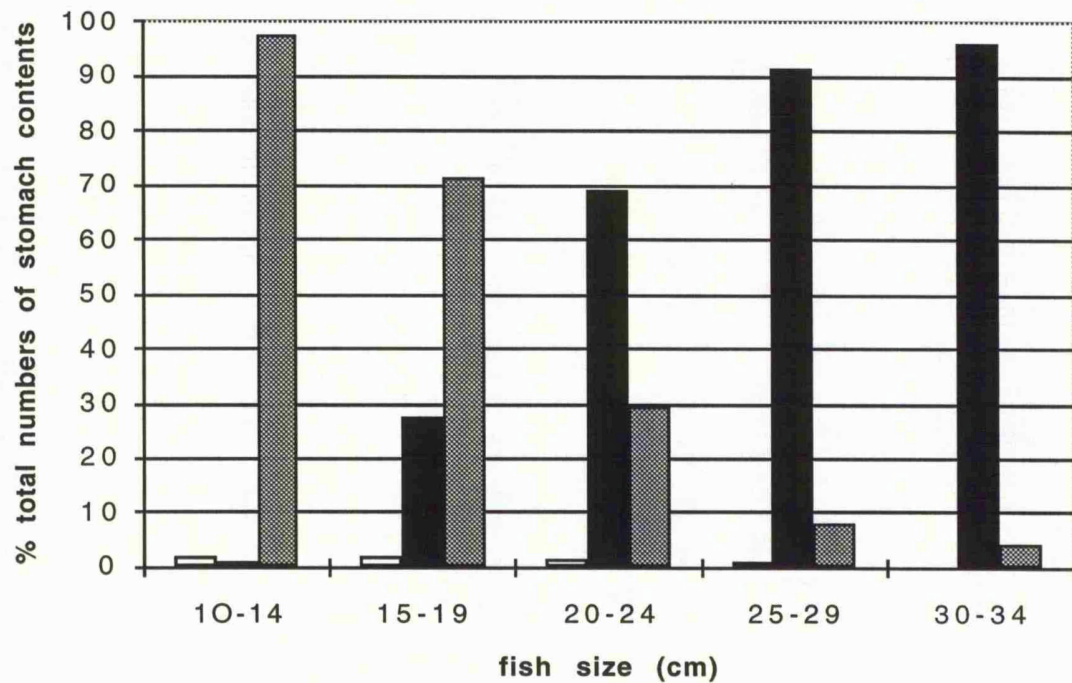


Figure 2.7: The contribution of each prey item in terms of percentage total weight to each 5cm fish size category

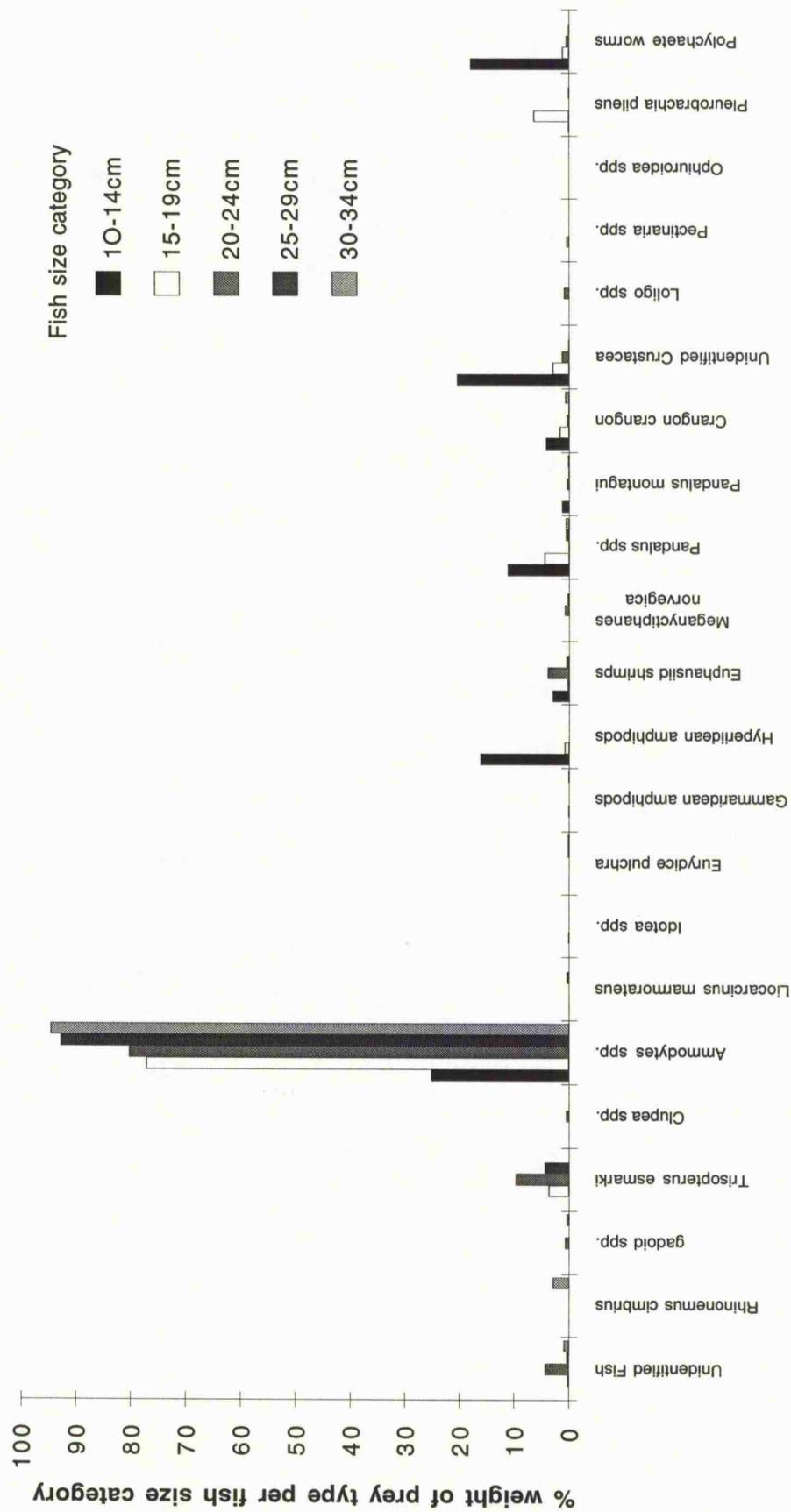
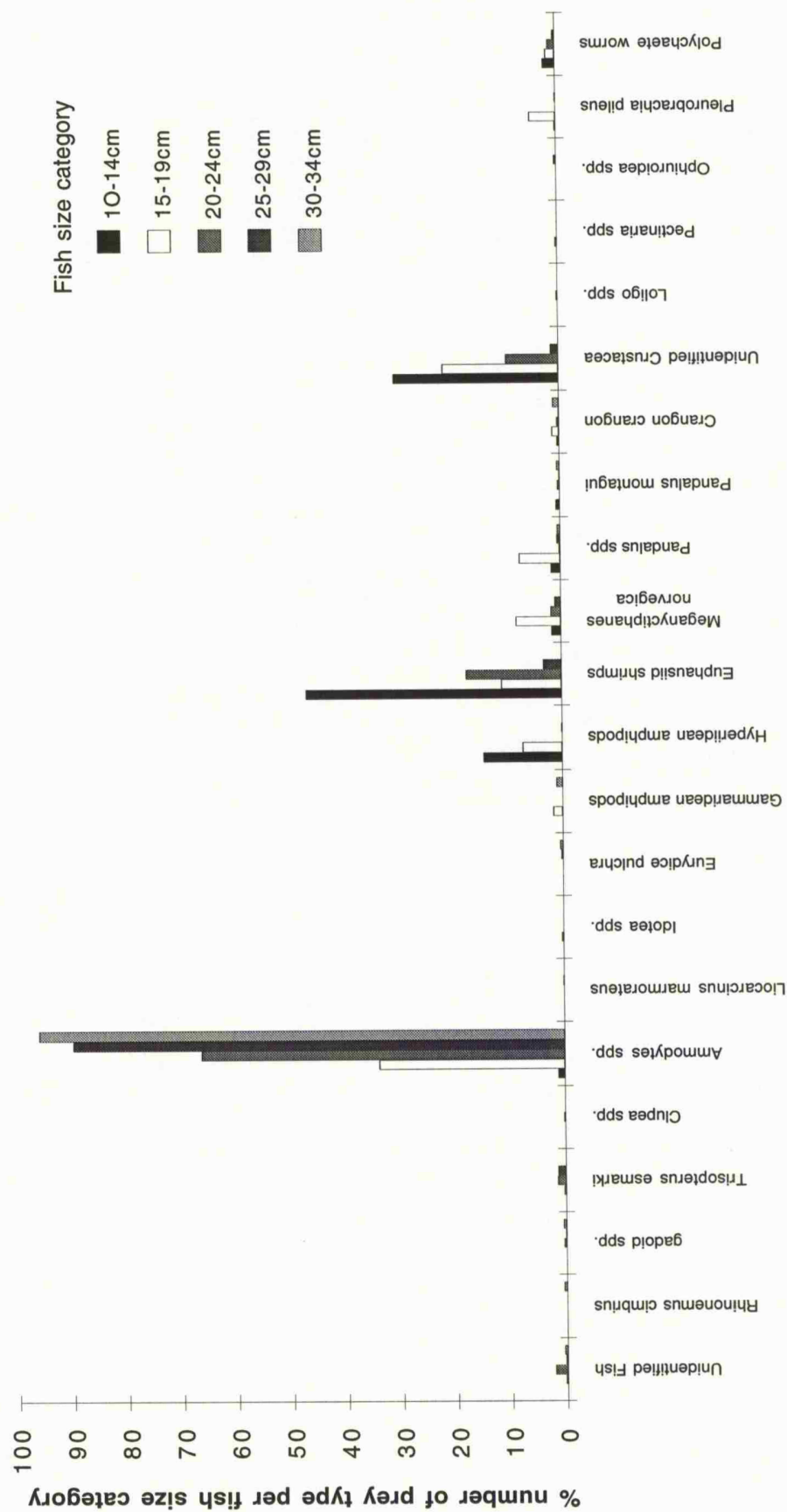


Figure 2.8: The contribution of each prey item in terms of percentage total number to each 5cm fish size category



The predator prey size relationship

The mean prey length for all prey types, for each size group is shown in Figure 2.9. Table 2.5 shows the results of the ANOVA and Table 2.6 shows the results from the SNK procedure. The mean prey length eaten increases with the length of the fish up to a maximum of around 8cm. The mean of the 10-14cm fish size is significantly smaller than the mean size at 15-19cm which is in turn significantly smaller than the 20-24cm mean prey size. There is no difference between the 20-24cm, 25-29cm and 30-34cm mean prey sizes.

Figure 2.9: Mean length of all prey types in each 5cm fish size group with standard error mean bars.

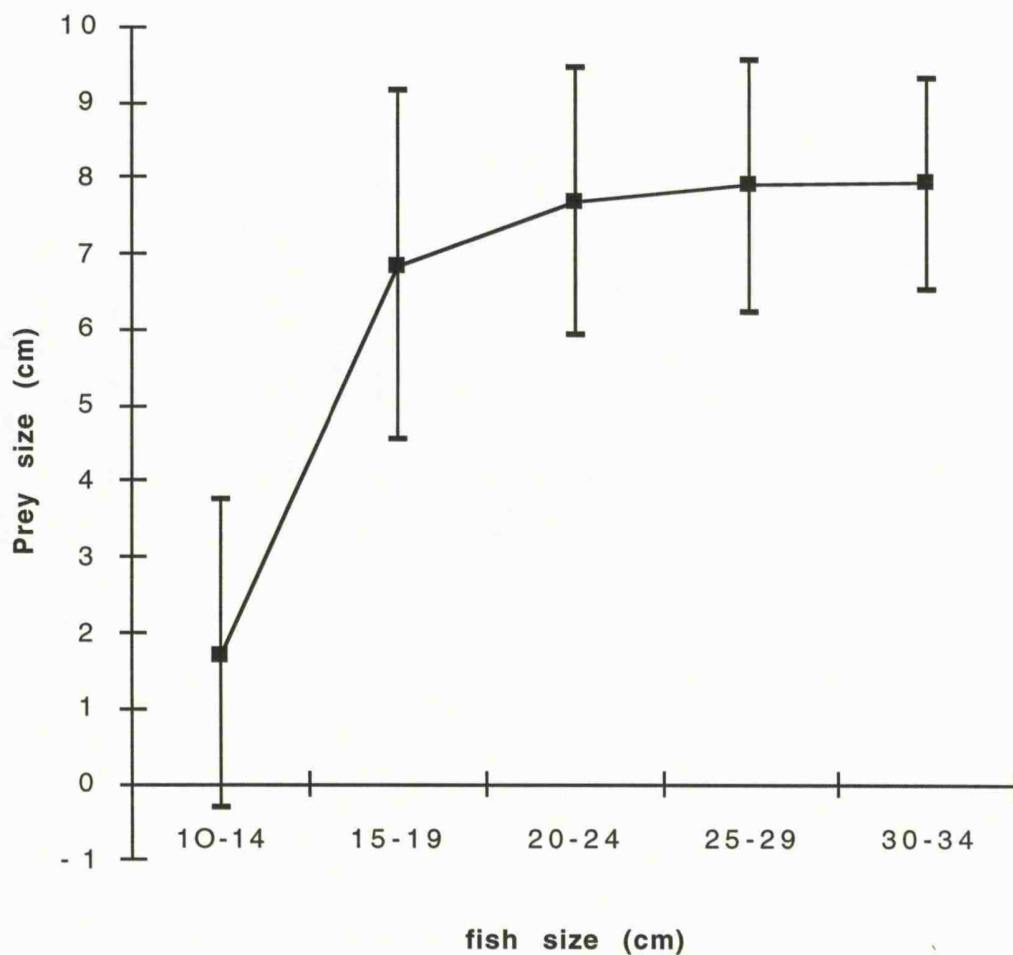


Table 2.5: The results of an ANOVA test on the mean length of prey eaten by each 5cm fish length category.

Categories (cm)	Count	Mean	Variance
10-14	61	1.70	4.05
15-19	75	6.85	6.35
20-24	180	7.69	3.15
25-29	332	7.90	2.78
30-34	98	7.93	1.91

ANOVA source of variation

	Sum of Squares	degrees of freedom	Mean Squares	F	P-value
Between Groups	2107.65	4	526.91	163.88	<0.05
Within Groups	2382.50	741	3.21		
Total	4490.16	745			

Table 2.6: The results of an SNK procedure on the mean length of prey eaten by each 5cm fish length category. (N.B. the ranges that are not significantly different are underlined).

	rank		1	2	3	4	5
	mean		1.70	6.85	7.69	7.90	7.93
rank	mean	count	61	75	180	332	98
1	1.70	61	-				
2	6.85	75	5.15*	-			
3	7.69	180	5.98*	0.83*	-		
4	7.90	332	6.19*	1.04*	0.21	-	
5	7.93	98	6.23*	1.08*	0.25	0.04	-

(* tested and found to be significant at P = 0.05)

Size category (cm)	10-14	15-19	20-24	25-29	30-34
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Feeding patterns

The number of stomachs that contain one type of prey (fish, crustacean or other) is significantly higher than the number of those with two, or all three types (Table 2.7). The contents of stomachs with two types of prey were mainly made up of crustaceans and fish. At the taxonomic group level most of the stomachs contained one prey type with less than 17% of the stomachs containing two or more prey items. None of the stomachs sampled contained more than three types of prey. The number of different prey types per station is shown in Table 2.8. The mean number per station is 4.12, this was calculated for all stomachs with food in, including part-regurgitated ones.

The percentage of stomachs, irrespective of fish size, containing each prey type per station is shown in Figure 2.10. Fish at each station had a dominant prey type with a few other prey types found in only a small percentage of the stomachs. There were two stations that do not fit this pattern, 38 and 74. At station 38 over 50% of the stomachs contained *Crangon crangon* but a large percentage also contained Polychaete worms. At station 74 the majority of stomachs contained Hyperiid amphipods and *Pandalus* prawns.

The mean number of each prey per stomach is shown in Figure 2.11. Only four species occur more than once in any stomach, and with all these species there was considerable variation in this number. The percentage of non-regurgitated stomachs at a station containing each prey type is shown in Figure 2.12. Sandeels and *Pleurobrachia pileus* both occur in the majority of stomachs if predated on at a station.

Figure 2.10: The percentage of non-regurgitated stomachs at each station containing each prey type (N.B. Station numbers 50-62 were along the same tow line)

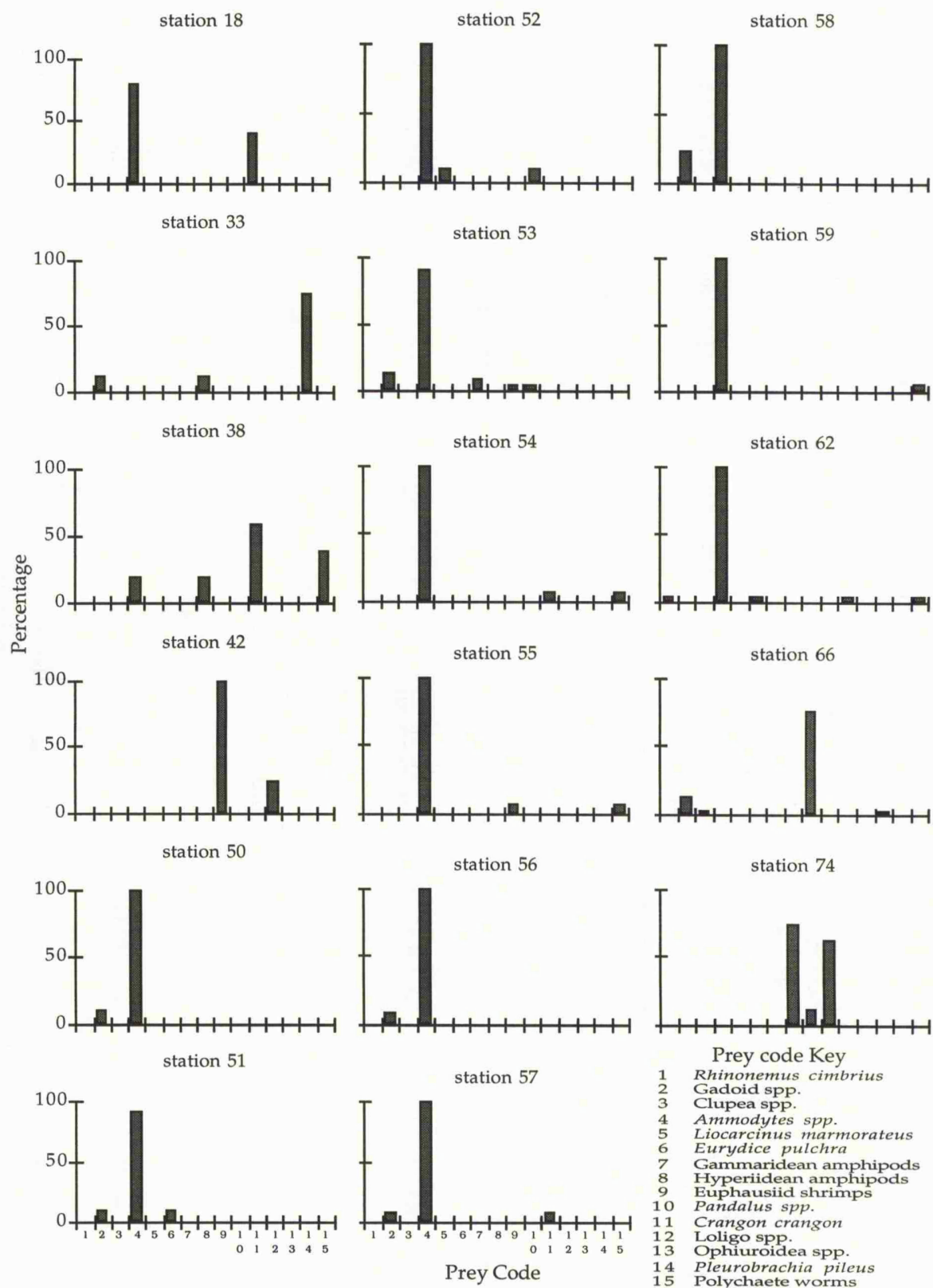


Figure 2.11: The mean number of each prey type occurring in non-regurgitated stomachs. (Bars show standard error means)

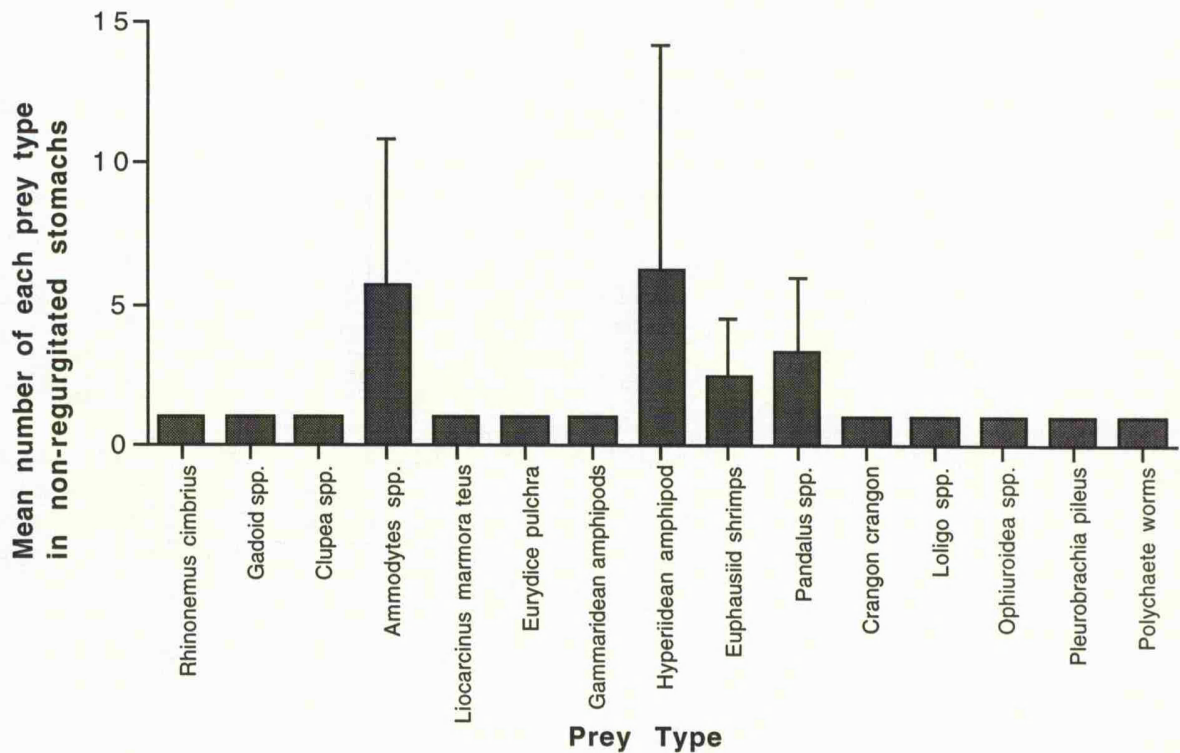


Figure 2.12: The percentage of non-regurgitated stomachs per station containing each prey type. (Bars show standard error means)

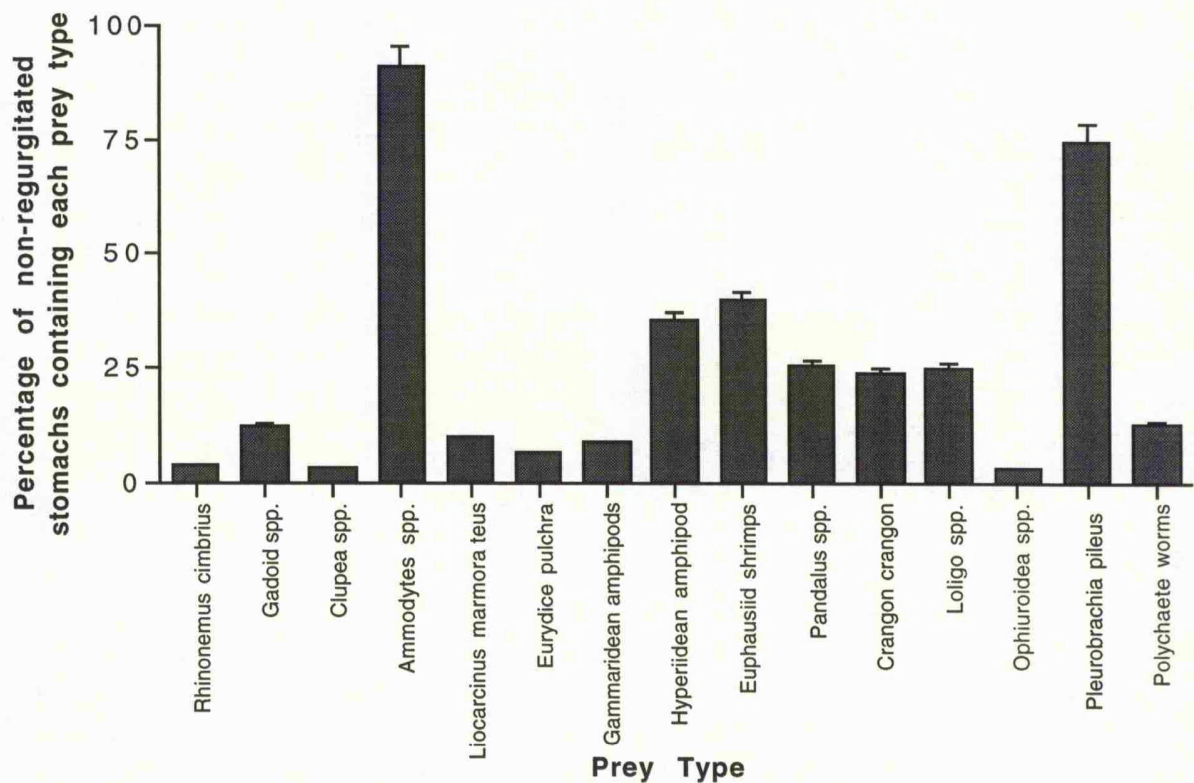


Table 2.7: The number of different prey types from non-regurgitated stomachs containing food

Level of identification		1 prey type	2 prey types	3 prey types
Crustacean/fish/other				
	Total	199	25	1
	%	88.44	11.11	0.44
Taxonomic level				
	Total	165	29	4
	%	83.33	14.65	2.02

Table 2.8: The number of different prey types consumed per station (The station numbers refer to the positions shown in Figure 2.2)

Station	No. species	Station	No. species
18	6	55	5
33	4	56	3
38	5	57	4
42	4	58	4
50	2	59	4
51	6	62	5
52	4	66	4
53	5	74	2
54	3	mean	4.12

Location of Feeding

The stomachs mostly fell into the indeterminate category (Table 2.3) containing no species which indicated decisively either pelagic or benthic feeding (Table 2.9). The largest number of stomachs that did contain representative prey items contained species which indicated pelagic feeding. Only three stomachs contained both prey of pelagic and benthic origins. When these data are studied in terms of station, the division between benthic and pelagic feeding stations was almost equal, four stations were uncategorised.

Table 2.9: The location of feeding as determined by prey type in stomach
(N.B. Station numbers 50-62 were from the same tow line)

Station Number	benthic	pelagic	indeterminate	benthic and pelagic	station category
18	1	10	27		pelagic
33	1	18	1		pelagic
38	11		16	1	benthic
42	1	5	3		pelagic
50			18		
51	2		24		benthic
52	2		18		benthic
53		1	28		pelagic
54	1		14		benthic
55	1	2	15		
56	1		22		benthic
57			16		
58	1		25		benthic
59		1	24		pelagic
62	2		31		benthic
66		31	8	2	pelagic
74		9	14		pelagic
Total	24	77	304	3	pelagic = 6 benthic = 7

Four stations contained stomachs that had benthic indicators and stomachs that contained pelagic indicators. In these stations there was

usually one 'odd' stomach and so the largest number was used to determine the station category.

Temporal changes in feeding

Figure 2.13 shows the occurrence of empty stomachs over the sampling period. The highest number of empty stomachs was observed at 06:00 and 18:00 hours and the lowest during the middle of the day between 10:00 and 14:00 hours. The highest proportion of stomachs that contained at least one fresh sandeel was at 14:02 hours (Figure 2.14). The occurrence of stomachs with fresh sandeels is lowest at 6:07 hours and between 18:14 to 22:15 hours.

A similar pattern is seen for the occurrence of non-regurgitated stomachs containing fresh sandeels (Figure 2.14) with a peak at 14:00 hours and a smaller one at 22:00 hours. There is a peak in the mean number of fresh sandeels occurring in non-regurgitated stomachs at 14:00 hours (Figure 2.15) but there is also a peak at 02:00 hours which is not seen on Figure 2.14.

Figure 2.13: The percentage of all stomachs sampled in an empty state over the continuous sampling period

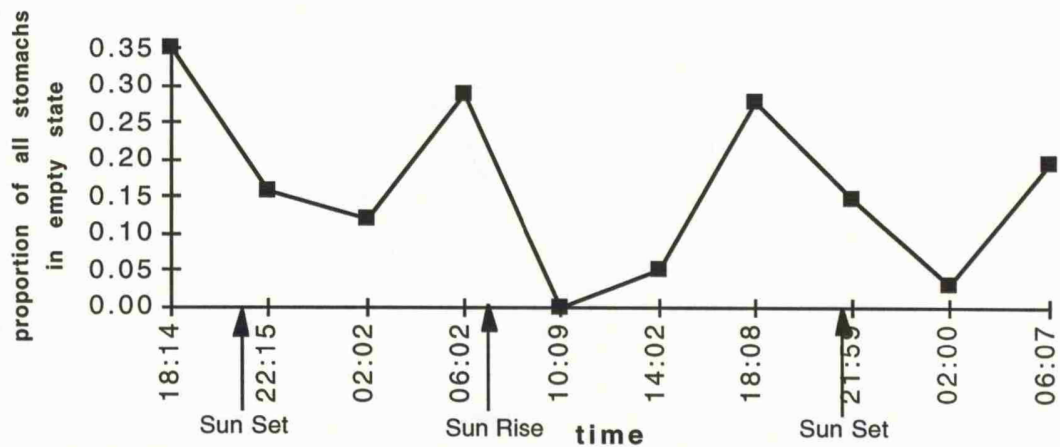


Figure 2.14: The percentage of non-regurgitated stomachs containing fresh sandeels over the continuous sampling period

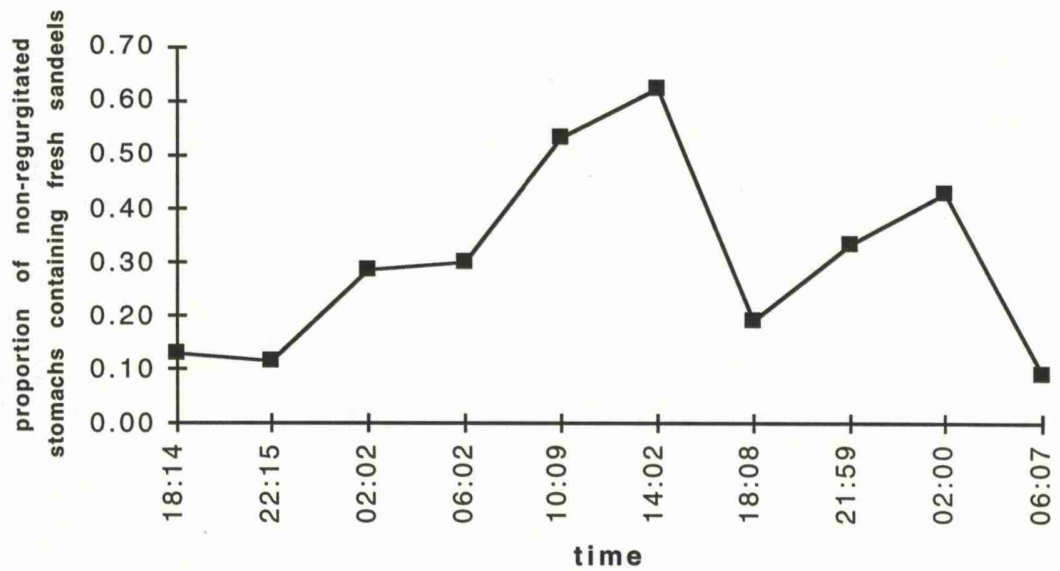
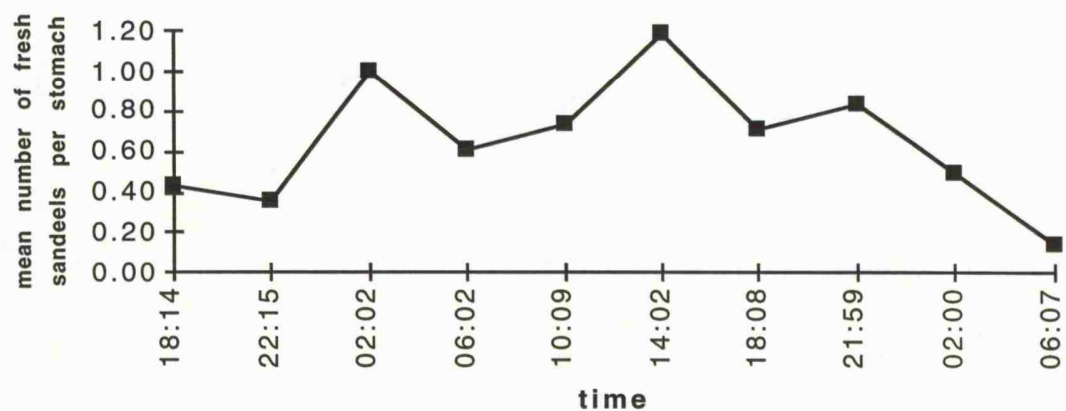


Figure 2.15: The mean number of fresh sandeels occurring in non-regurgitated stomachs over the continuous sampling period



DISCUSSION

Regurgitation

Over 50% of all the fish showed some signs of regurgitation. Both empty stomachs and stomachs with food in had a positive relationship with increasing fish size. This was possible because the proportion of stomachs showing signs of regurgitation decreased with increasing fish size. Significantly more regurgitation occurred in the smallest whiting sampled (Fig 2.4). This could be due to a number of reasons. The main reason for regurgitation in this study is probably the distension of the swimbladder pushing on the stomach. It is likely that some change in this correlated with fish size, caused the observed trend. Perhaps the different sized fish had different pressures in their swimbladders even though they were caught at the same depth. Swimbladders containing relatively more gas would expand more relative to their original size as a result of pressure changes on being brought to the surface. Regurgitation induced by the compression of the fish in the cod end might affect the smaller sizes of whiting more than the sturdier large ones. There is also some evidence that the larger fish have a stronger musculature in their oesophageal sphincter which can resist the pressure exerted from experimental stomach pumping techniques (pers. obs.). The increased resistance of the oesophageal sphincter could reduce the amount of regurgitation that would otherwise occur. The smaller fish maybe more prone to regurgitation through the stress of being captured and have a stronger regurgitation reflex. No published accounts of this size related regurgitation have been found which may be because it is limited to whiting or because no other studies have investigated such factors.

Regurgitation is a source of error in stomach sampling which must be accounted for in stomach sampling studies. Little is known about how the type of food in the stomach or how recently the meal was eaten, affects regurgitation. From personal observations during gastric lavage experiments where regurgitation is forced by filling the stomach with sea water (Chapter 3), a difference in the ease with which food items could be removed was noted. Freshly eaten prawns with their irregular body shape and many appendages were much harder to extract than sandeel prey or heavily digested prey. Also fuller stomachs will be affected more by the

expansion of the swimbladder and so fish that have recently fed may regurgitate more often.

Importance of prey

The gravimetric and numerical methods of analysis highlight different patterns of the important prey items in the diet. Gravimetric analysis can overemphasise single large prey items that are only found in a few stomachs (Hyslop 1980). The gravimetric analysis indicates that crustacean prey were the dominant part of the diet in only the smallest whiting sizes, and fish prey almost totally dominated the diet of the whiting over 15cm. The fish component of the diet was mainly sandeels but the largest whiting did take other fish such as gadoid and clupeid species.

Using numerical analysis small prey that are taken in large quantities are emphasised (Hyslop 1980) and the crustacean component of the diet is much larger. The switch from a mainly crustacean to a mainly piscivorous diet occurs at a larger size than when the diet is examined by gravimetric analysis. The 'Other' prey items were soft bodied organisms such as polychaetes and tunicates. Neither of the two methods of analysis used can overcome the problem of the under representation in the stomach samples of these types of prey. They are evacuated from the gut quickly and leave little or no identifiable remains to weigh or count (Hyslop 1980). The importance of these prey is hard to quantify in stomach sampling data so their low values should be regarded with reservation. The best method of analysis for fish like whiting with the large range of prey items is to use both gravimetric and numerical techniques. Although weight probably reflects the energy gained from a prey type numerical analysis can relate information about energy expended in foraging.

Previous studies (Jones 1954, Nagabhushanam 1964, Hislop *et al* 1991) have concluded that the diet of whiting is made up of mainly crustaceans and fish. The change from a crustacean dominated diet to a fish dominated one as the fish length increases has also been documented. Hislop *et al* (1991) found that the diet of whiting switched at around 20-25cm (using prey weight) slightly larger than the 15-19cm found in this study. The Hislop *et al* (1991) study was over the entire North Sea and also over the

year. There is good evidence that the abundance of prey items varies considerably in different areas (Singh-Renton 1990). Daan (1973) found that the switch in prey type in cod occurred at a smaller size in the northern North Sea compared to the southern North Sea. From catch sizes and landings Zijlstra (1988) calculated that there are more fish per square meter in the northern North Sea than the southern. Inter- and intra-year differences in prey abundance and availability can affect the species eaten through migration, aggregations and reproduction (Mehl 1986). These factors could all explain the differences between the Daan (1973), Singh-Renton (1990), Hislop *et al* (1991) and the current study.

The importance of sandeels in the diet of whiting has not been recorded by all workers. Casey *et al* (1986) found that sandeels did not feature in a greater frequency than about 10% for any length category of whiting. They concluded that there was no pattern to the feeding on sandeels and suggested that such feeding was opportunistic. However Hislop *et al* (1991) found sandeels were the most important fish species by weight in whiting of 10-29 cm length. This difference between studies may be due to the changes in prey abundance. The almost total domination of sandeels as fish prey in the present study may also be because of the continuous sampling in an area where sandeels were very prevalent. This non-random sampling may have overestimated the sandeel contribution to the diet.

In both the present work and that of Hislop *et al* (1991), a large part of the diet was sandeels but the proportion of the other fish taken increased with increasing whiting size. Smaller whiting with a corresponding smaller gape are limited to feeding on prey items below a certain size. Sandeels, despite being long, are thin and so can be eaten by the smaller whiting. Other fish prey tend to have a deeper body shape and unless they are very small cannot be handled by the smallest whiting. It may be that if sandeels are present the whiting can consume fish at a smaller size than would be possible with other fish prey species. There is some evidence that a fish diet allows the predator to grow at a faster rate (Bromley 1990). This would make sandeels a very important aspect of the diet of smaller fishes enabling them to reach a larger size more quickly.

The occurrence of other commercially important fish species in the stomach samples was low, but the study was limited to whiting below

35cm. The work by Hislop *et al* (1991) found that the predation by whiting on the other commercially important species (e.g. *Gadus morhua*, *Melanogrammus aeglefinus* and other whiting) occurred in the largest fish (>30cm). They concluded that whiting was probably one of the most important piscivorous fish in the North Sea.

The smallest sized fish (11-14cm) took the largest proportion of crustaceans in their diet. The dominant species in the crustacean component of the diet depends on the type of analysis used. Gravimetric analysis showed the Hyperiid amphipods to be the most important species with *Pandalus* prawns the next. Euphausiid shrimps were not a large component of the diet when expressed by weight but in numerical analysis they were the largest identified group by over 32%. The crustacean species recorded in this study have also been found in other work. Hislop *et al* (1991) reported the most important prey types by weight in the smallest fish (10-14cm) were Euphausiid shrimps (10.84%) and Crangonidae (22.12%). The species of Crangonidae were found in the stomachs of whiting sampled in the present study but they were of much less importance than found by Hislop *et al* (1991) and made up only 4.2% of the diet in the same fish size category. Another crustacean group found to be important by Hislop *et al* (1991) is the Brachyura, which were prevalent in the smaller whiting sizes. Only one member of this group (the marbled swimming crab, *Liocarcinus marmoratus*) was found in any stomachs in this study. This individual occurred in the larger 25-29cm fish size category. These differences are again probably due difference in timing and the much broader sampling of the 1991 study.

Prey size

The increase in mean prey size with increasing predator size was expected, as the maximum size of prey the fish can consume increases with increasing jaw size. The greatest difference is between 10-14cm and 15-19cm whiting, which is also when the diet switches to a fish dominated diet. Prey size was measured as length and so the inclusion of long and thin sandeels in the diet causes the ratio to increase dramatically. The prey size in the larger whiting is not significantly different, this is probably because larger prey items were not available to be eaten and so their diet still consisted of mainly sandeels. Hislop *et al* (1991) found that bigger fish

tended to eat larger prey, and that with fish prey the predator/prey length ratio was highly correlated.

Method of Feeding

The majority of stomachs sampled contained only one type of prey, and no fish had more than three different types of prey in their stomachs. It would appear that the whiting were concentrating on one type of prey at a time. This may be because that prey type was the most abundant, or the fish actively chose that type of prey over the other prey available. If the fish are grouped by station and the prey eaten per station are analysed then an interesting pattern is seen. Figure 2.10 shows the percentage of stomachs at each station that contain each type of prey. It is clear that at most of the stations one type of prey dominates the diet with a few other stomachs having an 'odd' prey type. At two stations 38 and 74 this pattern is not evident. Station 38 has only five non-regurgitated stomachs with food present and this may be the reason that no clear pattern can be seen. Station 74 also has only eight stomachs represented and seven of these stomachs contain more than one prey item.

Patterns in the predation of species are shown by Figure 2.12. Sandeels and *Pleurobrachia pileus* both occur in the majority of stomachs if predated on at a station. *Pleurobrachia pileus* were only found at one station and over three quarters of the stomachs at that station contained them. There are other species which occur in very few stomachs e.g. *Eurydice pulchra*, Polychaete worms and *Gadoid spp.*. There are also species such as Krill (*Meganyctiphanes norvegica*), Hyperiid amphipods and *Crangon crangon* which are sometimes found in the majority of the stomachs at one station but at other stations appear in just one or two stomachs. The prey items which are usually found in the majority of stomach are species which shoal or form into large aggregations. The 'odd' species are usually solitary benthic prey or are not eaten by the entire whiting size range e.g. *Clupea* and *Gadoid* species which were only eaten by the very largest whiting. It would appear that whiting, also a shoaling species, exploit aggregations of prey animals when feeding and occasionally take the odd prey of another species to supplement their diet.

The mean number of each prey species in the stomach shows that only four appear more than once in a single stomach. These species are also the ones which are fed on at each station by the majority of fish suggesting that they were fairly common where the fish were feeding. The exceptions are *Pleurobrachia pileus* and *Crangon crangon*, which were eaten by more than one fish per station but never occurred more than once in a stomach. These species were eaten by only the smaller fish and as they are relatively large the fish may not have been able to consume more than one at a time. The mean number of prey per station in all the stomachs was 4.12 which, compared to the sixteen groups eaten in total in this study and the 51 species found in stomachs by Hislop *et al* (1991) would suggest that whiting feeding in a particular area are only exploiting a small number of different prey types. No method of sampling the available prey items was possible on this cruise so no selectivity could be calculated. It maybe that the fish are choosing a small range of the available prey or simply taking what is accessible.

Foraging Habitat

The number of stations classified as pelagic and benthic feeding are similar. In three fish, both pelagic and benthic indicator species were found. In these fish prey items may have been taken in the trawl or one of the prey items may have remained in the stomach from feeding previously. Unfortunately, in all three cases, one of the prey items was a polychaete worm for which it was difficult to determine the stage of digestion, so no estimate of time of ingestion could be made. Stomachs containing pelagic prey occurred at the same station as stomachs with benthic prey on four occasions, but in every case the benthic feeding was only indicated by one stomach. This again may have been because of feeding in the trawl or from a previous feeding bout.

The indeterminate class of prey types may have been taken in a different location to the indicator species but the data on percentage of stomachs containing each prey type point to the fact that most fish at a station are feeding on the same prey. From this the presumption that all the fish caught are feeding at the same location seems fairly sensible. It would appear that the fish are feeding equally from the pelagic and the benthic zones. Hislop *et al* (1991) suggested that whiting were feeding on free

swimming prey which would suggest a pelagically oriented feeding strategy but Pawson (1974) showed that whiting were successful at locating buried food and digging it up. The larger whiting may feed more in the pelagic zone, when fish such as gadoids and clupeids become a more dominant part of their diet, than the smaller whiting which seem to forage on the bottom and in mid-water. A problem with the analysis of feeding location used in this study is that the species used to indicate pelagic feeding may have been taken when they were located just off the sea bottom. The precise location of the fishes feeding in the water column is difficult to judge using this prey species information. Echo-sounding can give information on where the fish are but whether they are actively feeding is then difficult to judge. No echo-sounding was possible in this trip but a combination of stomach sampling and echo-sounding could provide clues to where the fish are feeding. Another problem is the trawl used may sample the whiting feeding on the bottom more heavily than ones feeding pelagically but the trawl does have a headline that is 5m off the bottom so this effect should not be too great.

Feeding patterns

A drop in the observed number of empty stomachs is assumed to indicate an increase in the feeding intensity. The continuous sampling showed two drops one at around 02:00 hours and one around midday. The occurrence of stomachs containing fresh sandeels increased at 14:00 hours and again at 02:00 hours. The mean number of fresh sandeels per stomach also increased at 14:00 hours and also at 02:00 hours. The evidence suggests that the whiting were feeding on the sandeels in two strong bouts two hours after midnight and again around midday. Other fish sampled in the area showed different patterns of feeding intensity, cod showed almost the opposite pattern and fed on the sandeels most strongly at dawn and dusk (Bromley pers. com.). Saithe showed a similar pattern to the whiting but it was more marked with no feeding at the hours of dawn and dusk. The feeding pattern suggests the predators are exploiting the sandeels at different stages of their vertical migration. The timing of vertical migration of sandeels is still not fully understood, but the sandeel fishery is carried out in the day as very few sandeels are caught at night (Bertalsen and Popp Madsen 1958). There is also a great deal of variation in the

maximum number of sandeels caught during the day and the timing of their capture (Macer 1966). The non capture of sandeels in night trawls could be a result of them burying themselves in the sand, or from migrating to midwater. Bertalsen and Popp Madsen (1958) found that only one sandeel was caught in a grab during the day but 13 were captured at night. The same workers also found that large numbers of sandeels have been caught by midwater ring trawl at night. In the continuous sampling area the migration pattern was unclear as the trawl did not sample the sandeels.

Saithe are adapted to feeding pelagically (Gislason 1983) and so peaks in their feeding should coincide with the sandeels being in midwater to the surface. The evidence suggests that the more benthic oriented cod are preying on the sandeels when they are on the bottom and whiting predate upon them as they start to move up to mid water where they are then taken by the more pelagic saithe. It should be noted that the midday and two o'clock timings are merely periods of increased feeding intensity and that fresh prey items were found at every sampling time. The midday period of feeding found in this study agrees with the findings of Jones (1954). However it disagrees with the findings of Singh-Renton (1990) who found no fresh crustaceans in the stomachs of whiting between early morning and afternoon. Singh-Renton (1990) suggested that this was because of the difference in prey type. She suggested that the timing of feeding is influenced by the type of prey being eaten e.g. crustaceans are mainly eaten at night and fish during the day. Gordon (1977) found that small fish (7-8cm) preying predominately on crustaceans fed most from dusk to dawn yet the slightly larger fish (11-21) with a more piscivorous diet fed with the greatest intensity from dawn to late morning.

CHAPTER 3

GASTRIC EVACUATION

“What goes up must come down. What goes in must come out”

Dr. Peter Bromley

INTRODUCTION

Digestion rate studies provide essential information for a number of purposes. They can help estimate energy transfer within food webs and food conversion efficiency, if the energy content of the prey is obtained. Aquaculture can also benefit as maintenance and maximum rations can be determined. One of the most useful aspects of digestion studies is its use for interpreting stomach content data, in terms of daily and annual food consumption (Bromley 1994).

These data can then be used in the study of interspecific feeding interactions such as competition and predation. The interrelationship between fish species is important when considering the management of fish stocks. As a consequence of competition or predator-prey relationships, conservation measures for one species may well have adverse effects on other commercially important stocks (Chapter 1). There have been many studies on digestion rates and energy requirements of fish. It is very difficult to measure directly the actual digestion rate so most studies measure the rate at which food is emptied from the stomach (gastric evacuation rate, GER). It is then assumed that the GER is equal to the rate at which food is digested (Tyler 1970, Talbot 1985, Bromley 1994).

There are a number of methods for measuring gastric evacuation rate all of which have both advantages and disadvantages. The methods for measuring gastric evacuation are similar in that they all involve giving experimental fish a certain quantity of food, and then examining their stomach contents at several time intervals after feeding. The difference in the methods occurs in the following ways: treatment and presentation of the test meal, starving experimental fish for a specific period before and or after the test meal, and the technique for examining the stomach contents.

The simplest method is to remove the stomachs of the sample fish at each time period and retrieve the contents by dissection (Steigenberger and Larkin 1974, Macdonald *et al* 1982, Basimi and Grove 1985). The advantages are that no specialised equipment is needed, fish do not have to be force fed and food may also be dyed (Mills *et al* 1984) making periods of starvation unnecessary. The disadvantages are obvious in that each fish can only be used once which means that large numbers are needed for

each experiment, and a series of measurements on the same fish is not possible. The other methods all rely on sampling from live fish.

Radiological methods involve serial x-raying fish after a test meal, which shows up the presence of skeletal structures, swim bladder and otoliths (Molnar and Tolg 1960, Molnar *et al* 1967). Alternatively the test meal can be labelled with barium sulphate (Edwards 1973, Jobling *et al* 1977, Grove *et al* 1978, Flowerdew and Grove 1979, Ross and Jauncey 1981, Basimi and Grove 1985). These methods allow, by serial measurements, the passage through the gut to be followed and only a small sample of fish is required. There are a number of difficulties in that the fish need to be starved before and after the test meal. The fish in the barium meal method are also handled frequently and need to be force fed, resulting in excessive stress which could possibly affect the evacuation rate.

Radioisotopes have been used by some workers e.g. caesium (^{137}Cs) (Kevern 1966), iodine (^{131}I) and chromium (^{51}Cr) (Storebakken *et al* 1981). With this method serial measurements maybe made, but unlike the barium meal the test meal does not have to be force fed. However the use of radioactive substances is expensive; it can also be difficult requiring training and presents potential health risks.

The gastric lavage technique is less hazardous and relatively inexpensive. The technique involves inserting a tube, into either the mouth and stomach (Seaburg 1957, Foster 1977, Meehan and Miller 1978, Bromley 1987, Vondracek 1987) or into the anus (Baker and Fraser 1976), through which water is pumped so that the stomach contents are flushed out via the mouth. Fish are usually starved, prior to and after test feeding, and can only be used once during an experiment. Force feeding is unnecessary and fish do not have to be killed for sampling. With the retrieval of stomach contents the evacuation rate can be expressed in terms of weight per time as opposed to the subjective volume estimates of radiological techniques. There are some possible drawbacks in that this method does not always guarantee complete removal of the stomach contents (Talbot 1985), and the efficiency of the technique is negatively correlated with fish size (Hyslop 1980). Bromley (1988) found that after the gastric lavage procedure was used no food remained in the stomachs of 30 whiting and there was no evidence of food being forced through the duodenal sphincter into the hind gut. There is a possibility of damage to the oesophagus and walls of

the stomach but with careful handling this can be minimised or removed. All studies using this technique have reported quick recovery of fish and no obvious change in digestive physiology. Other methods of food recovery have been used, but they all have major disadvantages (Markus 1932, Wales 1962)

Gastric evacuation experiments have been performed on a very large range of fish species ranging from, Sacramento squawfish *Ptychocheilus grandis* (Vondracek 1987) to roach *Rutilus rutilus* (Persson 1982). The gastric evacuation rate is influenced by a number of biotic and abiotic factors. Generally GER increases as the temperature rises with a maximum rate at around the upper limit of the temperature range in which the fish species normally lives (Tyler 1970). The effect of the meal size does not appear to have a simple relationship in all fish, and different investigations have given contrasting results. Most studies found a positive relationship between meal size and evacuation rate (Windell 1967, Elliot 1972) though some found there to be no correlation (Bromley 1987, Tyler 1970) or even negative correlation (Ruggerone 1989). The size of the predator can affect the rate at which the meal is evacuated. The absolute rate increases with body size but the relative rate (grams evacuated per gram per hour) decreases (Flowerdew and Grove 1979).

The characteristics of the prey are known to be important in gastric evacuation. Elliot (1972) found prey size did not affect the GER of brown trout (*Salmo trutta*) fed on *Gammarus spp*, *Baetis spp*. or Chironomidae. However a study by Swenson and Smith (1973) found that walleye (*Stizostedion vitreum vitreum*) evacuated meals made up of small fish prey faster than those with a larger fish prey size.

The energy content of the prey, especially the protein and lipid concentrations affects the GER. Jobling (1980) showed that plaice (*Pleuronectes platessa*) evacuated high nutrient meals more slowly than meals of low nutritional value. This relationship is altered though when consecutive meals are offered and it has been shown that the energy available to the fish, rather than the total energy of the food is important.

Prey possessing a hard exoskeleton (e.g. Crustaceans) are evacuated more slowly than either fish prey (Tyler 1970, Singh-Renton 1990, Bromley 1989) or polychaetes (Jones 1974). Fish prey are in turn evacuated more slowly than the polychaetes as the fishes' scaled skin prevents digestion to some

degree (Singh-Renton 1990). As well as the skin providing a physical barrier the digestion of the prey can be affected by how it packs into the stomach and its subsequent surface area (Singh-Renton 1990, Kaiser *et al* 1992).

The way in which the skin of the prey item affects the evacuation means that whole prey should be used whenever possible as minced or pre-processed prey items will affect the rate of digestion. There is also evidence that prey items that have been frozen and then defrosted may be digested more quickly than fresh prey (Jackson *et al* 1987)

The data in gastric evacuation studies can be presented a number of ways including; absolute terms (grams of meal evacuated per hour), body weight terms (grams of meal evacuated per gram of body weight per hour), meal size (grams of meal evacuated per gram of initial meal size eaten per hour). The data may also be transformed in regards to meal size or described in terms of a percentage.

The way in which the food is evacuated from the gut is described by a gastric evacuation model. A wide range of models have been used but the two most common are linear and exponential (Table 3.1).

Table 3.1: The two most common models used to describe gastric evacuation.

Model	Equation
Exponential	$S_t = S_0 * e^{-bt}$
Linear	$S_t = S_0 - bt$

Where: S_t = stomach contents at time t
 S_0 = stomach contents at time 0
 t = time after feeding
 b = a constant

Which model to use is usually determined by the amount of variation explained, measured by the coefficient of determination (r^2). There is no formal statistical procedure to test if one model is significantly better than another and more complex models tend to lead to higher r^2 values. However more complex models also require more information so often it is better to choose a simpler model which is easier to use (Anon 1984).

The aim of these experiments was to quantify and compare the GER of fish prey with crustacean prey. The experiments also investigated whether the GER of the two prey types would change if they were fed in combination.

MATERIALS AND METHODS

The fish were housed in fibreglass tanks measuring 0.98 x 0.7 x 0.7m with undergravel filtration and circulated sea water. Four tanks (labelled A, B, C and D) were in a controlled temperature room (C.T.) and held at a mean temperature of $15.0 \pm 0.5^{\circ}\text{C}$. The other four tanks (labelled 1,2,3 and 4) were held in a separate room (hut) that had no means of temperature control so there was a greater range of temperatures (mean $17.2 \pm 1^{\circ}\text{C}$). Fluorescent tubes provided a 12hr L/D cycle in both rooms. The light intensity in the hut above the surface of the water ranged from 14-20 microeinsteins $\text{m}^{-2}\text{s}^{-1}$ and from 0.6 to 1.55 in the C.T. room.

The experimental fish used were whiting caught by rod and line near the Lowestoft laboratory in October 1991. Tanks were stocked with similar sized whiting (24.5 - 34.5 cm) 8 fish in each tank in the C.T. room (A - D) and 4 fish in each tank in the hut (1 - 4). The fish were allowed to acclimatise to the tanks for a week and were fed on a diet of live lugworm, defrosted fish and prawns.

The fish were fed as a group in each tank and prior to feeding the test meal, food was withheld for four days. This starvation period to ensure complete digestion of the previous meal, any remnants of which would bias the results. The fish fed voluntarily on the test meal that was presented by dropping individual pre weighed prey items from the water surface. The next item was not dropped until the previous one had been consumed. the fish in each tank were fed to satiation, this was judged when three items had been ignored and the fish showed no interest in feeding. The weight of meal consumed by all the fish in each tank was recorded with the time of feeding.

After this feeding the stomach contents were retrieved at 12 hourly intervals up to 48 hours. At each 12 hour interval the fish from one tank in each room were sampled. The bottom of the tank was checked for uneaten prey items and if any were found their weight was subtracted from the original meal weight. The fish were carefully netted to avoid any premature regurgitation from stress and were anaesthetised by submerging them for a few minutes in a mixture of 0.175ml of 2-phenoxyethanol per litre of sea water. The anaesthetic was required to immobilise the fish during handling to prevent them from damaging themselves. The

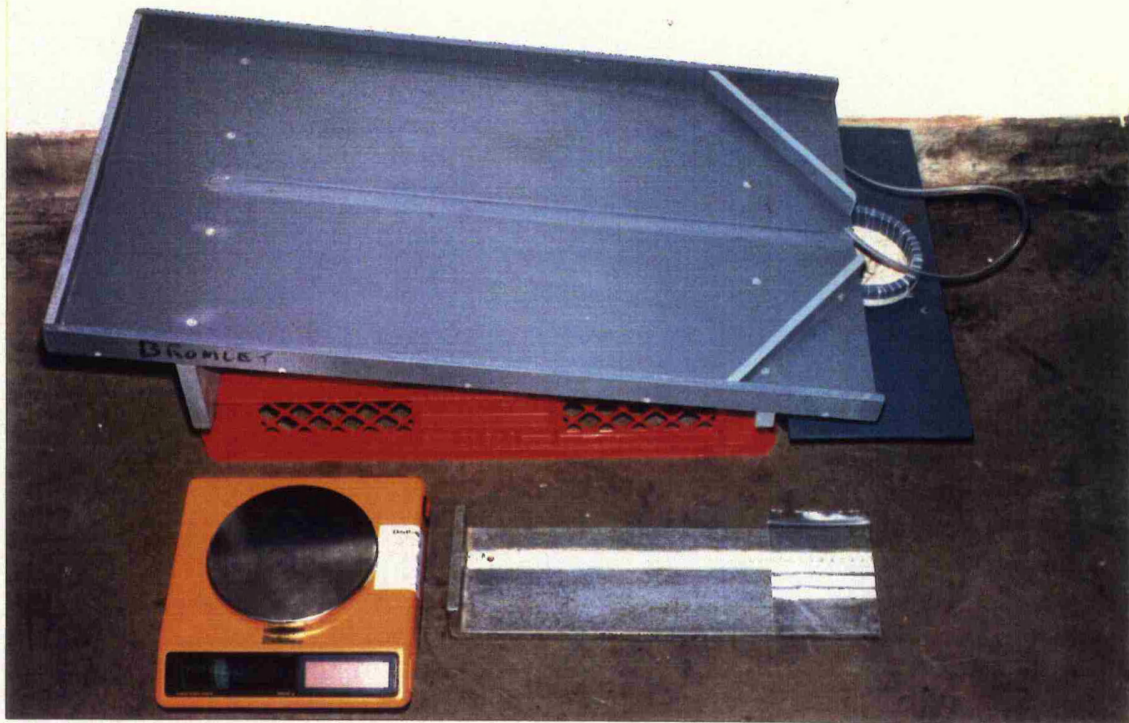


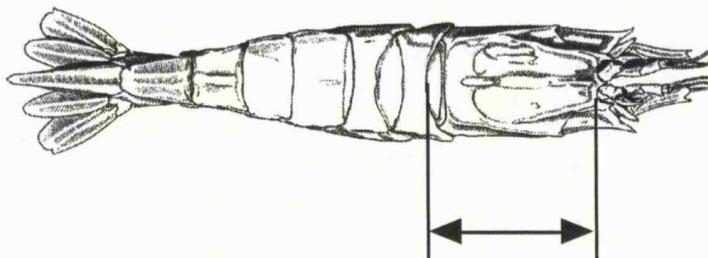
Plate 3.1: The sloped board used in the gastric lavage technique. The tube used to flush out the stomach contents, and the mesh collecting bag, are shown on the right hand side of the board. In the foreground the weighing scales and measuring board are shown.

anaesthetised fish was placed on a sloped board (Plate 3.1) and a plastic tube (1cm diameter), with rounded edges inserted into the stomach via the mouth and oesophagus .

A constant flow of sea water through this tube forced the stomach contents out through the mouth and into a collecting net (50 mesh cm^{-1}). When the stomach was empty the fish was measured and weighed and returned to the tank where it normally recovered within a few minutes. The stomach contents were emptied from the net and placed into plastic bags which were labelled and immediately frozen until later examination. Twenty fish were sacrificed after this procedure and dissected to check that the sampling technique was successfully retrieving all the stomach contents. Fish that were not sacrificed were used in subsequent trials up to a maximum of six. The trials were separated by at least one week to allow the fish to fully recover and to feed normally.

Three test diets were used; sandeels (*Ammodytes spp.*) prawns (*Pandalus spp.*) and a mixed meal of sandeels and prawns (Table 3.2). Each diet was tested twice in both of the rooms and the order in which the tanks were sampled randomised. The test diets were made up of individual items that were of approximately the same size, sandeels = 5.5 to 7.7 cm (to the nearest mm) and prawns 0.95 to 1.55 cm (to the nearest 50mg). In sandeels this was determined from the total length (Figure 2.3 Chapter 2). With the prawns the carapace length was used (Figure 3.1).

Figure 3.1 : Method of carapace measurement in prawns



The mixed meal was fed by alternately dropping a sandeel and then a prawn onto the water surface, and satiation was determined when three of

the same prey type had been ignored. The dates and number of fish sampled for each test meal are shown in Table 3.2

Table 3.2: The dates of gastric lavage sampling and the total number of fish sampled for each test diet

Diet tested	Dates of sampling		Total No. sampled
	repeat 1	repeat 2	
sandeel single	4/8/92 - 6/8/92	11/8/92 - 13/8/92	96
prawn single	18/8/92 - 20/8/92	25/8/92 - 27/8/92	96
prawn and sandeel mixed	8/9/92 - 10/9/92	15/9/92 - 17/9/92	96
	total=		288

Analysis

The amount of food that the fish in each tank ate was divided by the total weight of fish in that tank, which was then averaged over all the tanks for each prey type. This gave an estimate of the satiation level for each prey type. The satiation levels were compared between prey types by the method for testing the equality of two percentages, described by Sokal and Rohlf (1981, box 16.10).

The total weight of the stomach contents from each tank was recorded and this was expressed as a percentage of the total weight of prey eaten by the fish in that tank. These percentages were then tested for normality by plotting a normal probability scale. The lengths and weights of individual prey items were recorded when their digestion state allowed this. The digestion stage was recorded using the same scale used in Chapter 2 (Table 2.2).

Two different gastric models were fitted to the data to compare which described the evacuation of stomach contents the best. The least squares regressions (Sokal and Rohlf 1981) were calculated using Microsoft Excel™. The regressions were forced through the origin as at time zero no food had been evacuated providing a real datum. The significance of the correlation coefficient r was calculated using an F-test. Using analysis of covariance the linear evacuation models of sandeels fed in a single meal and prawns fed in a single meal were compared for homogeneity of slope (Sokal and Rohlf 1981, box 14.8). The same method was also used to compare the slopes of sandeels and prawns in single and mixed diets.

Individual lengths and weights

The lengths and weights of the ingested sandeels and prawns were compared until 24 hours had elapsed after feeding. Beyond the 24 hour time the prey items could not be separated easily into individuals and so accurate measurements could not be taken. The means of the length distributions were compared to check that samples were the same and then the mean weights were compared. The variances were checked with an F-test and the means then compared using the appropriate Students t-test. The mean weights of sandeels at 0, 12 and 24 hours were compared and the same was done with prawns. The mean weights were then compared between the mixed and single diets at 12 and 24 hours.

The gastric lavage technique described in this chapter was carried out under Home Office license PIL 80/02054.

RESULTS

Of the twenty fish sacrificed to check the success of the gastric lavage technique, no prey remains were found in any of the stomachs following the procedure. The oesophagus and stomach walls were checked for injury, but all were free of any obvious signs of damage.

The mean weight of each prey type consumed per gram of fish is shown in Figure 3.2. Although the means were expressed as a percentage, all the percentages were below 20% and it was not necessary to transform the data (Sokal and Rohlf 1981). The results of the t-tests all showed that the satiation levels were significantly different except for prawns in single and mixed diet (Table 3.3). The degrees of freedom for the comparisons of sandeels and prawns in single and mixed meals were calculated assuming unequal variances.

Table 3.3: The t-test statistics of the comparison of the satiation levels of the different meal types. Satiation levels were recorded as percentage prey weight of whiting weight.

Meal types compared	sandeel single	prawn single	sandeel single	sandeel mixed	prawn single	prawn mixed
Mean (%)	8.29	4.46	8.29	1.34	4.46	3.42
Variance	5.79	5.85	5.79	0.25	5.85	1.60
Observations	16	16	16	16	16	16
df	30		16.3		22.6	
t	4.49*		11.31*		1.52	
P(T<=t) two-tail	<0.05		<0.05		>0.05	

Gastric evacuation model

The regression statistics of the two evacuation models fitted to the data are shown in Table 3.4 and Figures 3.3 and 3.4. The equations shown are the models that describe the percentage of the meal evacuated against time. In every case the fitted model significantly described the variation. The normal probability scales calculated to test the normality of the distributions returned straight lines and so no transformation was necessary on the data.

Figure 3.2: The mean weight of prey consumed per gram of whiting for each of the meal types used (95% error bars shown)

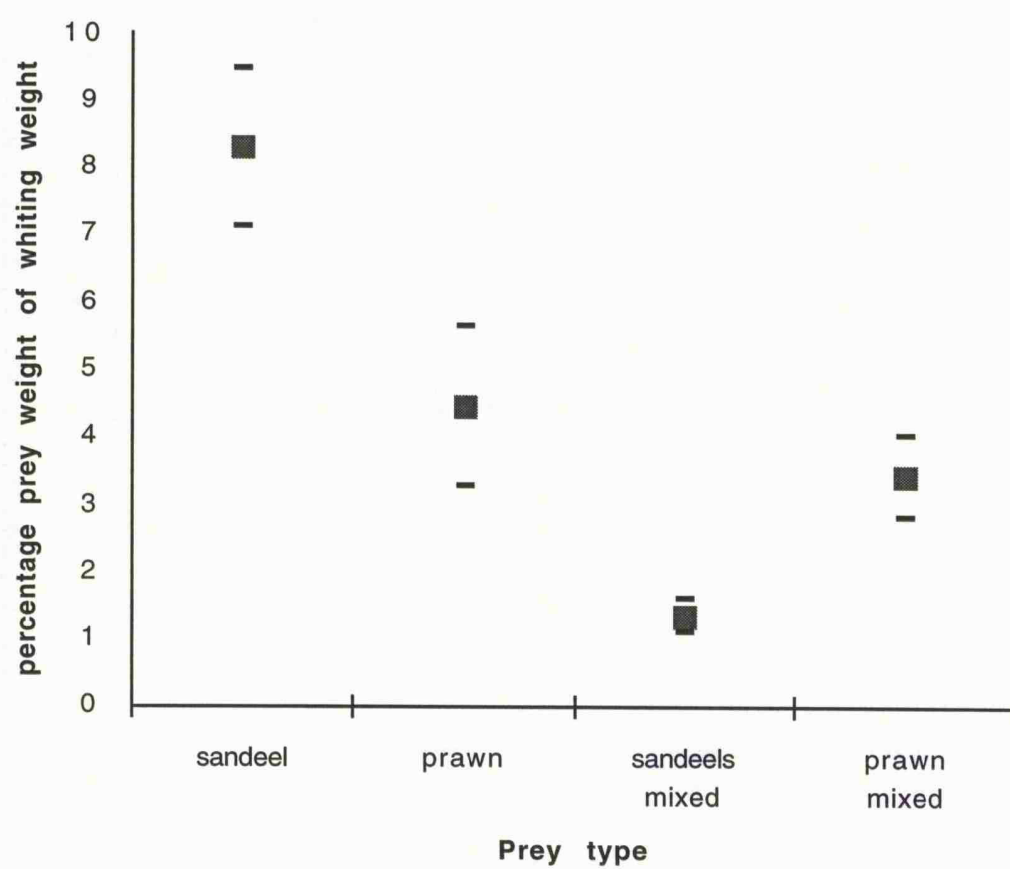


Table 3.4: Summary of linear and exponential gastric evacuation models fitted to data

Model	Test Meal	Equation	r ²	Probability
Linear	sandeels	$S_t = 100 - 2.004t$	0.974	$p < 0.05$
	prawns	$S_t = 100 - 1.749t$	0.822	$p < 0.05$
	mixed	$S_t = 100 - 2.246t$	0.870	$p < 0.05$
	sandeels			
	mixed	$S_t = 100 - 1.452t$	0.717	$p < 0.05$
	prawns			
Exponential	sandeels	$S_t = 100 * e^{-0.953t}$	0.829	$p < 0.05$
	prawns	$S_t = 100 * e^{-0.968t}$	0.801	$p < 0.05$
	mixed	$S_t = 100 * e^{-0.935t}$	0.661	$p < 0.05$
	sandeels			
	mixed	$S_t = 100 * e^{-0.976t}$	0.560	$p < 0.05$
	prawns			

The linear regression model accounts for 71% or greater of the variation of food remaining in the stomach over time in all the test diets. The slope coefficient is significant at the 0.05 level over all the diets. The exponential model slope coefficient is also significant but the amount of variation described is less than with the linear model in all of the test meals. In the rest of the analysis the linear model of gastric evacuation was used.

Prey type

The statistics for analysis of covariance used to test the homogeneity of the linear regression lines of sandeels and prawns in a single diet are shown in Table 3.5.

Table 3.5: Statistics from the comparison of slopes between sandeel and prawn in a single diet

H₀: The two prey types were sampled from populations of equal slopes.

H₁: The two prey types were sampled from groups of unequal slopes.

statistics	sandeels single meal	prawns single meal
b	2.004	1.749
number	20	20
Σx^2	19440	17280
$Sd^2_{Y.X}$		96.422
Fstat		6.16*
d.f.		36
Probability		<0.05

The F statistic calculated was significant so the null hypothesis is rejected and H₁ accepted. The slope describing the evacuation of sandeels is significantly steeper than the slope describing prawn evacuation.

Figure 3.3: Linear (solid line) and exponential (dashed line) models fitted to the evacuation over time of sandeels fed as a single meal

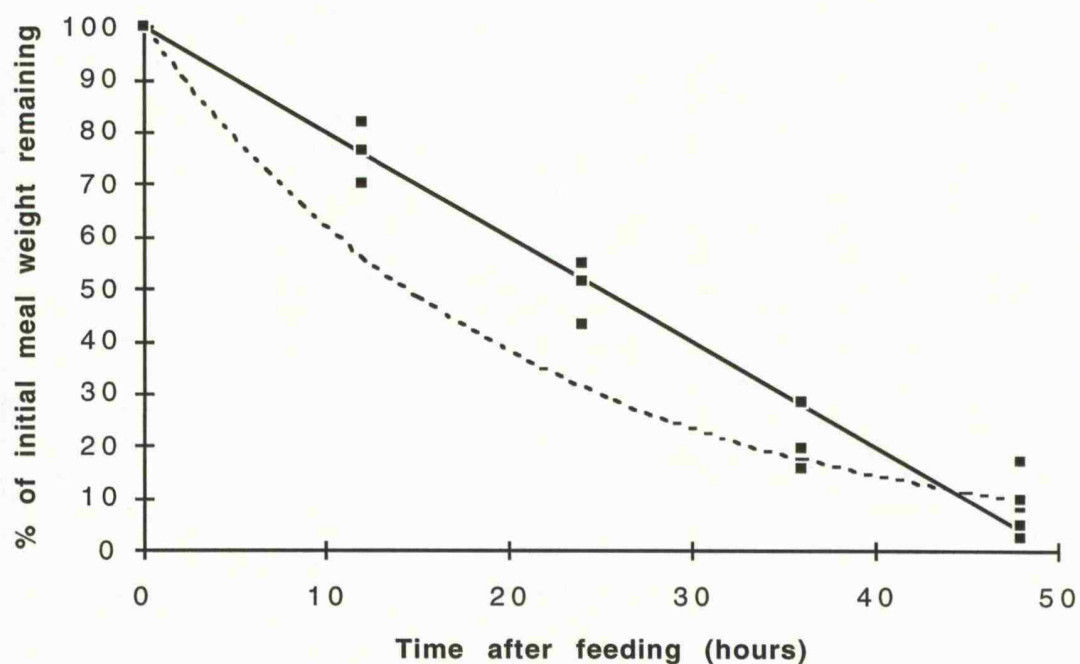
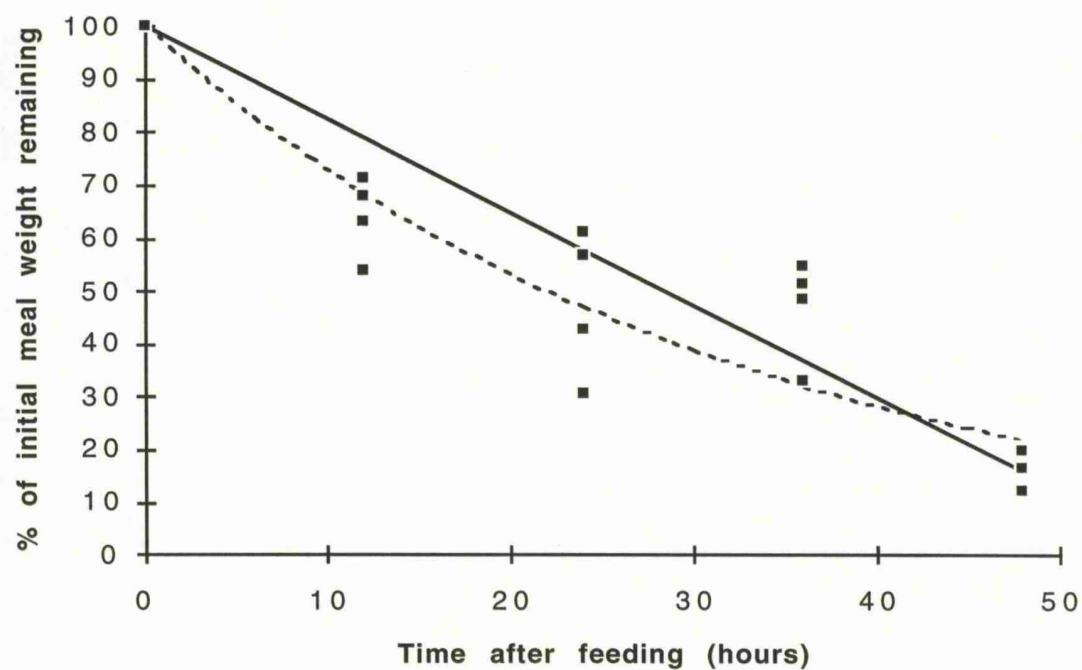


Figure 3.4: Linear (solid line) and exponential (dashed line) models fitted to the evacuation over time of prawns fed as a single meal



Mixed vs Single diet

The results from the comparison of the slope of sandeels in a single diet to sandeels in a mixed diet are shown in Table 3.6 and Figure 3.5.

Table 3.6: Statistics from the comparison of slopes describing the evacuation rate of sandeels fed on their own or when fed together with prawns

statistics	sandeels single meal	sandeels mixed meal
b	2.004	2.246
number	20	20
Σx^2	19440	17280
$Sd^2_{Y.X}$		107.858
Fstat		4.99*
d.f.		36
Probability		<0.05

The F statistic calculated was significant at the 5% level so the null hypothesis was rejected. Sandeels offered in a mixed meal were evacuated at a faster rate than sandeels on their own. The opposite is seen for the prawns which are evacuated quicker when on their own than when eaten in conjunction with sandeels (Table 3.7, Figure 3.6)

Table 3.7: Statistics from the comparison of slopes describing the evacuation rate of prawns fed on their own or when fed together with sandeels

statistics	prawns single meal	prawns mixed meal
b	1.749	1.452
number	20	20
Σx^2	17280	17280
$Sd^2_{Y.X}$		172.374
Fstat		4.43*
d.f.		36
Probability		<0.05

Figure 3.5: Linear (solid line) and exponential (dashed line) models fitted to the evacuation over time of sandeels fed as a mixed meal

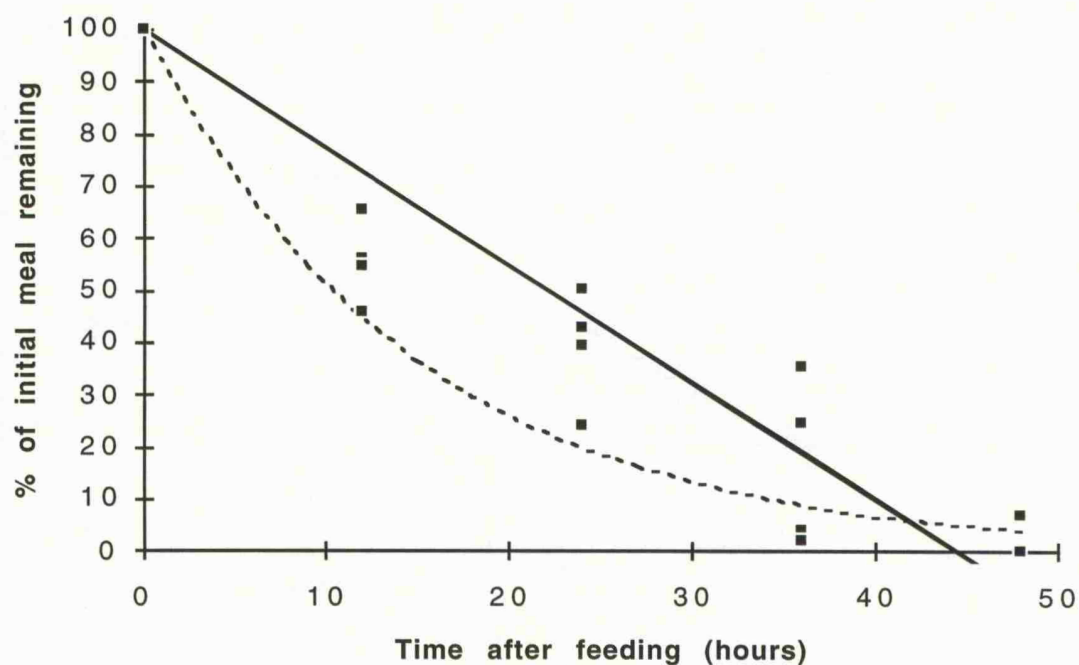
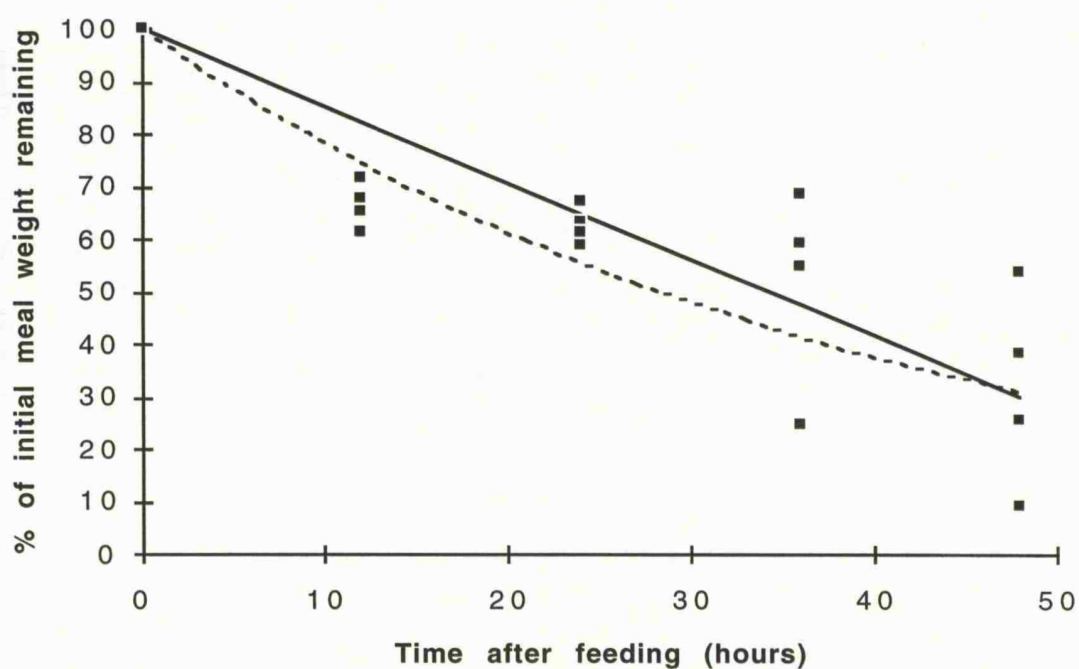


Figure 3.6: Linear (solid line) and exponential (dashed line) models fitted to the evacuation over time of prawns fed as a mixed meal



Individual Weights and Lengths

The changes in the mean length and weight of individual prawns and sandeels over the sampling times are shown in Figures 3.7 to 3.10.

Table 3.8: The results of t-tests between the mean lengths in cm and weights in grams of sandeels removed from whiting stomachs at the different sampling times

Sandeel lengths	0hrs	12hrs	12hrs	24hrs	0 hrs	24 hrs
Mean (cm)	6.47	6.44	6.44	6.43	6.47	6.43
Variance	0.17	0.16	0.16	0.24	0.17	0.24
Observations	55	41	41	85	55	85
df	94		97		129	
t	0.28		0.22		0.53	
Probability	>0.05		>0.05		>0.05	
Sandeel weights	0hrs	12hrs	12hrs	24hrs	0 hrs	24 hrs
Mean (grams)	0.51	0.47	0.47	0.40	0.51	0.40
Variance	0.01	0.02	0.02	0.01	0.01	0.01
Observations	55	48	48	136	55	136
df	101		182		189	
t	1.82		3.77*		6.56*	
Probability	>0.05		<0.05		<0.05	

The mean lengths of the prawns and sandeels were not significantly different at each of the sampling times 0, 12 and 24 hours. The results of the t-tests in Tables 3.8 and 3.9 show there is a significant difference between the weights of individuals over time in both sandeels and prawns. The exceptions to this are there is no significant difference between the weights of sandeels sampled at 0 and 12 hours and between prawns at 12 and 24 hours

Table 3.9: The results of t-tests between the mean lengths in cm and weights in grams of prawns removed from whiting stomachs at the different sampling times

Prawn lengths	0hrs	12hrs	12hrs	24hrs	0 hrs	24 hrs
Mean (cm)	1.21	1.22	1.22	1.24	1.21	1.24
Variance	0.02	0.01	0.01	0.00	0.02	0.00
Observations	47	29	29	9	48	9
df	73		27		35	
t	-0.25		-0.75		-0.90	
Probability	>0.05		>0.05		>0.05	
Prawn weights	0hrs	12hrs	12hrs	24hrs	0 hrs	24 hrs
Mean (grams)	1.42	1.08	1.08	0.93	1.42	0.93
Variance	0.16	0.15	0.15	0.12	0.16	0.12
Observations	48	35	35	51	48	51
df	81		84		97	
t	3.80*		1.95		6.46*	
Probability	<0.05		>0.05		<0.05	

Single vs mixed diet

The individual length and weight changes over time for sandeels in the single and the mixed test diet are shown in Figures 3.11 and 3.12. The mean lengths at the 12 and 24 sampling times are not significantly different between the two test diets. There is also no significant difference between the mean individual weights at the first sampling time 12 hours. There is a significant difference between the mean weight of individual sandeels in a single diet compared to a mixed diet at 24 hours (Table 3.10).

The individual length and weight changes over time for sandeels in the single and the mixed test diet is shown in Figures 3.13 and 3.14. The t-test results for the prawn data are shown in Table 3.11 and again no difference was found between the lengths of the prawns. The 12 hour sampling time has a significant difference between the mean prawn weights but the 24 hour sample does not.

Table 3.10: The results of t-tests between the mean lengths in cm and weights in grams of sandeels in mixed and single test diets at the different sampling times

Sandeel lengths	12 hours		24 hours	
	single	mixed	single	mixed
Mean (cm)	6.44	6.38	6.54	6.43
Variance	0.16	0.35	0.08	0.24
Observations	41	26	19	85
df	39		45	
t	0.45		1.31	
Probability	>0.05		>0.05	

Sandeel weights	12 hours		24 hours	
	single	mixed	single	mixed
Mean (grams)	0.47	0.41	0.40	0.30
Variance	0.02	0.01	0.01	0.01
Observations	48	31	136	55
df	77		131	
t	1.92		6.60*	
Probability	>0.05		<0.05	

Table 3.11: The results of t-tests between the mean lengths in cm and weights in grams of prawns in mixed and single test diets at the different sampling times

Prawn lengths	12 hours		24 hours	
	single	mixed	single	mixed
Mean (cm)	1.22	1.18	1.24	1.23
Variance	0.01	0.01	0.00	0.00
Observations	29	24	9	14
df	51		21	
t	1.55		0.53	
Probability	>0.05		>0.05	

Prawn weights	12 hours		24 hours	
	single	mixed	single	mixed
Mean (grams)	1.08	1.25	0.93	0.99
Variance	0.15	0.07	0.12	0.10
Observations	35	30	51	52
df	61		101	
t	-2.05*		-1.03	
Probability	<0.05		>0.05	

Figure 3.7: The changes in the mean length of individual sandeels against time after ingestion. (Bars show standard error on the means)

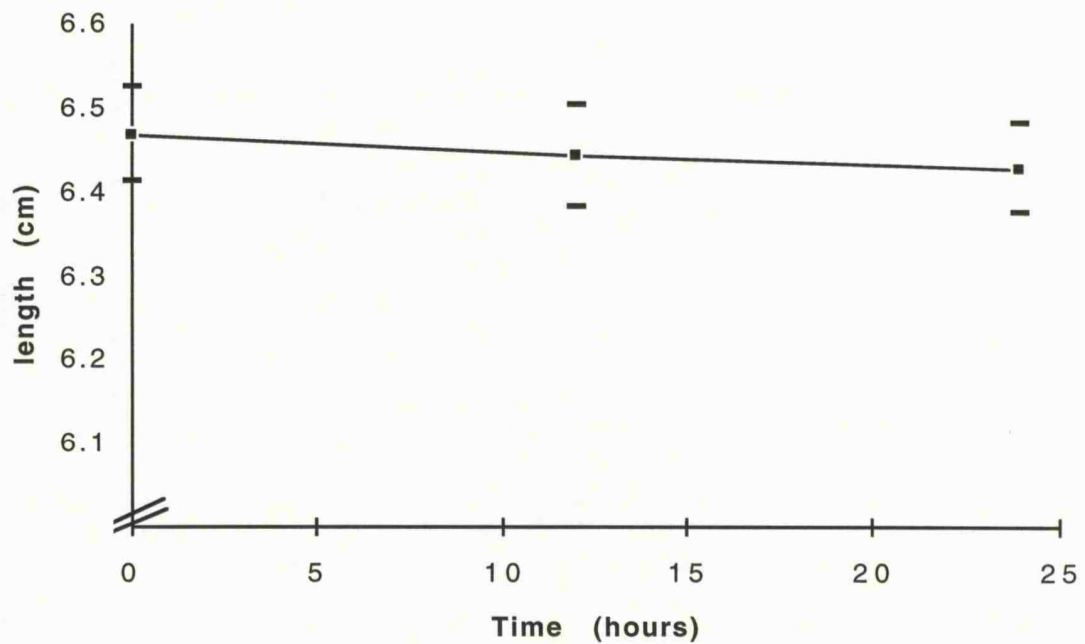


Figure 3.8: The changes in the mean weight of individual sandeels against time after ingestion. (Bars show standard error on the means)

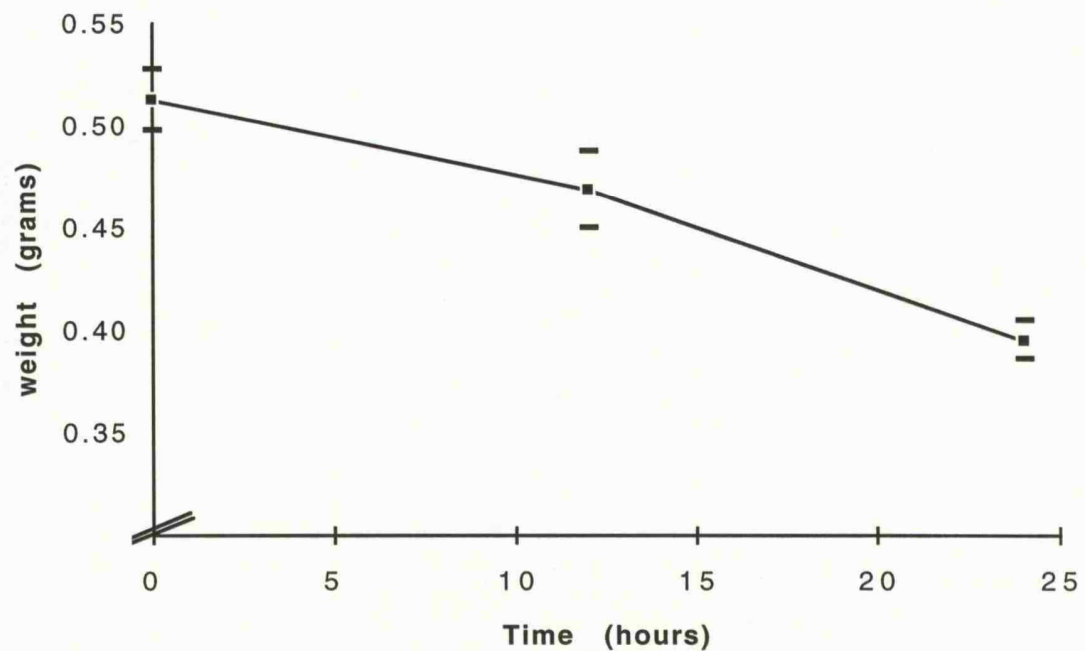


Figure 3.9: The changes in the mean length of individual prawns against time after ingestion. (Bars show standard error on the means)

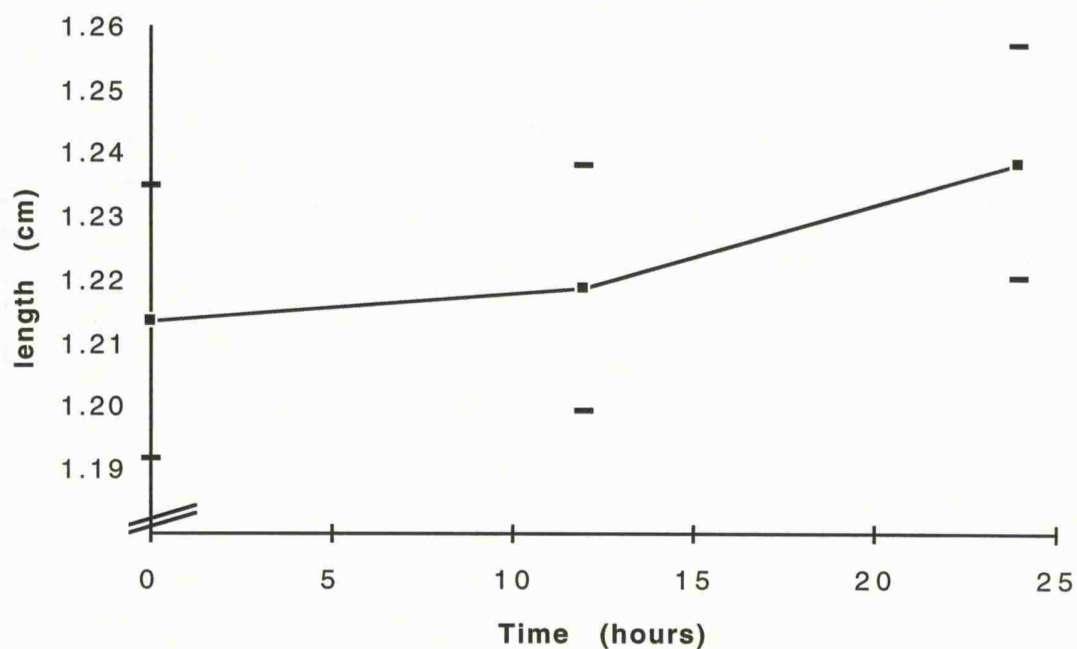


Figure 3.10: The changes in the mean weight of individual prawns against time after ingestion. (Bars show standard error on the means)

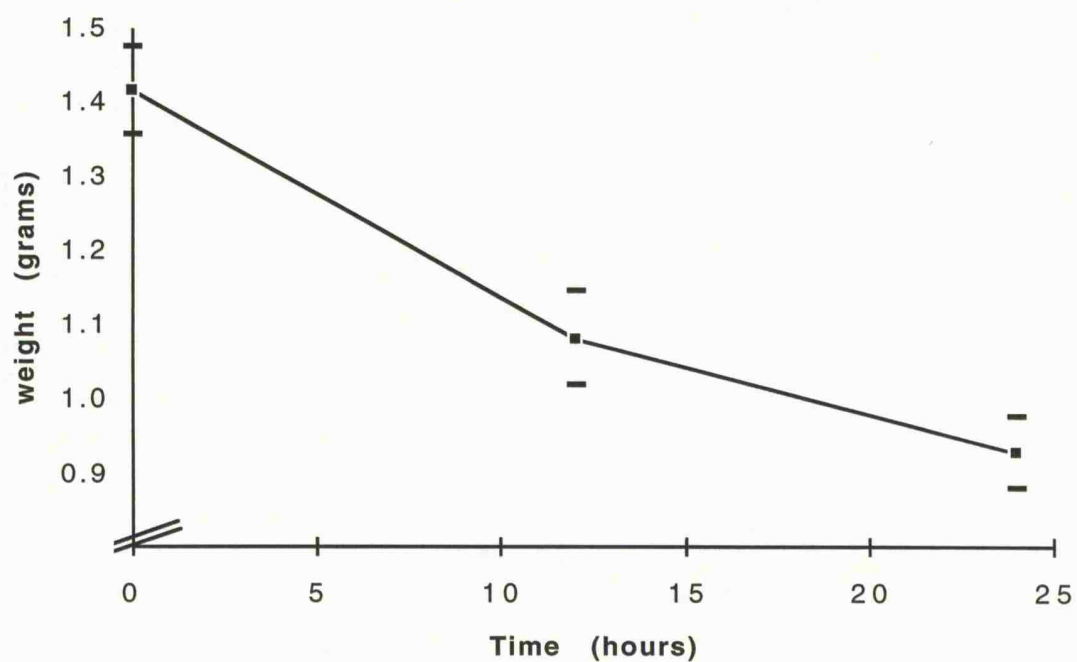


Figure 3.11: Mean lengths of individual sandeels in mixed and single diets against time after ingestion. (Bars show standard error on the means)

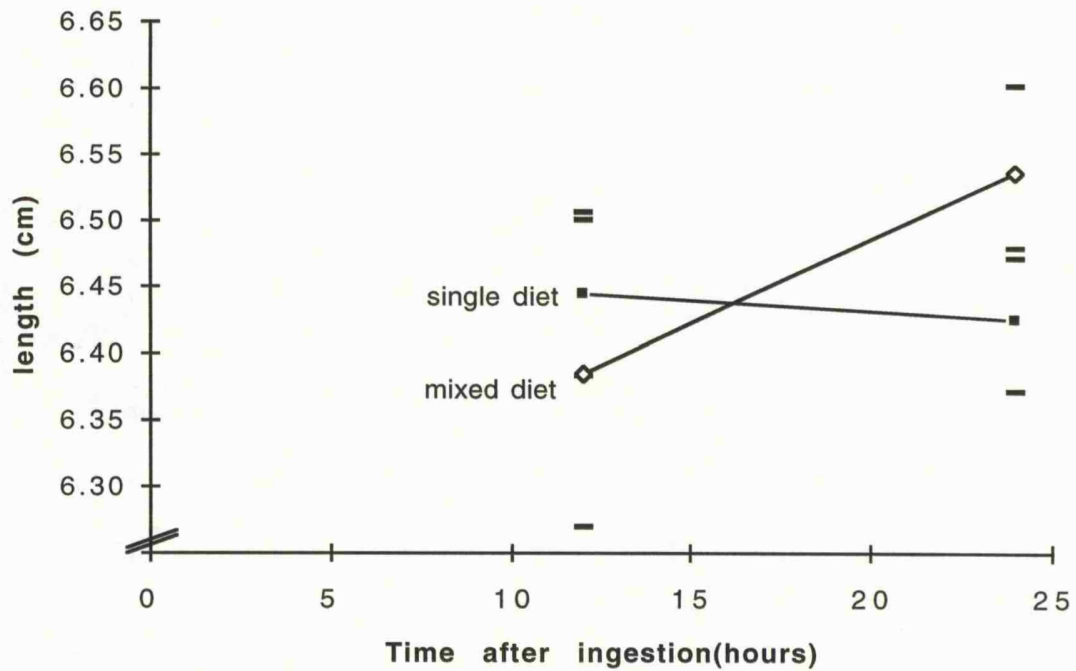


Figure 3.12: Mean weight of individual sandeels in mixed and single diets against time after ingestion. (Bars show standard error on the means)

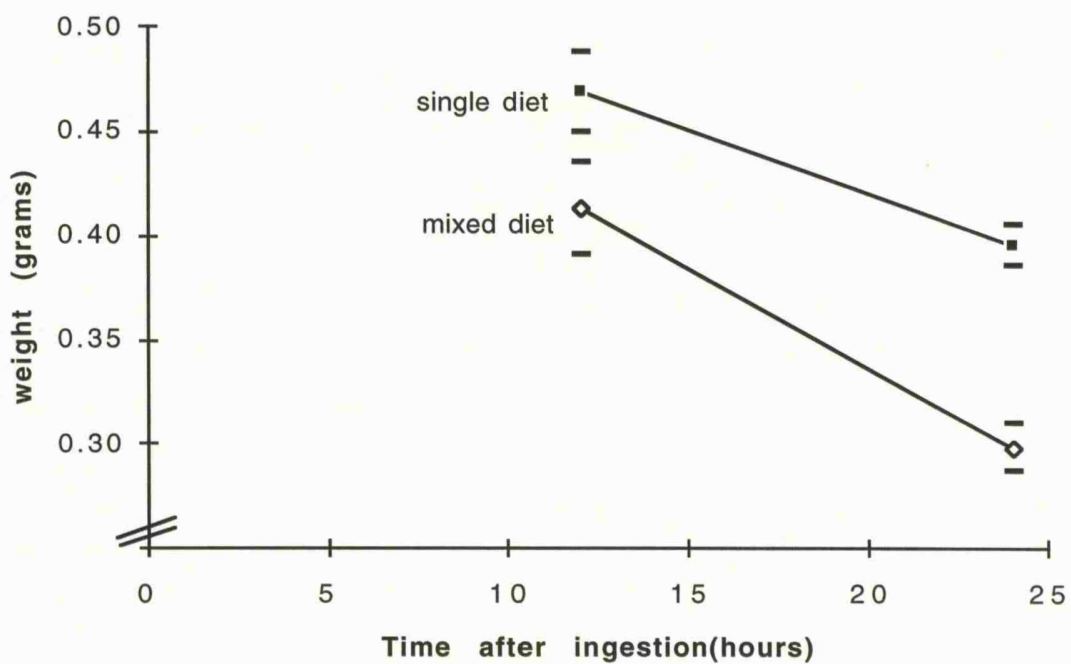


Figure 3.13: Mean length of individual prawns in mixed and single diets against time after ingestion (Bars show standard error on the means)

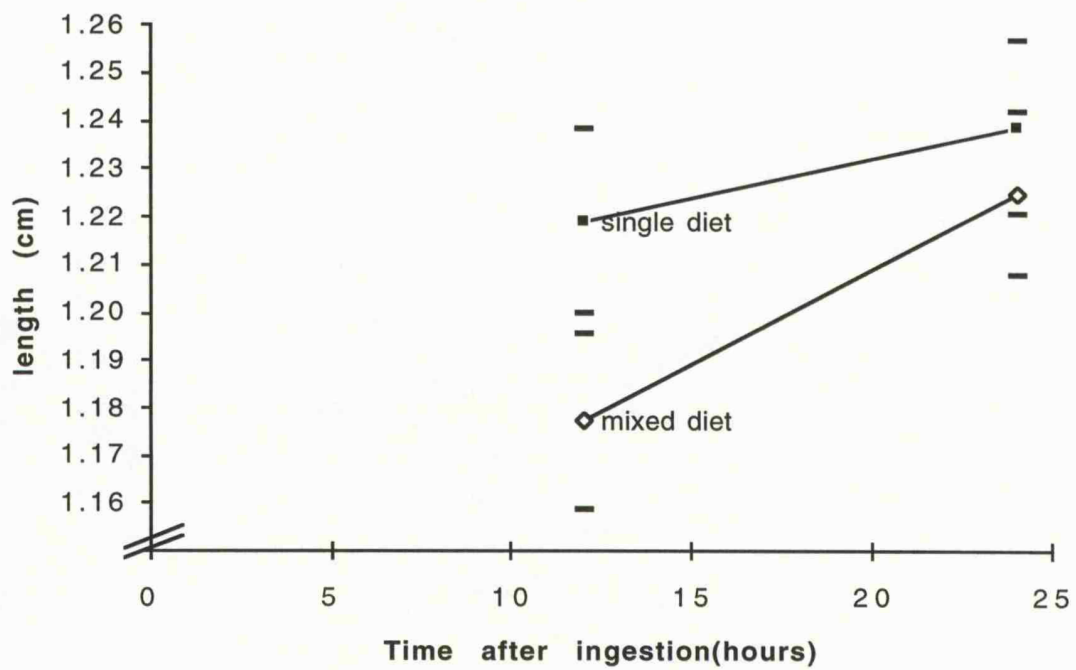
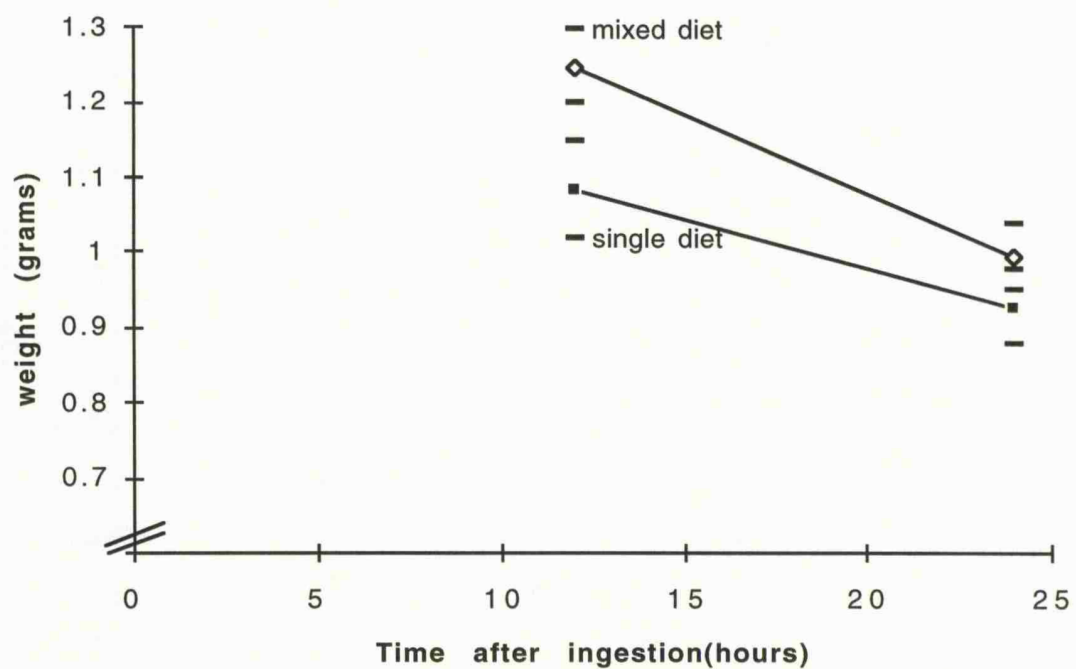


Figure 3.14: Mean weight of individual prawns in mixed and single diets over time after ingestion (Bars show standard error on the means)



DISCUSSION

The use of the gastric lavage technique to remove the stomach contents was found to be highly successful. All of the sacrificed fish had empty stomachs and all the fish allowed to recover from the anaesthetic did so almost immediately. This was also found by Bromley (1987) and Singh-Renton (1990).

The difference between the satiation levels with the prawn and sandeel diets could be due to the arrangement of the prey in the stomach. The sandeels are long and thin and form a tight bolus in the stomach. The prawns are an awkward shape and their appendages and rigid exoskeletons prevent tight packing. The stomach will reach fullness and prevent any more food from being swallowed at a much lower weight with prawns than with sandeels. The lower satiation level of fish feeding on crustaceans has been observed by other investigators (Bromley 1989, Singh-Renton 1990).

The results were expressed as a percentage of the meal weight originally ingested. This percentage was used because there was a large variation in the initial size of meal consumed per tank. The variation was mainly due to some fish in each tank which did not settle into the experimental conditions well and as a result took very little food or none at all. Expressing the evacuation as a percentage of meal size corrected for these differences so that they did not bias the observed pattern of evacuation. Sampling the tanks was randomised so any differences in fish performance was spread over all of the sampling times. There can be large inter-individual differences in the feeding of fish (Dos Santos and Jobling 1991) the effects of which can be lessened by communal feeding and randomised sampling. This communal feeding can lead to large variations in the amount of food taken, but as the stomach contents of fish in the wild also vary it probably reflects the natural situation more closely.

Comparing the linear and exponential evacuation models, both fitted the data well. Comparing the r^2 values it was clear that the linear model accounted for the most variation in percentage weight of meal remaining although the exponential model also described a significant amount of this variation. Judging the lines by eye the exponential model tended to predict values of food remaining in the stomach that were lower than those the observed at 24 and 36 hours and over estimated the amount of the meal

evacuated at these times. Over all the meals the linear evacuation was regarded to be the best description of the data and so this model was used in the rest of the analysis. The linear model also has the advantage that it is the simplest model and is easier to apply.

Other workers have used linear regressions to describe the evacuation of food by whiting. Robb (1990) found that in 24-29cm whiting at a temperature of 13°C, a meal of sandeels was evacuated at a rate of 1.82% of the initial meal per hour (%meal h⁻¹). Larger whiting 30-45 cm evacuated at 2.02%meal h⁻¹. Bromley (1987) found that meal size had no effect on evacuation rate but in 286g whiting feeding to satiation at 10°C the meal was evacuated at a rate of 1.297 %meal h⁻¹. These results are similar to the ones found in this study e.g. 2.004%meal h⁻¹ for whiting fed on a meal of sandeels (Table 3.4). The differences possibly resulting from the slightly different sized fish and the lower temperatures.

The measured lengths of the sandeels were the same in each time period. This meant that their weights could be compared as their original weights would have been the same. The same uniformity of length in the prawns meant that their weights could also be compared. In a linear regression the mean weight of each individual should decrease by a similar amount at each 12 hourly sampling period. The picture is complicated since the prey are in a food bolus, and individuals on the edge of the bolus are digested quicker than ones in the middle (pers obs., Singh-Renton 1990). This differential digestion is especially true in tight packing prey such as sandeels. The mean weight of sandeels at 12 hours was not significantly different than the mean weight at 0 hours but was significantly different at 24 hours from both 0 and 12 hours. This suggests that the digestion is not quite linear. This may be because the skin of the sandeels is still intact or there may be some delay in the release of the digestive enzymes. The prawns were significantly different between the mean weight at 0 and 12 hours, but were not between 12 and 24 hours. This suggests that the evacuation rate is slowing down but is probably due to the sampling method. In the gastric lavage technique the appendages which have been weakened by digestion tend to break off and are then hard to assign to individuals. This loss of appendages can have the effect of decreasing the mean weight in the early samples and thus decreasing the difference between this and the later samples. If the probability level is increased to

0.1 then all the weights would be significantly different, and looking at Figure 3.10 the relationship is still approximately linear.

The prawns were evacuated more slowly than sandeels which is a common finding in evacuation work. Bromley (1989) found that cod feeding on *Nephrops norvegicus* evacuated them almost 3 times more slowly than sprats (*Sprattus sprattus*). Singh-Renton (1990) showed that lugworm (*Arenicola marinus*) and herring (*Clupea harengus*) were evacuated four or five times more quickly than brown shrimp (*Crangon crangon*) in juvenile cod and whiting. The difference between the evacuation rates of prawns and sandeels in this work is smaller than these previous studies. However the results in this study are expressed as percentage of the meal eaten. Satiation levels were measured as grams of prey weight per gram of whiting weight. Whiting eating a meal of prawns had a lower satiation level than when they ate a meal of sandeels. This lower satiation level means that if the difference in evacuation rate was expressed in absolute terms, the difference would be much greater.

The slower rate for crustacean prey could be an effect of the hard exoskeleton acting as a barrier to the digestive juices (Bromley 1994). The soft inner flesh is protected and so the meal takes longer to digest as the exoskeleton must be penetrated first. The skin of the sandeels also acts as a barrier to digestion but it is not as effective a barrier as the crustacean exoskeleton (Singh-Renton 1990).

The faster evacuation of fish prey could be an advantage to the whiting if they were limited in their food intake by stomach constraints. Whiting consuming fish prey would be able to empty their stomachs more quickly than those on a crustacean diet and they can also consume a larger weight of sandeels before satiation. There may also be an advantage in that the energy expended in digestion to obtain the energy from the prey would be less, and the net profit would be higher. Increased intake and lower energy expenditure would increase the profitability of fish prey to whiting.

Mixed Diet

In terms of the percentage of the initial meal evacuated per hour, sandeels are evacuated more quickly when eaten with prawns, and the prawns are evacuated more slowly than when eaten on their own. The increased evacuation rate should be noted with some caution. The average weight of sandeels eaten in the two experiments were very different as the sandeels in the mixed diet were eaten with prawns. The ratio fed to the fish of prawns and sandeels was 1:1 in numbers but the prawns were heavier and larger. There was no way of controlling the ratio that each individual ate and so although most fish took a mixture of prey some fish did have a single prey type in their stomachs. These lower meal sizes and varying ratios reduce the confidence in the result and need to be taken into account when considering the implications.

The data on individual weight and length of prey also supports the hypothesis that the mixed diet changes the evacuation rate. The mean weight of the sandeels is lower in the single test meal experiment than in the mixed meal one at the 24 hour sampling time. The mean weights at the 12 hour sampling time were only different with 0.06 probability. The lower mean weights can be clearly seen in Figure 3.12. The prawn data are more varied. The 12 hour samples are significantly different but the 24 hour samples are approximately the same. Why this occurs is not clear but looking at Figure 3.14 both of the lines are still approximately linear. It may be that the effect on the evacuation of prawns is less than the effect on sandeels and that a significant difference is only apparent at the 12 hour stage.

The faster evacuation can be explained by two hypotheses, stomach packing and mechanical effects. The sandeels in a single diet pack into a very tight bolus and so the surface area on which the digestive enzymes can work is relatively small. When sandeels are eaten with prawns this tight bolus can not form and so the surface area is much greater and the digestion is speeded up. The slowing down of the prawn evacuation can also be explained by this theory as the sandeels decrease the surface area of the food bolus compared to prawns in a single diet.

The stomach is a muscular bag and there is some mechanical element to the digestion of food. The prawns with their hard exoskeleton and appendages are very abrasive and may increase the influence of the

muscular action. The skin of the fish provides some protection from the digestive enzymes and so if the abrasive quality of the prawns opens up this barrier then the GER may increase.

Singh-Renton (1990) investigated the evacuation of mixed diets involving lugworm, sandeels and brown shrimp in juvenile cod and whiting. She did not find any difference between the evacuation in single and mixed diets. This lack of difference maybe due to the methodology of the experiments or the prey characteristics. In her experiments the evacuation rate was expressed as a percentage of the weight of fish and no account of meal size was taken. If the results in the present study were expressed in the same way the evacuation rate for mixed sandeels would be much slower as the meal size was considerably smaller. The prey investigated by Singh-Renton (1990) were different to the ones in this study and it may be that the prawns are more abrasive than the brown shrimp or that the brown shrimp pack closer together than do the prawns.

The advantage to the whiting of sandeels being evacuated more quickly when eaten with prawns is not that great. If the whiting were limited in their food intake by stomach constraints the reduction in the amount they could eat would negate any benefits from a faster evacuation rate. The fish in this experiment were fed on an alternating diet of prawns and sandeels and to achieve this in the wild would probably require the fish to switch its feeding location which would cost it time and energy. In the cruise data presented in Chapter 2, the majority of the fish had a single prey type in their stomachs. However there maybe an even larger difference with other combinations of prey or in different sized fish.

CHAPTER 4

FEEDING BEHAVIOUR

“The difficulty in life is the choice”

George More: *from The Bending of the Bough*

INTRODUCTION

When fish are foraging they incur costs as well as benefits. The energy of any prey successfully ingested adds to the fish's energy levels, but the energy spent searching for, capturing and handling a prey item will decrease these reserves (Stephens and Krebs 1986). Different prey types will have different characteristics which will affect the net energy gain the fish will accrue if they eat them. The energy used in foraging for prey is difficult to measure and so the costs are generally recorded as time spent in each activity. The time spent foraging can have other costs as well as purely energetic ones. An actively foraging predator may be exposed to a greater risk of being predated upon itself, and time spent foraging may limit the time the fish can spend in other activities such as mating or protecting a territory. The searching time for a prey item will usually be dependent on its abundance. The time to capture and handle a prey item are regarded in most cases as the important factors in the differing profitability of prey types. The differences in the prey types and their subsequent profitability to the fish has led to the theory of optimal foraging. In optimal foraging theory it is postulated that the fish forages in such a way as to maximise the net energy it gains over time. Optimal foraging theory is discussed in greater detail in Chapter 5.

The detection of food in whiting by chemoreception was investigated by Pawson (1974). Pawson also studied the methods the whiting used to uncover buried food. Brawn (1969) studied the feeding behaviour of cod, mainly in terms of the detection of food. Løkkeborg *et al* (1989) investigated the way in which cod and haddock detected and attacked baited hooks observed in the natural environment.

The selection of prey by fish has been investigated by a large number of workers. Jolicœur and Brunel (1966) compared the availability of the prey fauna with the stomach contents of cod, and they showed a significant difference between the relative abundance of three pelagic crustacean species and the proportions of these eaten by cod. Daan (1973) showed that prey weight increased with cod length with a power relationship which he suggested maybe due to selection. Hislop *et al* (1991) found that prey size increased with whiting (predator) size and postulated that this was because of selection.

Prey selection can take two forms, active and passive (Stephens and Krebs 1986). In active selection the predator is deliberately choosing a prey type with certain characteristics over another or several other types. Passive selection is where the ratio of the prey items in the predator's stomach is due to differences in catchability, or availability to the predator. For example if a fish has the same probability of striking at two different prey types, but there is a difference in the probability that they will be successfully captured and eaten, then this could be described as passive selection. The reason for any differences will be because of prey characteristics such as size, shape or behaviour.

The selection of prey by fish, and factors that influence this selection have been widely studied. Werner (1974) showed a relationship between prey size and handling time in two species of sunfish. Magnhagen (1985) showed that prey size selection by three marine fish, was influenced by absolute and relative prey densities and also by the predator size. Prey and fish size have also been investigated by other workers. Gill and Hart (1994) studied the affect of increasing stomach fullness on profitability of a larger prey size to threespine sticklebacks *Gasterosteus aculeatus*. The affect of learning has been studied in terms of prey recognition and prey selection. Ware (1971) showed that rainbow trout (*Salmo gairdneri*) were more likely to attack a prey item, and would do so from further away when they had previous experience of it. Croy and Hughes (1991) found that sticklebacks would forage more efficiently on prey items as a result of experience. The affect of the digestive characteristics of prey were investigated by Kaiser *et al.* (1992). They found that although the physiological constraints influenced the net energy uptake in fifteen-spined sticklebacks (*Spinachia spinachia*) their prey choice was based on the characteristics of prey before digestion.

This chapter looks at the affect of various factors on the foraging of whiting. The factors investigated included learning, prey size, whiting size and stomach fullness. These factors were investigated in terms of their effect on the sequence of behaviours used to capture prey, and the time taken, to hunt and handle prey items.

MATERIALS AND METHODS

Background to the methods of behavioural analysis

The various methods used in the collection and analysis of behavioural data are well documented (Colgan 1978, Huntingford 1984). In direct observation the subject being studied is watched and the behaviours recorded in 'real time'. This technique is useful and simple requiring no sophisticated equipment, merely a pen, paper and stop watch. Sometimes direct observation is not possible, especially when the behaviours are so fast that accurate measurements cannot be taken. In these cases the use of video tape is vital. The subject is filmed and the behaviours played back in slow motion and analysed. Video recording allows the action to be saved and analysed in great detail. Video recording does have some disadvantages as often the area to be filmed must be specially designed with strong lighting and with a restricted size to obtain good quality pictures. The resulting image is two dimensional so some resolution and subsequent information may be lost or reduced. The analysis of video data can also be very time consuming if the subject is studied in detail.

The behaviours can be recorded in two main ways (Martin and Bateson 1986); time sampling and continuous recording. Time sampling is where the behaviour occurring at each specified time interval is noted. This sampling method is useful when the observer wishes to condense information, and it makes it possible to record several different categories of behaviour at the same time. In continuous sampling the observer records each occurrence of a behaviour and its duration. This method gives an exact record of the behavioural patterns and is most useful when the aim is to analyse behavioural sequences (Martin and Bateson 1986). Before the recording begins the start and end of each behaviour must be defined. The data is usually recorded onto recording sheets by hand, though special recording computers can be used.

With behaviours such as feeding that are ordered into a highly organised sequence the best model of the sequence is a Markov chain (Slater 1973, Crane 1978, Martin and Bateson 1986). Markov chain analysis shows whether a sequence is random, or if the probability of a behaviour occurring is influenced by previous behaviours. The probability that a behaviour follows another behaviour is first calculated, and this is called a

transition probability. If the transition probability of a behaviour is only calculated from the behaviour occurring immediately before, the Markov chain is first order. If the previous two behaviours were influential then the Markov chain is second order. Generally first order chains are used as the information required to construct higher order chains is very large. The transition probabilities are placed in a contingency table (Table 4.0) called a transition matrix.

Table 4.0: An example of a transition matrix including first order transition probabilities

		Previous behaviour		
		A	B	C
Following behaviour	A	$p(A A)$	$p(A B)$	$p(A C)$
	B	$p(B A)$	$p(B B)$	$p(B C)$
	C	$p(C A)$	$p(C B)$	$p(C C)$

(Where $p(A|B)$ equals the probability that A will occur given that B has happened.)

Some of the behavioural transitions may not be possible, this is usually the case with the repetition of a behaviour e.g. A cannot follow A. Usually repetition cannot take place as it is impossible to say where one expression of a behaviour ends and the next one begins. These behavioural transitions are replaced with logical zeros and the computation of any statistics must take these into account (Slater 1973).

To test whether the following behaviour is independent of the previous one, the actual number of times each transition occurs is compared to the expected numbers if the sequence were random. The expected numbers are usually calculated by multiplying the column and row totals and dividing by the total number of observations.

$$expected_{ij} = \frac{\sum observed_i \times \sum observed_j}{\sum observed_{ij}}$$

where:

i = row cells

j = column cells

The comparison between observed and expected numbers is usually done with a chi-squared test. Care should be taken as the assumptions of the test

are often broken by these matrices. This technique cannot be used in tables with logical zero values. In these tables the expected values must be interpolated using a technique, for example, as described by Goodman (1968). The sequences under different conditions can be tested by comparing their transition matrices against each other using one of a number of techniques; simultaneous confidence limits (Goodman 1968), information theory (Chatfield and Lemon 1970) or log-linear models (Colgan 1978).

The log-linear method tests models to find the one with the smallest number of parameters that still fits the data reasonably well. The models are tested by discrepancies between observed and expected cell frequencies as summarised by the chi-squared statistic. The log linear model is a combination of interaction terms e.g. [PREVIOUS, FOLLOWING] means that the previous behaviour and the following behaviour are dependent on each other. The significance of these terms indicate whether the edges (columns and rows etc.) are dependant or independent of each other. Interaction terms that are not significant are dropped from the model in sequence. When no more terms can be removed the remainder show which edges are dependant on each other. These terms are the least number of interactions that satisfactorily describe the data.

Another common method of studying behavioural changes is to record the time spent in each activity. The times spent performing behaviours can then be compared in different conditions and states of motivation. In feeding behaviour the times allocated to searching, hunting and handling prey are of particular importance in assessing how profitable a prey item is in terms of energy (Stephens and Krebs 1986).

$$profitability = \frac{e}{p+h}$$

p = pursuit time h = handling time

e = energy - (searching costs)

Experimental procedure

The apparatus was designed so that whiting could be video recorded whilst they predated upon *Crangon crangon*. The set-up was arranged so that fish could be separated into small groups for feeding with the least amount of

disturbance as possible. The experiments used three inter connecting tanks, set up as shown in Figure 4.1. The two end tanks were holding tanks connected to a central feeding tank by tubes measuring 30cm in diameter. The central feeding tank is shown in cross section in Figure 4.2. The bottom was a white plastic board that sloped from near the surface down to a non returning tray on the tank bottom. Water was circulated by a pump so that material in the tank would wash down this slope and into the tray. The tank was screened off from the surroundings by black plastic sheeting suspended from the ceiling. A video camera situated overhead was linked to a video recorder and monitor in an adjoining room. A clear plastic pipe of diameter 12.5mm ran into the tank through which shrimps were introduced. The shrimps were placed head first in the tube and flushed through with sea water.

The experimental apparatus was stocked with eleven whiting consisting of five small (23.5 - 25.5cm) and six large (27.0 - 30.0cm). These fish were then allowed to acclimatise for four weeks. They were fed only in the middle feeding tank so that they would be encouraged to enter this tank when allowed to do so. During the acclimatisation period the whiting were fed on defrosted sandeels.

Before a feeding trial the door between the holding tank and the feeding tank was opened and the fish allowed to swim through of their own accord, or gently guided using a small net. When two or three fish were in the feeding tank the door was closed and the fish allowed to settle for fifteen minutes, after which the first shrimp was introduced. The next shrimp was introduced after the previous one had either been eaten, or had dropped into the non-returning tray. The fish were deemed to be satiated when four shrimp had passed through the tank with little or no reaction from the fish i.e. they displayed no behaviours other than orientation. Once satiated the door to the opposite holding tank was opened and the fish guided through it. The next group of fish were then allowed into the feeding tank. When all 11 fish had been fed any uneaten shrimp were removed from the non returning tray and the tank cleaned. Each repetition of a feeding trial was separated by three days so that the fish had fully evacuated food from their gut and had empty stomachs.

The investigation was divided into two parts; Experiment one and Experiment two. Experiment one was designed to investigate the effects of

Figure 4.1: A top view of the experimental tank layout showing the central feeding tank connected to the two holding tanks. The sliding door arrangement is shown in detail.

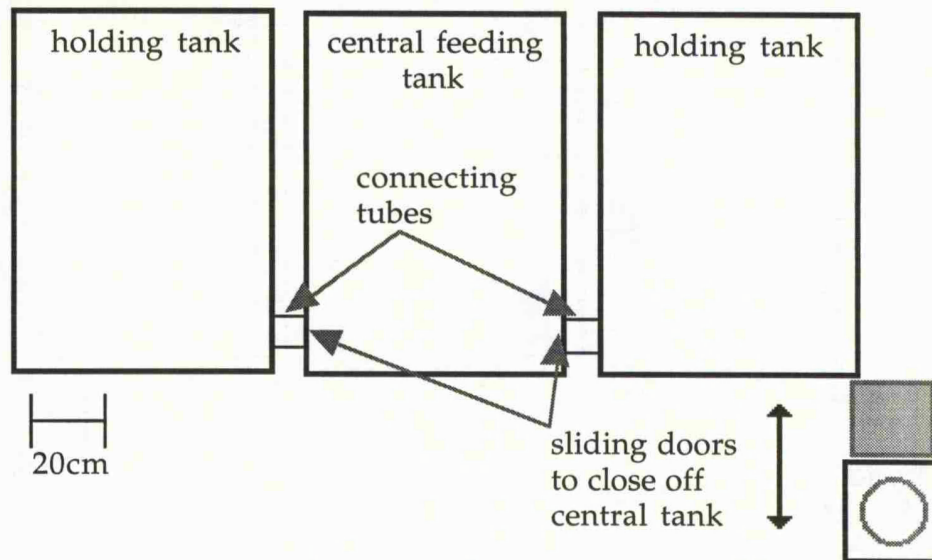
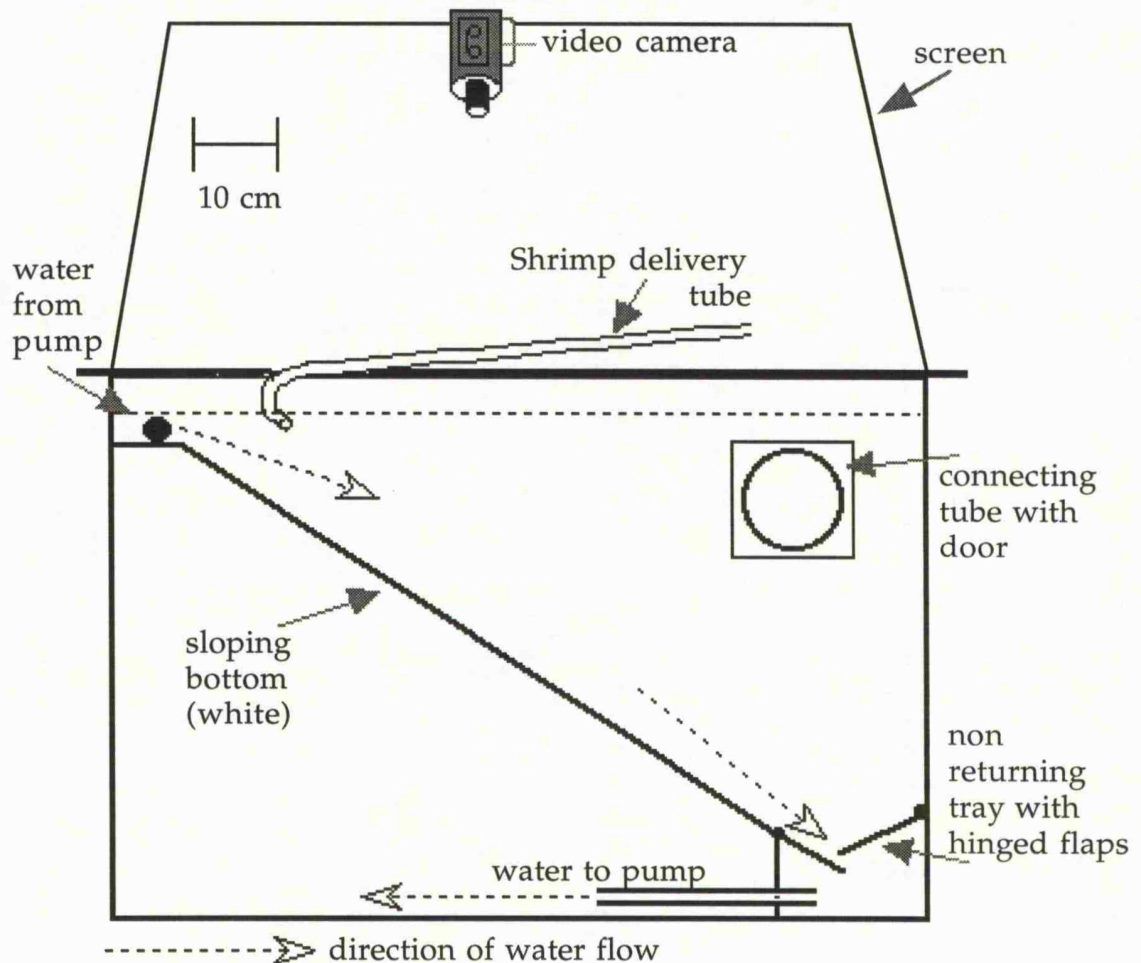


Figure 4.2: The central feeding tank in cross-section. The dashed lines with unfilled arrows indicate the flow of water within the tank.



stomach fullness, fish size and learning. The fish were presented with medium sized shrimps ranging from 6.5 - 7.5cm total length. Each fish was run through the feeding trial six times consecutively.

In Experiment two the aims were to investigate the effect of fish and shrimp size on the foraging behaviour of the fish. The experiment was also used to study whether the fish were selecting the size of shrimps eaten. The fish were presented with large (7.5 - 8.0cm) or small (5.9 - 6.5cm) shrimps. The presentation of large and small shrimp was alternated. In the first repetition the sequence was started with a large shrimp. In the second and third trial the sequence was started with a small shrimp.

Analysis

The video tapes of the feeding trials were viewed in slow motion using a video recorder with an electronic frame shutter facility. The behaviours were separated into the following categories:

Hunting Behaviours (concerned with the detection and capture of prey)

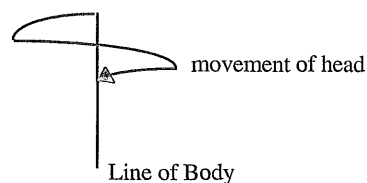
- Orientation:** movement of the fishes head to face the direction of the shrimp. The time was recorded from the first identified motion to the point when the fishes head pointed directly at the shrimp.
- Pursuit:** The action of the fish approaching the shrimp. The time was taken from the beginning of the first powerful tail flip until the next behaviour was recorded.
- Touch:** The action of the fish touching the shrimp. The time was recorded from the point of first contact until either the fish turned or the shrimp tail-flipped away.
- Strike:** The action of the fish lunging either sideways or forwards at the shrimp with its mouth open. The timing was taken from the first movement until the mouth closed.
- Capture:** This is when the fish caught part or all of the shrimp in its mouth.

End: This is the cessation of a behaviour when no other behaviour follows. e.g. turning away from shrimp.

Handling Behaviours (concerned with the manipulation and ingestion of the prey after capture)

Headshake: Where the fish with a shrimp protruding from its mouth shakes its head from side to side violently. One headshake is when the head passes back through the line of its body after going left and right.

1 Complete head-shake



Adjust: The movement of the head to the side distinguished from head shake by the opening of the mouth in order to adjust position of the shrimp.

SWallow: The exaggerated movements of the operculum when the shrimp is being ingested.

Loss: The escape or release of the shrimp from the mouth of the fish.

(N.B. The letters in **bold** were used as abbreviations of the categories in subsequent sections)

The video tapes were observed and the time spent performing a behaviour, and the sequence of the behaviours used by the fish were recorded into a log book. The time spent performing each behaviour was calculated to the nearest 1/50 second using the clock which was recorded onto each frame of the video tape during filming. Notes were also made on any observed interactions between the fish and the behaviour of the shrimp. Behaviours described in these notes are detailed later in this

chapter. The sequences and timings of the behaviours were analysed using statistical procedures outlined below.

Experiment one

For analysis the fish were divided into the two size groups, and for each fish at each level of stomach fullness, a behavioural transition matrix was calculated. The level of stomach fullness was determined by how many shrimps the fish had successfully ingested. The transition matrices were tested against each other using the log linear method described by Colgan (1978) and the calculations were performed using the computer package CoCo[©] (Badsberg 1995). The log linear method used is described in detail in the results section of this chapter, where the first analysis is used as an example.

Separate transition matrices were calculated for the hunting behaviours and handling behaviours so that the lower values for the handling behaviours were not obscured. The matrices were summarised in flow diagrams where the thickness of the arrow, indicating the transition, was proportional to the size of the probability. For clarity, probabilities of 0.1 or below were not shown.

The two fish size groups were compared using the behaviours of the fish summed over all levels of stomach fullness, except satiation, and over all trials. Evidence of learning, or changes in behaviour as the fish were exposed to more shrimps, were tested by comparing the transition matrices of each trial. The individual matrices were summed within the size groups and up to but not including satiation, so that only the behaviours of fish when feeding were compared.

The time taken for the hunting behaviour was measured from the start of orientation to the capture of the shrimp. The time taken to handle the shrimp was recorded from the capture, until the shrimp was completely swallowed. The timing data did not approximate to a normal distribution so the data were tested using non-parametric statistics as described by Sokal and Rohlf (1981). The Friedman randomised blocks method was used to test the influence of experience. To investigate the effect of stomach fullness the timings data were tested using Wilcoxon's signed ranks as the

data were paired. The differences between the two fish sizes in time spent hunting and handling were tested with a standard Mann-Whitney U-test.

Experiment two

The data in Experiment two were tested using the same methods as used in Experiment one except that the data were also divided between the two shrimp sizes. To investigate the selection of the shrimp sizes by the fish in the two size groupings the probability of a shrimp size being eaten was calculated. The probability of attack and the probability of success were also calculated for the two fish sizes. The probability of attack was calculated by dividing the number of strikes by the number of shrimps orientated to. The probability of success was calculated by dividing the number of shrimps successfully ingested by the number of strikes attempted. The probability of a shrimp size being eaten was calculated by dividing the number of a shrimp size eaten by the total number of shrimps eaten. These probabilities were calculated at each level of stomach fullness determined by the number of shrimps eaten. The levels of stomach fullness above four shrimps were not investigated as only one fish ate more than this.

DESCRIPTION OF BEHAVIOURS

The Fish

The first behaviour noted in almost all the attacks was orientation. This was where the fish, from a position of not facing a prey item, turned to face it head on. The orientation was initiated from varying angles to the shrimp up to 180°. The fish almost always turned through the smallest angle to face the shrimp and if they did not it was usually because the shrimp was moving too fast. The main methods used to detect the prey were probably sight and vibration as the response usually occurred to a moving shrimp. The fish did not swim around to face the shrimp, but rather one side of the body would contract pulling the head round to face the prey. If this movement was not sufficient to face the shrimp then the fish would straighten its body and repeat the contraction in a double movement. Sometimes the orientation was initiated so close to the shrimp that no pursuit was necessary and the fish would strike or touch the prey during the orientation. The transition into pursuit was smooth and no obvious 'fixation' in a stationary position was observed. Stationary fixating is a common behaviour in fifteen-spined sticklebacks when they are foraging (Croy and Hughes 1990). As soon as the head was lined up with the shrimp the tail would flick round in a powerful motion and the fish would accelerate towards the shrimp.

Often in the small area of the tank the powerful beat of the tail would be sufficient to reach the shrimp, else the fish would perform much smaller subsequent tail movements to propel itself. A pursuit ended in one of four different ways. If the shrimp was moving or moved during the approach the fish would reorientate, the fish could also end the pursuit before it reached the shrimp by turning away. Generally the fish would either touch or strike at the prey. Only twice was the fish observed to stop and coil before it reached the shrimp, as is sometimes seen in sticklebacks (Croy and Hughes 1991, Gill 1994). If the fish was struck at after a pursuit the fish did not usually slow down at all, instead the strike was a continuation of the pursuit movement (dependent on the type of strike employed). If the fish touched the prey it slowed down by spreading out its pectoral fins. The fish tended to touch the shrimp either in the middle or at the head. A couple of fish were observed to push the shrimp along the bottom of the tank as if to stimulate response. The response of the shrimp to being

touched tended to be a tail flip though a large number of shrimp did not respond at all.

Fish struck at prey in four ways; a straight lunge, a sideways strike, a suck or a bite. The straight lunge was characterised by the fish continuing in a straight line through the position of the shrimp. The motion was usually from a powerful tail flip and the fishes' mouth opened as it started the rapid forward movement. The shrimp either did not move, tail flipped in the opposite direction or towards the fish. The sideways strike was similar to the straight lunge except that the head motion was in sideways direction. This type of strike was usually associated with a shrimp that was moving in a tangent to the direction of the fish, or one that tail flipped sideways before the fish struck. In a suck the fish did not appear to move forward and the mouth would open wide and the shrimp sucked towards, or into the mouth. The bite was a strike that apparently had very little effort involved, the mouth did not appear to open very wide and little movement was involved. The strikes described are the extremes, many strikes observed comprised a combination of two or more of these types. The method of strike employed appeared to be influenced by the behaviour of the shrimp. However the video picture was not of high enough resolution to analyse this in greater detail.

A strike could end in two ways with either miss or capture. If the fish failed to capture the shrimp it would either rapidly reorientate, or simply turn away. Capture could occur in two ways; the shrimp would be swallowed in the same movement or the shrimp protruded from the fishes' mouth and some handling occurred.

The adjustment handling behaviour was a label for the behaviour by which the fish altered the position of the shrimp held in the mouth. The behaviour was very similar to the sideways strike, and was usually performed when the shrimp protruded from one side of the mouth. The fish rapidly moved its head sideways towards the side that the shrimp protruded and simultaneously opened its mouth. As a result of this adjustment the shrimp tended to become more centrally positioned. On three occasions the fish was observed to regurgitate the shrimp slightly and the tail was seen to move further out of the mouth. For the benefit of analysis this behaviour was labelled as an adjustment.

The headshake behaviour was recorded when the fish violently shook its head from side to side in what appeared to be an attempt to stun the shrimp. Headshakes occurred in bouts ranging from a single shake up to a rapid series of six.

The loss of a shrimp was where the shrimp either escaped or the fish let go of it. These two contrasting events were lumped together as it was usually impossible to distinguish them from each other. Loss, like a missed strike, was followed by either rapid reorientation or turning away.

The swallow category was composed of two similar behaviours. In the first type the shrimp was moved further into the throat by movements of the mouth. The second was when the shrimp was pushed in to the stomach, both were recognised by the exaggerated movements of the operculum. The shrimp were always swallowed head first with one exception. In this odd case the shrimp was caught in mid water tail first and swallowed in one continuous motion. It should be noted that in this case the shrimp to fish size ratio was very small.

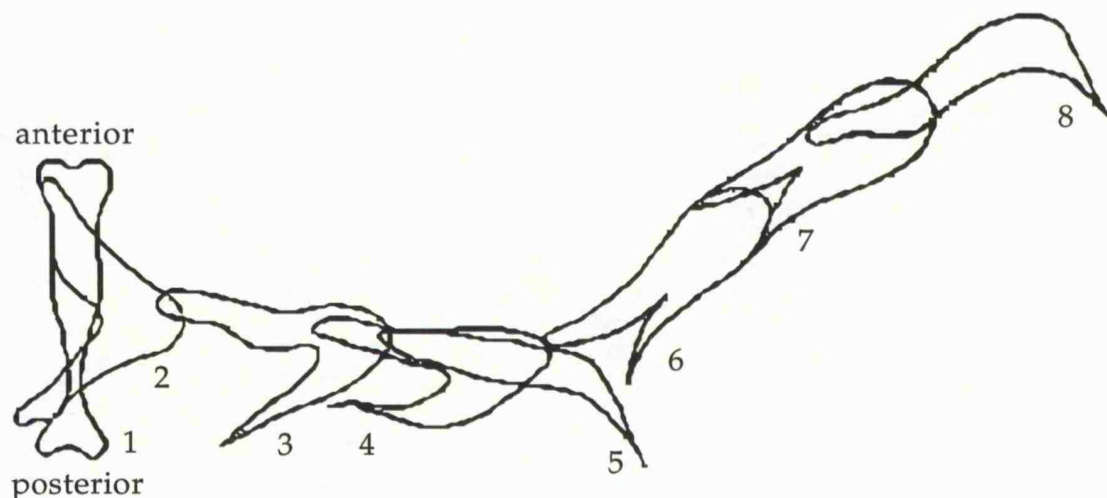
Comparing these behaviours to the attack and handling behaviours of fifteen-spined sticklebacks some basic differences were noted. Only twice did the whiting exhibit the S-shaped posture before striking at a prey item described by Croy and Hughes (1990). The attack by the whiting tended to be a continuous motion which could be an effect of studying the fish in groups. Often if a fish orientated towards a shrimp others in the tank would react to this and also orientate (pers obs). Therefore any pausing in the attack sequence after this would result in another fish attacking the shrimp first. In the wild, whiting are known to feed in shoals and so the pausing in the attack sequence would have the same affect.

In the handling behaviours the fish were never observed to spit out the shrimp and recapture it. This is quite a common behaviour in threespine sticklebacks especially when handling larger prey items (Gill and Hart 1994). The prey of the sticklebacks do not have the powerful escape response of the shrimp. The whiting may not have performed this spit behaviour as the recapture would have proved difficult and costly.

The Shrimp

The shrimp entered the tank head first through a tube flushed through by a stream of sea water. On entering the tank the current flow in the tank was designed to carry them down the slope and into the tray at the bottom. The tray's lid was arranged so that once the shrimp went into the tray they could not re-emerge and they were out of sight and reach of the fish. On entering the tank the shrimps usually swam using their pleopods but occasionally they emerged tail flipping. The tail flipping behaviour of the shrimp is an escape response which allows it to move very quickly over a fairly short distance. In the tail flip the shrimp rotates about its antero-posterior axis and rapidly contracts its fast flexor muscles so that the telson is pulled towards the head propelling the shrimp backwards (Figure 4.3).

Figure 4.3: The outline of a shrimp during a tail flip escape response. The numbers denote the sequence (After Arnott et al. 1994)



The initiation of the tail flip mainly came at one of two points in the fish's attack sequence. If the fish touched the shrimp this sometimes caused a tail flip response and it often appeared that the fish was trying to induce the shrimp to respond in this way. It has been noted that once the shrimp has rotated in the tail flip its direction of travel is limited (Arnott *et al* 1994). It maybe that the fish can read the shrimps movement and direct its strike accordingly. To investigate this would require a higher speed of video recording than this experiment used. The other main point at which a

shrimp tail flipped was as the fish initiated a strike. The video speed was not fast enough to determine the precise timings of this response but the two behaviours seemed to be instantaneous.

The further away a shrimp tail flipped from the attacking fish, the easier it was for the fish to adjust its direction and continue with the attack. The tail flip uses up energy in the shrimp and it is limited in its use, it would seem sensible for the shrimp to leave its tail flip until as late as possible. In the wild the shrimp would probably tail flip away and then bury itself into the sandy substrate over which it normally lives. As the tank that the experiments were held had a solid plastic bottom this was not possible.

If a shrimp was caught in the mouth of a fish there was a possibility that it may escape before it was ingested. A few of the captured shrimps were observed to tail flip, especially those with a large proportion of their bodies protruding from the mouth. Shrimps that did manage to escape from the mouth of the fish did not appear to be damaged in any way. This would suggest that the fish was not chewing or crushing the prey to any great extent.

Novel behaviours

During the trials some novel situations occurred that were too infrequent to be analysed in any detail but which did raise some interesting points. The tail flip of the shrimp did seem to be a two edged sword in that although it allowed the shrimp to escape from the attacking fish it also tended to attract the attention of the other fish. In two extreme cases of this, as the shrimp tail flipped it passed in front of another fish which then struck at, and successfully caught it.

Whilst handling the shrimps, an interesting interaction between fish was noted on a number of occasions. The tail flipping of a shrimp within the mouth of a fish would attract the attention of another fish, which then struck at the protruding tail. In two of these strikes the second fish successfully caught the tail of the shrimp. The two fish then pulled apart and in one case the original holder retained possession, in the other the second attacking fish ended up with the shrimp. This behaviour was also seen with the whiting and cod when they have been fed dead food. In

these cases the prey has usually ripped into two and both the fish ended up with a proportion of the food (pers obs, Brawn 1969). As a consequence of this behaviour the fish can handle more easily food items that would normally be too large . It could also be a way for the fish to obtain a 'cheap meal' for which they would not have to hunt.

The presence of a shrimp in the mouth of a fish was recorded as handling. However on three occasions these 'handling fish' pursued and struck at other shrimps entering the tank. The presence of the other shrimp in the mouth did not prevent capture as one of the handling fish successfully caught and ingested the second shrimp.

RESULTS

Experiment 1

The number of shrimp ingested by the different sizes of whiting before satiation are shown in Table 4.1. The mean number of shrimps eaten by the large fish was significantly higher than the small fish ($t = 6.67$, $p < 0.05$). Two large and two small fish did not feed at all throughout the experiment.

Table 4.1: The total number of shrimps eaten in each trial by each fish

Fish no.	Small fish			Large fish			
	1	2	3	1	2	3	4
Trial							
1	2	1	1	4	3	3	2
2	1	2	1	6	5	4	3
3	1	2	0	3	3	2	2
4	1	2	1	3	2	2	2
5	1	1	1	3	3	2	2
6	2	1	1	3	3	2	2
mean	1.33	1.5	.83	3.67	3.17	2.5	2.17
standard deviation	0.47	0.5	0.37	1.11	0.90	0.76	0.37

(N.B. the other fish did not eat any shrimps during the experiment.)

The remaining results from experiment one are organised into three sections relating to the three factors investigated; stomach fullness, fish size and learning. Each section reports the results from analysing the affect of the factor on four different aspects of the behaviour; the sequence of hunting and of handling behaviours, the time taken to hunt and to handle the shrimps.

Stomach Fullness

The totals of the behavioural transitions used by the fish in hunting the shrimps were calculated for the large and small fish separately. The data for each size category was divided further into groups of fish that ate the same total number of shrimps and a contingency table was calculated at each level of stomach fullness (not including satiation). The method used to analyse the behavioural sequences is shown in detail for the first grouping which was, large fish that ate two shrimps. The null hypothesis

tested was that the number of shrimps in the fish's stomach did not effect the sequence of hunting behaviours.

Table 4.2: A three dimensional contingency table including each level of stomach fullness in large fish that ate two shrimps

		previous behaviour			
1st shrimp eaten		O	P	T	S
following behaviour	O	-	0	0	1
	P	14	-	0	0
	T	0	5	-	0
	S	4	6	3	0
	E	2	3	1	4
	C	-	-	-	9
2nd Shrimp eaten		O	P	T	S
following behaviour	O	-	2	1	3
	P	18	-	0	0
	T	4	9	-	0
	S	4	5	9	0
	E	16	2	2	7
	C	-	-	-	9

N.B. (-) are cells that cannot occur and have a logical zero value

The contingency table was tested against an expected table. The expected table was calculated using the log linear technique with the special situation of logical zeros (Goodman 1968). The fit of the model is calculated by using a chi-squared test to quantify the deviation of the observed values from the expected ones. The chi-squared statistic is calculated using equation:

$$\chi^2 = 2 \sum_{i=1}^I \sum_{j=1}^J x_{ij} \log \frac{x_{ij}}{\hat{m}_{ij}} \quad (4.1)$$

where: x_{ij} = the observed value in cell i j

\hat{m}_{ij} = the expected value in cell i j in the model being tested

If the chi-squared test is significant the model is deemed to explain the data. The model finally chosen was the one that contained the least number of interaction terms that still explained the data. At the start the expected table for the saturated model was calculated, which included interaction terms for all the variables

The model can be written as:

[PREVIOUS,FOLLOWING,FULLNESS] = all factors are dependent on each other

The next level of interaction terms were then tested to see if they contributed a significant amount to the model's explanation of the data Table 4.3.

Table 4.3: The first and second order interaction terms and their significance for the large fish eating two shrimps

Interaction Term	Degrees of freedom	χ^2	probability level
[PREVIOUS,STOMACH]	18	12.33	0.136
[FOLLOWING,STOMACH]	10	15.97	0.100
[PREVIOUS,FOLLOWING]	8	88.50	<0.05

The interaction terms [PREVIOUS,STOMACH] (previous behaviour and the fullness of the stomach are dependent on each other) and [FOLLOWING,STOMACH] (following behaviour and the fullness of the stomach are dependent on each other) were dropped. These terms were dropped as they added the least amount to the model's explanation and were not significant at the 0.05 probability level. The last term [PREVIOUS,FOLLOWING] is significant and so cannot be dropped.

This left the model:

[PREVIOUS,FOLLOWING][STOMACH]= the previous and following behaviours are dependent on each other and independent of stomach fullness.

(N.B. the stomach term is now written on its own as it does not interact with the other two terms)

The model can be summarised as in Table 4.4 which shows the results of a chi-squared test on the fit of the model's expected values with the observed values. In Table 4.4 and subsequent tables the probability is marked with an asterisk to show that the model being tested is the accepted model. Although the probability for the model is not 0.95 the model is accepted because adding other interaction terms does not significantly increase the models fit of the data. The probability chi-squared test does give an idea of the goodness of fit of the tested model e.g. a probability of 1 would mean the model described the data perfectly (Colgan 1978).

Table 4.4: The results of a chi-squared test on the model 'hunting behavioural sequences are independent of stomach fullness'

Experimental condition	degrees of freedom	χ^2	probability
large fish eating 2 shrimps	23	18.63	0.72*

The acceptance of this model shows that the sequence of hunting behaviours did not change significantly with stomach fullness in large fish that ate two shrimps. The rest of the fish groupings were tested in the same manner and the results from the chi-squared tests are shown in Table 4.5.

Table 4.5: The results of a chi-squared test on the model 'hunting behavioural sequences are independent of stomach fullness' applied to the data for fish grouped by number of shrimp they ate.

number of shrimp eaten	degrees of freedom	χ^2	probability
Large fish			
2	23	18.63	0.72*
3	46	37.75	0.80*
4	69	64.10	0.64*
5	92	30.25	1.00*
6	115	40.63	1.00*
Small fish			
2	23	21.74	0.54*

In Table 4.5 the H_0 is accepted in all the different categories for the number of shrimps eaten. This significance shows that stomach fullness did not effect the hunting behaviour.

The hunting behaviours of the fish when they were feeding were then compared against the hunting behaviours of the fish when they were satiated. The fish were grouped into the two size categories, small and large, and contingency tables were calculated for the fish when they were feeding and satiated. These tables were tested using the method just described. The results in Table 4.6 show the probabilities that model describes the data are very small and are not significant e.g. the model requires more interaction terms to describe the data. this meant the null hypothesis that there is no difference in the sequence of hunting behaviours of the fish when they are feeding or satiated, was rejected.

Table 4.6: The results of a chi-squared test on the model 'hunting behavioural sequences are independent of satiation and feeding' applied to large and small fish.

	degrees of freedom	χ^2	probability
Large fish	23	94.10	<0.01
Small fish	23	60.03	<0.01

In order to determine which of the behavioural transitions are changing with satiation and how they are changing the technique of logical zeros was used (Colgan 1978). The technique involves replacing the behavioural transitions that deviate significantly from the expected model with a logical zero value. The first test of large fish is shown in detail to show how the technique works. The expected values for the model [PREVIOUS,FOLLOWING] [SATIATION] (i.e. Hunting behaviours are independent of satiation) were calculated. The deviation of these expected values from the observed values is called the residual value.

The residual values shown in Table 4.7 were calculated using the equation:

$$\text{Standardized residual} = \frac{(O - E)}{\sqrt{E}} \quad (4.2)$$

The behavioural transition that had the largest modular total was 'touch to end', $|-3.25| + |4.38| = 7.63$. The observed values for this transition were replaced with logical zero values and the log linear test was repeated. This replacement with a logical zero means that the influence of this residual is removed and the other residuals can be tested for importance. The null hypothesis was still rejected and so the behavioural transition with the next largest modular residual total was replaced with a logical zero. This replacement of transitions was continued until the null hypothesis was accepted. The resulting list of behavioural transitions removed are the ones which changed significantly once the fish was satiated (Table 4.8). The sign of the residual indicates whether the observed value is above (+) or below (-) the expected.

Table 4.7: The observed and expected and residual values in the model
[PREVIOUS,FOLLOWING] [SATIATION] for the large fish category

observed values					expected values				
feeding	O	P	T	S	feeding	O	P	T	S
O	-	6	7	19	O	-	7.74	7.74	14.83
P	131	-	0	0	P	133.49	-	0	0
T	23	45	-	0	T	28.37	56.10	-	0
S	29	63	43	0	S	23.86	48.37	35.47	0
E	69	18	18	43	E	78.03	21.93	38.05	40.63
C	-	-	-	78	C	-	-	-	57.39
satiated	O	P	T	S	satiated	O	P	T	S
O	-	6	5	4	O	-	4.26	4.26	8.17
P	76	-	0	0	P	73.51	-	0	0
T	21	42	-	0	T	15.63	30.90	-	0
S	8	12	12	0	S	13.14	26.63	19.53	0
E	52	16	41	20	E	42.97	12.07	20.95	22.37
C	-	-	-	11	C	-	-	-	31.61

residual values				
Feeding	O	P	T	S
O	-	-0.62	-0.27	1.08
P	-0.22	-	0	0
T	1.01	-1.48	-	0
S	1.05	2.10	1.26	0
E	-1.02	-0.84	-3.25	0.37
C	-	-	-	2.72
satiated	O	P	T	S
O	-	0.84	0.36	-1.46
P	0.29	-	0	0
T	1.36	2.00	-	0
S	-1.42	-2.84	-1.70	0
E	1.38	1.13	4.38	-0.5
C	-	-	-	-3.67

Table 4.8: The behavioural transitions and their standardised residual values that are significant in the model 'hunting behavioural sequences are dependent on satiation and feeding' for large fish.

Large fish	Feeding	Satiated
T \Rightarrow E	-3.25	4.38
S \Rightarrow C	2.72	-3.67
P \Rightarrow S	2.10	-2.84
P \Rightarrow T	-1.48	2.00
T \Rightarrow S	1.26	-1.70
O \Rightarrow S	1.05	-1.42

This method of logical zero replacement was used to investigate the important changes in the hunting behaviour of the small fish when they became satiated (Table 4.9).

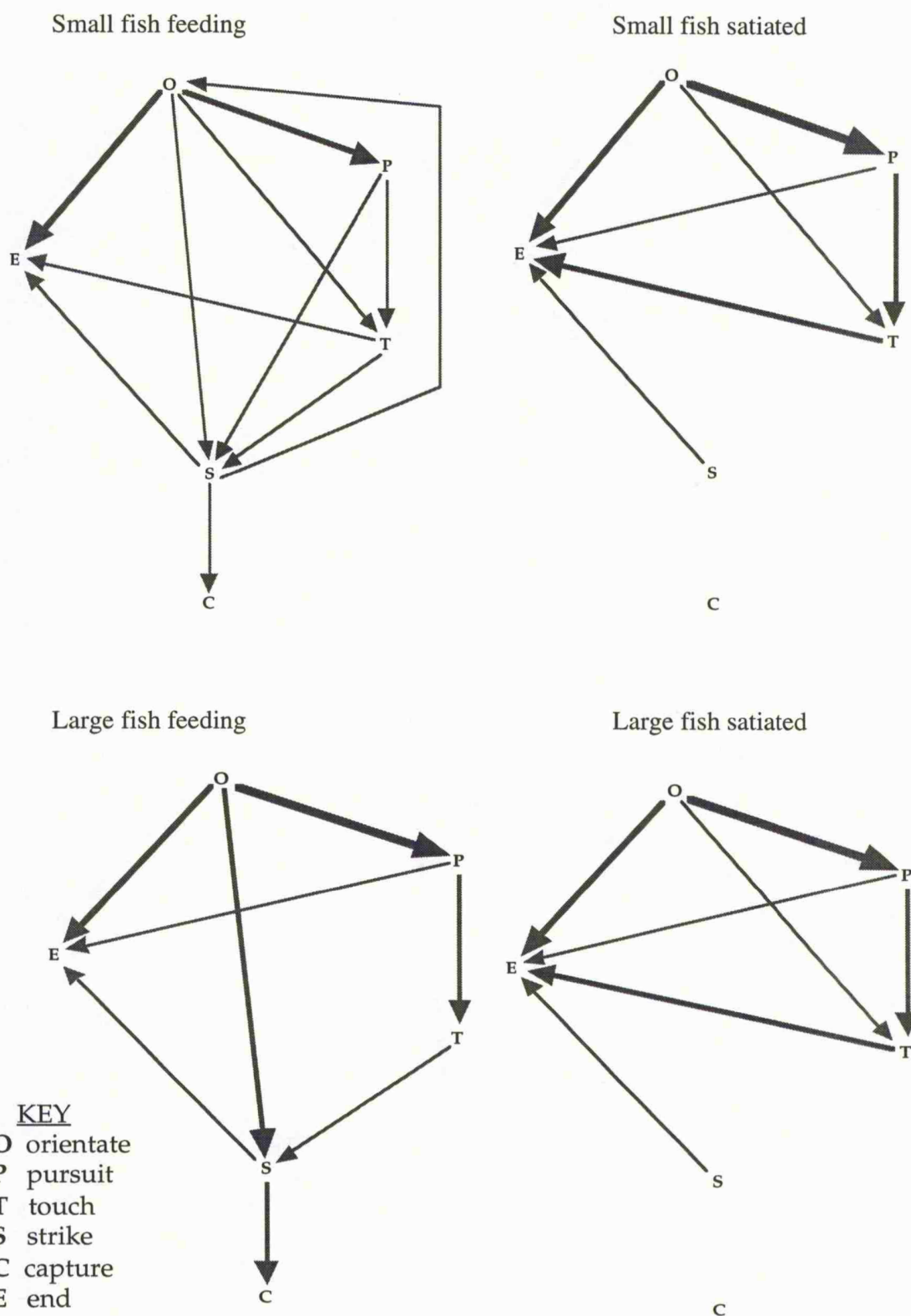
Table 4.9: The behavioural transitions and their standardised residual values that are significant in the model 'hunting behavioural sequences are dependent on satiation and feeding' for small fish

Small Fish	Feeding	Satiated
S \Rightarrow C	2.03	-2.13
T \Rightarrow E	-2.02	2.11
T \Rightarrow S	1.80	-1.88
P \Rightarrow T	-1.72	1.80
O \Rightarrow S	1.64	-1.72
S \Rightarrow E	1.37	-1.44

In both the small and the large fish the patterns in the residuals were very similar. The only residuals that were different are 'pursuit to strike' which was important only in the large fish and 'strike to end' which was only important in the small fish. The rest of the important behaviours were the same and all decreased in satiated fish except for 'touching to end' and 'pursuit to touch' which increased. With these residuals removed the matrices of feeding and satiated fishes were not significantly different. The flow diagrams of the hunting behaviours are shown in Figure 4.4 in which the thickness of the lines are related to the transition probabilities and the probabilities below 0.1 are not shown for clarity.

The behavioural transitions involved in handling the shrimps were tested in the same way as were the hunting behaviours. Table 4.10 shows the results from testing the effect of changing stomach fullness in fish of the same size eating the same total number of shrimps. The null hypothesis

Figure 4.4: Flow diagrams of the behavioural transitions in whiting hunting shrimp prey. The thickness of the arrow represents the probability of the transition occurring



tested was that stomach fullness had no effect on the sequence of behaviours used to handle a shrimp.

Table 4.10: The results of a chi-squared test on the model 'handling behavioural sequences are independent of stomach fullness' applied to the data for fish grouped by number of shrimp they ate.

number of shrimp eaten	degrees of freedom	χ^2	probability
Large fish			
2	29	6.07	1.00*
3	58	35.77	0.99*
4	87	10.40	1.00*
5	116	15.72	1.00*
6	145	14.87	1.00*
Small fish			
2	29	17.66	0.95*

The null hypothesis was accepted in all of the fish groupings. This means that stomach fullness was not a significant factor in the behaviours used to handle the shrimp. Within the two fish size categories the behaviours used to handle the shrimp when the fish were feeding, were compared to the behaviours used when they were satiated (Table 4.11).

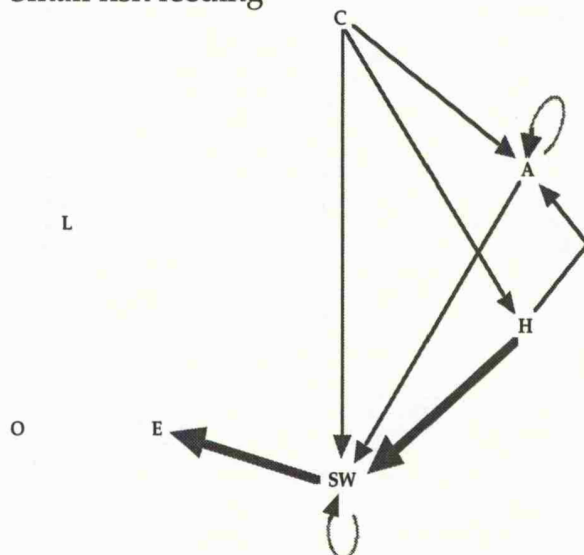
Table 4.11: The results of a chi-squared test on the model 'handling behavioural sequences are independent of satiation and feeding' applied to large and small fish.

	degrees of freedom	χ^2	probability
Large fish	29	92.83	<0.05
Small fish	29	57.54	<0.05

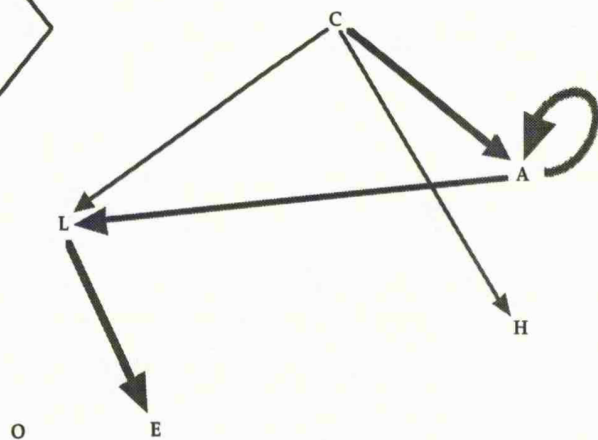
As with the hunting behaviours the fish behaved differently when they became satiated. The null hypothesis that there is no difference in the sequence of hunting behaviours of the fish when they are feeding or satiated, was rejected. The important behavioural transitions in causing this rejection are shown in Table 4.12.

Figure 4.5: Flow diagrams of the behavioural transitions in whiting handling shrimp prey. The thickness of the arrow represents the probability of the transition occurring

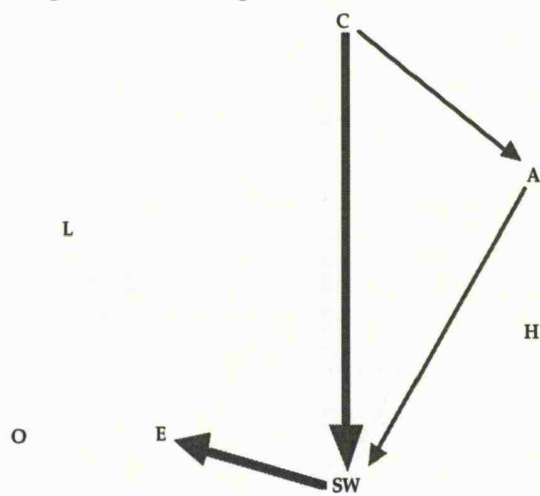
Small fish feeding



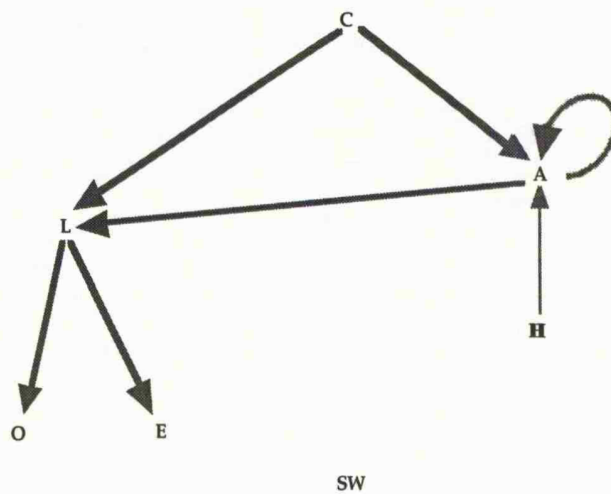
Small fish satiated



Large fish feeding



Large fish satiated



KEY

- C capture
- A adjust
- H headshake
- SW swallow
- L loss
- O orientate
- E end

Table 4.12: The behavioural transitions and their standardised residual values that are significant in the model 'handling behavioural sequences are dependent on satiation and feeding' for large fish

Large fish	Feeding	Satiated
L \Rightarrow O	-1.77	3.84
L \Rightarrow E	-1.34	2.89
C \Rightarrow L	-1.13	2.45
A \Rightarrow A	-1.24	2.68
SW \Rightarrow A	-0.91	1.96
SW \Rightarrow E	1.56	-3.38
A \Rightarrow L	-1.62	3.51
S \Rightarrow A	-0.22	0.47
Small Fish		
L \Rightarrow E	-1.91	3.60
C \Rightarrow L	-1.25	2.36
A \Rightarrow A	-1.30	2.46
A \Rightarrow L	-0.90	1.69
H \Rightarrow L	-0.45	0.85
C \Rightarrow A	-0.25	0.05

The same residuals that are important in the small fish were also important in the large fish although the number of important residuals in the large fish was much greater. Nearly all the residuals increased in the satiated fish except for 'swallow to end'. The difference between the feeding and satiated fish was very clear in Figure 4.5 which shows the flow diagrams of the fishes' handling when feeding and when satiated.

The affect of stomach fullness on the time taken to hunt and handle the shrimps was recorded. The time taken to hunt a shrimp was recorded from the start of the first orientation until the successful capture of the shrimp. The influence of stomach fullness was tested between large fish taking their first shrimp and their last shrimp (Table 4.13). The hunting times showed no significant difference between the empty and nearly full fish. The time taken to handle the shrimp did change with stomach fullness. The first shrimp to be eaten was handled for a significantly shorter time than the last shrimp.

Table 4.13: The summary statistics of Wilcoxon's signed ranks test examining effect of stomach fullness on hunting and handling times.

behaviour	rank	median	Σ rank	Z statistic	probability
hunting	-ve	1.94	120	-0.857	>0.05
	+ve	1.94	180		
handling	-ve	0	24	-2.678*	<0.05
	+ve	0.99	147		

Fish Size

The same methods used to analyse the affect of stomach fullness were used to test the affect of fish size on the sequence of behaviours. Comparing the hunting dynamics of the two fish size categories shows that size is important. The null hypothesis 'Fish size does not effect the sequence of behaviours used to hunt the shrimps' was rejected, until the transition of 'strike to capture' was removed (Table 4.14). The transition 'strike to capture' was observed with increased frequency in the large fish when compared to the small fish.

Table 4.14: The results of a chi-squared test on the model 'hunting behavioural sequences are independent of fish size' with residual values shown

Test	degrees of freedom	χ^2	probability
Large fish vs. Small fish	23	27.07	0.25
residual	small fish	large fish	
S \Rightarrow C	-1.75	1.31	

Table 4.15 shows that there was a significant difference in the handling sequences between small and large fish. The largest residuals were 'capture to swallow' and 'swallow to end'. When these were removed there was no difference between the two sizes of fish. The frequency of both the transitions increased in the large fish.

Table 4.15: The results of a chi-squared test on the model 'handling behavioural sequences are independent of fish size' with residual values shown

Test	degrees of freedom	χ^2	probability
Large fish vs. Small fish	29	46.92	0.02
Behavioural transition	small fish	large fish	
C \Rightarrow SW	-2.28	3.02	
SW \Rightarrow E	-2.05	1.61	

The time spent in hunting the shrimp did not change significantly with the size of the fish (Table 4.16). However the handling times were different between the two sizes. The smaller fish spent significantly longer handling the shrimps than the large fish.

Table 4.16: The summary statistics of Mann-Whitney U-test used to examine the effect of fish size on hunting and handling times.

behaviour	Fish size	median	W statistic	probability
hunting	large	1.94	465.0	>0.05
	small	2.54		
handling	large	0.00	418*	<0.05
	small	4.30		

Experience and learning

To investigate the effect of experience on the fishes' behavioural sequences during feeding, the transition matrices between trials were compared. The small fish showed no difference in their hunting patterns between trials, but the large fish did (Table 4.17).

Table 4.17: The results of a chi-squared test on the model 'hunting behavioural sequences are independent of experience'

	degrees of freedom	χ^2	probability
Large fish	115	131.96	0.13
Small fish	115	103.00	0.78*

The important behavioural transitions in the large fish were 'pursuit to strike' and 'strike to capture'. Although the pattern in magnitude of the residuals was not clear there was a pattern in the signs. Both residuals of the behavioural transitions were negative in the first two trials and positive in the rest (Table 4.18).

Table 4.18: The behavioural transitions and their standardised residual values that are significant for large fish in the model 'hunting behavioural sequences are dependent on experience'

Behaviour	Trial number					
	1	2	3	4	5	6
P \Rightarrow S	-2.85	-0.52	2.14	0.48	0.3	2.26
S \Rightarrow C	-1.89	-0.99	2.32	0.82	1.98	0.23

Increasing experience did not effect the handling behaviours displayed. The null hypothesis, that handling behaviours do not change with experience, was accepted (Table 4.19).

Table 4.19: The results of a chi-squared test on the model 'experience is independent of previous and following handling behaviours'

	degrees of freedom	χ^2	probability
Large fish	145	94.31	>0.99*
Small fish	145	91.82	>0.99*

The times spent hunting and handling the shrimps are shown in Figures 4.6 to 4.11. The time taken to hunt the shrimps showed no significant difference at the 0.05 confidence level, when considering experience (Table 4.20). However the large fish hunting their first shrimp did show a difference at the 0.1 probability level. Examining Figure 4.6 it can be seen that the first two trials contain long hunting times from individual fish which were the cause of the difference.

Table 4.20: The summary statistics of Friedman's randomised blocks used to test the effect of experience on hunting times.

Fish size	shrimp	median	d.f.	χ^2	probability
large	first	1.94	5	6.57	0.05<p<0.1
	last	1.94	5	9.28	>0.05
Small	first	2.54	5	4.00	>0.05

The large fish showed a significant difference between trials, in the time spent handling the last shrimp they ate. The reason for the difference can

seen in Figure 4.9, where the first two trials contained individual fish that spent a very long time in handling the shrimps. The handling times of the first shrimp taken were not different in either of the fish sizes between the trials (Table 4.21).

Table 4.21: The summary statistics of Friedman's randomised blocks used to test the affect of experience on handling times.

Fish size	shrimp	median	d.f.	χ^2	probability
large	first	0	5	5.867	>0.05
	last	0.99	5	11.808*	<0.05
Small	first	4.26	5	8.478	>0.05

Figure 4.6: Hunting times of large whiting feeding on their 1st shrimp over the six consecutive feeding trials.

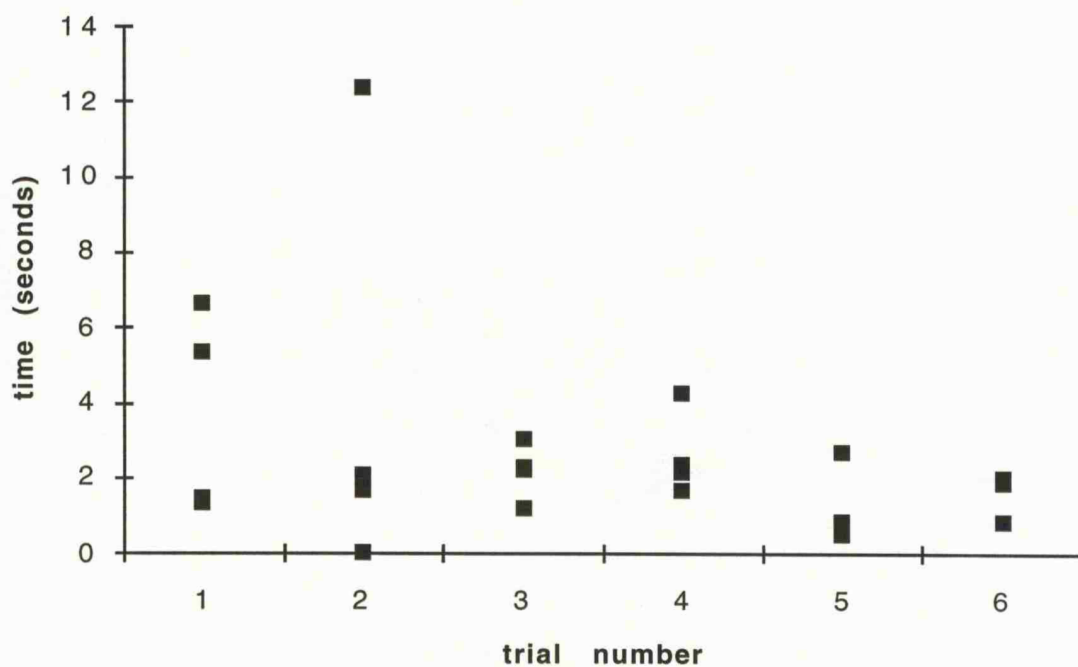


Figure 4.7: Hunting times of large whiting feeding on their last shrimp over the six consecutive feeding trials.

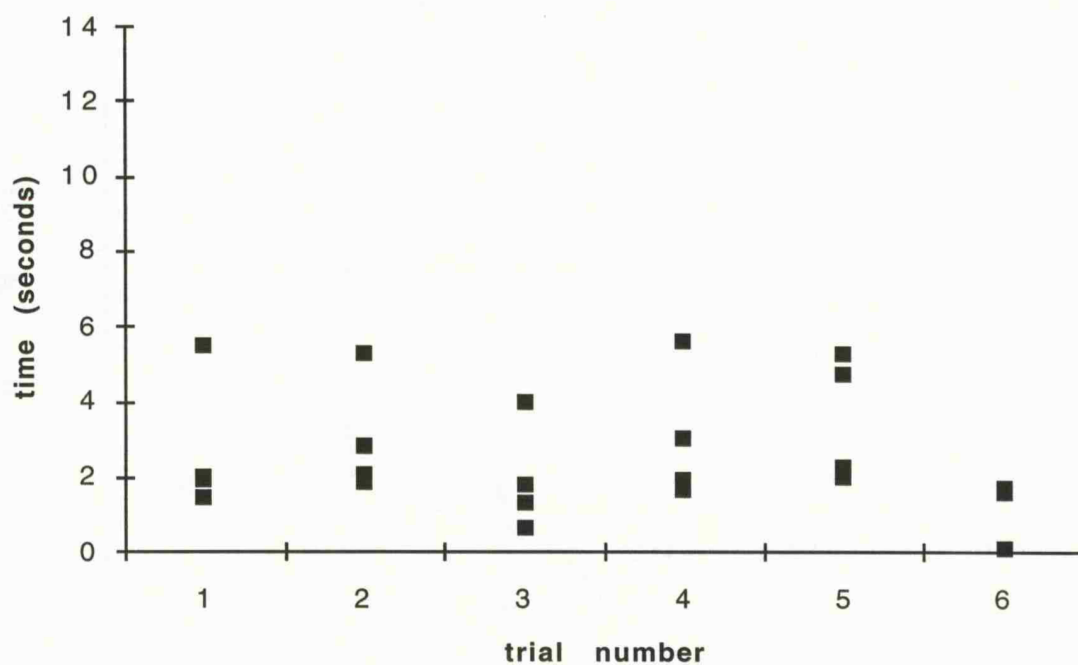


Figure 4.8: Handling times of large whiting feeding on their 1st shrimp over the six consecutive feeding trials.

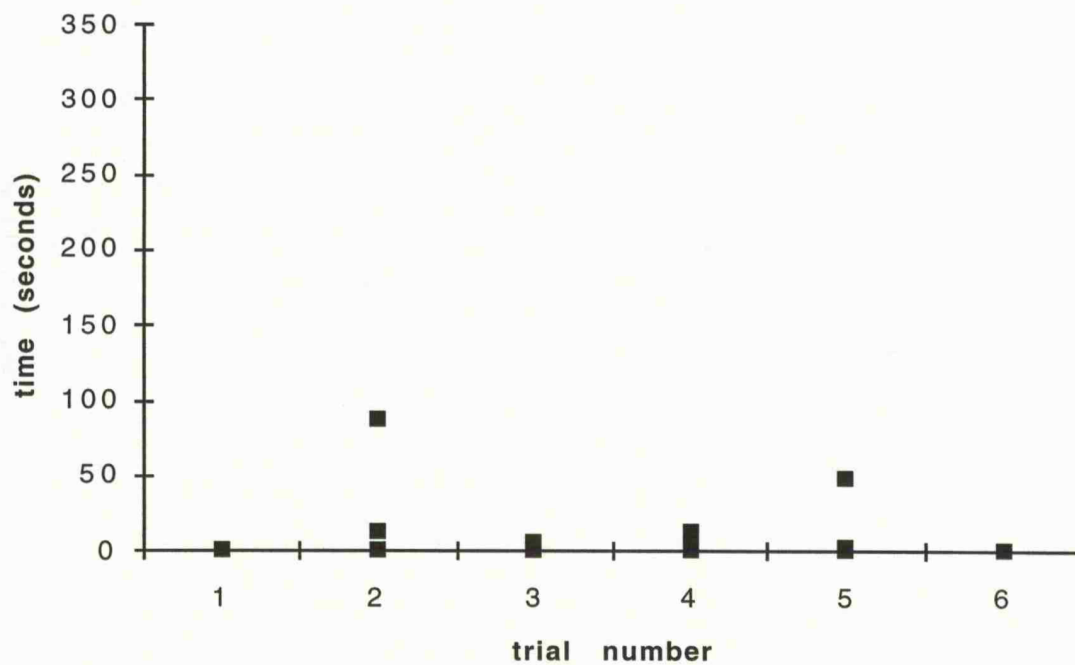


Figure 4.9: Handling times of large whiting feeding on their last shrimp over the six consecutive feeding trials. (N.B. Y axis maximum 1800)

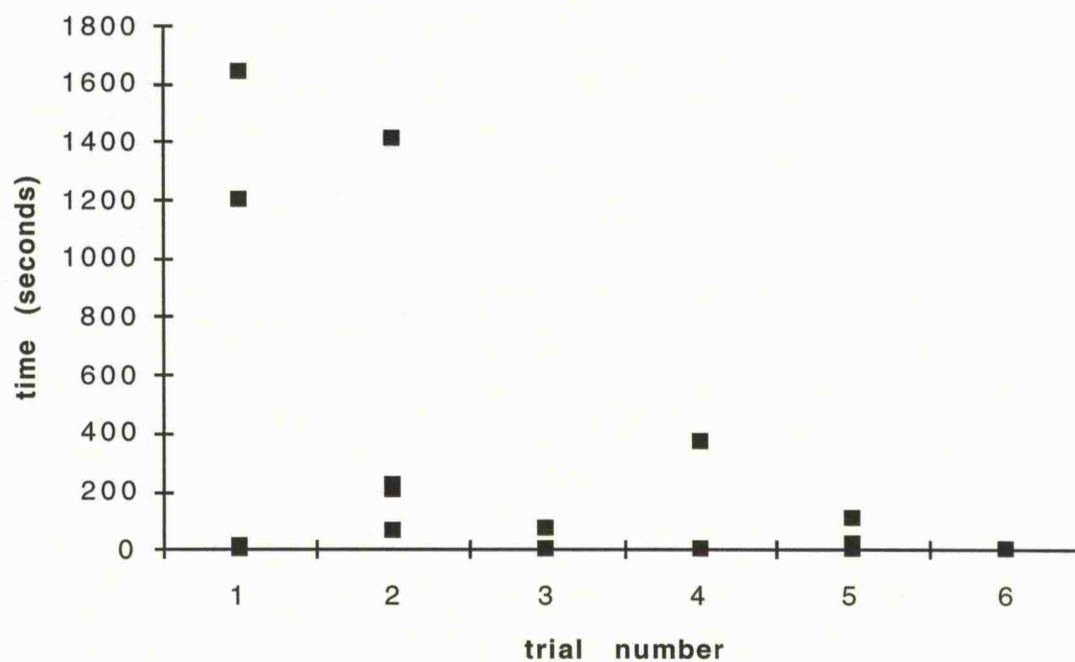


Figure 4.10: Hunting times of small whiting feeding on their 1st shrimp over the six consecutive feeding trials.

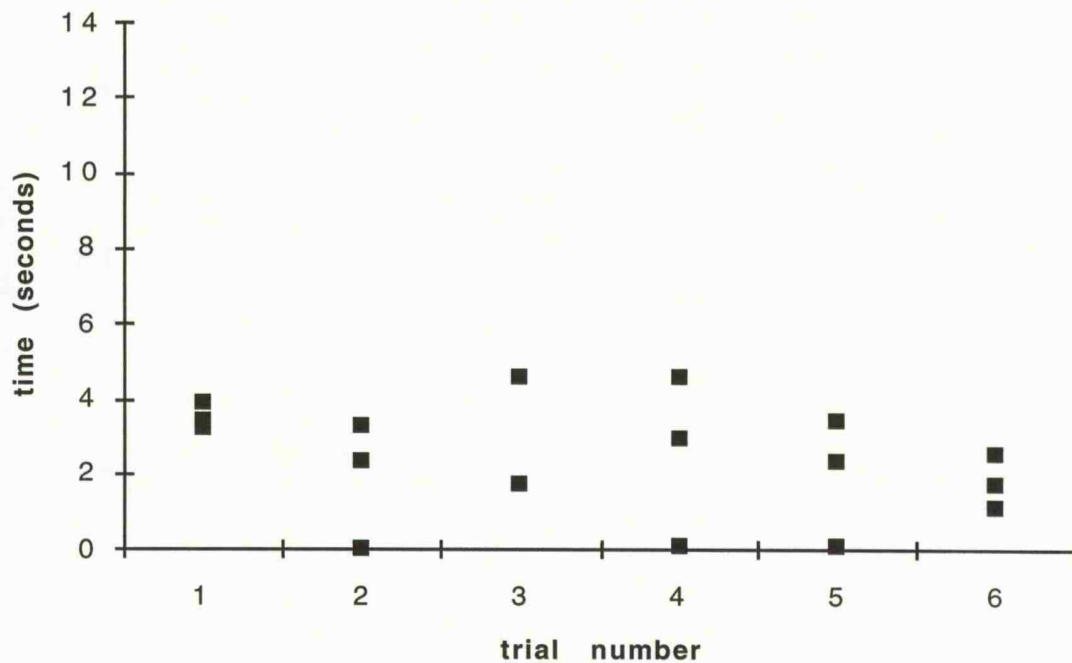
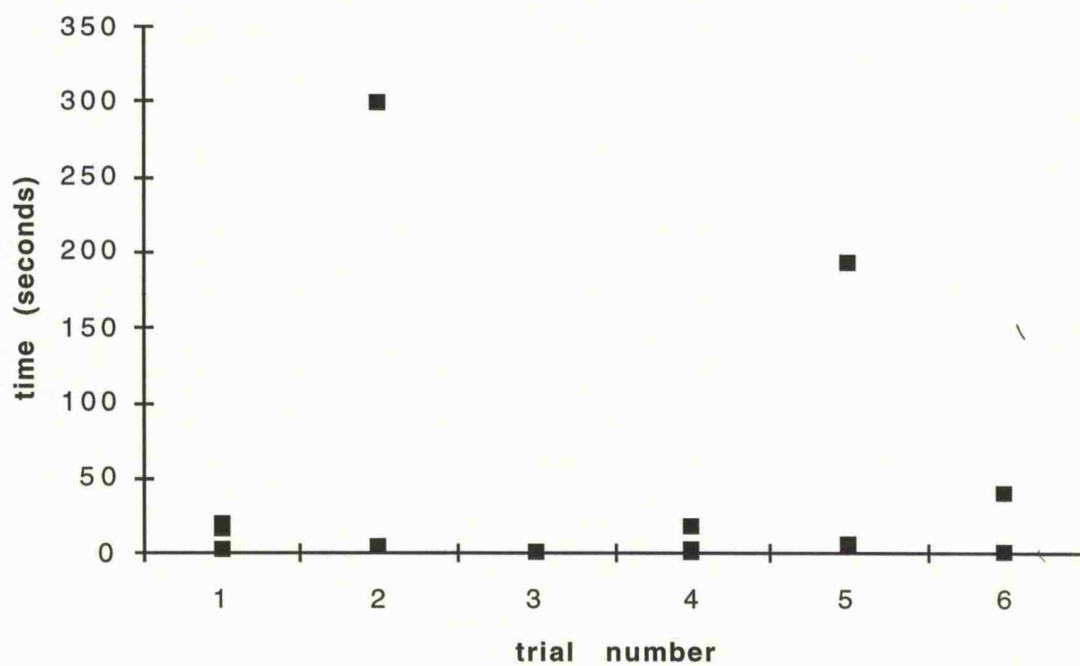


Figure 4.11: Handling times of small whiting feeding on their 1st shrimp over the six consecutive feeding trials



Experiment 2

The pattern of shrimp sizes ingested by the two different sizes of whiting are shown in Table 4.22 and in Figures 4.12 and 4.13. The probabilities were calculated using the methods described on page 84. The probability of a large shrimp being eaten by a small fish was much lower at $p=0.33$ than that for a small shrimp at $p=0.66$. The probability of a large shrimp being taken as the second shrimp was zero for small whiting.

Table 4.22: The total number of shrimps eaten in each trial by each fish

Fish	Small			Large			
	1	2	3	1	2	3	4
trial 1	S	L	S	L	S	L	L
		S		L	L	S	S
				S	L	S	S
				L			
trial 2	S	L	S	L	S	S	S
	S		S	S	L	S	S
				L	S	L	S
					S		
trial 3	L	S		S	S	S	DEAD
		S		L	S	S	
				S	S	S	
				L		L	
				L			
				S			

N.B. the other fish did not eat any shrimps during the experiment.

The small fish struck at almost every shrimp they orientated towards when they were empty, but when they had one shrimp in their stomach the probability that they attacked a prey dropped (Figure 4.14). The decrease in the probability of attack was more marked when the prey was a large shrimp. The probability of success in the small fish decreased with increasing stomach fullness. The probability of success was lower when the prey were large shrimp, and was zero when the small fish had one shrimp in their stomach (Figure 4.16).

The pattern in the large fish was not so clear (Figure 4.15). The large fish eating their first or second shrimp had a greater probability of attacking a small shrimp. With three fish in the stomach the large fish attacked the large shrimps more often. The probability of success in the large fish decreased with increasing stomach fullness (Figure 4.17). With the large shrimp the probability of success dropped after one shrimp was taken,

Figure 4.12: The probability of a shrimp size being eaten by a small whiting, against stomach fullness



Figure 4.13: The probability of a shrimp size being eaten by a large whiting, against stomach fullness



Figure 4.14: The probability of attack in small whiting hunting large and small shrimp, against stomach fullness

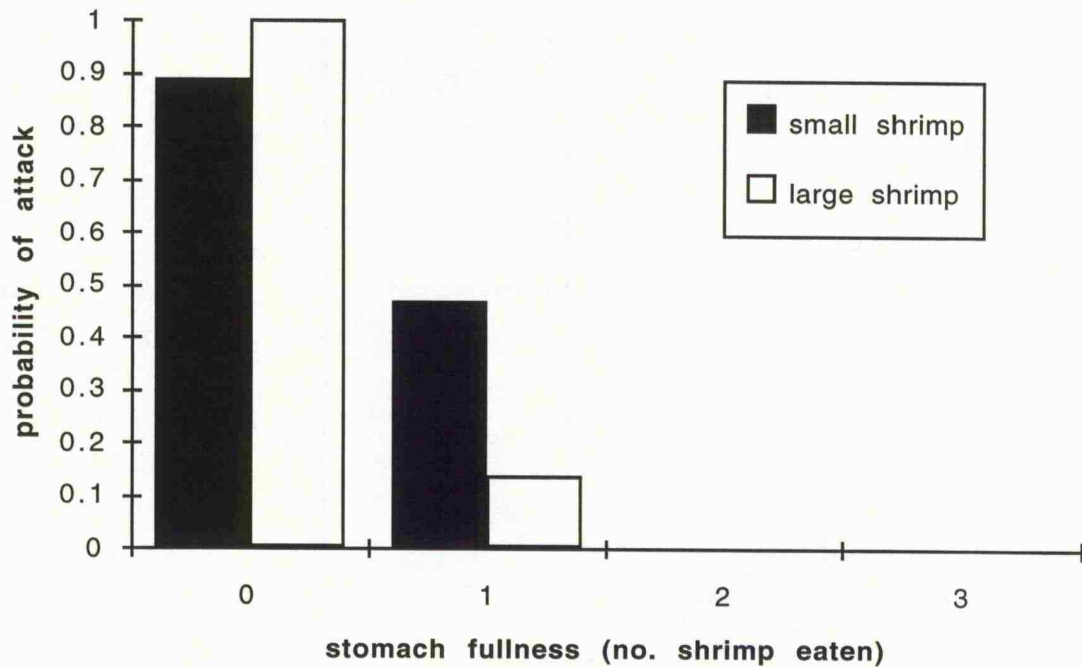


Figure 4.15: The probability of attack in large whiting hunting large and small shrimp, against stomach fullness.

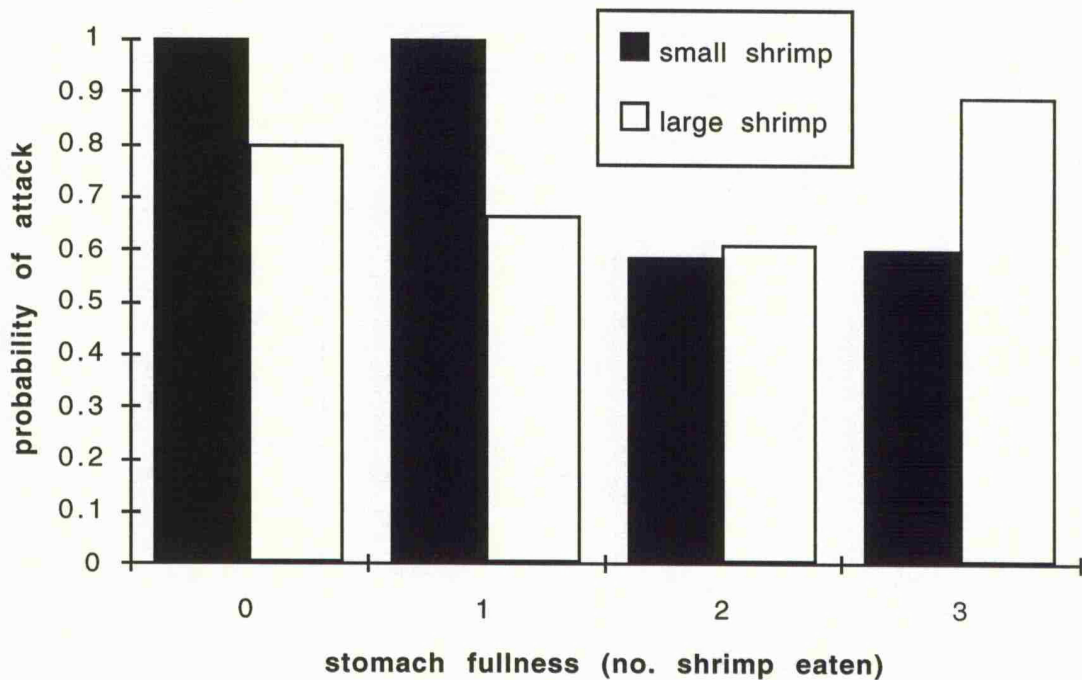


Figure 4.16: The probability of success in small whiting hunting large and small shrimp against stomach fullness.

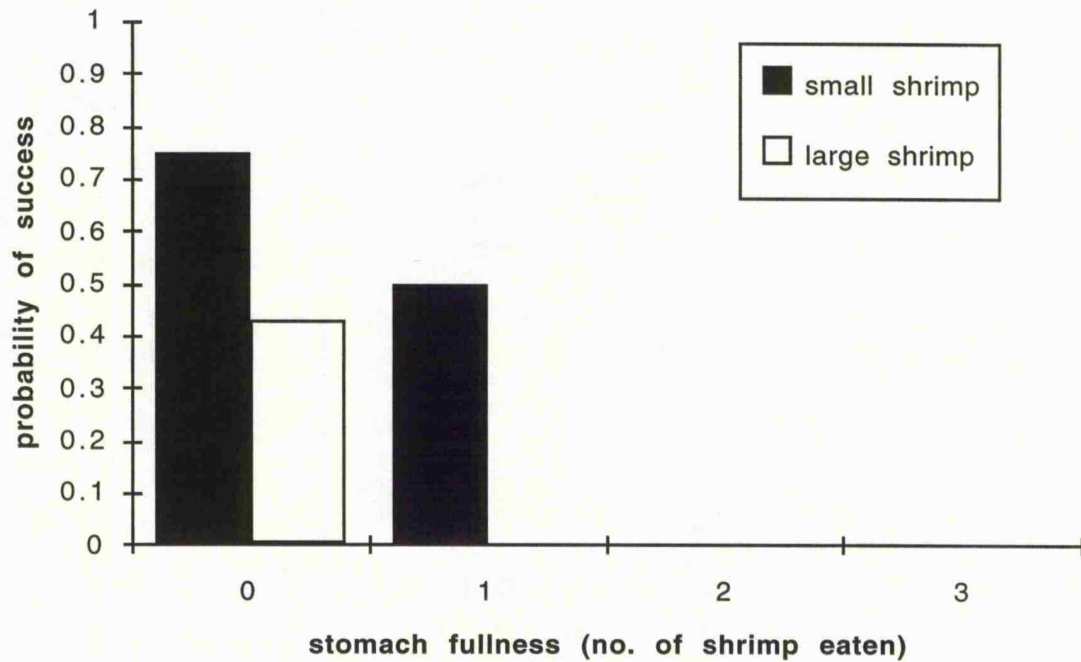


Figure 4.17: The probability of success in large whiting hunting large and small shrimp against stomach fullness.



though with the small shrimp the drop in success did not occur until the third shrimp had been eaten.

The rest of the results in Experiment 2 are arranged into two sections. The first section deals with the affect of shrimp size on the hunting and handling behaviours of the whiting and the second with the affect of fish size on the same behaviours. The effects of these factors were investigated using the same variables and methods employed in Experiment one.

Shrimp Size

The comparison between large fish eating large and small shrimps showed no significant difference in the hunting behavioural transitions (Table 4.23). There was also no difference in the behaviours of the small fish hunting large or small shrimps. The null hypothesis that shrimp size does not effect the sequence of hunting behaviours used by the fish, was accepted for both sizes fish.

Table 4.23: The results of a chi-squared test on the model 'hunting behaviour is independent of shrimp size' for large and small fish

	degrees of freedom	χ^2	probability
Large fish	23	4.53	1.00*
Small fish	23	11.49	0.98*

There was a difference between large fish handling small shrimps and large shrimps (Table 4.24). The important behaviours were 'headshake to adjust' and 'headshake to headshake' (Table 4.25). The same behaviours were important in the small fish handling small and large shrimps. Both of these two transitions increased in their frequency when the fish were handling the large shrimps.

Table 4.24: The results of a chi-squared test on the model 'handling behaviour is independent of shrimp size' applied to data from large and small fish

	degrees of freedom	χ^2	probability
Large fish	29	32.79	0.28
Small fish	29	33.13	0.27

Table 4.25: The behavioural transitions and their standardised residual values that are significant in the model 'handling behaviour is independent of shrimp size' applied to data from large and small fish

Large fish	small shrimp	large shrimp
H \Rightarrow A	-1.76	1.81
H \Rightarrow H	-1.43	1.48
Small fish	small shrimp	large shrimp
H \Rightarrow A	-1.31	1.52
H \Rightarrow H	-1.31	1.52

The time taken to hunt the two different sizes of shrimp was not significantly different in either of the fish sizes (Table 4.26). However the sample size for the small fish eating large shrimps was very small ($n = 3$) and so any interpretation should be done with caution.

Table 4.26: The summary statistics of Mann-Whitney U-test used to test the affect of shrimp size on hunting times.

Fish size	shrimp size	number	median	W statistic	probability
large	large	23	1.46	437.50	0.813
	small	16	1.48		
small	large	3	2.41	80.00	0.108
	small	10	0.66		

The differences in the time taken to handle the two different sizes of shrimp, for both sizes of fish, were only significant at the 0.1 level (Table 4.27). At this 0.1 probability level both sizes of fish handled the smaller shrimps more quickly than the larger ones.

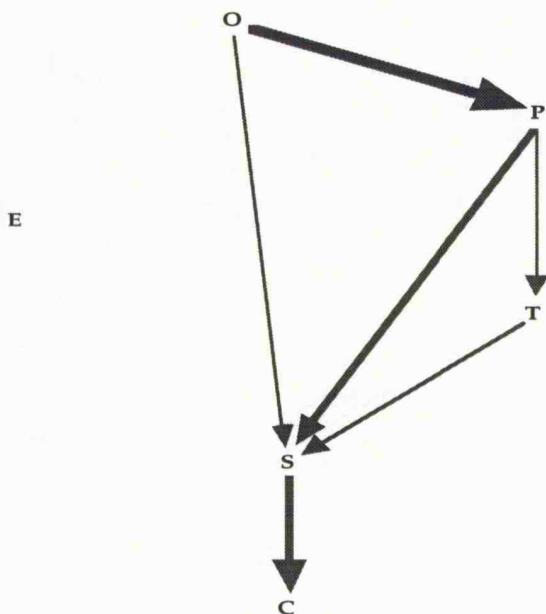
Table 4.27: The summary statistics of Mann-Whitney U-test used to test the affect of shrimp size on handling times.

Fish size	shrimp size	number	median	W statistic	probability
large	large	14	2.20	371.00	0.05<p<0.1
	small	23	0.11		
small	large	3	10.80	59.00	0.05<p<0.1
	small	9	0.74		

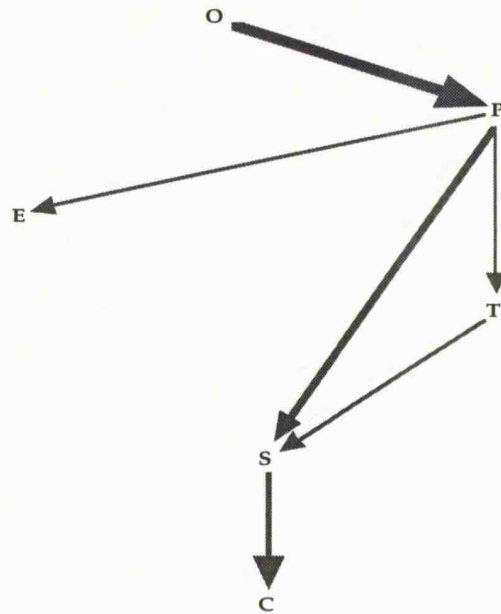
The flow diagrams for the large and small fish hunting the two different sizes of shrimp are shown in Figure 4.18. In this figure it is obvious that the hunting behaviours used to capture the two sizes of shrimp were very similar. The differences in the way the fish handled the two shrimp sizes are clear in Figure 4.19, especially for the large fish.

Figure 4.18: Flow diagrams of behavioural transitions in whiting hunting large and small shrimp prey. The thickness of the arrow represents the probability of the transition occurring.

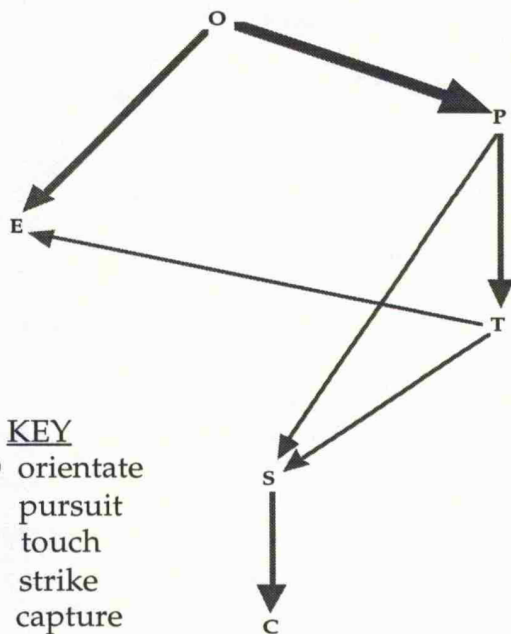
Large fish: small shrimp



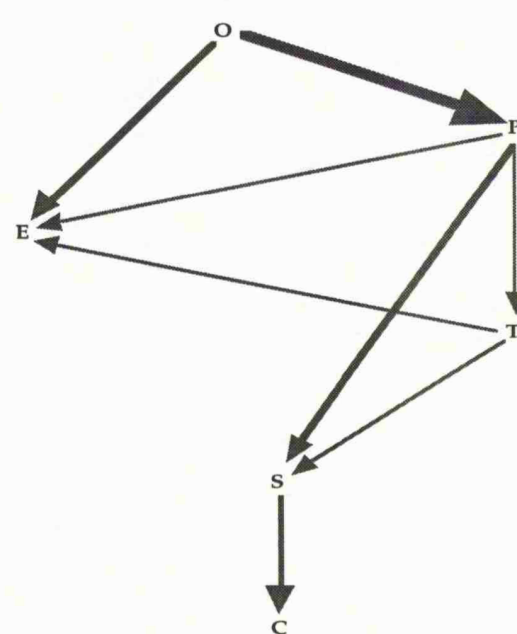
Large fish: large shrimp



Small fish: small shrimp



Small fish: large shrimp

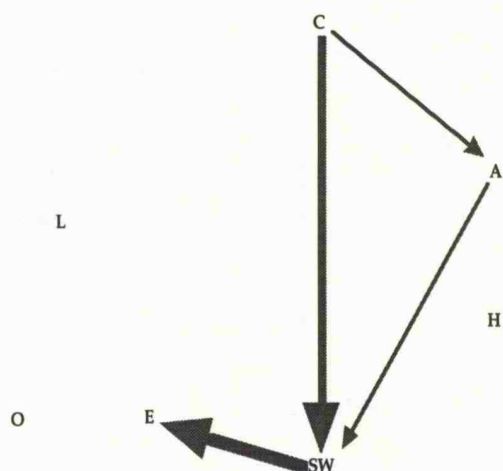


KEY

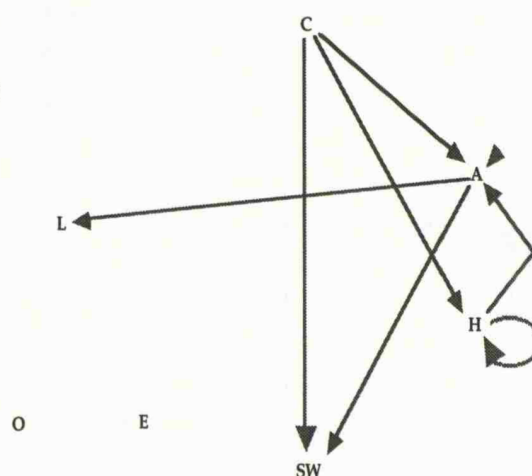
O orientate
P pursuit
T touch
S strike
C capture
E end

Figure 4.19: Flow diagrams of behavioural transitions in whiting handling large and small shrimp prey. The thickness of the arrow represents the probability of the transition occurring

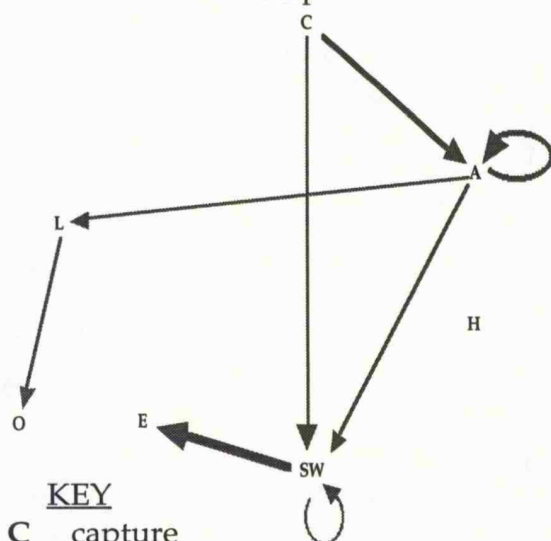
Large fish: small shrimp



Large fish: large shrimp



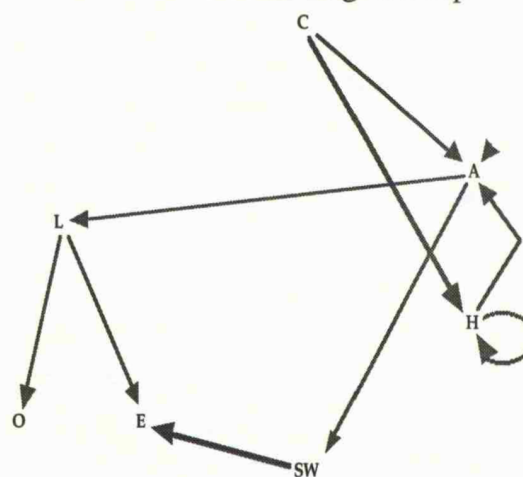
Small fish: small shrimp



KEY

- C capture
- A adjust
- H headshake
- SW swallow
- L loss
- O orientate
- E end

Small fish: large shrimp



Fish Size

The results from testing the affect of fish size on the hunting behavioural transitions are shown in Table 4.28. There was no difference between the two fish sizes when they were feeding on small or large shrimps. The null hypothesis, that fish size does not effect the behaviours used in hunting, was accepted.

Table 4.28: The results of a chi-squared test on the model 'hunting behaviour is independent of fish size' applied to data from large and small shrimp

	degrees of freedom	χ^2	probability
Large shrimp	23	19.0036	0.70*
Small shrimp	23	4.7228	0.99*

The handling behaviours of the large and small fish were the same when the prey were large shrimps (Table 4.29). The null hypothesis, that handling behaviours do not change with fish size, was accepted. When the fish were handling the small shrimps there was a significant difference and the null hypothesis was rejected.

Table 4.29: The results of a chi-squared test on the model 'handling behaviour is independent of fish size' applied to data from large and small shrimp

	degrees of freedom	χ^2	probability
Large shrimp	29	8.08	1.00*
Small shrimp	29	22.96	0.78

Table 4.30: The behavioural transitions and their standardised residual values that are significant in the model 'handling behaviour is independent of fish size' for data from small shrimp

small shrimp	small fish	large fish
H \Rightarrow A	2.20	-1.87

The important residual was for the behavioural transition 'headshake to adjust' (Table 4.30). The frequency of this transition was significantly lower in the large fish compared to the small ones

In the time spent hunting the small shrimp, the size of the fish had no effect (Table 4.31). There was a difference in time spent hunting the large shrimps between the two fish sizes. However this difference was only at the 0.1 probability level and as before the sample size of the small fish was small.

Table 4.31: The summary statistics of Mann-Whitney U-test used to test the affect of fish size on hunting times.

Shrimp size	fish size	number	median	W statistic	probability
large	large	16	1.48	175.50	0.05<p<0.1
	small	3	0.66		
small	large	23	1.46	344.00	>0.05
	small	10	2.41		

When the effect of fish size on time spent handling was investigated there was no difference. In both of the shrimp sizes the smaller fish took longer to handle but the difference was not significant (Table 4.32)

Table 4.32: The summary statistics of Mann-Whitney U-test used to test the affect of fish size on handling times.

Shrimp size	fish size	number	median	W statistic	probability
large	large	14	2.20	153.00	>0.05
	small	3	10.80		
small	large	23	0.11	340.50	>0.05
	small	9	0.74		

DISCUSSION

Experiment 1

The number of shrimp eaten by the fish was highly variable which shows the large inter- and intra-fish differences with regards to satiation. This was also found in the gastric evacuation experiments (Chapter 3). There were a number of fish that did not eat anything at all during the trials. The difficulty in laboratory based experiments is that some fish do not adapt well to the conditions and remain stressed. One of the effects of this stress is that the fish will not eat (Pawson 1974). In their natural environment the whiting do not tend to encounter barriers such as the walls of tanks and some fish have problems in settling in this limited space. Large free swimming marine fish such as whiting are not ideal fish with which to do these laboratory based feeding experiments compared to 'lab rats' like sticklebacks. However these fish are an important resource to man and a major predator in the North Sea ecosystem (Hislop *et al* 1991), so that neglecting large marine fish because of problems in their adaptation to laboratory experiments would be unwise. The extrapolation of results from one type of fish has only limited use as fish species employ many varied foraging strategies, from ambush predators such as pike *Esox lucius*, to speculative hunters such as goatfishes (Mullidae) (Curio 1976). To make the feeding of the fish in this work slightly closer to the natural situation, they were fed in groups. This also helped the fish settle. When the fish were held singly in tanks they became very nervous and easily stressed.

The comparisons of transition matrices provided a useful tool in analysing the fishes' foraging sequences. The effect of the skewed data in the contingency tables and the resulting cells with low values was reduced by dividing the foraging sequences into hunting and handling behaviours. The computer program used adjusted the calculations for cells with logical zero values. The analysis confirmed what was observed visually in the fishes' feeding behaviour. A problem with the method is that the sample size can dictate the sensitivity of the test. A very large sample size causes very small differences to be highly significant and no model will fit the data. Too small a sample size and the significance of the tests becomes invalid (Colgan 1978). The method used in this analysis is a good alternative to the previous methods used such as regression analysis or reduction to two way contingency tables. The time spent by the fish in

hunting and handling was highly variable and did not approximate to a normal distribution, so non-parametric statistics were used. The distributions deviated from the normal because the data values tended to take on either zero values or high values with intermediate values being rare.

Stomach fullness

As the stomachs of the fish filled up there were no observed changes in their hunting behavioural patterns. A fish that was empty had the same approach to capturing a shrimp as one that was hunting the last shrimp eaten. The time taken for the fish to capture the first shrimp it ate was not significantly different from the time taken to capture the last shrimp eaten. The changes in the hunting behaviour when the fish became satiated were virtually the same in both small and large fish. The most important change was the probability of a strike leading to the capture of a shrimp becoming lower in the satiated fish. The other important behaviours could be classed as motivational indicators and were mainly concerned with whether a strike was initiated or not. An interesting transition was the probability that a fish orientated after a strike was unsuccessful. In both small and large fish this probability dropped which would suggest that the motivation of the fish was reduced. The motivational state of the fish in regards to capturing the shrimp did not seem to change until a point in stomach fullness when the fish did not eat any more shrimps. After this point the fishes' behaviour changed considerably and their motivation appeared to be dramatically reduced.

The handling behaviours in either small or large fish were also not effected by stomach fullness. The sequence of behaviours used to handle the shrimp did not change as the fishes' stomachs filled up. In terms of the time taken to handle the shrimp there was a difference with stomach fullness. The last shrimp to be eaten took significantly longer to handle than the first one to be eaten. The handling behaviours of the fish when they were feeding differed significantly from the behaviours when they were satiated. In the feeding fish the biggest probabilities were towards the swallowing behaviour and in the satiated ones nearly all the behaviours were towards or from the loss behaviour. The frequency of behavioural transitions associated with the adjustment of the prey increased in satiated

fish. This would suggest that the fish were trying to orientate the prey in their mouths in order to be able to swallow it. Unlike the hunting behaviours the handling of the shrimps was effected by stomach fullness. There was no observed difference within the sequence but the time spent handling did increase. The changes in handling with satiation were expected, as by the definition of satiation no shrimps could be successfully swallowed. As some shrimps were handled, it would appear that the fish were still attempting to eat the shrimps even when they could not swallow them.

The affect of stomach fullness (or hunger) on the handling time of a prey item was noted by Werner (1974). He found that in bluegill sunfish, *Lepomis macrochirus* and Green sunfish, *Lepomis cyanellus* the time spent handling the prey increased in a curvilinear way with increasing stomach fullness. The increase in handling time with stomach fullness has also been found in fifteen-spined sticklebacks feeding on mysids (*Neomysis integer*) (Kislalioglu and Gibson 1976).

Fish Size

There was a significant difference in the hunting behaviours of the large and small fish when they were feeding. In the small fish the probability that a strike ended in successful capture was smaller than for the large fish. The shrimp size was constant and so the fish to shrimp size ratio was much smaller for the small fish. The analysis suggests that this fish to shrimp size ratio did not affect the sequence of behaviours by which the fish attacked the shrimp but did affect the outcome of the attack. The size of the fish had no effect on the time taken to hunt the prey. The conclusion from this is that the large and small fish did not differ in terms of speed or acceleration. The larger fish probably are faster swimmers, but the difference was not detectable over the limited distances in the small feeding tank.

The size of the fish did affect the handling behaviours. The large fish had a higher probability of directly swallowing a prey on capture and were more likely to swallow a prey successfully. This result is what would be expected as the larger fish to shrimp size ratio should make handling easier for the large fish. The size of the fish also affected the time taken to handle the

shrimps. The smaller fish having smaller fish to shrimp size ratio took longer to handle the shrimps. The difficulties associated with handling the relatively larger prey meant that the small fish took more time to swallow the prey. The instances of the fish striking and swallowing the prey in the same movement were much higher in the large fish.

Experience and Learning

Any influence of learning on the foraging behaviour should have been shown up by comparing the fish over the series of six successive trials. The fish were inexperienced in the first trial, and in each subsequent trial the total number of shrimps they had encountered increased. The small fish showed no significant differences between trials, but the large fish did. The important transitions in the large fishes' behaviour were the probability of a strike being initiated after a pursuit, and the probability that a strike would be successful. The pattern in the frequencies of both the transitions was the same. In the first two trials the frequencies were less than expected by the model of independence and in the other trials they were higher. This pattern suggests that the experienced fish are more likely to strike as soon as they come within range of the shrimp without touching it. The experienced fish are also more successful in capturing a prey when they do strike at it. The improvement in the strike success may have come from the methods employed though it was not possible to analyse this for the reasons outlined in the section describing behaviours. The small fish may not have shown any effect of learning as they are less successful in capturing the shrimps anyway and any improvement in their striking success was probably too small to be significant.

The affect of learning and experience on the time taken to capture a prey item was only detected in the large fish eating their first shrimp. The difference was only significant at the 0.1 probability level. By examining Figure 4.6 it is clear that the difference is caused by the first two trials. In the first trial, two of the fish took over four seconds to capture the shrimp, in the second trial one fish took over twelve seconds. The rest of the trials all have values around two seconds. In the other situations of small fish eating their first shrimp, and large fish eating the last shrimp, the affect of experience is not significant. The time taken to capture the shrimp may be longer in the inexperienced large fish as they do not capture the shrimp at

the first attempt. The probability of a strike being successful increases with experience in the large fish and so, if the inexperienced fish fail to capture the shrimp at the first attempt the time taken will increase.

Neither the small or large fish showed any differences between the trials in terms of handling behaviours. This would suggest that the handling did not change with experience. A more likely explanation is that because of the small number of handling situations in each trial the methods of analysis did not highlight any significant differences. The handling times of the first shrimp taken did not change with increasing experience, in either of the two fish sizes. The last shrimp taken by the large fish did decrease from a long period of handling in the first two trials to a significantly quicker time in the last four trials. It is also interesting to note that in the first two trials the some of large fish took more than three shrimps whereas in the later trials they did not. This may have been because they learnt that the more shrimps they consumed the longer they had to handle them. These longer handling times would reduce the profitability of the prey.

Croy and Hughes (1990) who studied the affect of experience on fifteen-spined stickleback foraging found that the hunting behaviour was simplified, and the probability of an attack being successful was increased. They also found that the complexity of the handling behaviours used, and the time spent handling, decreased with increasing experience. Although no differences in the handling behaviours were found in the current study the time taken to handle the last shrimp eaten by large fish did decrease. The Croy and Hughes (1990) experiments did show that sticklebacks began to lose learned skills after two days. As the trials in the current experiment were three days apart this may have affected the amount of learning observed.

Experiment 2

The small fish ate proportionally fewer large shrimps than the large fish. The probability that a small empty fish attacked a large shrimp was the same as for a small shrimp, but the probability that the large shrimp was successfully caught and ingested was lower. The probability of attack decreased when the small fish had one shrimp in their stomach and was particularly small when the prey was a large shrimp. These data would suggest that the small fish were choosing not to attack the large prey when their stomachs filled up and were only predating on the small prey. The empty small fish did not seem to choose between the two shrimp sizes. The difference in the proportions eaten was because the large shrimps were less likely to be successfully eaten. When the small fish had eaten two shrimps they no longer initiated any attacks on shrimps, and some of the small fish were satiated after eating only one shrimp.

The small shrimps were the largest proportion of the prey taken by the large fish. The probability of attack by the large fish had no real pattern over stomach fullness though the probability of success did decrease. The small shrimp were more likely to be attacked than the large ones and, if attacked the small shrimp had a greater probability of being eaten successfully. The larger fish did seem to select the smaller prey, though it is unclear if this was a result of passive or active selection.

Shrimp Size

The size of the shrimp did not alter the sequence of behaviours by which the fish attacked the prey. The time taken to capture the shrimp was also not affected by the difference in their size. The way in which the two shrimp sizes were handled did change. In both the large and small fish the headshake to adjust transition increased in frequency when handling the large shrimp size. The increase of this behaviour is shown clearly in the flow diagrams (Figure 4.19). The large fish has a very simple flow diagram with most of the small shrimps being swallowed directly after capture. The pattern with the large shrimps is more complicated with 'adjust', 'headshake' and 'loss' coming into the sequence. The change in complexity

is also visible in the small fish but not quite as clear. The affect of the shrimp size on the time spent handling was significant in both the sizes of fish at the 0.1 probability level. The time taken to handle the small shrimp was significantly shorter in both sizes of fish. This was expected as the sequence of handling for these shrimps is simpler. The occurrence of the 'headshake and adjust' behaviours are less with the small shrimp the time taken to handle the shrimps should be much shorter.

Fish Size

There was no difference between the two sizes of fish, in terms of hunting behaviours. However in the first experiment there was a significant difference between the small and large fish which was caused by the probability of a successful strike being reduced in the small fish. The lack of difference is not surprising when the fish were hunting the small shrimps as the affect of the fish size would be reduced. It would be expected that when hunting the large shrimps the size of the fish would have a greater influence on factors such as capture success. One reason for the lack of difference is the low sample size, the small fish only consumed three large shrimps during the three trials and so the differences may not have been highlighted. The difference in the probability of success can be seen in Figures 4.16 and 4.17 where probability is much lower in the small fish especially with the large shrimp. The time taken to capture a prey item is not affected by fish size except in the case of large shrimp. The small fish take a shorter time to capture the large shrimp than the large fish. However the small sample size of the small fish eating large shrimps means that this result is probably spurious.

Comparing the two fish sizes when they were handling the same sized shrimps a difference was observed in the small shrimps but not in the large ones. The lack of difference in the handling sequence when the prey were the large shrimp is again probably a factor of the small sample size. In the small shrimp the probability of headshake to adjust decreases. These behaviours are concerned with the subduing the shrimp and orientating it within the mouth of the fish in order for it to be swallowed. The frequency of these behaviours was greater when handling the large shrimp size. This would suggest that a smaller fish to shrimp size ratio caused the fish to have to handle the shrimp more in order to successfully swallow it. The size of the fish did not affect the time taken when handling either large or small shrimp. In the first experiment fish size was found to affect the handling time. The results from the first experiment are based on a larger number of replicates and are probably more accurate than the results in Experiment 2. From the results of fish size and shrimp size it would seem that the fish to shrimp size ratio is important in the way in which the shrimp is handled. The smaller the ratio the longer the fish takes to handle the prey and the more complex the sequence of handling is.

The effects of fish and prey size have been investigated by other workers. Hart and Gill (1992) found that a larger 8mm prey was included in the diet less often as the size of the stickleback predator decreased. They also showed that smaller sticklebacks were more likely to handle prey, and took longer to do so than larger fish. Kislalioglu and Gibson (1976) found that handling time increased with larger prey items. These findings agree with the ones in this study the handling time and probability of success are the factors which are affected most by changing the shrimp to fish ratio.

In general it would appear that the handling of the prey is the most variable part of the fishes feeding behaviour. The method of capture is fairly constant through out the various situations.

The whiting feeding on the shrimps tended to attack them on the bottom of the tank. The shrimps rarely moved off the bottom and hence the fish came into contact to them in this situation. The shrimp prey would also normally be able to hide themselves by burying in the substrate which was not possible in these experiments. Whiting are known to feed on the bottom taking other benthic prey types (Chapter 2). However they also take prey in the water column and this should be taken into account. The shrimp prey also have some unique characteristics with the fast tail flip but their slow swimming speed. In order to gain a full picture of the whiting feeding mechanics other prey types would need to be studied.

CHAPTER 5

FEEDING MODEL

"To ERR is human, to really mess things up you need a computer."

Anon.

INTRODUCTION

Modelling is a method of describing nature, and in recent times this has been done using quantitative mathematical models. These mathematical models are conceptual tools that can be used to interpret observations, and generate predictions. Models allow general theories and specific hypotheses to be brought together spanning the gap between theory and observed information. The use of models in ethology is widespread, and this is a field to which it is particularly suited. The Markov chain analysis used in Chapter 5 is a form of modelling that allows the patterns in a behaviour to be studied, in this case hunting and handling behaviours. The study of feeding has led to the development of optimal foraging theory which was first proposed by Emlen (1966) and by MacArthur and Pianka (1966). Optimality theory states that the behaviour an animal performs will be the one that confers the greatest fitness upon it. Optimal foraging theory is concerned with the behaviours relating to the finding and consumption of food. There are three basic principles involved in optimal foraging theory (Pyke *et al* 1977). Firstly the behaviours concerned must show heritable variation so that differences in the behaviours of animals are passed onto subsequent generations. Secondly there must be a range of possible foraging behaviours which the animal can perform that will alter its fitness. Finally natural selection must occur so that animals with a better fitness will contribute the most to the following generations. If these principles hold true then the foraging behaviour in a population should, on average, be very close to the optimal.

In order to model behaviour in terms of optimisation, a currency that is to be optimised must be chosen. The choice of this currency is crucial if the model is to correctly mirror the optimal choice of the animal. The currency used in most foraging models is net energy gained. How the animal's choices affect the currency needs to be determined in terms of both costs and benefits. The equations of the model can then be solved to optimise the currency.

One of the simplest foraging models is the basic prey model, which assumes that net energy gain per unit time is a function of fitness (Stephens and Krebs 1986). The choice of a prey item is based on its profitability which is calculated from its energy content, and how long the animal takes to handle it. Like any model the basic prey model has some

assumptions (Stephens and Krebs 1986). Prey items are encountered sequentially in a Poisson process. The prey is either eaten or rejected and the animal loses no fitness if a prey is rejected. Encountering a prey without attacking it takes no time and fitness is not gained or lost in this process. Prey are also not encountered whilst handling another prey item. The basic prey model can be written mathematically as:

$$\text{Fitness} \propto \frac{E}{T} = \frac{\sum P_i \lambda_i e_i}{1 + \sum P_i \lambda_i h_i}$$

P_i = probability a prey type i will be taken

λ_i = the encounter rate with prey type i

e_i = the energy gained per encounter

h_i = the handling time of prey type i

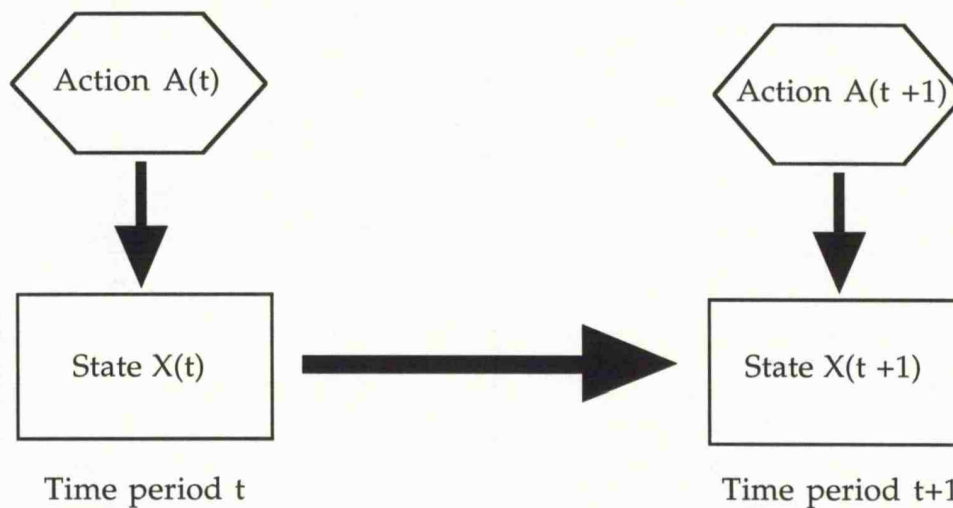
The major problem with this type of model is that it assumes that the behaviour of the animal is not affected by its internal state. This assumption is clearly erroneous as a fish with a full stomach will not behave in the same manner as one which is empty as was shown in Chapter 4.

Dynamic modelling takes into account the changing state of the animal and allows for this in the calculation of the optimal behaviour (Mangel and Clark 1988). In the simplest type of dynamic model one state variable is used. A state variable is a characteristic of the organism which will affect and be affected by its behaviour. The state variable will have constraints which will limit the values that it can take. The animal makes optimal choices at each value of the state and these are called the strategy set. How these choices affect the state variable over time is called the state dynamics and a simple case is shown in Figure 5.1. The division of time is discrete so that the computation and interpretation of the model is much simpler than with continuous time models. The one state variable is the simplest type and models can be expanded to include two or many more, if these are deemed to be important. Burrows (1994) uses three state variables; energy, stomach fullness and vertical position, to model the migration and foraging behaviour of juvenile plaice.

The phenotypic character which the animal in the model is trying to maximise, through the choices it makes, is called the optimisation

criterion. In natural selection this would be life-time fitness, but this is hard to measure and so another simpler variable is usually used e.g. fecundity or growth. The choice of the criterion is dependant on the behaviours that are being modelled. In dynamic modelling the optimisation criterion is determined from the state variables at the end time T .

Figure 5.1: Schematic diagram of a simple stochastic system subject to periodic choices of action $A(t)$ (after Clark 1985).



Dynamic modelling is a highly versatile technique and has been used to model a large variety of optimisation problems in biology, from the reproduction of insects, to movement in spiders and raptors (Mangel and Clark 1988). The technique has been used extensively in the study of foraging behaviour on animals such as; Dogwhelks, *Nucella lapillus* (Burrows and Hughes 1991), three-spined sticklebacks (Hart 1994) and small birds (Bednekoff and Houston 1994).

This chapter describes a stochastic dynamic program developed to model whiting feeding on different sizes of shrimp. The model is used to predict the optimal choices of large and small whiting in terms of prey size eaten during a feeding bout. The functions used to describe the probability of successful capture and handling time in the model were tested to investigate their effect on the optimal choices predicted. The predicted prey size choices were compared to actual choices observed in the feeding trials described in Chapter 4.

THE MODEL

The model was written using Microsoft Quickbasic 4.5 on an Apricot XEN-S IBM clone personal computer. The computer program printout is shown in Appendix 2. The symbols and variable names used in the program are shown in Table 5.1.

Table 5.1: The variables and their symbols used in the model

Symbol	Description	Units
i	prey item	-
α_0	Basal metabolic rate	C min ⁻¹
x_c	critical energy value of fish	Calories
C	energy capacity of fish	Calories
y_i	energy of prey item	Calories
x	energy value of the fish	Calories
vol	stomach volume	grams
vol_{min}	minimum stomach volume	grams
vol_{max}	maximum stomach volume	grams
τ_i	handling time of prey item i	minutes
ϵ	evacuation rate	g min ⁻¹
$preyvol_i$	volume of prey item i	grams
λ_i	probability of encountering prey item i	-
λ_u	probability of encountering prey item 1 and 2	-
λ_0	probability of not encountering a prey item	-
Success(i)	the probability of successfully eating prey i	-
Horizon	length of the feeding period	-
$F(vol, x, t, T)$	fitness value at; stomach state = vol , energy state = x at time t from until T	g day ⁻¹

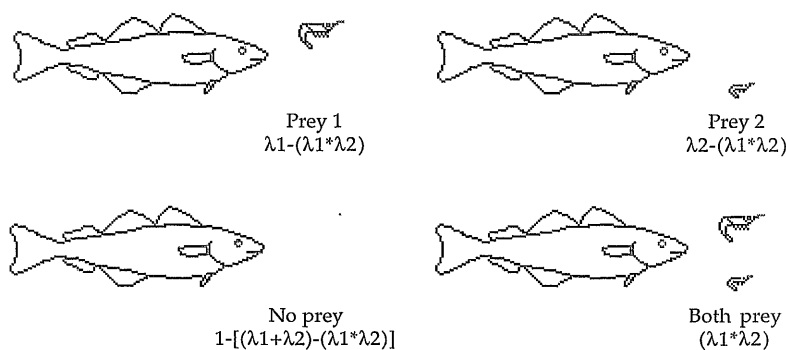
The computer model uses two state variables; energy reserves, and stomach fullness. Initially the model works backwards from the end point T . Time T is defined as the end of a feeding bout and the growth for each level of the state variable energy is calculated at time T , using the equation from Jones and Hislop (1972);

$$growth \text{ (grams day}^{-1}\text{)} = (0.361 \times \text{energy levels}) - 0.336 \quad 5.1$$

The equation gives the fish with higher energy values in the final time a higher value of the optimization criterion, in this case a larger weight

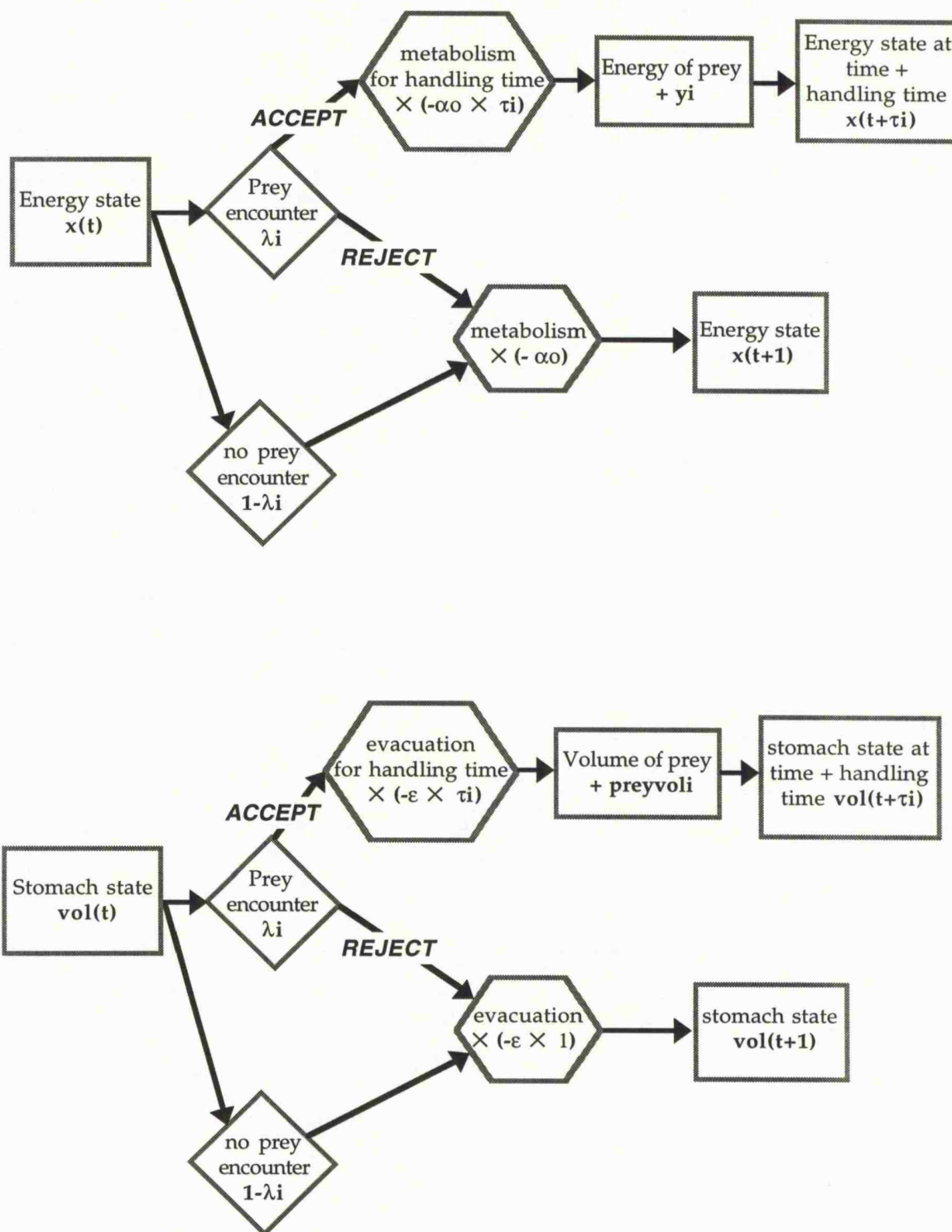
increase. It is assumed that the fish is trying to maximise its energy intake over the time of the feeding bout. The fitness at time T is known for each state variable, and from these values the fitness values in the previous time period $T-1$ or t are calculated. At any one time the program calculates, for each combination of the two state variables, the fitness from the probability of a prey encounter occurring and the fitness resulting from the optimal choice for that encounter. The fish can encounter prey in one of four ways (Figure 5.2). Either of the prey can be met on its own and can either be rejected or eaten. The fish also has a probability of not encountering any prey in the time period. There is also a special case in this model when the two prey items are met simultaneously. The probabilities of these encounter scenarios occurring are calculated from the probabilities of encountering the two prey types, λ_i and the equations used are shown in Figure 5.2

Figure 5.2: The encounter scenarios and their probabilities including simultaneous prey



The effect of eating a prey item on the energy level and stomach volume is shown by the flow diagram in Figure 5.3. The energy contained in the prey is added to the fish's energy levels. The time taken to handle the prey is then multiplied by the basal metabolic rate and subtracted from the fish's reserves. If a prey is eaten the stomach volume is increased by the volume of the prey, and is decreased by the evacuation rate multiplied by the handling time. If an attempt to eat a prey item is made then the resulting fitness is a combination of the fitness gained from successfully eating the prey, and the fitness from an unsuccessful attempt. The fitness from successfully ingesting a prey item is taken from the time period after the prey has been handled and from the resulting levels of the two state

Figure 5.3: The dynamics of the two state variables; energy levels, and stomach fullness in the whiting foraging model.



variables. The fitness gained from successful ingestion is multiplied by the probability of success. The probability of a fish being unsuccessful in its attempt to eat a prey item (1-prob(success)) is multiplied by the fitness gained from not eating the prey item. This unsuccessful fitness is the same as if the prey item had been rejected. The two components of successful and unsuccessful ingestion are added together to give the fitness in the time period calculated.

If the prey is rejected the energy levels of the fish are simply decreased by the basal metabolic rate for one time period. The stomach state is decreased by the evacuation rate multiplied by one time period. The fitness resulting from rejecting a prey is taken from the previous time period $t+1$ together with the resulting levels of the two state variables. The fitness resulting from a prey type being eaten is compared with the fitness resulting from rejection. The behavioural choice which leads to the largest fitness value is optimal. The fitness resulting from the optimal choice for the prey encounter is multiplied by the probability of that prey encounter occurring. This acceptance or rejection value is calculated for all the encounters with the two prey types. The situation when no prey is encountered is calculated in the same way as if a prey item was rejected. In the special situation of meeting both prey types only one prey can be eaten. In this case the fitness of eating prey type one, prey type two or rejecting both prey types are compared. The fitness values of the optimal choice from each encounter scenario are summed and the new fitness value is recorded for the state of the fish in the new time period. The calculation for this fitness in the simultaneous encounter model is, using the notation of Mangel and Clark (1988),

$$F(vol, x, t, T) = \lambda_0 \times F(vol_0'', t+1, T) + \sum_{i=1}^2 [\lambda_i \times \max\{F(vol_o'', x_o'', t+1, T), F(vol_i', x_i', t + \tau_i, T)\}] + [\lambda_u \times \max\{F(vol_o'', x_o'', t+1, T), F(vol_1', x_1', t + \tau_1, T), F(vol_2', x_2', t + \tau_2, T)\}]$$

Written out as:

$$\begin{aligned} \text{fitness} = & \text{Prob}(\text{not encounter prey}) \times \text{fitness}(\text{not eating food}) + \\ & \text{prob}(\text{encounter prey 1}) \times \max[\text{fitness}(\text{eating prey 1}) \text{ or } \text{fitness}(\text{not eating prey 1})] \\ & + \text{prob}(\text{encounter prey 2}) \times \max[\text{fitness}(\text{eating prey 2}) \text{ or } \text{fitness}(\text{not eating prey 2})] \\ & + \text{prob}(\text{encounter prey 1 and 2}) \times \max[\text{fitness}(\text{eating prey 1}) \text{ or } \text{fitness}(\text{eating prey 2}) \\ & \text{or } \text{fitness}(\text{not eating food})] \end{aligned}$$

The two state variables have constraints on the values that they can take. The energy state variable has a maximum capacity and if the energy levels exceed this then they are forced to this value. If the energy levels fall below a minimum level, called the critical value (x_c) then the fish is deemed to have starved and has a fitness of zero. The stomach volume also has a minimum value which it cannot fall below. If the volume of the stomach is less than this minimum then the volume is corrected up to the minimum. The maximum volume of the stomach cannot be exceeded, and if taking a prey item would result in a higher stomach volume, then the prey must be rejected. This rejection is forced by setting the fitness to zero when the stomach capacity is exceeded so that it is always optimal to reject the prey rather than eat it. These constraints can be shown mathematically using the same notation as before:

$$\begin{aligned}
 x_i' &= chop(x - (\tau_i \times \alpha_o) + y_i; x_c, C) \\
 x_0'' &= chop(x - \alpha_o; x_c, C) \\
 vol_i' &= \begin{cases} chop((vol + preyvol_i) - ((vol + preyvol_i) \times \epsilon); volmin) & \text{if } preyvol_i + vol \leq volmax \\ F(vol_i', x_i', t + \tau_i, T) = 0 & \text{if } preyvol_i + vol > volmax \end{cases} \\
 vol_0'' &= chop(vol - (vol \times \epsilon); volmin)
 \end{aligned}$$

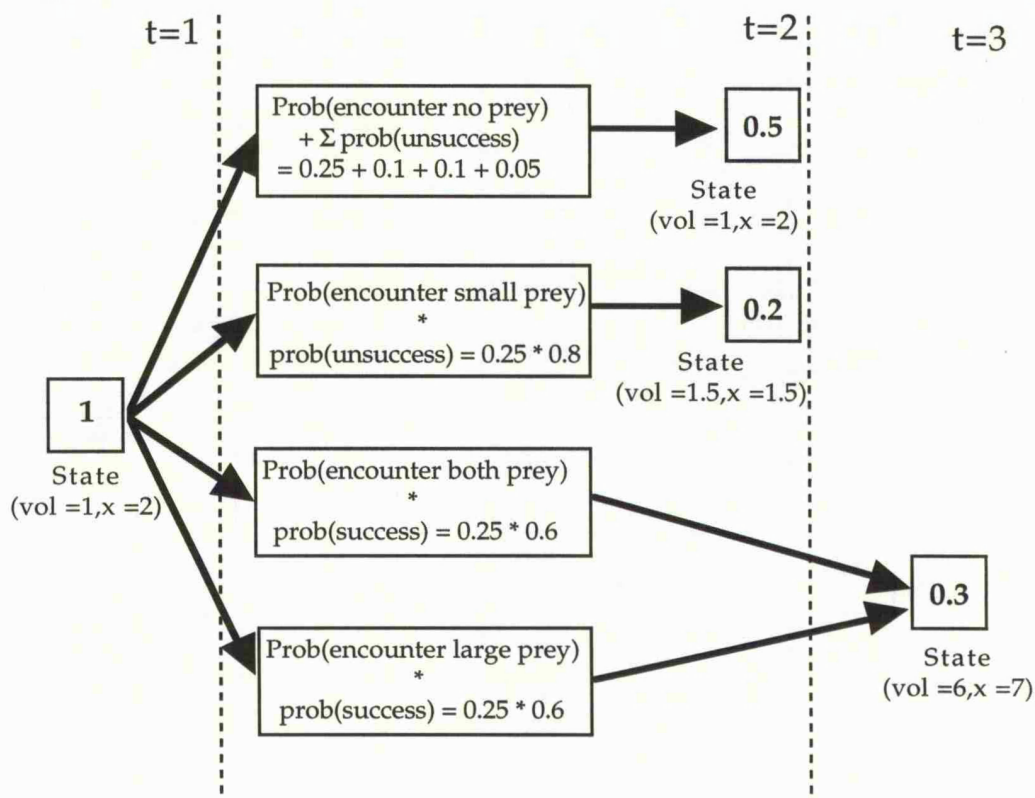
Forward iteration

The program stores the optimal choices at each state in a file along with the resulting state in terms of energy, stomach contents, and the time period in which the fish finished handling the prey. The optimal choices can then be used to compare models to each other, and to observed results. The resulting tables of optimal choices can be large and difficult to summarise so other ways of viewing the data were devised. To investigate the predictions of different models a forward iteration program was developed. This program returns a predicted sequence of choices that the fish makes. These sequences can then be used to compare different models against each other, and against actual observations. The program calculates the optimal choices and their probability of occurring starting from an initial state. A probability of 1 is entered into the starting state in the first time period ($t = 1$). The starting state can be any combination of the two state variables, but in the following experiments a standard state of, $vol=1$ and $x=2$ was used.

In the starting state, the program calculates the probability of each encounter, and multiplies it by the probability of success for the optimal choice (Figure 5.4). The result is multiplied by the initial probability, in this case 1. The resulting probability of this multiplication is placed into the state that would result from the choice being made and in the time period when the fish has finished handling (e.g. a probability of 0.3 in the state $\text{vol}=6$ $x=7$). This calculation is done for all of the possible encounter scenarios.

The time period t is moved on one and the program searches for combinations of the state variables that have had a probability of occurring given to them (e.g. the states $\text{vol}=1$ $x=2$ and $\text{vol}=1.5$ and $x=1.5$, at $t=2$). When such a probability is encountered the program repeats the calculation as described for the starting state. The difference in this time period is that the initial probability will not be 1, but will be the result of a previous calculation (e.g. probability of 0.5 in state $\text{vol}=1$ $x=2$). If the fish is still handling the prey in the time period, the probability is ignored (e.g. the state $\text{vol}=6$ $x=7$ is not calculated until $t=3$). The time is moved on one period at a time, calculating the probabilities, until the horizon is reached.

Figure 5.4: A flow diagram example of one step of the forward iteration program



Parameter Values

Parameters for the model were estimated using results from the feeding experiments described in Chapter 4. Each time period was set as 1 minute and the whole model was run over ten of these periods. The energy levels were calculated in Calories with a critical value of 1C, below which the fish would be deemed to be dead. The metabolic rate (α_0) was assumed to be a negative linear function so that energy values decreased over time. The rate was set at $0.001C \text{ min}^{-1}$ which was estimated from a value of 0.93 g day^{-1} needed for zero growth in small whiting (Jones and Hislop 1972). As the model was run over a short time only, this rate did not have a big influence. If the fish did not eat throughout the feeding bout T then the energy levels would decrease by the equation,

$$X(t) = X(T) - (\alpha_0 * t)$$

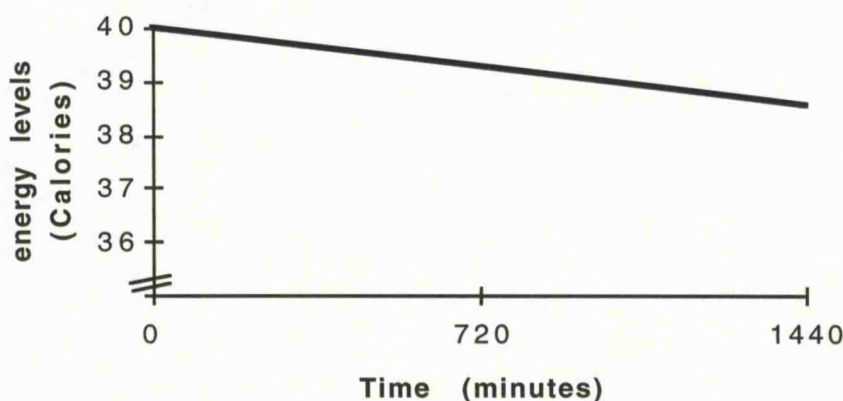
Where:

$X(t)$ is the energy level at time t

$X(T)$ is the original energy level

α_0 is the basal metabolic rate

Figure 5.5: The decrease in energy levels over time, if the fish ate no prey, as a consequence of the basal metabolic rate. (N.B. the y axis starts at 35 and the x axis is 1 day for clarity)



The stomach volume was calculated in grams as the two prey items were of the same density. The minimum stomach volume was set at 1 gram and the evacuation rate was set as a linear function of stomach contents with 0.5 g h^{-1} being removed from the stomach contents. This value was estimated from the evacuation rate of *Pandalus* prawns in Chapter 3. The decrease of the fishes' stomach contents over time was described by the equation,

$$\text{Vol}(t) = \text{Vol}(T) - (\epsilon * t)$$

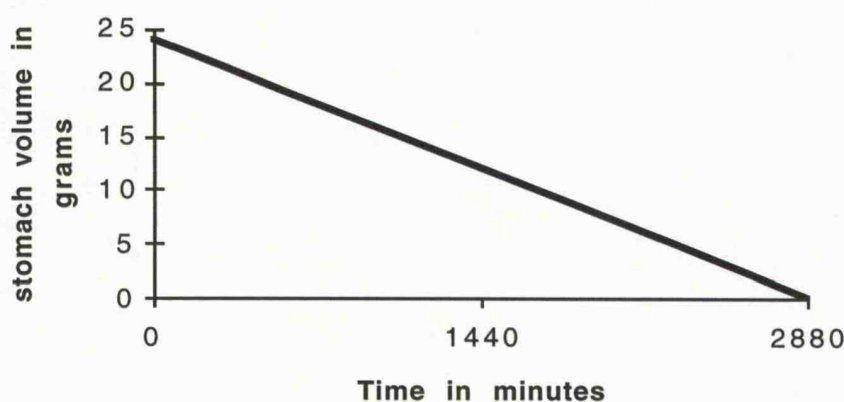
Where:

Vol(t) is stomach volume at time t

Vol(T) is the original stomach volume

ϵ is the evacuation rate

Figure 5.6: The decrease in the weight of stomach contents over time, if the fish ate no prey, by the evacuation function (N.B. the x axis is 2 days).



The two types of prey included in the model were set-up as a large shrimp and a small shrimp. The large shrimp was given a weight of 5 grams and an energy content of 5 Calories. The small shrimp had a weight of 1.5 grams and an energy content of 1.5 Calories. The weight values for the two sizes of shrimp were similar to the weights of the large and small shrimps used in the feeding trials described in Chapter 3. The energy values of the shrimp were estimated using a weight to energy ratio of 1C per gram (Rumohr *et al.* 1987)

Table 5.2: Summary table of parameters values used in all of the models

Parameter	Values used
α_0	0.001 C min ⁻¹
x_c	1 Calorie
ϵ	0.0083 g min ⁻¹
volmin	1 gram
preyvol _i	large = 5g small = 1.5g
y_i	large = 5C small = 1.5C
λ_i	large=1 small=1
horizon	10 min

The probability of encounter (λ_i) for each of the two prey types was set at 1. This meant that in every time period the fish would meet both prey sizes simultaneously. The rest of the parameters were varied in the experiments and their characteristics are described in each test of the model.

Interpolation

The model uses discrete values of the state variables with which to calculate the fitness in each time period. The choices made by the fish lead to intermediate values of the state variables from which fitness is not calculated. By taking the fitness from the nearest value of state variable important information could be lost so the model uses linear interpolation. Intermediate fitness values were calculated from the following equation.

$$F(x,t,T) = \frac{(x - x_i)B(i+1) + (x_{i+1} - x)B(i)}{x_{i+1} - x_i}$$

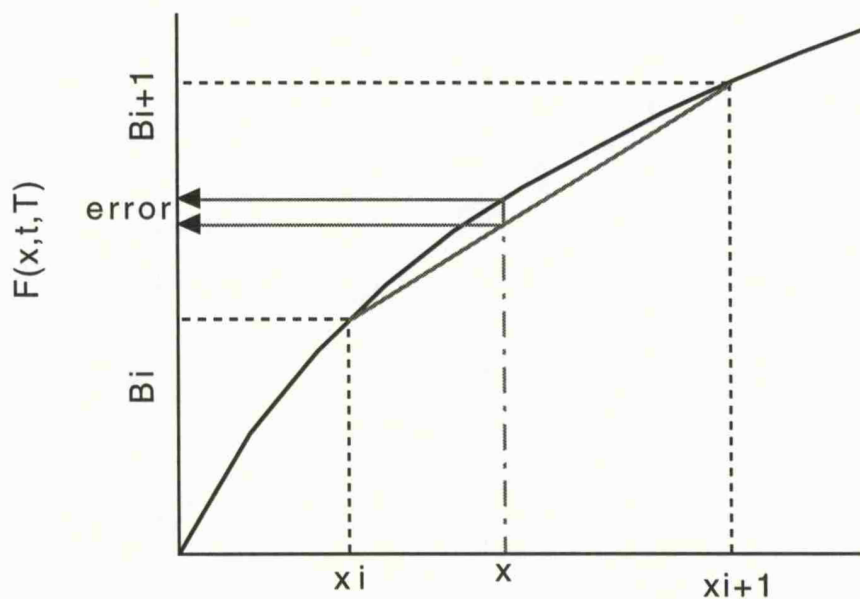
where:

$$x_i < x < x_{i+1}$$

$$B(i) = \text{fitness at } x_i$$

$$B(i+1) = \text{fitness at } x_{i+1}$$

Figure 5.7: Linear interpolation of the fitness function $F(x,t,T)$ (after Mangel and Clark 1988)



The program in this thesis uses two state variables and when they both take on intermediate values the calculation becomes more complicated but works in a similar manner as before. Intermediate fitness values are calculated from;

$$F(x, y, t, T) = \frac{1}{PQ} [pqB(i+1, j+1) + p(Q-q)B(i+1, j) + (P-p)qB(i, j+1) + (P-p)(Q-q)B(i, j)]$$

where:

$$p = x - x_i \quad P = x_{i+1} - x_i$$

$$q = y - y_i \quad Q = y_{i+1} - y_i$$

This interpolation technique is based on a linear relationship between fitness and the state variables. If the fitness is non-linear then the result will have an error (Figure 5.7). To keep this error as small as possible it is useful to keep the gap between the discrete variables small.

TESTING THE MODELS

Fish size models

The computer program was first used to run two models of different fish sizes. The first model labelled the 'small fish model' was based on the results from the small fish size category used in Chapter 4. The second model labelled the 'large fish model' was based on the large fish size category used in Chapter 4. The predictions of these two models could then be compared to the actual observed choices of the fish in the feeding trials. The maximum stomach capacity for each size of fish was estimated from the largest weight of shrimps eaten by any of the fish in the category. There was a large difference in the number of shrimps eaten by the fish within each size category. To test the effect of changing stomach size the small fish model was run with two different maximum stomach capacities.

The small fish model

In this model the energy capacity of the fish was set at 20 Calories and the maximum weight in the stomach at 8 grams. The probability that the fish would successfully eat a prey was described using a decreasing linear function with a different slope for the two types of prey.

$$\text{success (i)} = [s(i) * \text{weight in stomach}] + 0.8$$

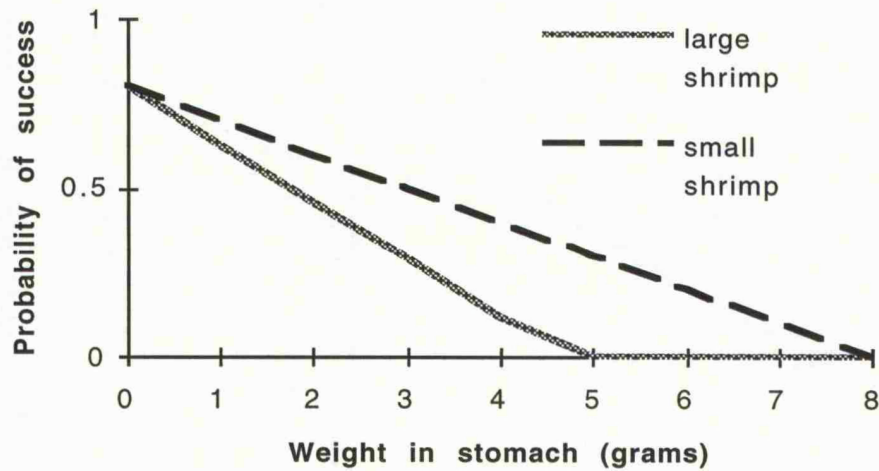
Where:

Large shrimp: $s(1) = -0.17$

Small shrimp: $s(2) = -0.1$

These values were estimated from the probability of success calculated in Chapter 4 (Fig 4.16).

Figure 5.8: The change in probability of success with increasing weight of stomach contents in the small fish model.



The time taken to handle the two prey sizes also changed with the weight in the stomach and was different between the two sizes of shrimp. The relationship was an exponential one with the larger shrimp taking longer to handle than the smaller ones (Figure 5.9).

$$\tau(i) = \frac{\text{handle}(i) \times 10^{(0.21 \times \text{weight in stomach})}}{60}$$

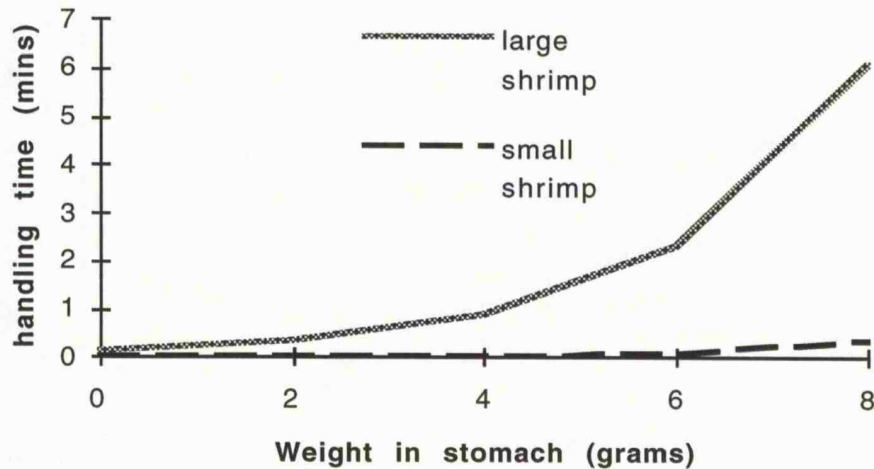
Where:

Large prey: $\text{handle}(1) = 7.62$

Small prey: $\text{handle}(2) = 1$

An exponential curve was chosen as this was the function fitted by Werner (1974) to the handling times of Sunfish. The values for the prey sizes were estimated from Chapter 4.

Figure 5.9: The change in handling time with increasing weight of stomach contents in the small fish model.



The small fish model was also run with two other reduced levels of stomach size. The maximum stomach capacity was reduced to 6 and then 5 grams with all of the other parameters the same.

The large fish model

The parameters used in the large fish model were the same as in the small fish model except for: capacity, volmax, probability of success and the handling time. The energy level capacity was increased to 40 Calories and the maximum weight the stomach could hold was set at 19 grams. The probability that the fish would successfully eat a prey was the same except for the success factor $s(i)$ for each size of shrimp.

$$\text{success}(i) = [s(i) * \text{weight in stomach}] + 0.8$$

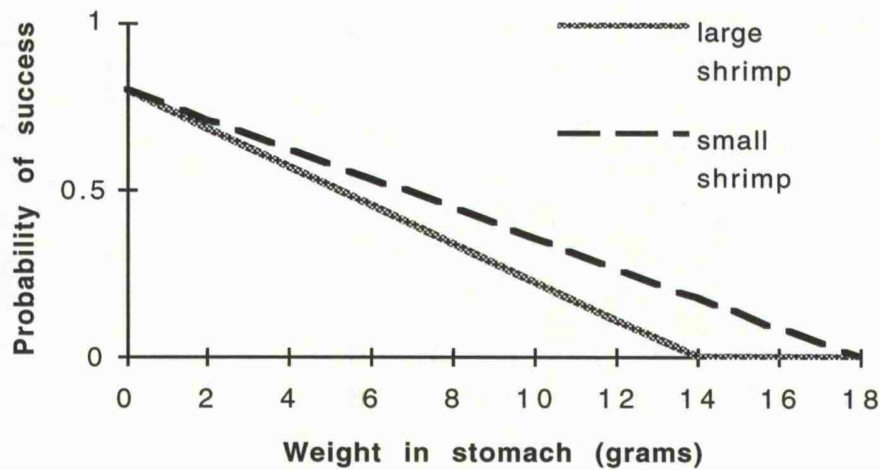
Where:

Large shrimp: $s(1) = -0.57$

Small shrimp: $s(2) = -0.044$

These values were estimated from the probability of success calculated in Chapter 4 (Fig 4.17).

Figure 5.10: The change in probability of success with increasing weight of stomach contents in the large fish model.



The equation used to calculate the handling time was also slightly different in this model compared to the small fish model. The exponential constant multiplying the volume was changed. This change meant that the handling times allowed for the greater stomach capacity of the large fish. The constants for the two sizes of shrimp stayed the same.

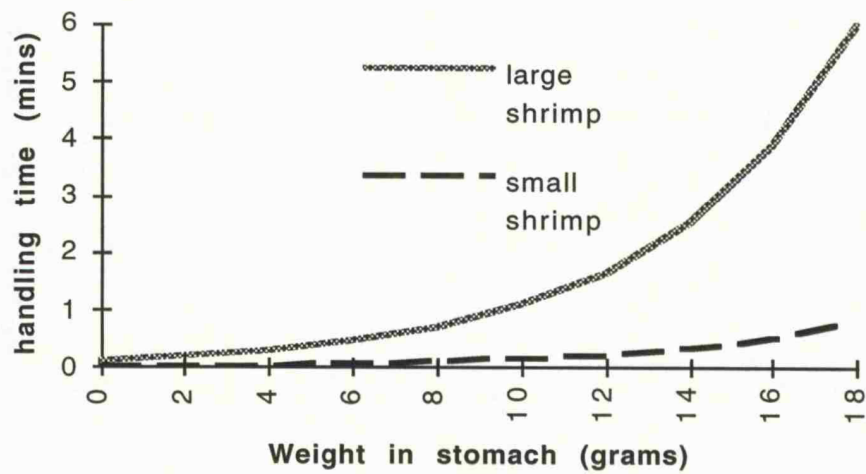
$$\tau(i) = \frac{\text{handle}(i) \times 10^{(0.093 \times \text{weight in stomach})}}{60}$$

Where:

Large prey = handle(1) = 7.62

small prey = handle(2) = 1

Figure 5.11: The change in handling time with increasing stomach contents in the large fish model.



Testing the effects of the handling and success functions

The main difference between the models described in this thesis and previous foraging models such as those discussed in Hart and Gill (1993), Burrows (1994) and Bednekoff and Houston (1994) is the dynamic nature of the functions describing the probability of success and the handling time. In order to test the effects of these two functions on the predictions of the models the equations used to describe them were changed. Varying the equations used tested the sensitivity of the model to these functions and gives an indication of the model's robustness.

Probability of Success

Examining the observed changes in the probability of success over stomach fullness (Figures 4.16 and 4.17, Chapter 4) there is no one pattern that describes all of the situations. Three different equations were used to describe the probability of success. The first equation was the linear function used in the small fish model (p142) in which, the slope was different for the two sizes of shrimp, but the intercept was the same. In the second equation the slope was the same but the intercept was different between the two sizes of shrimp. The model with this second equation was labelled the larger difference model because the difference between the two sizes of prey was much bigger in the near empty stomach states. The third equation removed the dynamic nature of the probability of success so that it remained constant over all of the stomach states. This model was labelled the fixed difference model. The actual equations used in each model are described below.

The larger difference model

The equation giving the probability of successful capture (p142) was changed so that the difference between the two prey types was larger for the lower stomach states. This larger difference function was used as it fitted the data the for the small whiting (Figure 4.16) better than the original function in the small fish model. Using this equation the difference in the probability of success between the two prey sizes is

constant, but their probabilities both decrease with increasing stomach fullness. In this linear equation the success factor ($s(i)$) was used as the intercept constant as opposed to the slope constant in the previous 'small fish model'.

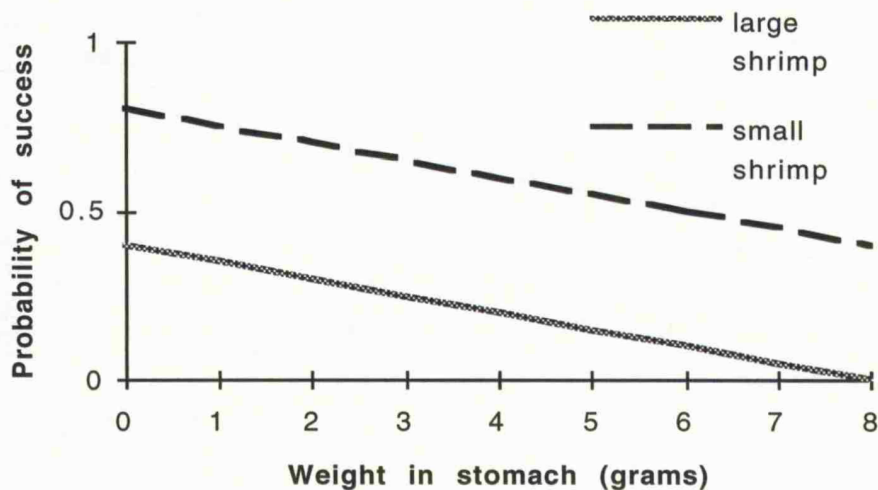
$$\text{success}(i) = [-0.05 * \text{weight in stomach}] + s(i)$$

Where:

Large shrimp: $s(1) = 0.4$

Small shrimp: $s(2) = 0.8$

Figure 5.12: The change in probability of success with increasing weight of stomach contents in the larger difference model.



The fixed difference model

In this alternative the probability of success was fixed so that it did not change with stomach fullness. The probability of success was fixed so that the effect of this could be compared with the dynamic models (e.g. the small fish model and the larger difference model). There was still a difference in success between the two prey sizes.

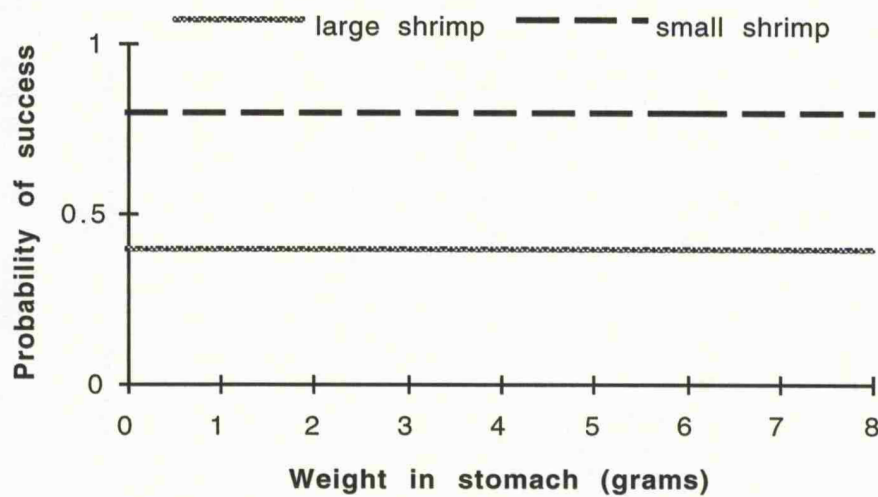
$$\text{success}(i) = s(i)$$

Where:

Large shrimp: $s(1) = 0.4$

Small shrimp: $s(2) = 0.8$

Figure 5.13: The change in probability of success with increasing weight of stomach contents in the fixed difference model.



Handling Time

The equation used to describe the time spent in handling (p143) was tested in the same way as the equation for the probability of successful capture. The parameters from the 'small fish model', and the original linear probability of success equation were used. The first equation used to describe the change in handling time with stomach fullness was the exponential equation used in the small fish model (Figure 5.9). This exponential equation caused there to be very little difference between the handling times of the two different shrimp sizes in the lower states of stomach fullness. Therefore a second linear equation was used that gave a larger difference at these times. This second linear equation was labelled the 'linear handling model'. The final equation described non-dynamic handling. The two shrimp sizes had a different but constant handling time over all the states of stomach fullness. This was labelled the fixed handling model. The first model was described previously as the small fish model and the two modifications to it are described below.

The linear handling model

In this model the handling time was related to stomach fullness using a linear equation. The time taken to handle a prey item increased with an increase in the weight of food in the stomach.

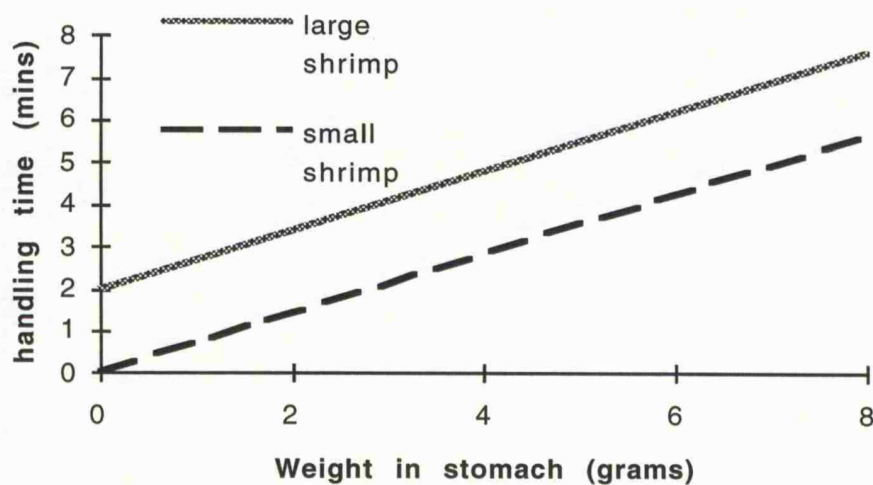
$$\tau(i) = (\text{weight in stomach} \times 0.7) + \text{handle}(i)$$

Where:

Large prey: $\text{handle}(1) = 2$

small prey: $\text{handle}(2) = 0$

Figure 5.14: The change in handling time with increasing weight of stomach contents in the linear handling model.



The fixed handling model

The handling equation was then fixed so that it was not affected by changing the stomach contents. The difference between the two prey sizes was maintained.

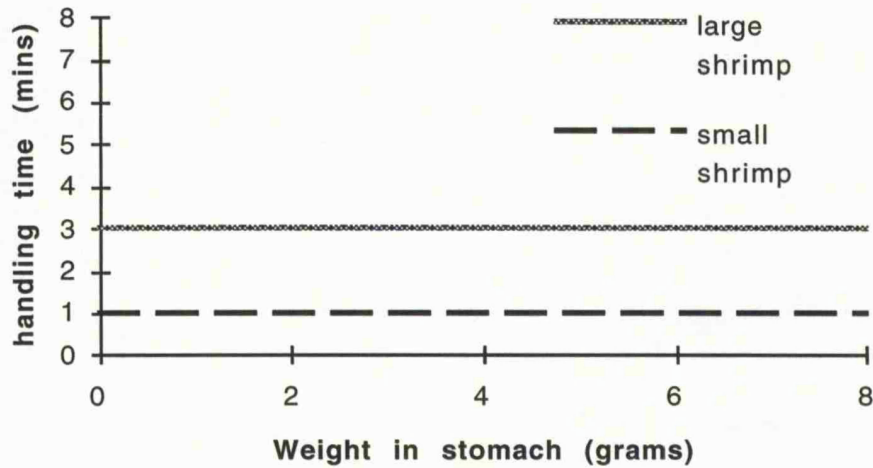
$$\tau(i) = \text{handle}(i)$$

Where:

Large prey: $\text{handle}(1) = 3$

small prey: $\text{handle}(2) = 1$

Figure 5.15: The change in handling time with increasing weight of stomach contents in the fixed handling model.



Testing the Robustness of the Model

The sensitivity of the model to changes in the other important parameter values; horizon and encounter probability (λ_i), was tested by altering the magnitude of these values. The small fish model was run in its original state and the value for the horizon was decreased to 5 and then increased to 20. The probability of encountering a prey was reduced to 0.5 for both prey sizes together and then each one separately. The effects of altering these parameters on prey choice and final energy levels were investigated.

Analysis

To compare the models their pattern of optimal choices (the strategy set) over the range of states were studied. The choices in the first time period were used as at this point the pattern had stabilised so that the optimal strategy was time independent being a function of state only. This is usually the case with SDP modelling (Mangel and Clark 1988). To aid the comparison between different alternatives of the model a sequence of choices, and their probabilities, was calculated using the forward iteration program.

In each time period the probabilities of the fish making each choice; rejection, handling, eating prey 1 and eating prey 2 were calculated. The probability of rejection also included fish that attempted to eat a prey item but were unsuccessful. These unsuccessful attempts were grouped with rejection for clarity as they had the same effect on the fishes state. These probabilities were displayed in a bar chart called a probability sequence of choices. The probability that a fish would eat each type of prey was also summed over all of the time periods. This sum of probabilities gave a predicted number of that size of shrimp eaten in the feeding bout. The predicted numbers were usually decimal values that could be rounded to the nearest integer. However the values were displayed in their original form so that they could be compared. Examples of these three calculations derived from forward iteration are given in the results section of the small fish model.

The probability that a fish would have each combination of the two state variables was also calculated from the forward iteration program, in each time period. The time periods when the fish were making the important decisions, e.g. eating one of the two prey items, were displayed in a 3-dimensional bar chart. This allowed the probability of the choices being made in the time period to be related to the fishes' internal state. The state probabilities were also calculated and shown for the final period T.

The effect of the optimal choices made, and their probabilities of occurring, on the net energy gain of the fish throughout the feeding bout was calculated. This effect on energy was quantified by multiplying the energy state by its probability of occurring. These probabilities were summed and an example of this calculation is detailed in the small fish model results

section. In order to calculate growth the end time energy was placed in the fitness function equation 5.1.

The models tested are summarised in Table 5.3. This table shows how the subsequent models used differ from the standard small fish model.

Table 5.3: Summary of the models tested and their differences

Label	Differences from small fish model
small fish model	standard model
small fish model (reduced gut capacity)	volmax = 6 and volmax = 5
large fish model	capacity = increased volmax = increased $s(1) = -0.57$ $s(2) = -0.044$ $\tau(i) = \frac{\text{handle}(i) \times 10^{(0.093 \times \text{weight in stomach})}}{60}$
larger difference model	success (i) = [-0.05 * weight in stomach] + s(i) $s(1) = 0.4$ $s(2) = 0.8$
fixed difference model	success (i) = s(i) $s(1) = 0.4$ $s(2) = 0.8$
linear handling model	$\tau(i) = (\text{weight in stomach} \times 0.7) + \text{handle}(i)$ handle(1) = 2 handle(2) = 0
fixed handling model	$\tau(i) = \text{handle}(i)$ handle(1) = 3 handle(2) = 1

The results of the investigations into the whiting foraging model described in this thesis are set out in four sections. In the first section the model is set-up to reflect the foraging dynamics of the two different sizes of fish used in the feeding trials (Chapter 4). The difference between the small fish model, which was used as the standard model, and the large fish model is summarised in Table 5.3. In Chapters 3 and 4 it was found that satiation level was a highly variable between similar sized fish (Figure 3.2, Tables 4.1 and 4.22). To investigate the effect of gut capacity on prey choice the small

fish model was also run with two lower values for volmax of six and five grams.

The second section investigates the influence of the shape of the probability of success function on the prey choice of the fish. The linear function, with differing slopes for the two sizes of shrimp, used in the small fish model (Figure 5.8) is compared to a larger difference model (Figure 5.12) and a fixed difference model (Figure 5.13).

The third section is concerned with the function describing the handling time of the two sizes of shrimp with gut fullness. The influence of this function on the prey choices of the fish is explored by comparing the exponential equation used in the small fish model (Figure 5.9) with a linear handling model (Figure 5.14) and a fixed handling model (Figure 5.15)

The last section describes the sensitivity of the model to changes in the encounter rates for the two sizes of prey, and the duration of the feeding bout. The encounter rates for the two sizes of shrimp were changed in the standard small fish model and their effect on the prey choices examined. The length of the feeding bout that the standard small fish model was run over was altered from a horizon of ten minutes to five and then 20 minutes.

RESULTS

Investigating the Influence of Fish Size

Small fish model

The optimal choices when $t=1$ are shown in Table 5.4. If it is optimal to reject a prey size when it is encountered the table shows a value of zero. If eating the prey size is optimal over rejecting it the table shows a 1 or a 2. A prey size with a value of two is also the optimal choice if both of the prey items are encountered together.

Table 5.4: The optimal choices made for each combination of state variable in the small fish model with a stomach capacity of 8 grams at $t=1$.

2 = optimal choice if both shrimp are encountered
or if the prey is the only one encountered

1 = optimal choice if the prey is the only one encountered

0 = reject if encountered

		Weight of stomach contents (grams)															
		1		1.5		2		2.5		3		3.5		4		4.5	
		L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S
energy reserves of fish (Calories)	2	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	4	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	6	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	8	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	10	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	12	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	14	1	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	16	2	0	2	0	2	0	2	0	2	0	0	2	0	2	0	2
	18	1	2	1	2	1	2	1	2	1	2	0	2	0	2	0	2
	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

		Weight of stomach contents (grams)															
		5		5.5		6		6.5		7		7.5		8			
		L	S	L	S	L	S	L	S	L	S	L	S	L	S		
energy reserves of fish (Calories)	2	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	4	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	6	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	8	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	10	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	12	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	14	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	16	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	18	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0		

The model predicted that the small fish should take a small shrimp when the stomach contents were equal to or less than 1.5 grams (Table 5.4). When the stomach contents were 2.5 and 3 grams the optimal choice switched to the large prey in the majority of energy states. In the stomach states 3.5 to 8 grams the large shrimps were rejected. Both sizes of shrimp should be rejected when the weight of the stomach contents is above 6.5 grams. The shaded cells show states where the optimal choices vary with energy state compared to the optimal choice in the rest of that stomach state e.g. with a stomach state of 2 grams the optimal choice is to eat a large shrimp except when the energy state is 18 C it becomes optimal to eat a small shrimp. No prey are taken in any of the stomach states when the energy level is at the capacity of 20 Calories.

The optimal choices shown in Figure 5.4 and the choices calculated for the other time periods were used in the forward iteration program to produce the probability sequence (Table 5.5, Figure 5.16).

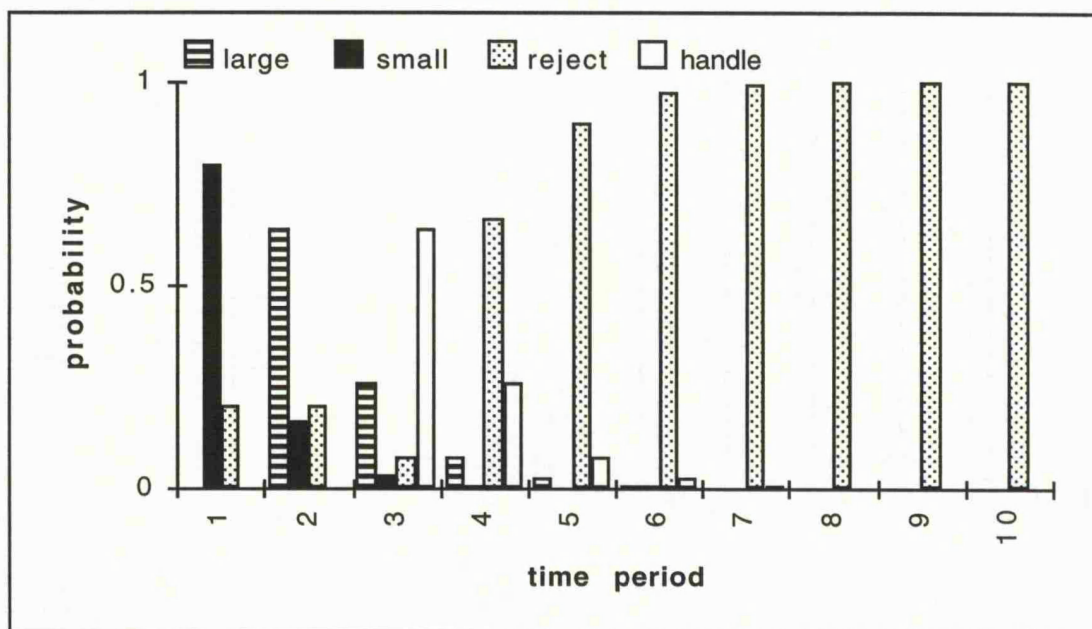
Table 5.5: The values for the probability sequence of choices predicted by the small fish model with a stomach capacity of 8 grams (zero values are not shown). The totals for each column are the predicted number that the behaviour will occur in the duration of the feeding bout.

		Behaviour			
		eat large	eat small	reject	handle
Time period	1		0.800000	0.200000	
	2	0.640000	0.160000	0.200000	
	3	0.256000	0.032000	0.072000	0.640000
	4	0.076800	0.006400	0.660800	0.256000
	5	0.021760		0.901440	0.076800
	6	0.004352	0.001024	0.974144	0.020480
	7	0.000870	0.000410	0.994624	0.004096
	8	0.000174	0.000123	0.990000	0.009703
	9	0.000035	0.000033	0.999768	0.000164
	10			0.999967	0.000033
Total		0.999991	0.999989	6.992744	1.007276

The probability sequence was calculated by summing the probabilities for each of the choices in each of the time periods. In the first time period $t=1$ the fish had a probability of 1 of encountering a small and a large shrimp and as they had a state of $vol=1$ and $x=2$ then the optimal choice was to eat a small shrimp (Table 5.4). The probability that they would successfully eat the small shrimp in this state was 0.8 (Figure 5.8) and so the probability

sequence (Figure 5.16) shows a probability of 0.8 (1×0.8) for eating a small shrimp and a probability of 0.2 (1×0.2) for rejection. An unsuccessful attempt at eating a shrimp is classed as rejection as the resulting stomach and energy state is the same. Looking at the probability sequence in Figure 5.16 the fish were most likely to take a small shrimp in the first time period and then a large shrimp in the second. The rest of the time periods were then spent in either handling the large shrimp or both of the prey sizes were rejected.

Figure 5.16: The probability sequence of choices predicted by the small fish model with a stomach capacity of 8 grams



All of the fish were empty when they consumed the small shrimp. At $t=2$ when the majority of the fish had stomach contents of 3 grams (Figure 5.17) the large shrimps were most likely to be taken. As the probability of successfully eating this size of shrimp was less, the probability transfer to the higher state took more time periods. At the higher state of stomach volume (Figure 5.17) the large weight in the stomach meant that both of the shrimp sizes were rejected. The predicted number of each size being eaten are shown in Table 5.6. This predicted number eaten was calculated by summing the probability that a shrimp size would be eaten in a time period over all of the time periods (Table 5.5)

Figure 5.17: The probability that the fish will have the values of the state variables shown as the feeding bout proceeds. The results of forward iteration using the optimal policy derived from the small fish model.

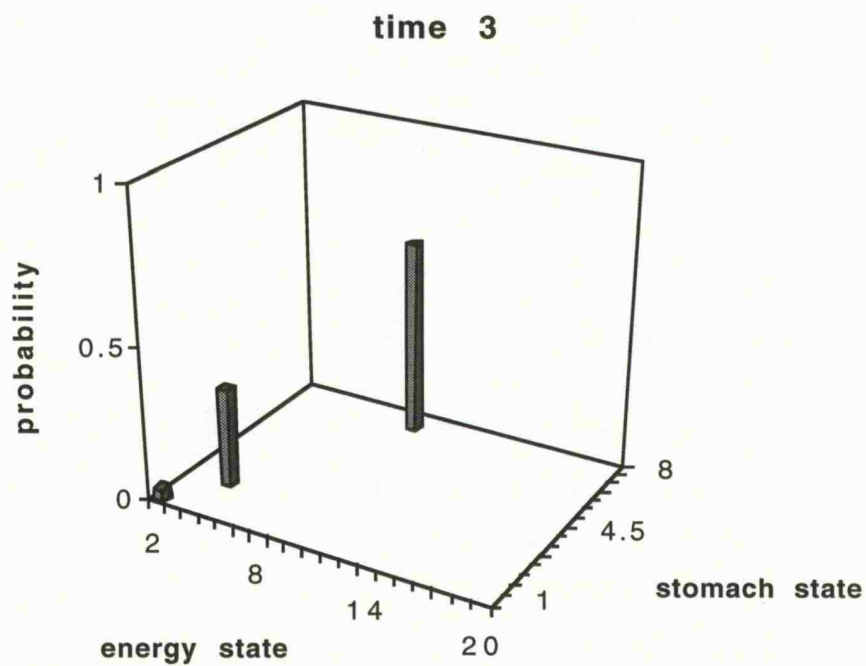
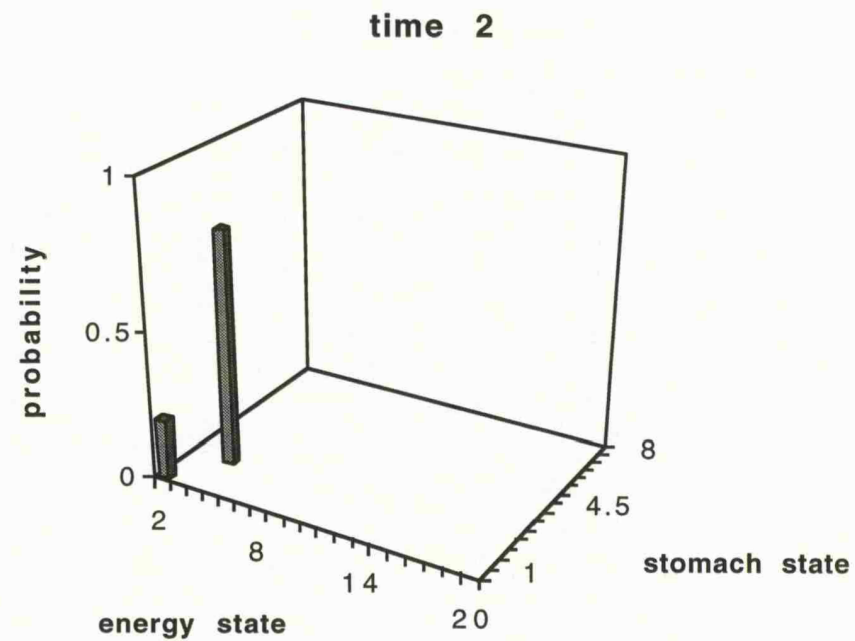


Figure 5.18: The probability that the fish will have the values of the state variables shown as the feeding bout ends. The results of forward iteration using the optimal policy derived from the small fish model. The values of the probabilities greater than zero are given.

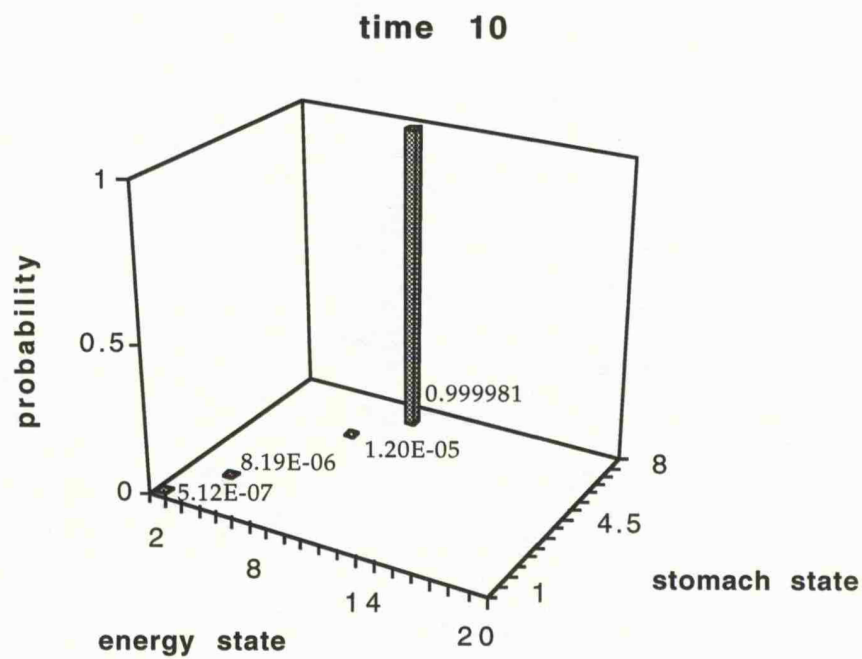


Table 5.6 The predicted number of each shrimp size eaten in the small fish model with a stomach capacity of 8 grams

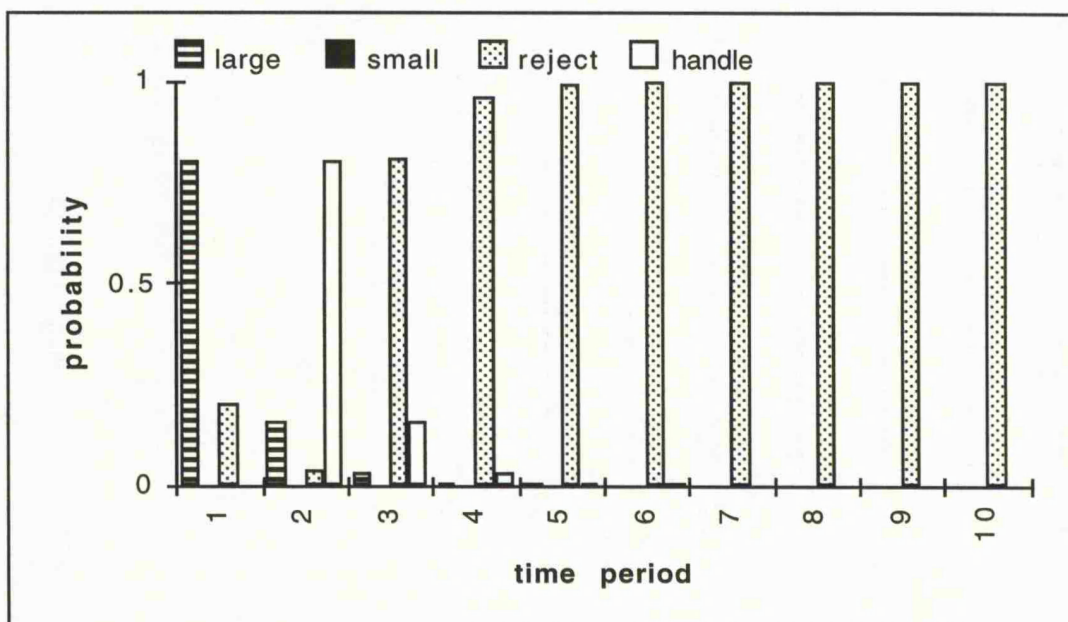
	Large shrimp	Small shrimp
predicted number eaten	0.999991	0.999989

In the final time period at $t=10$ (Figure 5.18) the fish were most likely to have $vol=7.5$ and $x=9$. The energy value was $=8.999935C$ which would translate to a growth in weight of 2.905 grams per day. This energy value was calculated by summing the probability that the fish would be in each energy state at $t=10$ by the energy level of that state, e.g. from Figure 5.18 $(5.12E-07 \times 2) + (8.19E-06 \times 4) + (1.02E-05 \times 7) + (0.999981 \times 8)$.

The small fish model with reduced stomach size

When the maximum stomach state was reduced to 6 grams and all the other variables were kept the same the optimal choices changed.

Figure 5.19: The probability sequence of choices predicted by the small fish model with a stomach capacity of 6 grams



The small fish with a stomach capacity of 6g were most likely to simply take one large shrimp in the first time period and then reject both of the prey sizes until the horizon was reached (Figure 5.19). The predicted

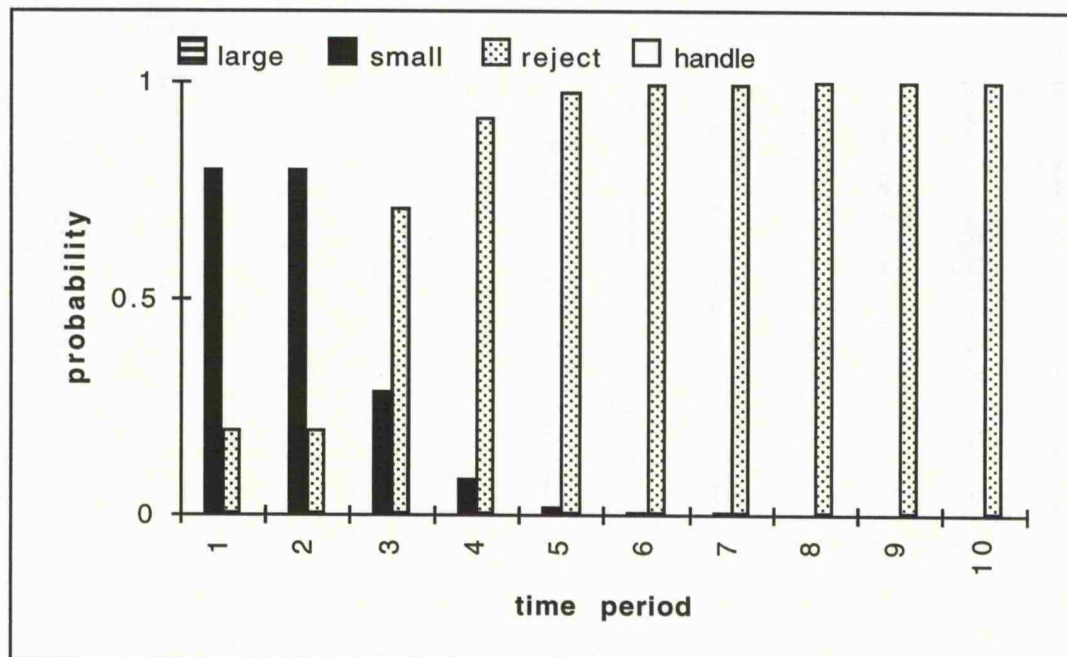
number of shrimps eaten shows that the small shrimp were not included in the diet (Table 5.7).

Table 5.7: The predicted number of each shrimp size eaten in the small fish model with a stomach capacity of 6 grams

	Large shrimp	Small shrimp
predicted number eaten	0.99999	0

When the maximum stomach state was reduced even further to 5 grams the pattern of choices changed again. The highest probability was for the small fish to eat two small shrimps in the first two time periods and then reject all other prey (Figure 5.20).

Figure 5.20: The probability sequence of choices predicted by the small fish model with a stomach capacity of 5 grams



The predicted numbers show that the large prey were rejected throughout the feeding bout and that two small shrimps were taken (Table 5.8).

Table 5.8: The predicted number of each shrimp size eaten in the small fish model with a stomach capacity of 5 grams

	Large shrimp	Small shrimp
predicted number eaten	0	1.99998

The large fish model

The large fish model predicted that for fish with a stomach state of 12g or below, and an energy state of 24C or below, the optimal choice would be to eat the large shrimp (Table 5.9). In these states if only a small shrimp was encountered then eating it would be optimal over rejection. However because the probability of encountering both shrimp sizes is 1 this single encounter will not occur. In stomach states from 12 to 16g the optimal choice became the small shrimp in all but the very highest states of energy i.e. 40C. At stomach states above 16g and at an energy state of 40C both shrimp sizes should be rejected. In the shaded cells the optimal choice varies in each stomach state as the energy level increases.

Table 5.9: The optimal choices made in each combination of state variables in the large fish model at t=1.

- 2 = optimal choice if both shrimp are encountered
or if the prey is the only one encountered
1 = optimal choice if the prey is the only one encountered
0 = reject if encountered

		Weight of stomach contents (grams)																	
		2		4		6		8		10		12		14		16		18	
		L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S
energy reserves of fish (Calories)	2	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	4	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	6	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	8	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	10	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	12	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	14	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	16	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	18	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	20	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	22	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	24	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	26	1	2	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	28	2	1	2	1	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	30	2	0	2	0	2	1	2	1	2	1	2	1	1	2	0	2	0	0
	32	2	1	2	1	1	2	2	1	2	1	2	1	1	2	0	2	0	0
	34	1	2	2	1	2	1	2	1	2	0	2	1	1	2	0	2	0	0
	36	2	0	2	0	2	0	2	0	2	0	2	1	1	2	0	2	0	0
	38	1	2	1	2	2	1	1	2	1	2	1	2	1	2	0	2	0	0
	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

The probability sequence in Figure 5.21 was derived using the forward iteration program which was run with the strategy set shown in Table 5.9 and the sets from the other nine time periods. The predicted number of shrimps eaten (Table 5.10) show that if the large fish fed optimally they should have taken three large shrimps and approximately two small ones.

Table 5.10: The predicted number of each shrimp size eaten in the large fish model

	Large shrimp	Small shrimp
predicted number eaten	2.999667	1.818624

Figure 5.21 shows that the large shrimp were taken first as these had the largest probability of being eaten in the first three time periods. In these periods the fish were in stomach states with a low weight of contents (Figure 5.22). In the fourth and fifth time periods the fish were mainly handling, though if they had failed to successfully take a shrimp in any of the previous periods they took a large shrimp. In time periods six to nine the fish ate the two small shrimps when their weight of stomach contents was high. The predicted number of small shrimps eaten is 1.82 which shows there is a probability ($2 - 1.82 = 0.18$) that the fish will not be able to eat the optimal quantity of shrimps within the time of the feeding bout.

Figure 5.21: The probability sequence of choices predicted by the large fish model

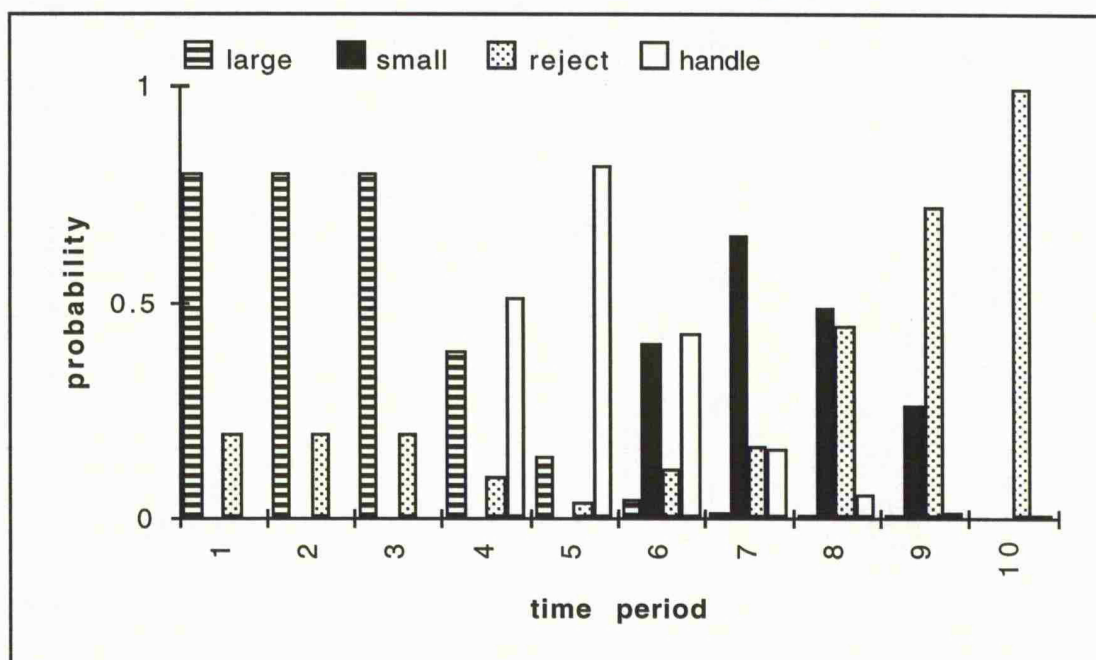


Figure 5.22: The probability that the fish will have the values of the state variables shown as the feeding bout proceeds. The results of forward iteration using the optimal policy derived from the large fish model

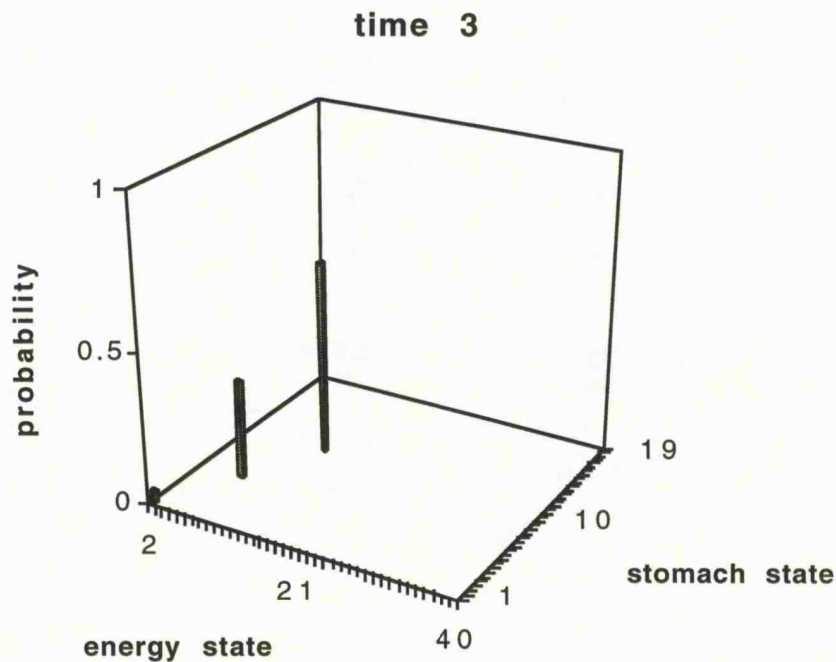
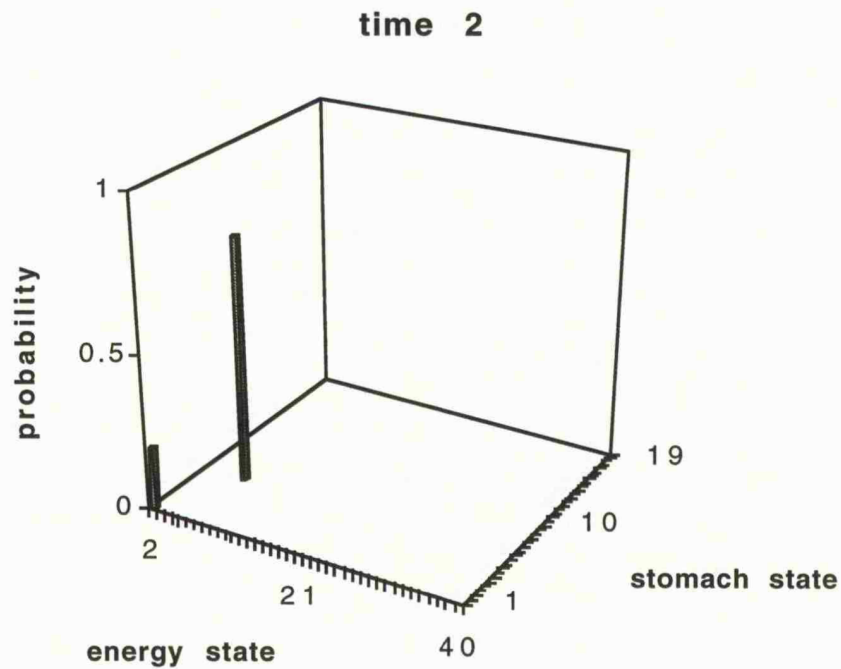
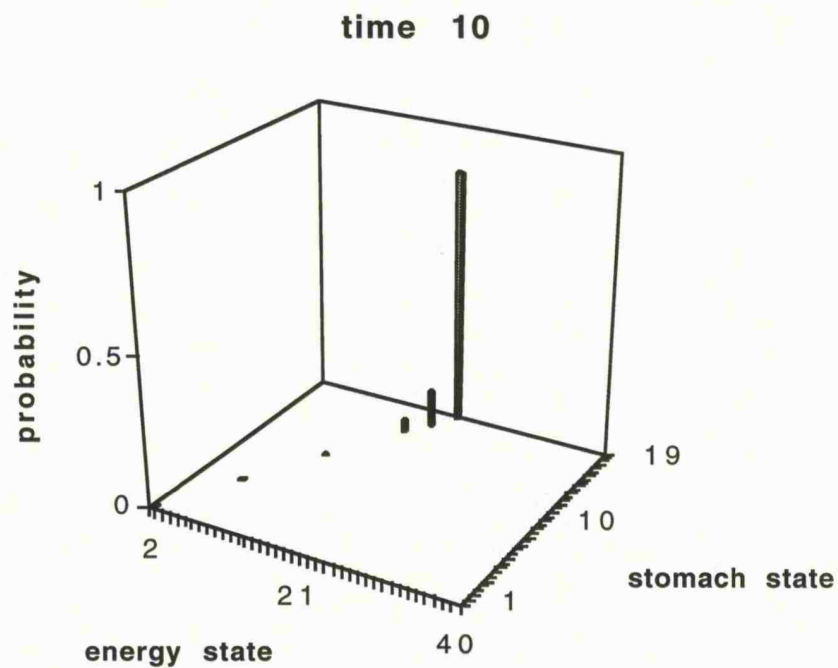
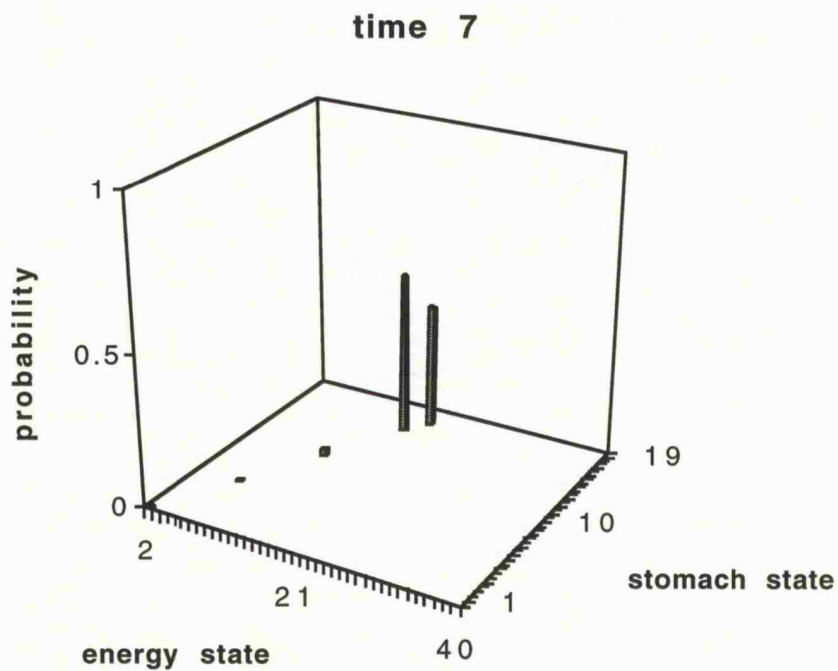


Figure 5.23: The probability that the fish will have the values of the state variables shown as the feeding bout proceeds. The results of forward iteration using the optimal policy derived from the large fish model



In the final time period (Figure 5.23) the largest probability was for the state to be at vol=19 and x=21. The energy value was =20.61999C which would translate to a growth in weight of 7.4231964 grams per day.

Investigating the Influence of the Probability of Success Function

The larger difference model

In this model the probability of success function produced a larger difference between the two sizes of shrimp at the lower levels of stomach fullness than in the standard small fish model (Figure 5.12).

Table 5.11: The optimal choices made for each combination of state variables in the larger difference model at t=1.

2 = optimal choice if both shrimp encountered
or if the prey is the only one encountered

1 = optimal choice if the prey is the only one encountered

0 = reject if encountered

		Weight of stomach contents (grams)															
		1		1.5		2		2.5		3		3.5		4		4.5	
		L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S
energy reserves of fish (Calories)	2	2	0	2	0	0	2	2	0	2	0	0	2	0	2	0	2
	4	2	0	2	0	0	2	2	0	2	0	0	2	0	2	0	2
	6	2	0	2	0	0	2	2	0	2	0	0	2	0	2	0	2
	8	2	0	2	0	0	2	2	0	2	0	0	2	0	2	0	2
	10	2	0	2	0	0	2	2	0	2	0	0	2	0	2	0	2
	12	2	0	2	0	0	2	2	0	2	0	0	2	0	2	0	2
	14	2	0	2	0	0	2	2	0	2	0	0	2	0	2	0	2
	16	1	2	1	2	1	2	2	1	2	1	0	2	0	2	0	2
	18	1	2	1	2	0	2	0	2	0	2	0	2	0	2	0	2
	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

		Weight of stomach contents (grams)															
		5		5.5		6		6.5		7		7.5		8			
		L	S	L	S	L	S	L	S	L	S	L	S	L	S		
energy reserves of fish (Calories)	2	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	4	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	6	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	8	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	10	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	12	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	14	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	16	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	18	0	2	0	2	0	2	0	2	0	0	0	0	0	0		
	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0		

The pattern of choices were different to those predicted using the exponential function in the small fish model (Table 5.11). In the empty fish (stomach states 1 to 1.5g) the large shrimp were the optimal prey in all but the highest states of energy ($\geq 16C$). With a stomach state of two grams the optimal choice switched to the smaller shrimp and then from 2.5 grams to 3 grams the optimal prey was the large shrimp again. At and above a stomach state of 3.5 grams the large prey could not be eaten and the small shrimps became the optimal choice, until at 7 grams they too were excluded from the diet. As with the other tables of optimal choices (Tables 5.4 and 5.9) the shaded cells show the states of energy where the optimal choice is different from the rest of in the stomach state. At the highest level of energy (i.e. 20C) both of the shrimp sizes were rejected.

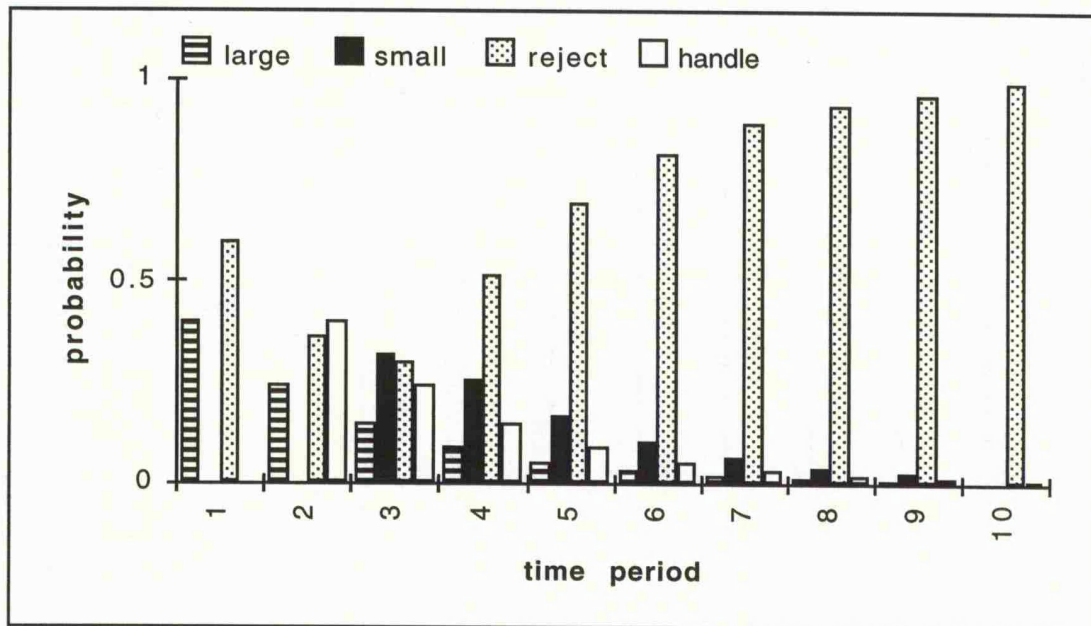
The larger difference model predicted that the optimal diet should consist of one large shrimp and one small shrimp which was the same as in the standard small fish model (Table 5.12).

Table 5.12 The predicted number of each shrimp size eaten in the larger difference model

	Large shrimp	Small shrimp
predicted number eaten	0.989922	0.96641

The probability sequence shows that the fish ate the large shrimp first, and then took the smaller shrimp once they had finished handling the large one (Figure 5.24). Once the two shrimps had been successfully handled the fish rejected both of the shrimp sizes. The fish took longer to accrue energy than the previous small fish model, as the probability of success was lower (Figures 5.25 to 5.26). With this lower probability a larger proportion of the fish failed to eat a shrimp first time and had to try for another in the next period.

Figure 5.24: The probability sequence of choices predicted by the larger difference model



In the final time period $t=10$ (Figure 5.25) the largest probability was for the fish to be in the state $vol=7.5$ and $x=9$. The energy value was $=8.882433$ which would translate to a growth in weight of 2.86287588 grams per day.

Figure 5.25: The probability that the fish will have the values of the state variables shown as the feeding bout proceeds. The results of forward iteration using the optimal policy derived from the larger difference model

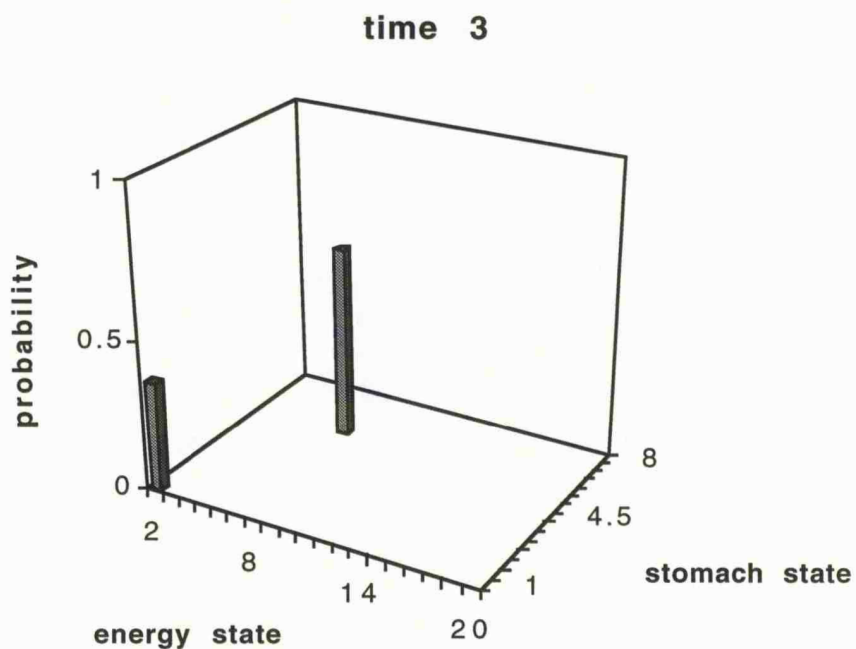
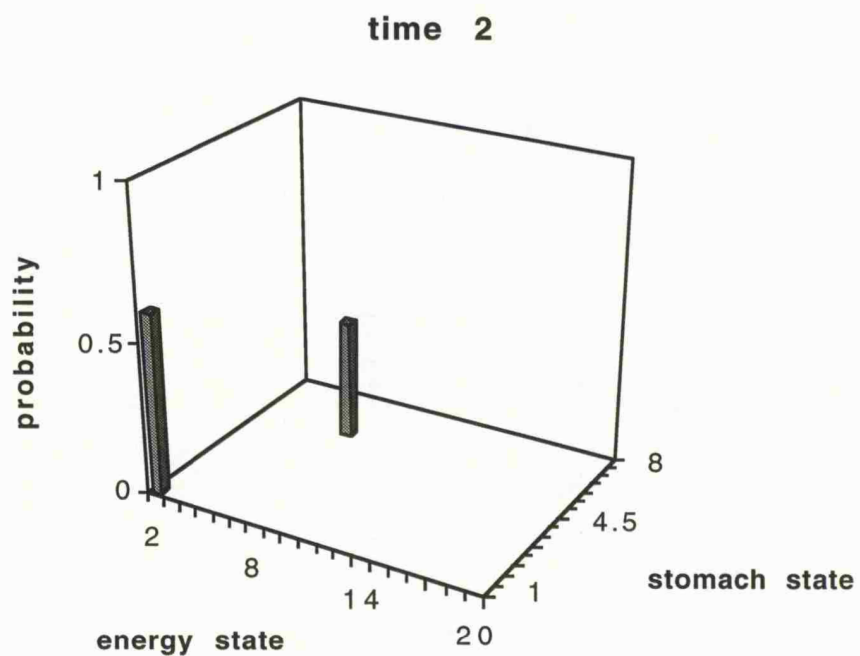
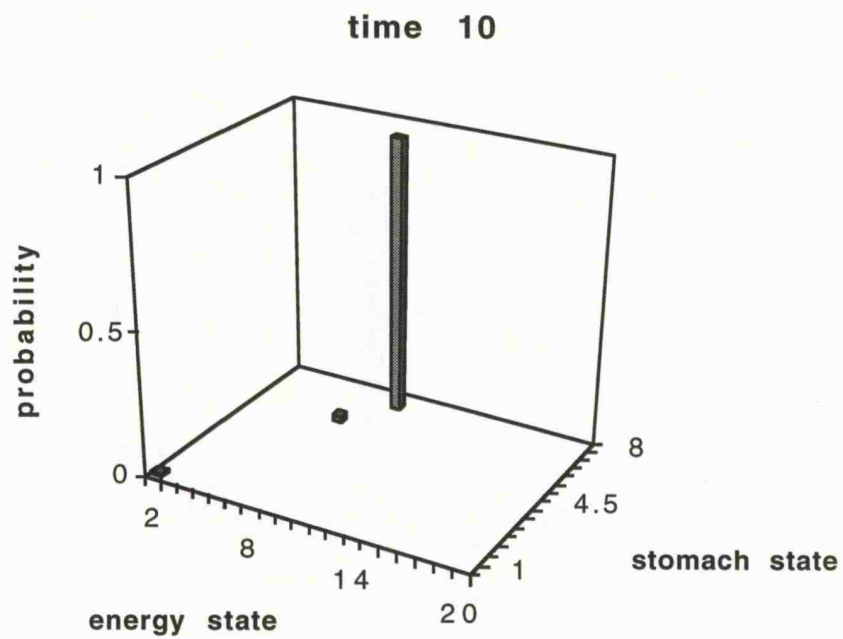


Figure 5.26: The probability that the fish will have the values of the state variables shown as the feeding bout ends. The results of forward iteration using the optimal policy derived from the larger difference model



The fixed difference model

When the probability of success was uncoupled from the state of the stomach the model predicted that an empty fish (vol = 1g) should take a small shrimp (Table 5.13). Fish with a stomach state of 1.5 or 2.5 to 3 grams should take a large shrimp but fish with a stomach state of 2 grams should take a small shrimp. The higher values of stomach state were limited to taking a small shrimp until again these are limited by the maximum stomach capacity (vol>=7g). The energy levels only affected the choice when the fish neared its maximum capacity in the shaded cells and when the fish should reject both sizes of shrimp at the energy capacity of 20 Calories.

Table 5.13: The optimal choices made for each combination of state variables in the fixed difference model t=1.

2 = optimal choice if both shrimp encountered

or if the prey is the only one encountered

1 = optimal choice if the prey is the only one encountered

0 = reject if encountered

		Weight of stomach contents (grams)															
		1		1.5		2		2.5		3		3.5		4		4.5	
		L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S
energy reserves of fish (Calories)	2	1	2	2	1	0	2	2	0	2	0	0	2	0	2	0	2
	4	1	2	2	1	0	2	2	0	2	0	0	2	0	2	0	2
	6	1	2	2	1	0	2	2	0	2	0	0	2	0	2	0	2
	8	1	2	2	1	0	2	2	0	2	0	0	2	0	2	0	2
	10	1	2	2	1	0	2	2	0	2	0	0	2	0	2	0	2
	12	1	2	2	1	0	2	2	0	2	0	0	2	0	2	0	2
	14	2	1	2	1	0	2	2	0	2	0	0	2	0	2	0	2
	16	1	2	1	2	0	2	2	0	2	0	0	2	0	2	0	2
	18	1	2	1	2	0	2	0	2	0	2	0	2	0	2	0	2
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

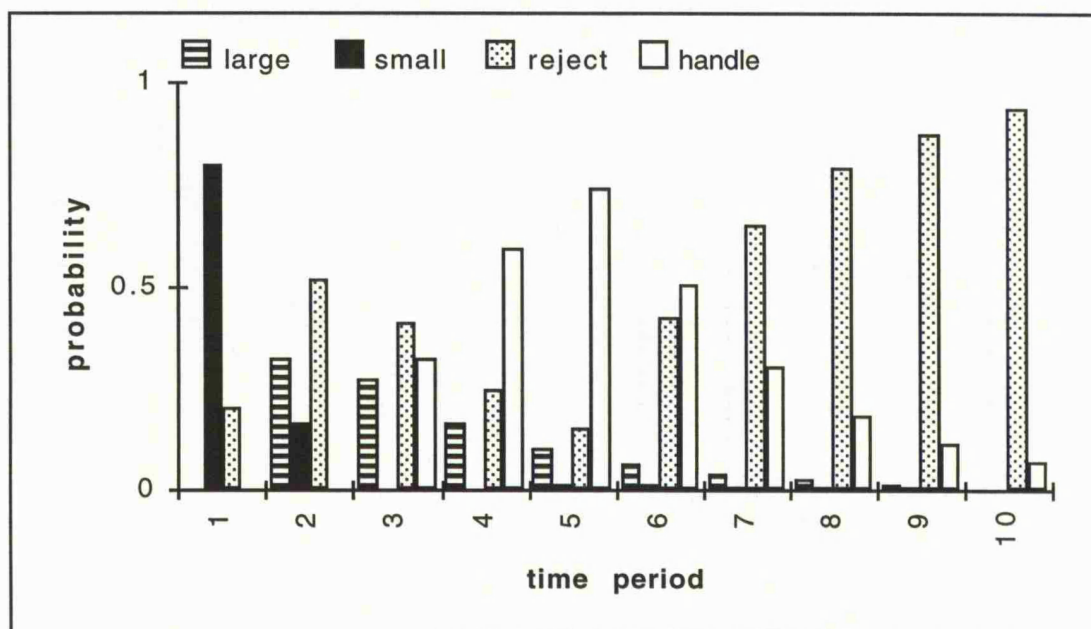
		Weight of stomach contents (grams)													
		5		5.5		6		6.5		7		7.5		8	
		L	S	L	S	L	S	L	S	L	S	L	S	L	S
energy reserves of fish (Calories)	2	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	4	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	6	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	8	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	10	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	12	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	14	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	16	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	18	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5.14: The predicted number of each shrimp size eaten in the fixed difference model

	Large shrimp	Small shrimp
predicted number eaten	0.980964	0.99627

The forward iteration program run with the optimal choices derived from the fixed difference model predicted that the fish should eat one shrimp of each size (Table 5.14). The probability sequence calculated from the same forward iteration program shows the small shrimp should be taken first and then the larger shrimp eaten (Figure 5.27). The larger prey had a fairly low probability of being taken (Figure 5.13) and so a proportion of the fish were still attempting to eat the larger prey even in the ninth time period. The effect of the low probability of success is shown in Figure 5.28, where the majority of the fish were still in the lower energy and stomach state ($\text{vol}=2.5$ $\times=4$) in time 3. In the middle time periods ($t = 4-6$) the majority of the fish were handling prey items.

Figure 5.27: The probability sequence of choices predicted by the fixed difference model



In the final time period $t=10$ (Figure 5.29) the largest probability was for the fish state to be $\text{vol}=7.5$ and $\times=9$. The energy value was $=8.610708C$ which would translate to a growth in weight of 2.7650548 grams per day.

Figure 5.28: The probability that the fish will have the values of the state variables shown as the feeding bout proceeds. The results of forward iteration using the optimal policy derived from the fixed difference model

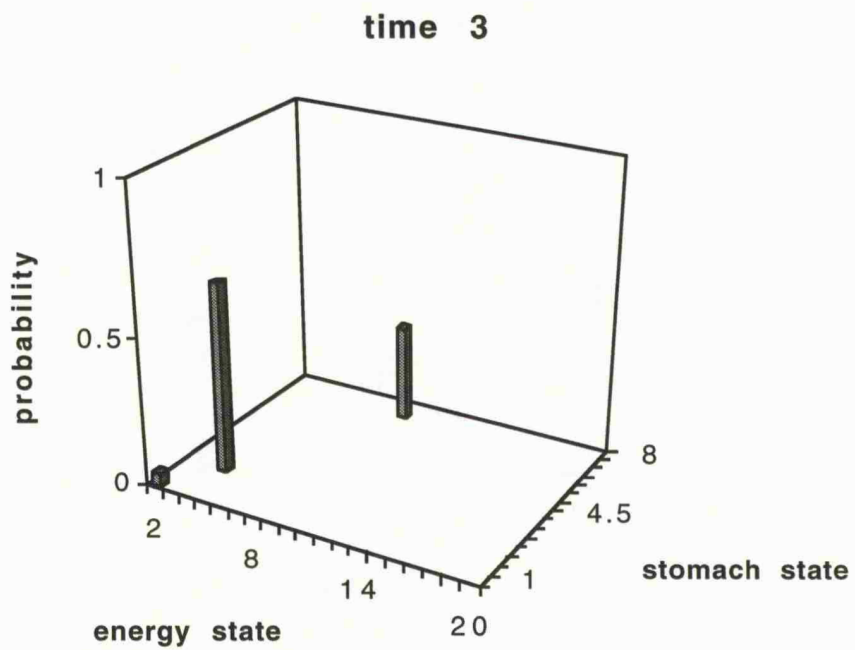
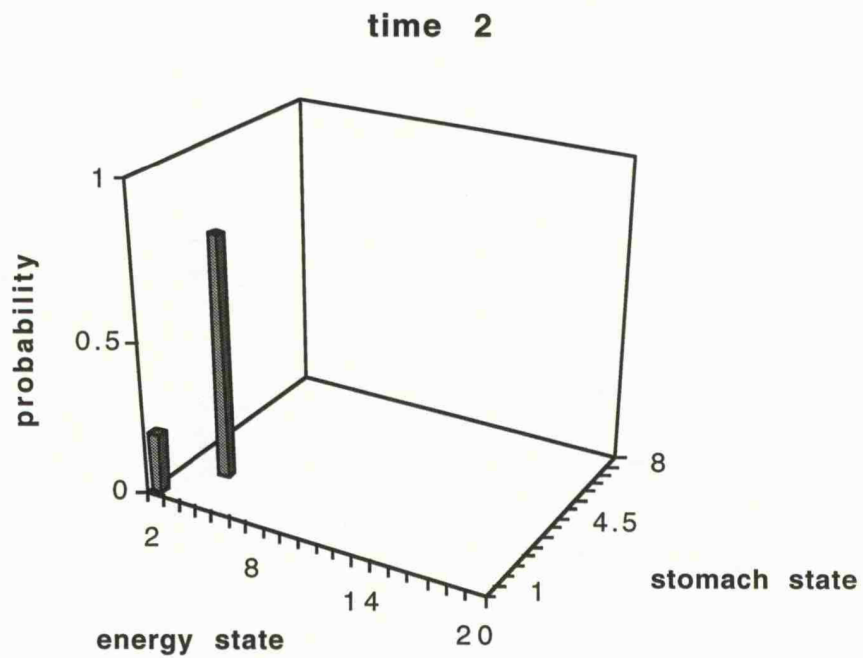
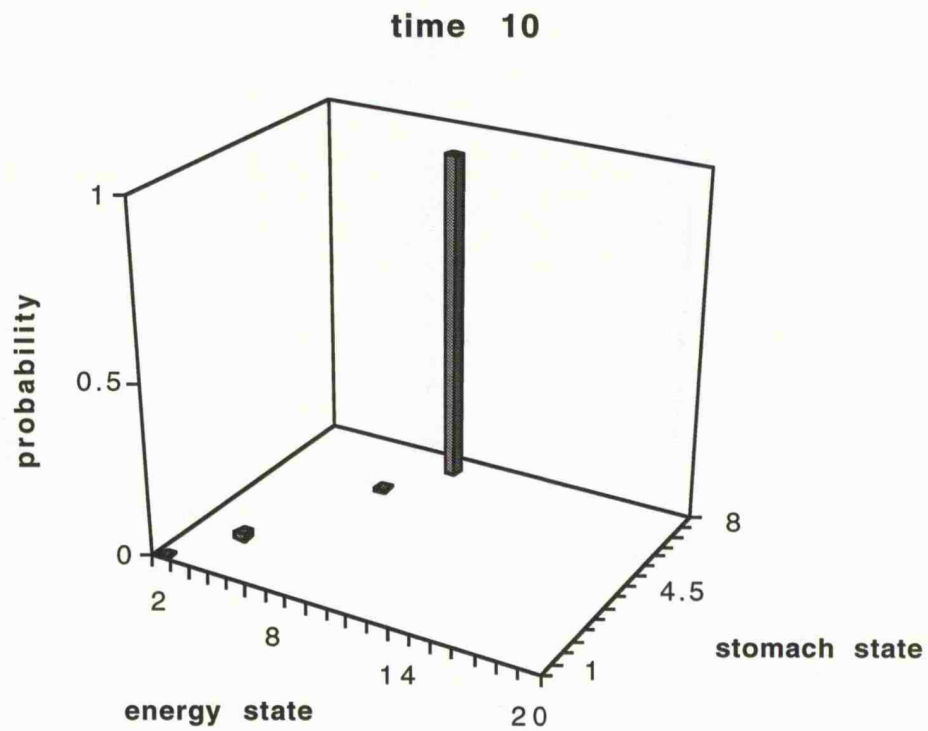


Figure 5.29: The probability that the fish will have the values of the state variables shown as the feeding bout ends. The results of forward iteration using the optimal policy derived from the fixed difference model.



Investigating the Influence of the Handling Time Function

The linear handling model

The pattern in the optimal choices over the range of stomach states showed that for the fish with empty stomachs (vol =1 to 1.5g) the optimal choice was to eat the smallest shrimp (Table 5.15). The optimal choice switched to taking the larger shrimps when the state was between 2 and 3g. Above this value the optimal choice was to take the small shrimp until the stomach volume became limiting (vol ≥ 7 g).

Table 5.15: The optimal choices made for each combination of state variables in the linear handling model at $t=1$.

2 = optimal choice if both shrimp encountered

or if the prey is the only one encountered

1 = optimal choice if the prey is the only one encountered

0 = reject if encountered

		Weight of stomach contents (grams)															
		1		1.5		2		2.5		3		3.5		4		4.5	
		L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S
energy reserves of fish (Calories)	2	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	4	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	6	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	8	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	10	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	12	0	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	14	1	2	1	2	2	0	2	0	2	0	0	2	0	2	0	2
	16	2	0	2	0	2	0	2	0	2	0	0	2	0	2	0	2
	18	0	2	1	2	1	2	1	2	1	2	0	2	0	2	0	2
	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

		Weight of stomach contents (grams)													
		5		5.5		6		6.5		7		7.5		8	
		L	S	L	S	L	S	L	S	L	S	L	S	L	S
energy reserves of fish (Calories)	2	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	4	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	6	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	8	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	10	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	12	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	14	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	16	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	18	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0

The state of the energy levels affected the choice in the shaded cells where the optimal choice changed. At the highest level of energy (20C) both of the shrimp sizes were rejected.

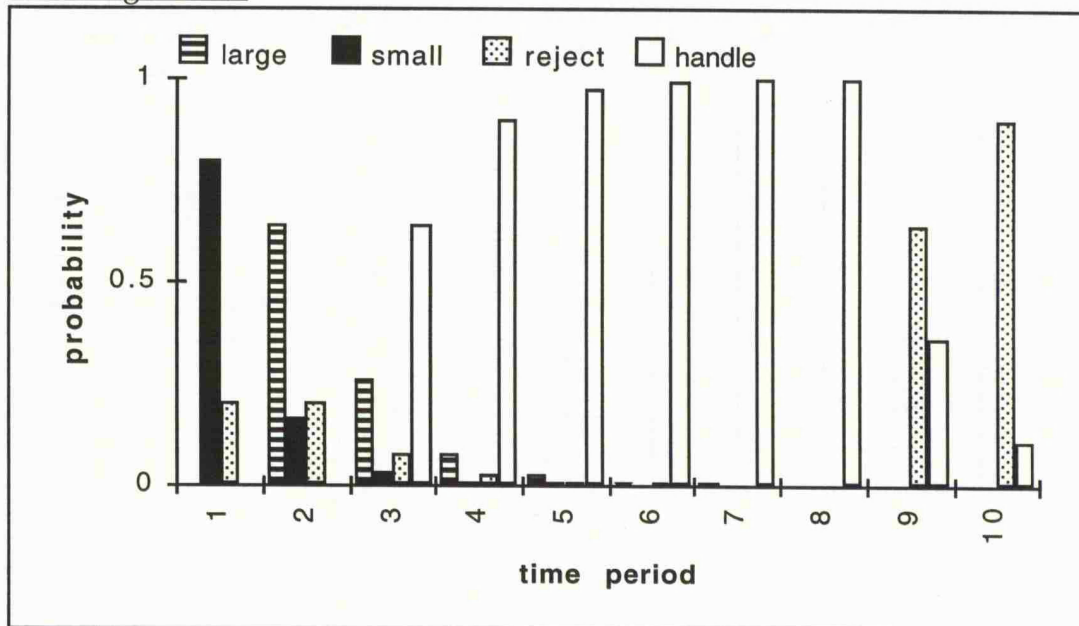
The predicted number of shrimps eaten derived from the forward iteration of the linear handling model showed a similar pattern as the other small fish models with one shrimp of each size being eaten (Table 5.16).

Table 5.16: The predicted number of each shrimp size eaten in the linear handling model

	Large shrimp	Small shrimp
predicted number eaten	0.999741	0.999928

The probability sequence derived from the linear handling model was dominated by the probability of handling the prey (Figure 5.30). This handling was the largest probability from the third to the eighth time period (Figure 5.31). The small shrimp were most likely to be eaten in the first time period and the large shrimp in the second period. The rest of the time periods were dominated by handling except in the last two time periods when the largest probability was rejection.

Figure 5.30: The probability sequence of choices predicted by the linear handling model



In the final time period $t=10$ (Figure 5.32) the fish were most likely to be in the state $vol=7.5$ and $x=9$. The energy value was $=8.758517C$ which would translate to a growth in weight of 2.81826612 grams per day.

Figure 5.31: The probability that the fish will have the values of the state variables shown as the feeding bout proceeds. The results of forward iteration using the optimal policy derived from the linear handling model

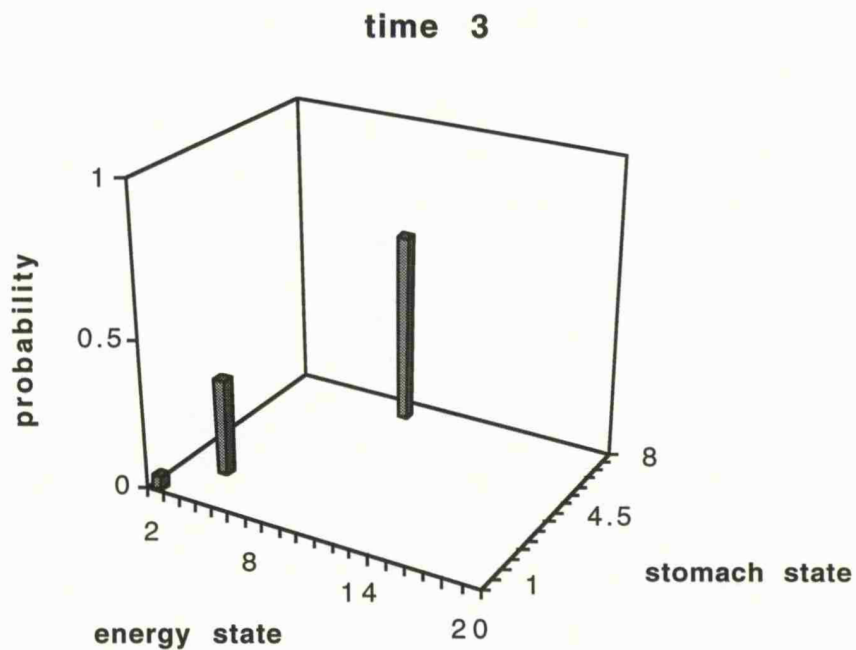
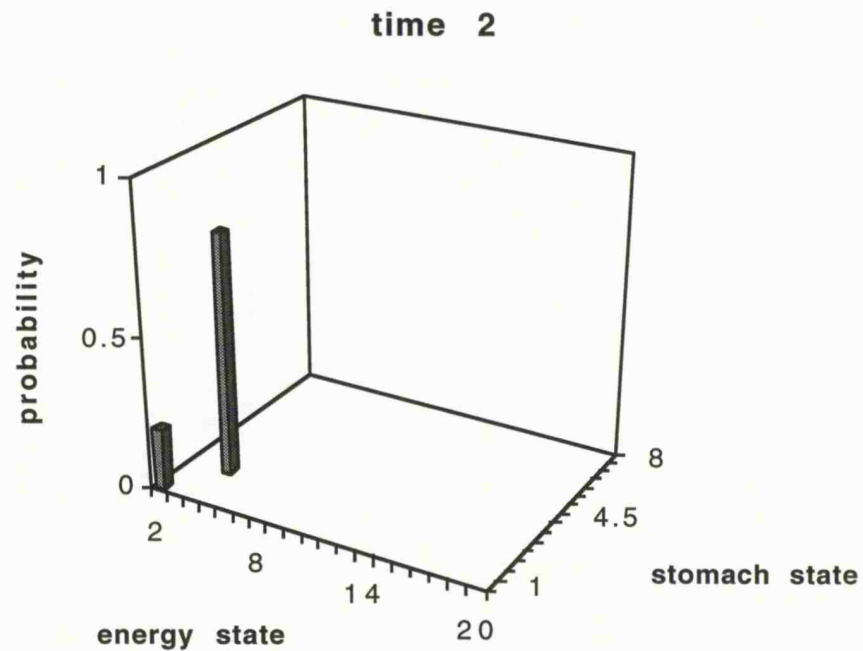
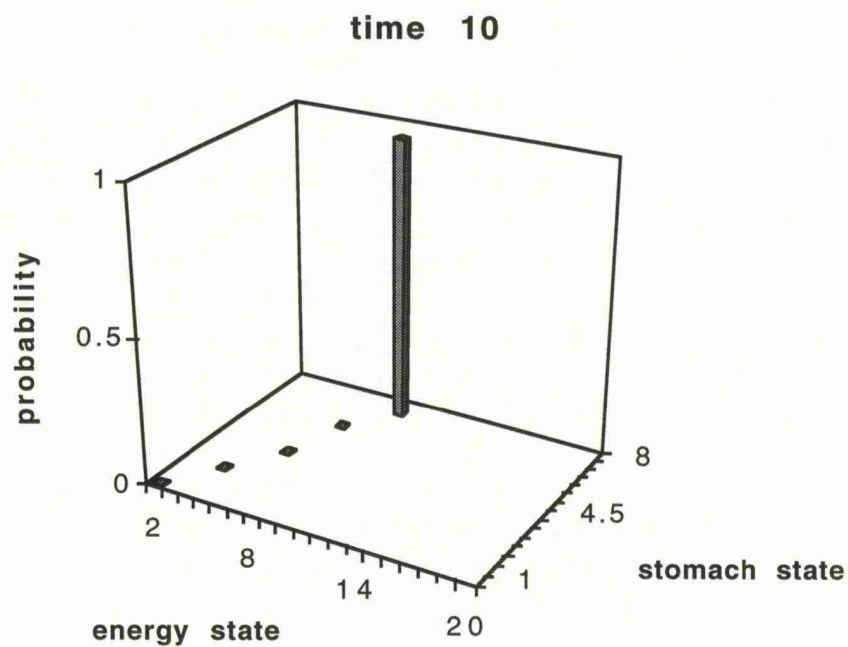


Figure 5.32: The probability that the fish will have the values of the state variables shown as the feeding bout ends. The results of forward iteration using the optimal policy derived from the linear handling model



The fixed handling model

The pattern in the optimal choices was again influenced strongly by the state of the stomach (Table 5.17). The empty fish (vol = 1g) should take a small shrimp but the largest shrimp became the optimal choice when the stomach contained between 1.5 and 3g. When the stomach state reached 3.5 grams the optimal choice switched back to the small shrimp as the stomach capacity became limiting. Both of the shrimps sizes were rejected when the fishes' state was 7g or above. The shaded cells show the states where the energy level become limiting and the optimal choice is affected. At the very highest energy level 20C both of the shrimp sizes are rejected.

Table 5.17: The optimal choices made for each combination of state variables in the fixed handling model.

2 = optimal choice if both shrimp encountered
or if the prey is the only one encountered

1 = optimal choice if the prey is the only one encountered

0 = reject if encountered

		Weight of stomach contents (grams)															
		1		1.5		2		2.5		3		3.5		4		4.5	
		L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S
energy reserves of fish (Calories)	2	0	2	2	1	2	0	2	0	2	0	0	2	0	2	0	2
	4	0	2	2	1	2	0	2	0	2	0	0	2	0	2	0	2
	6	0	2	2	1	2	0	2	0	2	0	0	2	0	2	0	2
	8	0	2	2	1	2	0	2	0	2	0	0	2	0	2	0	2
	10	0	2	2	1	2	0	2	0	2	0	0	2	0	2	0	2
	12	0	2	2	1	2	0	2	0	2	0	0	2	0	2	0	2
	14	0	2	2	1	2	0	2	0	2	0	0	2	0	2	0	2
	16	2	0	2	0	2	0	2	0	2	0	0	2	0	2	0	2
	18	1	2	1	2	1	2	1	2	1	2	0	2	0	2	0	2
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

		Weight of stomach contents (grams)													
		5		5.5		6		6.5		7		7.5		8	
		L	S	L	S	L	S	L	S	L	S	L	S	L	S
energy reserves of fish (Calories)	2	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	4	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	6	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	8	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	10	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	12	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	14	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	16	0	2	0	2	0	2	0	2	0	0	0	0	0	0
	18	0	2	0	2	0	2	0	2	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

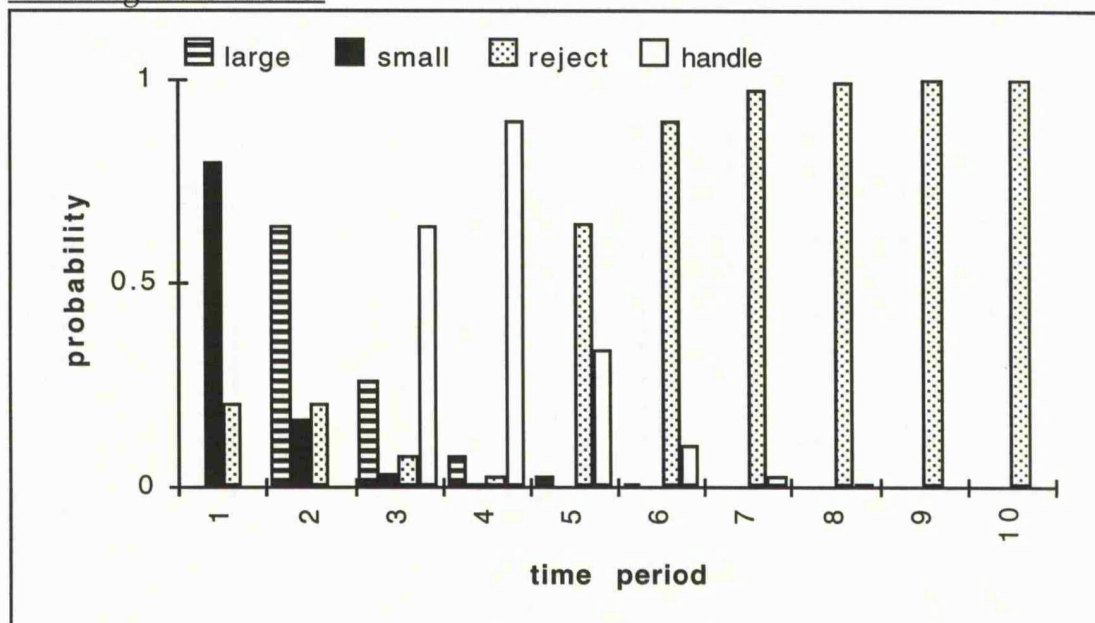
The forward iteration program was run on the results of the fixed handling model. The predicted number of shrimps eaten showed a similar pattern as the other models of the small fish with one shrimp of each size being included in the diet (Table 5.18).

Table 5.18 The predicted number of each shrimp size eaten in the fixed handling time model

	Large shrimp	Small shrimp
predicted number eaten	0.998963	0.999395

The probability sequence showed that the fish took the small shrimp first when they were empty (Figure 5.33). The large shrimp were taken second with the greatest probability in the second period the large shrimp were most likely to be handled in the third and fourth periods. From the fifth period, until the horizon, the largest probability was for the fish to reject both the shrimp sizes. The state of the fish in the important feeding periods two and three can be seen in Figure 5.34. In period two, most of the fish were in the state $vol=2.5$ and $energy=4$ after eating a small shrimp. In time period three the majority of the fish were in the state $vol=7.5$ and $energy=9$.

Figure 5.33: The probability sequence of choices predicted by the fixed handling time model



In the final time period (Figure 5.35) the largest probability was for the fish to be in a state of $vol=7.5$ and $x=9$. The energy value was $=8.993607C$ which would translate to a growth in weight of 2.90289852 grams per day.

Figure 5.34: The probability that the fish will have the values of the state variables shown as the feeding bout proceeds. The results of forward iteration using the optimal policy derived from the fixed handling model.

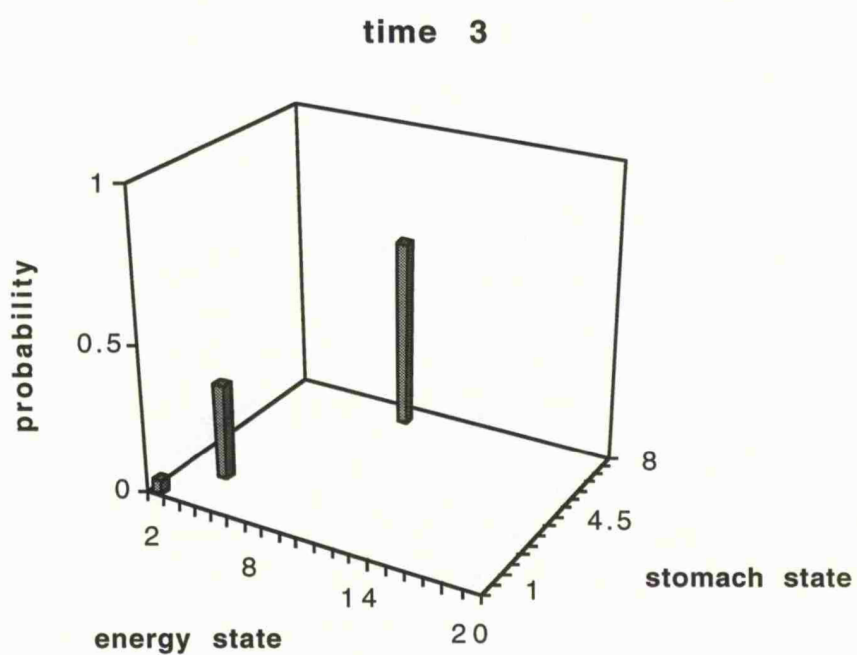
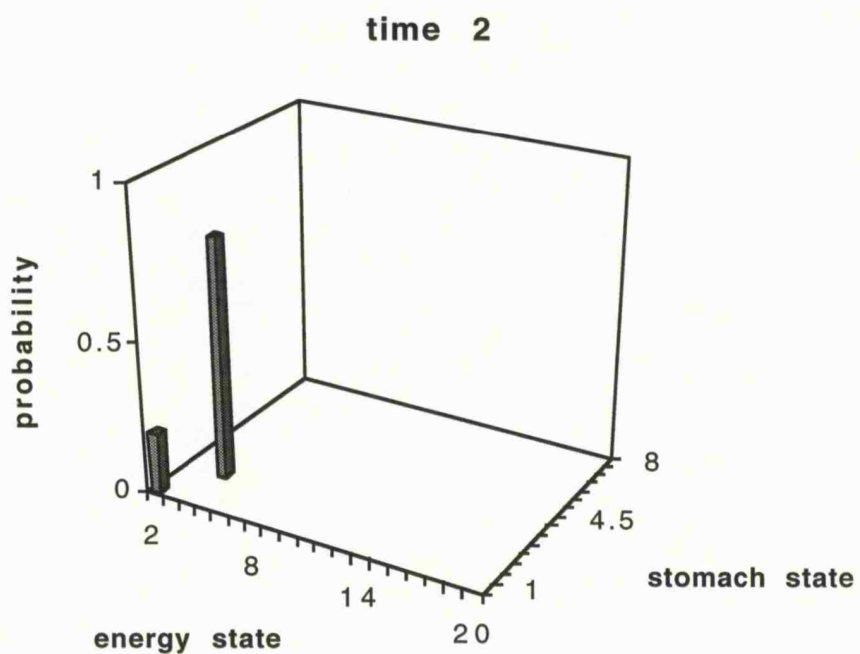
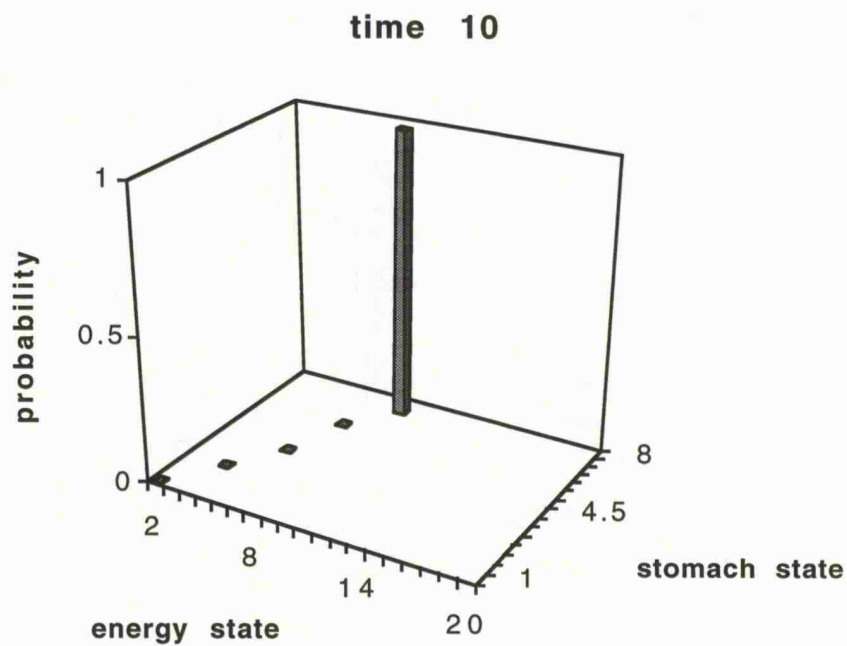


Figure 5.35: The probability that the fish will have the values of the state variables shown as the feeding bout ends. The results of forward iteration using the optimal policy derived from the fixed handling model.



Testing parameter values

Testing the robustness of the model showed that the predictions did not change greatly with any of the parameters altered (Table 5.19). Decreasing the horizon slightly decreased the energy at the end but the difference was only 0.215C. Decreasing the horizon value to 5 also changed the predicted number of small shrimps eaten. Increasing the horizon did not change the energy or the predicted number of each shrimp size eaten.

Table 5.19: The effects on the small fish model predictions from varying key parameter values.

Parameter	values	predicted no. large shrimp	predicted no. small shrimp	Energy function time T
Horizon	5	0.9984	0.8960	8.784
	10	0.9999	0.9999	8.999
	20	1	1	8.999
Lambda	large = 1 small = 1	0.9999	0.9999	8.999
	large = 0.5 small = 1	0.9459	1.1548	9.026
	large = 1 small = 0.5	0.9999	0.9814	8.947
	large = 0.5 small = 0.5	0.9830	0.9890	8.802

The lambda value, which is the encounter rate with each prey type, despite large changes did not greatly alter the energy values. The reduction of the large shrimp encounter rate to 0.5, when the encounter rate with the small shrimp was kept at 1, actually increased the energy slightly. The reduction of just the small shrimp encounter rate to 0.5 (large shrimp $\lambda=1$) and the reduction in both the encounter rates decreased the energy factor. In terms of the predicted number eaten the largest change was seen when the encounter rate with only the large shrimp was reduced to 0.5 (small shrimp $\lambda=1$). In this case the small shrimp prediction increased at the expense of the large shrimp prediction.

DISCUSSION

The effects of energy and stomach state

The pattern of choices predicted by the models changed with both energy state and with stomach state. The energy contents affects the choice because when the energy capacity is reached no more energy can be gained. The optimal choice at the lower levels of energy state remain constant up to a certain level of energy when the pattern of choices changes (e.g. the shaded cells). This occurs when the energy gained from eating the optimal sequence of prey, added to the current energy levels, results in the energy capacity being exceeded. At this point the optimal sequence of prey sizes eaten will change and therefore the optimal choice for each stomach state will also change. At the highest energy level the fish would gain nothing from eating a shrimp. The fish cannot increase its energy level further, and so both sizes are rejected. When the energy levels are less than 1.5 Calories from the maximum only one small shrimp needs to be eaten before the maximum is reached. Further from the capacity it is usually optimal to eat one large prey or two small prey.

The maximum capacity of the stomach state influences the optimal sequence that the fish eats. The pattern is complicated by the dynamic nature of the handling and probability of success which change with stomach state. At the highest levels of the stomach state the choice of whether to reject a prey depends on whether the stomach has room. The upper stomach constraint works differently from the energy capacity as, if the maximum is exceeded the prey must be rejected. In the standard small fish model when the stomach contents are at 3.5g eating a large shrimp of 5g would exceed the capacity of 8g and so the shrimp size must be rejected (Table 5.4). In the lower states the optimal choice is influenced by the maximum number of shrimps that can be eaten and the most efficient order in which the prey can be eaten.

The Effect of Fish Size

The small fish model

The small fish model fails to predict what was observed in the feeding trials described in Chapter 4. In these trials if the small fish ate a large shrimp it was always the first shrimp taken. The model predicts that if a large shrimp is eaten in the feeding bout then the optimal sequence is to eat the large shrimp after a small shrimp. The model predicts that the optimal diet for an empty fish, not constrained by energy levels, is to eat two shrimps, one small and one large. In the feeding trials there was a large variation in the observed diet of the small fish with only one instance of a small fish eating a large and a small prey. The other combinations of prey selected can be predicted by changing the size of the stomach. When the maximum stomach size is reduced the optimal choices change and the observations of eating one large shrimp or two small shrimps are predicted (Figures 5.19 and 5.20). The effect on prey choice of changing the probability of success and handling functions in the small fish model are discussed later.

Large fish model

The strategy set of the large fish model could predict some of the size choice patterns observed in the feeding trials (Table 4.22, Chapter 4). Forward iteration showed that the empty large fish should take three large shrimps first and then two smaller shrimps (Figure 5.21). At the lower stomach states ($< 12g$) when the large shrimp is the optimal choice the strategy set also shows that the small shrimp should be eaten if they are the only prey encountered. In the forward iteration program the single prey encounter could not occur as the probability of encountering both prey together was 1. In the feeding experiment the prey were fed sequentially so that they were always encountered singly. This encounter difference would account for the inclusion of the smaller shrimps early in the choice sequence of the large fish in the feeding trials. The model does not predict that the large shrimps should be taken when the fish are almost full which occurred in five of the trial fish (Table 4.22, Chapter 4).

This failure to predict the choice may be because the probability of success or the equation of handling time penalises too heavily the taking of a large shrimp when the fish is full.

Comparing the small fish model and the large fish model highlights the effect of changing the stomach capacity. The small fish can only consume a maximum of two shrimps but the large fish can consume 5. The models also differ slightly in handling and probability of success equations but the major difference is the stomach capacity. The estimated energy gained from the forward iteration program is very different between the two models. The large fish end up with 20.61 Calories which is more than double the 8.99 Calories gained by the small fish. This is because the large fish can consume more prey though the large fish may have a higher basal metabolic rate (Jones and Hislop 1972) which would lower the actual growth observed.

The set-up of the feeding trial could explain the difference between the observed feeding patterns and the ones predicted by the models. In the feeding trial the fish were in competition with other fish for any food in the tank. The prey sizes in the model are fixed and do not vary, but in the feeding experiments the small and large prey categories were ranges of sizes. The fish sizes in the experiments were also ranges and there is natural variation in the morphological characteristics of the fish. The model describes simultaneous meeting of prey but in the tank experiments the shrimps were introduced sequentially. Simultaneous encounters were used in the model for simplicity. With forward iteration it was not possible to alternate the encounters between small and large shrimp so both of their encounter rates were set at 1.

The Influence of the Probability of Success Function

Altering the probability that a prey would be successfully eaten had a large effect on the optimal choices and their patterns. By changing the equation to a linear function with a larger difference between the two shrimp sizes the optimal prey sequence switched from small shrimp first then large shrimp second, to large shrimp first then small shrimp second. This was also the pattern observed in the experimental feeding trials. This switch occurs because the probability of taking a large shrimp when the stomach

is not completely empty is very low. When fixed probabilities are used the model is very similar to the first small fish model, which used a negative linear equation. The probability of successful capture effects the energy reserves at the end of the feeding period. The fixed model provided the lowest estimate of energy because it predicted the lowest number of the large shrimps included in the diet. The energy factor difference between the exponential model and the larger difference model is only very small. The feeding trial (Chapter 4) showed that the probability of success did change with stomach fullness. The prediction of the model would suggest that this variation in success could be a reason why, if a large shrimp was eaten, it was eaten first. This larger difference model was the same one that predicted the correct order of prey size selection observed in Chapter 4 (Table 4.22)

The Influence of the Handling Time Function

The handling time equation did not drastically change the choice made by the small fish. The linear handling model did increase the probability that a fish would be handling within the probability sequence (Figure 5.30) meaning the fish were handling for a longer time. In terms of energy and the predicted number of shrimps eaten, very little effect was observed. The linear model predicted a slightly lower energy value but the two other models were virtually identical in their predictions. The influence of handling time may be underestimated in these tests as the fish could easily consume the optimal number of prey within the 10 minute feeding bout, under the conditions described. In a shorter time period or with scarcer prey the affect of handling time may become more important.

The Robustness of the Model

The problem of error generated by using interpolation to calculate intermediate values was shown when the encounter rates with the shrimps were changed. When the encounter rate with the large shrimps was reduced to 0.5 and the encounter rate with the small shrimps was 1 the energy function actually increased. This is because the calculation gap for the energy state of the fish is 1 Calorie and the small shrimp contain 1.5

calories. The forward iteration does keep track of the actual state of the fish but it has to use the calculated values to represent the data. Thus the estimate was rounded up and the energy level appeared artificially higher.

From testing the models under the standard prey conditions described in Table 5.2, it would appear that the most important factor is the probability of success. Previous models of feeding behaviour have tended to ignore this as a variable or have used it as a fixed parameter (Hart and Gill 1993, Burrows 1994). The handling time of prey has been regarded as an important cost in foraging for a long time (Werner 1974) but has again tended to be modelled as a fixed parameter, though it is often proportional to prey size (Hart 1994).

The influence of the other variables on the predictions of the model was not strong. The parameters were tested individually and their effect would probably change if they were tested in combination. The interactions of all the variables can be quite complex and the testing performed in this chapter should not be considered comprehensive. The parameters of metabolic rate and evacuation would be much more important if the model were run over a day or a week instead of the ten minute feeding bout used in these tests. As highlighted previously, the influence of handling time would increase were the fish to be limited in the duration of its foraging.

Conclusions

The modelling described is an evolving process and can be adapted and added to so that new situations and problems can be investigated. The program currently does not model the effect of energy reserves in a realistic way. The forward iteration model was run from a state ($vol = 1 \times = 2$) so that the choice of prey was limited by the stomach size before energy capacity had an effect. In the present model all of the energy in the shrimp passes to the fish immediately on ingestion. The fish does not need to convert the energy into reserves or expend any extra energy in handling or digesting the prey items. Love (1980) showed that fish can slow down their metabolic rate when they approach starvation which is not included in the model. The size of the maximum capacity of energy reserves of different sized whiting is not documented. The level at which no more reserves can be created has only been estimated. It may also be that the metabolic rate alters as this energy capacity is approached. For the energy reserves to be

properly modelled, further experimentation on the energetic dynamics of the whiting would be required.

Expansion of the model could be done in a number of ways. The size range and type of prey encountered could be increased. A new type of prey with new characteristics, e.g. a fish prey, would allow the change in diet with whiting size to be investigated. Predation is a major influence that has not been incorporated in to the model at present. The choices of the fish maybe influenced by the risk of predation e.g. handling fish maybe more prone to predation which would greatly increase the influence of this variable.

CHAPTER 6

GENERAL DISCUSSION

"To go on investigating without the guidance of theories is like attempting to walk in a thick mist without a track and without a compass. We should get somewhere under these circumstances, but chance alone would determine whether we should reach a stony desert of unintelligible facts or a system of roads leading in some useful direction; and in most cases chance would decide against us"

August Friedrich Leopold Weismann

DISCUSSION

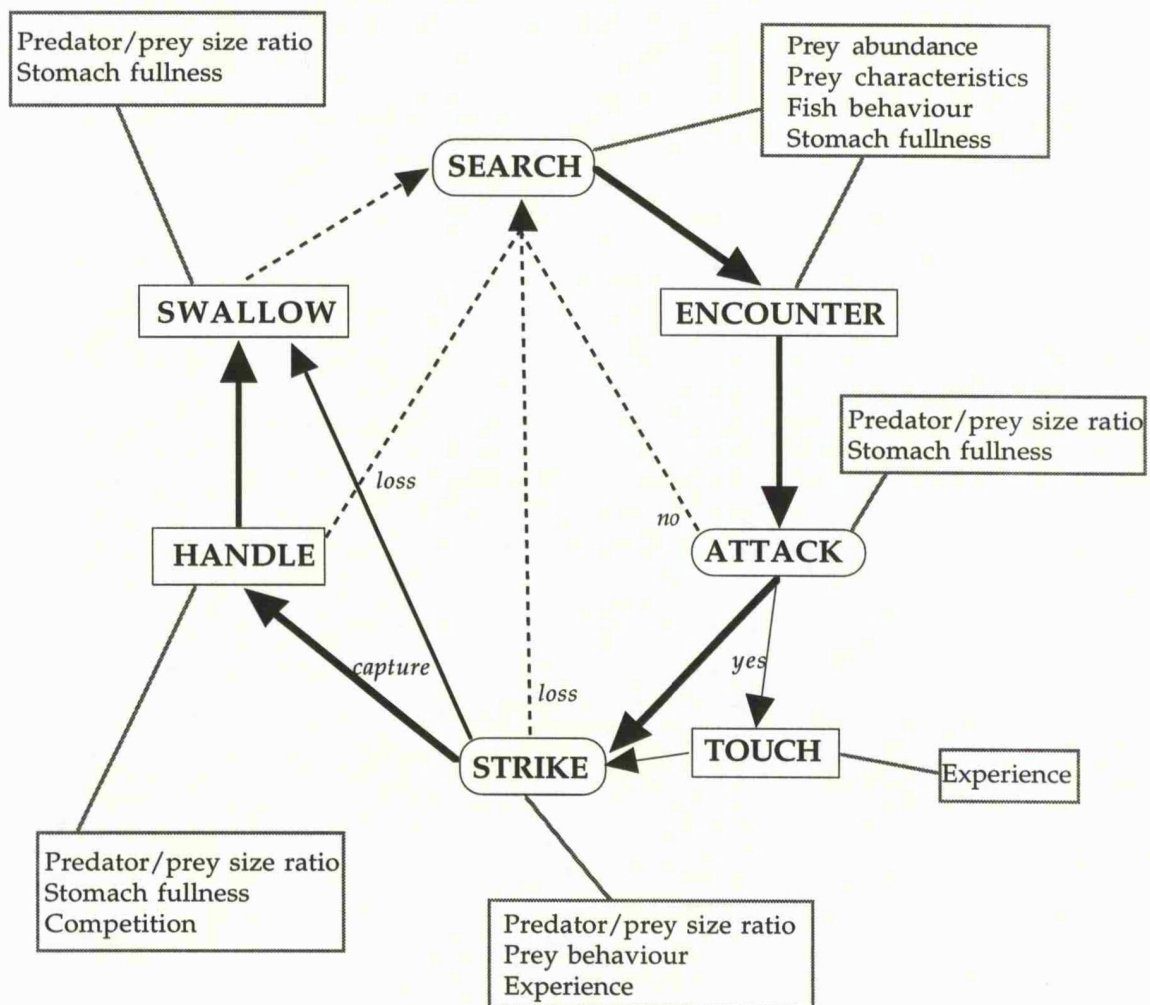
For the fisheries manager there are three important aspects of the interactions between fish species; by catch, competition and predation (Hilborn and Walters 1992). By catch occurs when one species of fish is caught at the same time as a targeted species. This interaction is not discussed in the present study. The other two interactions of competition and predation are mainly concerned with the feeding ecology of the fish. Competition takes place because one species consumes the same food type as another (Hilborn and Walters 1992). Predation occurs when one species at some stage of its life is eaten by another. Both of these interactions cause the numbers in the species' populations to be dependant on each other. As outlined in Chapter 1 fisheries management has become concerned with inter-specific interactions and methods to quantify the effects have been developed. The main thrust of these methods has been to quantify:

- The mean contribution, by weight, of each prey group to the stomach contents of each predator age group.
- The mean body weight at time of ingestion of each prey age group for each predator age group.
- The average rates of food intake for each predator age group (Daan 1989).

The results from previous studies such as the International Stomach Sampling Project (Anon 1980), have been interpreted so as to estimate the points above, for use in models like multispecies virtual population analysis (MSVPA). In MSVPA the natural mortality rate for each species, at each age depends upon the abundance of species that prey on it (Pope and Knight 1982, Daan 1987). A better understanding of the foraging ecology of the predators would lead to a better estimation of this mortality. If the optimal prey size of a predator is known or, how the predator changes its choice under different prey abundance conditions, managers could produce more reliable estimates of mortality.

The foraging ecology of the whiting is summarised in Figure 6.1, which shows the major decision making points and the influencing factors.

Figure 6.1: A summary of the major points in the foraging of whiting. The grey rectangles indicate factors which influence each of the behaviours and their outcome (adapted from Gill 1993).



Search and Encounter

The motivation to forage is thought to be influenced by gut fullness and a systemic factor reflecting metabolic balance (Holmgren *et al* 1983). Gut fullness is related to the evacuation rate, which will determine when the fish will be motivated to feed again. This dependence on stomach fullness is behind the assumption that the intake of food is equal to the output

from the gut. The output from the gut is used in estimating the consumption rates of fish.

The searching and encounter of whiting is also influenced by its shoaling behaviour. Fish foraging in shoals can gain, through faster location of food, more time for feeding, more effective sampling, information transfer and opportunity for copying (Pitcher 1986). Patchy food can be located faster in larger shoals with members of a shoal recognising when others have located a food source (Pitcher *et al* 1986). The dominance of one prey type in the stomachs of the fish sampled at a station suggests that the whiting are feeding on aggregations of prey species (Chapter 2). When one fish locates a food source its behaviour will attract the attention of other fish in the shoal (Magurran 1984). This passive information transfer was observed in the feeding experiments described in Chapter 4 when the orientation of a fish often appeared to cause the other fish to orientate in the same direction. Brawn (1969) found that cod rapidly approached other cod that began to feed. The attraction of other fish means that if one fish exploits a prey source then there is a high probability that the other fish in the area will do the same, if the source is large enough. Large aggregations of food are also usually more easily detected by the fish than single prey items (Pitcher 1986). There are costs of shoaling, mainly through intra-specific competition for food. The small fish may be at a disadvantage when shoaling with larger whiting as they may be forced out of the feeding area as occurs in minnows, *Phoxinus phoxinus* (Pitcher *et al* 1986).

Brawn (1969) found that cod used two distinct methods of locating food according to whether the food was pelagic, on the bottom or buried. Cod feeding pelagically used vision to locate their food whereas food on the bottom or buried was located by smell. Whiting can also locate buried food through olfaction (Pawson 1974). Food that is buried is uncovered using a digging action achieved through thrusting the head into the substrate with rapid side to side movements.

Attack and Strike

When a prey item was encountered the probability that a whiting would attack a shrimp was found to be dependent on the fish to shrimp size ratio, and stomach fullness (Chapter 4). In small whiting the probability that a large shrimp would be attacked fell from 1 when empty, to 0.1 with one shrimp in their stomachs. Small whiting were more likely to attack a small shrimp than a large one when they already had a shrimp in their stomachs. When the fish were satiated the probability of attack was approximately zero. The effects of prey size and stomach fullness have also been studied in other fish. Gill and Hart (1994) found that in threespine sticklebacks the probability of attack for a given sized prey increased with fish size, but decreased with prey size and stomach fullness.

The sequence of behaviours used by whiting when attacking shrimps changed with increasing experience (Chapter 4). Inexperienced fish were more likely to touch the shrimp before striking at it than whiting that had experienced more feeding trials. The time taken to attack the shrimp was also faster in the experienced fish, this was probably because of the simplified attack sequence. Gill (1993) found that in competition the threespine stickleback which was first to attack a prey had the highest probability of capturing it. Whiting feeding in shoals would be competing against each other for any available prey and could gain an advantage by the ability to attack more quickly.

The probability that a strike would end in capture was higher when the fish had experienced more feeding trials. The successful capture of a shrimp after a strike was also dependent on the fish to shrimp size ratio (Chapter 4). The larger the ratio the greater the probability that a shrimp was caught successfully. There is also evidence that the way in which the whiting struck at the shrimp was influenced by the shrimp's behaviour, though this needs further investigation.

Handle and Swallow

After the successful capture of a shrimp by a whiting, two events could occur. The shrimp was either handled, or swallowed in the same motion as the strike. The whiting to shrimp size ratio was an important factor in

whether the shrimp was handled or not. The size ratio also effected the length of time the whiting spent in handling the shrimp. A large size ratio meant the probability that the shrimp would be handled was low. As the size ratio decreased the need to handle the shrimps, and the time spent doing so increased. Stomach fullness also affected the time spent in the handling of a shrimp. It was found that as stomach fullness increased the probability of a prey item being handled increased and the handling time lengthened.

In Chapter 4 it was found that experience reduced the time whiting spent handling shrimps. The effect of experience decreasing handling times has also been observed in fifteen-spined sticklebacks (Croy and Hughes 1991). They found that with experience the sequence of behaviours the sticklebacks used in handling *Artemia* and *Gammarus* was simplified and the time spent in handling decreased.

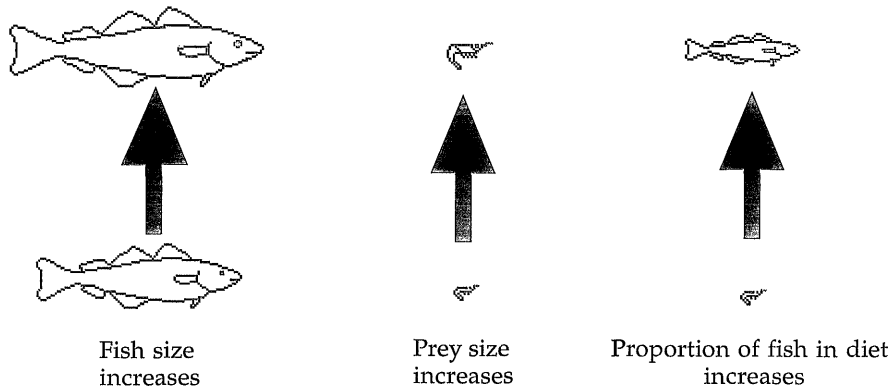
Handling time is associated as a cost of foraging (Werner 1974). Time spent in handling prey is time when the fish could be foraging for more food, or engaged in other activities. Chapter 4 showed an affect of competition on the handling of prey items. Fish that had food protruding from the mouth were at risk of loosing the prey item through another fish striking at it. This loss of food would further increase the costs of handling as with more fish around the chances of loosing a prey item in handling would increase. Brawn (1969) observed that when small cod were chased by larger cod they would release the food they were handling.

Whether a shrimp that has been attacked will be captured and successfully swallowed depends on the whiting to shrimp size ratio, and the whiting's stomach fullness (Chapter 4). As the size ratio decreases the probability of successful ingestion decreases. It was also found that as the level of stomach fullness increased, the probability of success decreased. The model described in Chapter 5 suggested that the probability of success is an important factor in determining the optimal choice of the whiting.

Whiting to prey size ratio

The factors that appear to have the greatest influence on the foraging of whiting are stomach fullness and the whiting to prey size ratio. The influence of the size ratio could account for some of the observed trends in the diet composition of whiting foraging in the North Sea. It has been found that as the size of the whiting increases so the average prey size eaten and the proportion of fish in the diet increases (Figure 6.2)(Hislop *et al* 1991).

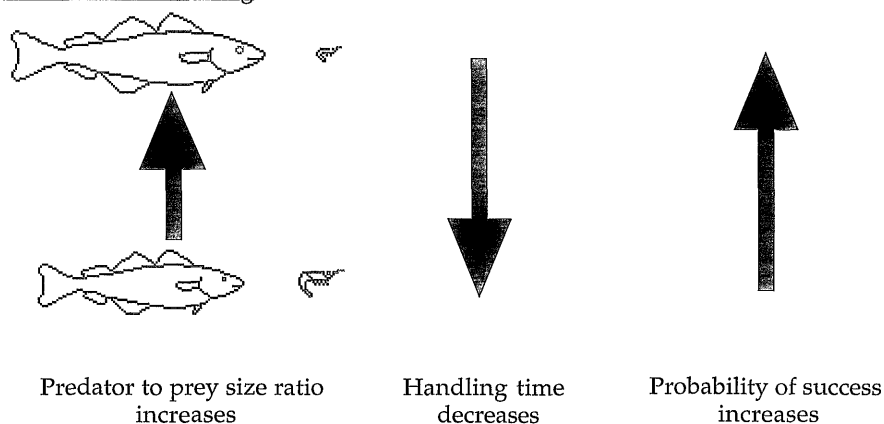
Figure 6.2: The effect of increasing fish size on the diet of whiting



Chapter 5 showed that as the predator to prey size ratio decreased the handling time of the prey increased and the probability that a prey would be successfully caught and ingested decreased (Figure 6.3).

The changes in these foraging costs could explain some of the observed diet changes with increasing fish size. Handling time and the probability of success are factors that change the profitability of a prey item. A long handling time or a very low probability of success for a prey type would cause that prey to be unprofitable, and the fish to reject it. As the prey becomes larger in proportion to the fish size there will come a point when rejecting the prey is more profitable than attempting to eat it. There is also a predator prey size ratio when the prey is simply too large for the predator to physically swallow.

Figure 6.3: The effect of predator to prey size ratio on the foraging behaviours of whiting



When the model in Chapter 5 was used to compare the foraging of large and small fish, the average prey size increased as proportionally more large shrimps were eaten. When the small fish model was run with a maximum stomach size of 5 grams the large prey were excluded from the diet.

The trend of larger fish having a larger proportion of fish in their diet could also be explained through considerations of prey profitability. In the North Sea the average size of all the fish species is larger than the average size of the crustaceans. The majority of the smaller prey available are crustacean species, and smaller whiting are limited to these smaller prey sizes. This availability of prey sizes could explain the dominance of the crustacean prey in the diet of the smaller whiting. Fish prey were not excluded from the diet of small whiting and a large number of small fish prey were found in their guts. The whiting sampled in Chapter 2 fed on sandeels and small individuals of other fish species.

The large whiting are not so constrained in their choice by prey size and take a much larger proportion of fish in their diet. It may be that when possible whiting consume fish prey in preference to other prey, though this has not been demonstrated. This possible preference for fish is supported by the changes in diet with area in the North Sea discussed in Chapter 2. There are proportionally less fish in the diet of whiting in the southern than the northern North Sea (Hislop *et al* 1991). This is thought to be because the abundance of fish prey is less in the southern area. Daan

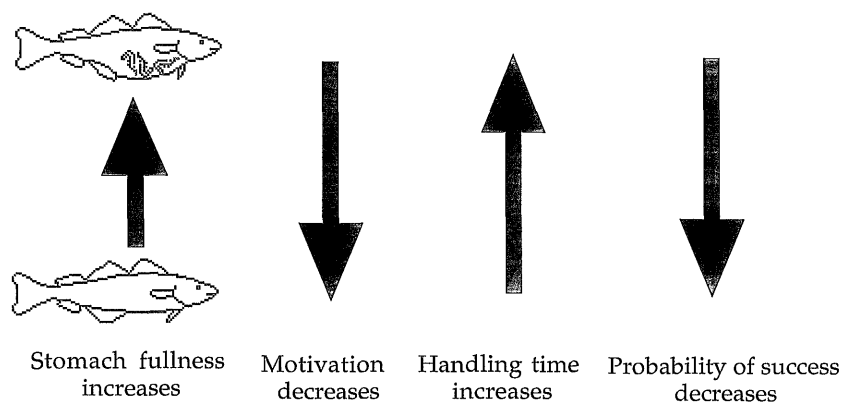
(1973) suggested that cod were feeding sub-optimally in the southern North Sea, where they had to consume a larger proportion of crustaceans.

Why should fish prey be consumed in preference to other types? The other major prey type eaten by whiting are crustaceans. Although crustaceans can grow to larger sizes they are less abundant at these sizes and heavily armoured, so making capture difficult. Large whiting can eat smaller prey items but they have to consume more before satiation, making it more profitable to eat less of the larger items. The model in Chapter 5 predicted that the large shrimps were more profitable to the large fish in all but the fullest stomach states.

Stomach fullness

Stomach fullness has been shown to affect the foraging behaviour of whiting in terms of motivation, handling time and the probability of successfully eating a prey item (Figure 6.4)(Chapter 4).

Figure 6.4: The effect of increasing stomach fullness on the foraging behaviour of whiting



These changes in the foraging behaviour of the whiting with increasing stomach fullness cause changes in the optimal choices of the whiting. The large fish model in Chapter 5 showed that optimal choice switched from eating a large shrimp to eating a small shrimp as the fish became full. The

affect of this change in prey size profitability will complicate the effect of a particular sized whiting on the size structure of its prey population. A prey size that might normally be ignored in favour of a larger size might become the favoured prey at a certain level of stomach fullness.

If the aim of the fish is to maximise its energy gain over time then it would be expected that the whiting's foraging behaviour would be adapted to maximise the rate at which the stomach is emptied. In Chapter 3 the gastric evacuation experiments showed that prawns were digested at a much slower rate than sandeels. The faster evacuation of fish prey compared to crustacean prey has been demonstrated in other investigations (Bromley 1989, Singh-Renton 1990). Fish prey also have the advantage that a larger weight of prey can be consumed before satiation. These satiation and digestive factors mean that the whiting can gain more energy in a time period by consuming fish than it could consuming crustacean prey. Table 6.1 shows the difference in satiation weight and evacuation time for the different meals fed to the fish in Chapter 3. It is clear that a larger weight of sandeels can be consumed and the stomach will empty more quickly, than with a meal of prawns. Of course the fish does not necessarily empty its stomach before consuming more food. If the evacuation rate is linear as suggested in Chapter 3 then fish consuming sandeels will be able to start feeding again earlier than fish consuming prawns.

Table 6.1: The satiation weights and evacuation times for different prey types based on a 250g whiting, using data from Chapter 3.

Meal	Satiation weight	Evacuation time for meal
Sandeels	20.7g	49hrs
Prawns	11.2g	57hrs
Mixed meal		
of sandeels	3.1g	44hrs
and prawns	8.5g	69hrs

Chapter 3 also found that in a mixed meal that consisted of both sandeels and prawns, the sandeels were evacuated more quickly. The majority of stomachs sampled in Chapter 2 contained only one type of prey. If the fish gains an advantage through having a faster evacuation rate then the

mixed meal situation would be expected to be usual, but in Chapter 2 it was shown that single prey meals were the normal situation. By consuming prawns as well as the sandeels the weight of food consumed before satiation is reduced (Table 6.1). The total meal also takes longer to be evacuated as the evacuation rate of the prawns is slower. Any advantage gained from the faster evacuation is probably cancelled out by the reduced satiation weight and the slower evacuation of the prawns.

Whiting interactions

In the North Sea the important commercial species that interact with whiting in terms of feeding are cod, saithe, haddock and mackerel (Daan 1989). The interaction of these species was noted in the area of the continuous sampling (Chapter 2). In this area a large number of whiting were sampled whilst they were feeding on aggregations of sandeels. Also sampled in large numbers in the area were cod and saithe. It was clear from stomach samples that all of the piscivorous fish in the area were foraging upon the sandeels (Bromley pers com.), but they were exploiting the sandeels at different times of the day. The small whiting were also under predation pressure and were often found in the stomachs of the large piscivorous fish. By feeding on the sandeels the small whiting were increasing their probability of being eaten but also increased their intake of food. The aggregations of the fish species into relatively small areas will increase the affect of any interactions. These aggregations will also mean that the interactions will remain important even at reduced numbers of the fish species (Daan 1987).

The competition and predation interactions are complicated by the changes in diet with the increasing size of the fish. The way in which fish interact will change at different stages of their life cycles. A number of prey species of adult whiting are also predators of whiting juveniles e.g. cod, haddock and saithe (Anon 1984). Cannibalism is also found in whiting where adults predate upon juveniles and larvae (Hislop *et al* 1991). Because of these life history interactions it is important to know the affect of the predator size upon the size distribution of the prey.

Conclusion

The ultimate aim of fisheries management is to exploit fish populations as a renewable resource and in the most productive way. Multispecies models appear to be a positive step towards this goal and their development should be aided by a better understanding of the foraging ecology of the exploited fish. The present study has showed how a more behavioural approach to the work can help in advancing our understanding of the processes involved in shaping the diet of exploited fish such as North Sea whiting.

APPENDIX I
Arcsin transformation

Arcsin transformation for percentages

An arcsin transformation (or angular transformation) it is appropriate for percentages or proportions. The transformation expands the variance in the lowest and highest number to prevent the problem of variance becoming a function of the mean.
the transformation is:

$$q = \arcsin (p^{0.5})$$

where:

$$p = \text{a percentage}$$

To convert back to percentage

$$p = [\sin (q)]^2$$

APPENDIX II
Computer program listings

```

REM ****PREY selection model including volumes and interpolation****
REM **** program parameters stored in details.dat ****
REM **** program results stored in 1opt*.dat ****

CLEAR

RESTORE
CLS : PRINT "copyright IAINSOFT (tm) 1994"

OPEN "c:\dos\iaintemp\smchoice.dat" FOR OUTPUT AS #250
nprey = 2: REM ****number of prey items need to change print out****

DIM s(nprey), success(nprey), lambda(nprey), y(nprey), alpha(nprey), r(nprey),
preyvol(nprey)

GOSUB 1000: REM ****enter parameters values****
GOSUB 4000: REM ****to print parameter values****
REM $DYNAMIC
DIM f0(volmax * 10, capacity): REM f1 tracks f(X,t+ri,T)****
DIM evacvol(volmax * 10, capacity, nprey): REM ****tracks evacuation vol****
DIM xprim((volmax) * 10, capacity, nprey): REM ****tracks fitness choice****
DIM volvalues((volmax) * 10): REM ****values of calculated volues
DIM fitvalues(capacity): REM **** values of calculated fitness****
DIM rhs(nprey): REM ****rhs(i) is value for accepting prey i****

REM ****set fields for file 1opt*.dat****
TYPE filedata
optimum1 AS INTEGER
volume1 AS SINGLE
fitness1 AS SINGLE
handle1 AS SINGLE
optimum2 AS INTEGER
volume2 AS SINGLE
fitness2 AS SINGLE
handle2 AS SINGLE
volume0 AS SINGLE
fitness0 AS SINGLE
handle0 AS INTEGER
growth AS SINGLE
END TYPE
DIM choice AS filedata: REM ****sets length of fields****
DIM fone AS filedata
GOSUB 2000: REM ****initialize F1****
REM ****start iterations****
FOR t = horizon - 1 TO 1 STEP -1
PRINT t;

baseline$ = "c:\dos\iaintemp\1opt" + LTRIM$(STR$(t)): REM **** sets file
name to linear+time value****
OPEN baseline$ + ".dat" FOR RANDOM AS #t LEN = LEN(choice): REM
****sets length and opens as #time value****
GOSUB 3000: REM ****solve dpe****
CLOSE #t

```

```

      REM ****update f1****

NEXT t
CLOSE #250
END:      REM ****end program****

1000      REM ****set up parameter values****
capacity = 20: REM ****maximum X value****
xcritical = 1: REM ****minimum X value****
evacrate = .0083: REM ****evacuation rate constant****
volmax = 8: REM ****maximum stomach volume****
volmin = 1: REM ****minimum stomach volume****
gap = .5: REM ****increment for stomach volume****
fitgap = 1: REM ****increment for energy values****
l1 = 0: REM ****prob encountering food variable****
x0 = 1: REM ****Terminal fitness parameter****
horizon = 10: REM ****No. time periods****

alphaO = .001: REM ****basic metabolic rate****
DIM optimum(npred): REM ****tracks whether prey should be eaten or
rejected****

DATA -0.17,-0.1: REM ****success factor slope****
FOR i = 1 TO npred
  READ s(i)
NEXT i

DATA 1,1: REM ****lambda values (prob encountering food) ****
FOR i = 1 TO npred
  READ l(i)
NEXT i
lambda(1) = l(1) - (l(1) * l(2))
lambda(2) = l(2) - (l(1) * l(2))
lambdaO = 1 - ((l(1) + l(2)) - (l(1) * l(2))): REM **** lambda0 prob not
encountering food****

DATA 5,1.5: REM ****y values (energetic value of food)****
FOR i = 1 TO npred
  READ y(i)
NEXT i

DATA 7.62,1: REM ****handle base****
FOR i = 1 TO npred
  READ handle(i)
NEXT i
rmax = INT(handle(1) * 10 ^ (.21 * (volmax)) / 60): REM ****maximum
handling time (n.b. handle(1) as largest)****

DATA 5,1.5: REM ****prey volumes****
FOR i = 1 TO npred
  READ preyvol(i)
NEXT i
RETURN

```

```

2000      REM ***initialization sub routine***
      basename$ = "c:\dos\aintemp\1opt" + LTRIM$(STR$(horizon))
      OPEN basename$ + ".dat" FOR RANDOM AS #horizon LEN = LEN(choice)
      FOR vol = (volmin * 10) TO (volmax * 10) STEP (gap * 10)

        recordnumber = (capacity - xcritical) * vol
        FOR i = xcritical + 1 TO capacity: REM **** fitness < xcritical values****
          recordnumber = recordnumber + 1
          choice.growth = .36 * (i - .93)
          PUT #horizon, recordnumber, choice
          f0(vol, i) = 0:
        NEXT i
      NEXT vol
      CLOSE #horizon
      j = 0: REM **** sets values to those calculated****
      FOR i = volmin TO volmax STEP gap
        volvalues(j) = i
        j = j + 1

      NEXT i
      j = 0: REM **** sets values to those calculated****
      FOR i = xcritical TO capacity STEP fitgap
        fitvalues(j) = i
        j = j + 1

      NEXT i
      RETURN: REM **** end of initialization****

```

```

3000      REM ****SOLVE DPE****
      REM ****cycle over vol then cycle over x****
      FOR vol = (volmin * 10) TO (volmax * 10) STEP (gap * 10)
        REM IF vol MOD 20 = 0 THEN PRINT vol;
        recordnumber = (capacity - xcritical) * vol: REM ****defines address in file for
each set of data****
        FOR x = xcritical + 1 TO capacity

          REM ****compute rhs(i)****

          REM **** calculates the affect of rejecting prey ****
          evacvol(vol, x, 0) = (vol / 10) - (1 * evacrate): REM **** volume if prey
rejected ****
          IF evacvol(vol, x, 0) < volmin THEN evacvol(vol, x, 0) = volmin
          xprim(vol, x, 0) = x - alphaO: REM **** x value if prey i
rejected ****

          IF xprim(vol, x, 0) < xcritical THEN xprim(vol, x, 0) = xcritical
          p = INT((evacvol(vol, x, 0) - volmin) / gap)
          q = INT((xprim(vol, x, 0) - xcritical) / fitgap)
          change = fitvalues(q)
          change2 = fitvalues(q + 1)
          change3 = volvalues(p + 1)
          IF fitvalues(q + 1) > capacity THEN
            fitvalues(q + 1) = capacity
          END IF
          IF volvalues(p + 1) > volmax THEN

```

```

        volvalues(p + 1) = volmax
    END IF
    IF fitvalues(q) = xcritical THEN
        xprim(vol, x, 0) = xcritical + fitgap
        fitvalues(q) = xcritical + fitgap
    END IF
    storage$ = "c:\dos\iaintemp\1opt" + LTRIM$(STR$(t + 1))
    OPEN storage$ + ".dat" FOR RANDOM AS #100 LEN = LEN(fone)
    place = (((capacity - xcritical) * volvalues(p) * 10) + fitvalues(q)) - xcritical
    place1 = (((capacity - xcritical) * volvalues(p + 1) * 10) + fitvalues(q)) - xcritical
    place2 = (((capacity - xcritical) * volvalues(p) * 10) + fitvalues(q + 1)) - xcritical
    place3 = (((capacity - xcritical) * volvalues(p + 1) * 10) + fitvalues(q + 1)) -
xcritical
    GET #100, place, fone
    normalboth = fone.growth
    GET #100, place1, fone
    oddstomach = fone.growth
    GET #100, place2, fone
    oddenergy = fone.growth
    GET #100, place3, fone
    oddboth = fone.growth
    CLOSE #100
    IF evacvol(vol, x, 0) = volvalues(p) AND xprim(vol, x, 0) = fitvalues(q) THEN
vmax = normalboth
        IF evacvol(vol, x, 0) <> volvalues(p) AND xprim(vol, x, 0) = fitvalues(q) THEN
vmax = (((evacvol(vol, x, 0) - volvalues(p)) * oddstomach) + ((volvalues(p + 1) -
evacvol(vol, x, 0)) * normalboth)) / .5
            IF evacvol(vol, x, 0) = volvalues(p) AND xprim(vol, x, 0) <> fitvalues(q) THEN
vmax = (((xprim(vol, x, 0) - fitvalues(q)) * oddenergy) + ((fitvalues(q + 1) -
xprim(vol, x, 0)) * normalboth)) / fitgap
                IF evacvol(vol, x, 0) <> volvalues(p) AND xprim(vol, x, 0) <> fitvalues(q)
THEN
                    pea = evacvol(vol, x, 0) - volvalues(p)
                    bigpea = volvalues(p + 1) - volvalues(p)
                    que = xprim(vol, x, 0) - fitvalues(q)
                    bigque = fitvalues(q + 1) - fitvalues(q)
                    vmax = (1 / (bigpea * bigque)) * ((pea * que * oddboth) + (pea * (bigque - que) *
oddstomach) + (que * (bigpea - pea) * oddenergy) + ((bigpea - pea) * (bigque - que) *
normalboth))
                END IF:
                REM ***** interpolation calculation*****
                IF xprim(vol, x, 0) <= xcritical THEN vmax = 0
                fitvalues(q) = change
                fitvalues(q + 1) = change2
                volvalues(p + 1) = change3
                REM ***** section calculates affects of accepting prey*****
                FOR i = 1 TO nprey: REM ***** cycle over number of prey items*****
                    r(i) = INT(handle(i) * (10 ^ (.21 * (vol / 10))) / 60) + t
                IF r(i) > horizon THEN
                    rhs(i) = 0
                ELSE
                    IF r(i) - t < 1 THEN r(i) = 1 + t
                    success(i) = (s(i) * (vol / 10)) + .8
                    IF success(i) < 0 THEN success(i) = 0
                    xprim(vol, x, i) = x - ((r(i) - t) * alphaO) + y(i): REM ***** x value if eats
prey i*****
                    IF xprim(vol, x, i) > capacity THEN xprim(vol, x, i) = capacity - ((r(i) - t) *
alphaO)
                    IF xprim(vol, x, i) < xcritical THEN xprim(vol, x, i) = xcritical

```

```

      rvol = preyvol(i) + (vol / 10);          REM **** initial stomach vol if
eats prey i****
      evacvol(vol, x, i) = rvol - ((r(i) - t) * evacrate); REM **** stomach volume
after handling and evacuation****
      IF evacvol(vol, x, i) < volmin THEN evacvol(vol, x, i) = volmin
      IF rvol > volmax THEN
        rhs(i) = 0
        evacvol(vol, x, i) = volmax: REM ****done so that does not affect forward
iteration****
      ELSE
        REM **** interpolation calculation****

        p = INT((evacvol(vol, x, i) - volmin) / gap)
        q = INT((xprim(vol, x, i) - xcritical) / fitgap)
        full = 0
        change = fitvalues(q + 1)
        change1 = volvalues(p + 1)
        IF fitvalues(q + 1) > capacity THEN
          fitvalues(q + 1) = capacity
        END IF
        IF volvalues(p + 1) > volmax THEN
          volvalues(p + 1) = volmax
        END IF

        storage$ = "c:\dos\aiantemp\1opt" + LTRIM$(STR$(r(i)))
        place = (((capacity - xcritical) * volvalues(p) * 10) + fitvalues(q)) - xcritical
        OPEN storage$ + ".dat" FOR RANDOM AS #100 LEN = LEN(fone)
        GET #100, place, fone
        normalboth = fone.growth
        place2 = (((capacity - xcritical) * volvalues(p + 1) * 10) + fitvalues(q)) -
xcritical
        GET #100, place2, fone
        oddstomach = fone.growth
        place3 = (((capacity - xcritical) * volvalues(p) * 10) + fitvalues(q + 1)) -
xcritical
        GET #100, place3, fone
        oddenergy = fone.growth
        IF evacvol(vol, x, i) = volvalues(p) AND xprim(vol, x, i) = fitvalues(q)
THEN rhs(i) = (success(i) * (normalboth)) + ((1 - success(i)) * vmax)
        IF evacvol(vol, x, i) <> volvalues(p) AND xprim(vol, x, i) = fitvalues(q)
THEN rhs(i) = success(i) * (((evacvol(vol, x, i) - volvalues(p)) * (oddstomach) +
((volvalues(p + 1) - evacvol(vol, x, i)) * (normalboth)))) / (volvalues(p + 1) -
volvalues(p))) + ((1 - success(i)) * vmax)
        IF evacvol(vol, x, i) = volvalues(p) AND xprim(vol, x, i) <> fitvalues(q)
THEN rhs(i) = success(i) * (((xprim(vol, x, i) - fitvalues(q)) * (oddenergy) +
((fitvalues(q + 1) - xprim(vol, x, i)) * (normalboth)))) / (fitvalues(q + 1) -
fitvalues(q))) + ((1 - success(i)) * vmax)
        IF evacvol(vol, x, i) <> volvalues(p) AND xprim(vol, x, i) <> fitvalues(q)
THEN
        place4 = (((capacity - xcritical) * volvalues(p + 1) * 10) + fitvalues(q + 1)) -
xcritical
        GET #100, place4, fone
        oddboth = fone.growth
        pea = evacvol(vol, x, i) - volvalues(p)
        bigpea = volvalues(p + 1) - volvalues(p)
        que = xprim(vol, x, i) - fitvalues(q)
        bigque = fitvalues(q + 1) - fitvalues(q)

```



```

rhs(i) = (1 / (bigpea * bigque)) * ((pea * que * oddboth) + (pea * (bigque - que) *
oddstomach) + (que * (bigpea - pea) * oddenergy) + ((bigpea - pea) * (bigque - que) *
normalboth))
rhs(i) = (rhs(i) * success(i)) + ((1 - success(i)) * vmax)
END IF
fitvalues(q + 1) = change
volvalues(p + 1) = change1

```

```

END IF
END IF

```

```

CLOSE #100
NEXT i

```

```

REM ***** compares rejection with accepting takes largest values*****
optimum(1) = 0: optimum(2) = 0
reject = vmax
imax = 0: REM ***** stays 0 if rejection best choice

```

```

*****
summax = 0
FOR i = 1 TO nprey
IF rhs(i) <= reject THEN
summax = summax + (lambda(i) * reject)
ELSE
summax = summax + (lambda(i) * rhs(i))
optimum(i) = 1
END IF
NEXT i
FOR i = 1 TO nprey: REM ***** loop compares each
choice to find optimum *****
test = rhs(i)
IF vmax < test THEN
vmax = test
imax = i
END IF
NEXT i
IF imax = 0 THEN
summax = summax + ((l(1) * l(2)) * reject)
ELSE
summax = summax + ((l(1) * l(2)) * vmax)
optimum(imax) = 2
END IF
IF optimum(1) = optimum(2) AND optimum(1) <> 0 THEN END
equat = (lambdaO * reject) + (summax): REM ***** ACTUAL SDP EQUATION

```

```

*****
f0(vol, x) = equat
REM ***** sets data to go in file *****
choice.optimum1 = optimum(1): REM **whether accept or reject prey1**
choice.volume1 = evacvol(vol, x, 1): REM **stom volume if prey1
encountered**
choice.fitness1 = xprim(vol, x, 1): REM **energy if prey 1 encountered**
choice.handle1 = handle(1): REM **period if prey1 encountered**
REM PRINT ""
REM LPRINT "prey 1: "; optimum(1), evacvol(vol, x, 1), xprim(vol, x, 1), r(1)
choice.optimum2 = optimum(2): REM **whether accept or reject prey2**
choice.volume2 = evacvol(vol, x, 2): REM **stom volume if prey2
encountered**
choice.fitness2 = xprim(vol, x, 2): REM **energy if prey2 encountered**

```

```

choice.handle2 = handle(2):          REM **period if prey2 encountered**
REM PRINT "prey 2: "; optimum(2), evacvol(vol, x, 2), xprim(vol, x, 2), r(2)
choice.volume0 = evacvol(vol, x, 0): REM **stom volume if no prey
encountered**
choice.fitness0 = xprim(vol, x, 0): REM **energy if no prey encountered**
choice.handle0 = 1:          REM **period if no prey encountered**
choice.growth = equat
IF vol MOD 20 = 0 AND x MOD 2 = 0 THEN
WRITE #250, t, vol, x, optimum(1), optimum(2)
END IF
REM PRINT x; "p1: "; optimum(1); evacvol(vol, x, 1); xprim(vol, x, 1); r(1),
"p2: "; optimum(2); evacvol(vol, x, 2); xprim(vol, x, 2); r(2), "p0: "; evacvol(vol, x, 0);
xprim(vol, x, 0); r(0), equat
REM IF t = 1 THEN
REM PRINT t; vol; x; "L"; rhs(1); "S"; rhs(2); "R"; reject; equat
REM END IF
recordnumber = recordnumber + 1:          REM ***** moves record
number onto next space in file*****
REM PRINT recordnumber, vol, i, x
PUT #t, recordnumber, choice:          REM ***** puts data into file
linear 't'.dat*****
NEXT x
NEXT vol
RETURN:          REM *****end of solving dpe*****

```

```

4000 PRINT "linear evacuation St = So - bt"
PRINT "parameter values:"
PRINT "evacuation rate: "; evacrate
PRINT " capacity="; capacity
PRINT "xcritical="; xcritical
PRINT "stomach volume capacity "; volmin; " to "; volmax
PRINT " i      lambda      y      alpha      r      preyvol"
PRINT "-----"
FOR i = 1 TO nprey
PRINT i, lambda(i), y(i), r(i); " "; preyvol(i)
NEXT i
PRINT "-----"
PRINT

```

```

REM *****section puts parameters into file details.dat*****
REM ***** for use in forward iteration*****
TYPE detail
rmax AS INTEGER
xcrit AS INTEGER
cap AS INTEGER
vmin AS SINGLE
vmax AS SINGLE
hori AS INTEGER
fitspace AS SINGLE
space AS SINGLE
i1 AS SINGLE
i2 AS SINGLE
beta1 AS SINGLE
beta2 AS SINGLE
s1 AS SINGLE
s2 AS SINGLE

```

```
END TYPE
DIM prodet AS detail
prodet.rmax = rmax
prodet.xcrit = xcritical
prodet.cap = capacity
prodet.vmin = volmin
prodet.vmax = volmax
prodet.hori = horizon
prodet.fitspace = fitgap
prodet.space = gap * 10
prodet.i1 = l(1)
prodet.i2 = l(2)
prodet.beta1 = 0
prodet.beta2 = 0
prodet.s1 = s(1)
prodet.s2 = s(2)
OPEN "c:\dos\aintemp\details.dat" FOR RANDOM AS #1 LEN = LEN(prodet)
PUT #1, 1, prodet
CLOSE #1
RETURN:      REM *** end of parameter values***
```

RESTORE: CLS

```
1 REM ***** Non sequential probability version of program *****
  REM ***** module that shows probabilities of optimal choices *****
  REM ***** includes procedure to account for iterations *****
  REM ***** data store in sequential files pbdata*.dat *****
  REM ***** N.B. delete all pbdata*.dat and prob*.dat files *****
  REM ***** have to load qb45 with qb/ah to run *****
```

REM ***** gets parameters from backward iteration*****

TYPE detail

```
rmax AS INTEGER
xcrit AS INTEGER
cap AS INTEGER
vmin AS SINGLE
vmax AS SINGLE
hori AS INTEGER
fitspace AS SINGLE
space AS SINGLE
i1 AS SINGLE
i2 AS SINGLE
beta1 AS SINGLE
beta2 AS SINGLE
s1 AS SINGLE
s2 AS SINGLE
```

END TYPE

DIM prodet AS detail

OPEN "c:\dos\aintemp\details.dat" FOR RANDOM AS #1 LEN = LEN(prodet):

REM ***** gets data from file details.dat *****

GET #1, 1, prodet

```
rmax = prodet.rmax: REM ***** rmax = maximum handling time *****
xcritical = prodet.xcrit: REM ***** xcritical = minimum energy value *****
capacity = prodet.cap: REM ***** capacity = maximum energy value *****
volmin = prodet.vmin: REM ***** volmin = minimum stomach volume *****
volmax = prodet.vmax: REM ***** volmax = maximum stomach volume *****
horizon = prodet.hori: REM ***** horizon = end time T *****
fitgap = prodet.fitspace
gap = (prodet.space) / 10: REM ***** gap = step between calculated values*****
gap10 = prodet.space: REM ***** gap10 = gap * 10 for calculation *****
prey1 = prodet.i1: REM ***** prey1 = prob encountering prey1 *****
prey2 = prodet.i2: REM ***** prey2 = prob encountering prey2 *****
beta(1) = prodet.beta1
beta(2) = prodet.beta2
s(1) = prodet.s1
s(2) = prodet.s2
```

CLOSE #1: REM ***** closes file details.dat*****

REM ***** calculations of probability assuming events are independent *****

```
p1 = prey1 - (prey1 * prey2): REM ***** prob(only encounter prey1)
p2 = prey2 - (prey1 * prey2): REM ***** prob(only encounter prey2)
p12 = prey1 * prey2: REM ***** prob(encounter prey1 and prey2)
p0 = 1 - ((prey1 + prey2) - (prey1 * prey2)): REM ***** prob(encounter no prey)
```

REM ***** results of calculations in file 1opt*.dat *****

TYPE filedata

```
optimum1 AS INTEGER
volume1 AS SINGLE
fitness1 AS SINGLE
handle1 AS SINGLE
```

```

optimum2 AS INTEGER
volume2 AS SINGLE
fitness2 AS SINGLE
handle2 AS SINGLE
volume0 AS SINGLE
fitness0 AS SINGLE
handle0 AS INTEGER
growth AS SINGLE
END TYPE

DIM choice AS filedata: REM *****sets length of fields in 1opt*.dat *****
DIM voldata AS SINGLE
DIM fitdata AS SINGLE
DIM probdead AS SINGLE
DIM probdata AS SINGLE
DIM probdat3 AS SINGLE
DIM probat AS SINGLE
REM $DYNAMIC : REM *****allows flag() to be more than 64K *****
DIM flag(rmax + 1, volmax * 2, capacity): REM ***** flag() tracks whether file has
been written to *****
DIM flag2(rmax + 1, volmax * 2, capacity): REM ***** flag2() tracks whether file
has been written to *****
FOR i = volmin * 2 TO volmax * 2 STEP gap * 2: FOR j = xcritical TO capacity
LET flag(rmax + 1, i, j) = 0: LET flag2(rmax + 1, i, j) = 0
NEXT j: NEXT i
DIM probab(3)
CLS
PRINT "copyright IAINSOFT (tm) 1994"
PRINT "nonseq4.bas program giving probability distributions"
PRINT "output to sequential file pbdata*.dat"

REM ***** input starting point vol and fit *****
10 PRINT
PRINT "Enter starting volume, between "; volmin; " and "; volmax; " step .5 ";
INPUT stom
IF stom * 10 MOD 5 <> 0 THEN
PRINT " must be divisible by .5"
GOTO 10
END IF
IF stom < volmin THEN
PRINT "Below minimum level!"
GOTO 10
END IF
IF stom > volmax THEN
PRINT "Above stomach capacity!"
GOTO 10
END IF
20 PRINT
PRINT "Enter starting fitness, between "; xcritical + 1; " and "; capacity;
INPUT energy
IF energy < xcritical + 1 THEN
PRINT "Below Critical value!"
GOTO 20
END IF
IF energy > capacity THEN
PRINT "above capacity!"
GOTO 20
END IF

```

```

REM **** fields to go in file random access file prob*.dat ****
TYPE st1
  st2 AS SINGLE
  st3 AS SINGLE
END TYPE
DIM start AS st1
period = 1: REM **** period tracks time****
start.st2 = 1: REM **** start.st2 = probability value (set to 1 in first period)****
start.st3 = 0: REM **** st3 records active and non active fish ****
OPEN "c:\dos\aintemp\prob1.DAT" FOR RANDOM AS #1 LEN = LEN(start):
REM **** opens prob1.dat and puts in initial probability****
PUT #1, (((capacity - xcritical) * (stom * 10)) + (energy - 1)), start
flag(1, stom * 2, energy) = 1
flag2(1, stom * 2, energy) = 0
start.st2 = 0
start.st3 = 0
PUT #1, (((capacity - xcritical) * (volmin * 10)) + (xcritical - 1)), start
flag(1, volmin * 2, xcritical) = 1
flag2(1, volmin * 2, xcritical) = 0
CLOSE #1: REM **** closes prob1.dat ****

REM **** main program ****
PRINT : PRINT "probability of 1 starting from stomach volume ="; stom; " and
energy ="; energy
PRINT "horizon ="; horizon
PRINT "time period currently being calculated: ";
OPEN "choices.dat" FOR OUTPUT AS #4
DO
  REM **** open prob(period).dat to get initial probability ****
  basename$ = "c:\dos\aintemp\prob" + LTRIM$(STR$(period))
  OPEN basename$ + ".dat" FOR RANDOM AS #1 LEN = LEN(start)

  REM **** open lopt(period).dat to get choices at each state ****
  basename$ = "c:\dos\aintemp\lopt" + LTRIM$(STR$(period))
  OPEN basename$ + ".dat" FOR RANDOM AS #3 LEN = LEN(choice): REM
  **** opens appropriate time file for reading****

  FOR stom = volmin * 10 TO volmax * 10 STEP gap10: REM **** cycle over
  volume ****
    FOR fit = xcritical + 1 TO capacity: REM **** cycle over fitness ****
      IF flag(1, stom / 5, fit) <> 1 THEN GOTO 30: REM **** checks if file
      record has been written to (if not skips to 30) ****
      recordnumber = (((capacity - xcritical) * stom) + (fit - xcritical)): REM ****
      recordnumber = area in file where data stored ****
      GET #3, recordnumber, choice: REM **** extracts data from opened
      lopt*.dat file****
      GET #1, recordnumber, start: REM **** extracts data from opened
      prob*.dat file ****
      FOR i = 1 TO 3: probab(i) = 0:
      success(i) = (s(i) * vol / 10) + .8
      IF success(i) < 0 THEN success(i) = 0
      NEXT i: REM **** probab(i) = probability of fish meeting prey(i) ****
      REM **** multiplies out probabilities ****
      IF choice.optimum1 >= 1 THEN LET probab(1) = start.st2 * (p1 - (p1 *
      beta(1))) * success(1)

```

```

IF choice.optimum2 >= 1 THEN LET probab(2) = start.st2 * (p2 - (p2 *
beta(2))) * success(2)
IF choice.optimum1 = 2 THEN probab(1) = probab(1) + ((start.st2 -
(p12(p12 * beta(1)))) * success(1))
IF choice.optimum2 = 2 THEN probab(2) = probab(2) + ((start.st2 -
(p12(p12 * beta(2)))) * success(2))
IF choice.optimum1 <> 2 AND optimum2 <> 2 THEN probab(3) =
probab(3) + (start.st2 * p12)
REM might not work with predation
probab(3) = start.st2 - (probab(1) + probab(2))
REM ***** finds resulting state if optimal choices are made *****
stomach(1) = choice.volume1 * 10
stomach(2) = choice.volume2 * 10
stomach(3) = choice.volume0 * 10
energy(1) = choice.fitness1
energy(2) = choice.fitness2
energy(3) = choice.fitness0
handle(1) = choice.handle1
handle(2) = choice.handle2
handle(3) = choice.handle0

FOR i = 1 TO 3: REM ***** cycles over prey items *****
IF probab(i) = 0 THEN GOTO 27
GET #1, recordnumber, start: REM ***** extracts probability each
time*****
volreal = stomach(i)
fitreal = energy(i)

REM ***** section that corrects stomach value to one above interpolated
value *****
factor = 1
FOR position = 1 TO LEN(LTRIM$(STR$(stomach(i))))
IF MID$(LTRIM$(STR$(stomach(i))), position, 1) = "." THEN
factor = LEN(LTRIM$(STR$(stomach(i)))) - position
factor = 10 ^ factor
position = LEN(LTRIM$(STR$(stomach(i))))
ELSE
factor = 1
END IF
NEXT position

IF factor = 1 THEN GOTO 21
actual = (stomach(i) * factor) MOD (gap10 * factor): REM *****multiplied
up because evac = 0.03 and mod needs integers*****
actual = actual / factor
IF actual <> 0 THEN
LET actual = FIX(stomach(i) / gap10)
stomach(i) = (actual * gap)
stomach(i) = stomach(i) + gap
stomach(i) = stomach(i) * 10
END IF
21 actual = energy(i) / fitgap
IF actual <> INT(actual) THEN
actual = FIX(energy(i) / fitgap)
energy(i) = actual * fitgap
energy(i) = energy(i) + fitgap
END IF
r(i) = INT(handle(i) * 10 ^ (.21 * (stomach(i) / 10))) / 60)

```

```

IF r(i) < 1 THEN r(i) = 1
r(3) = 1
FOR gapfill = 1 TO r(i)
  GET #1, recordnumber, start
  basename$ = "c:\dos\iaintemp\prob" + LTRIM$(STR$(period + gapfill))
  OPEN basename$ + ".dat" FOR RANDOM AS #2 LEN = LEN(start):
REM ***** opens prob(period + handling time) to put new prob in *****
  IF energy(i) <= xcritical THEN
    energy(i) = xcritical: REM ***** checks if fish dead *****
    stomach(i) = volmin * 10
  END IF

  IF gapfill = r(i) THEN

    IF flag(gapfill + 1, stomach(i) / 5, energy(i)) = 1 THEN
      GET #2, ((capacity - xcritical) * stomach(i)) + energy(i) - 1, start
      start.st2 = start.st2 + probab(i): REM ***** if address already has a
value then new probability is added to it *****
    ELSE
      GET #2, ((capacity - xcritical) * stomach(i)) + energy(i) - 1, start
      start.st2 = probab(i)
    END IF
    PUT #2, ((capacity - xcritical) * stomach(i)) + energy(i) - 1, start
    flag(1 + gapfill, stomach(i) / 5, energy(i)) = 1: REM ***** records in
flag() that address has been written to *****
  ELSE

    IF flag2(gapfill + 1, stomach(i) / 5, energy(i)) = 2 THEN
      GET #2, ((capacity - xcritical) * stomach(i)) + energy(i) - 1, start
      start.st3 = start.st3 + probab(i)
    ELSE
      GET #2, ((capacity - xcritical) * stomach(i)) + energy(i) - 1, start
      start.st3 = probab(i)
    END IF
    PUT #2, ((capacity - xcritical) * stomach(i)) + energy(i) - 1, start:
REM ***** puts probability in address relating to stom and fit of choice *****
    flag2(1 + gapfill, stomach(i) / 5, energy(i)) = 2
  END IF
END IF

25  CLOSE #2: REM*****closes file after
calculations*****
  NEXT gapfill
27  NEXT i
  IF probab(1) + probab(2) + probab(3) <> 0 THEN WRITE #4, period, stom,
fit, probab(1), probab(2), probab(3)
30  NEXT fit: REM ***** line jumped to if no probability for the state *****
  NEXT stom
  CLOSE #3

  basename$ = "c:\dos\iaintemp\prob" + LTRIM$(STR$(period + 1))
  OPEN basename$ + ".dat" FOR RANDOM AS #2 LEN = LEN(start): REM *****
opens prob(period + 1) to put new mortality prob in *****
  GET #1, ((capacity - xcritical) * (volmin * 10)), start: REM ***** updates value of
fish mortality *****
  previous = start.st3
  IF flag2(2, volmin * 2, xcritical) = 2 THEN
    GET #2, ((capacity - xcritical) * (volmin * 10)), start: REM ***** gets current
value of fish mortality *****

```



```

    start.st3 = start.st3 + previous
ELSE
start.st3 = previous
END IF

PUT #2, ((capacity - xcritical) * (volmin * 10)), start
probdead = start.st3
CLOSE #2

wfl = 1
REM ***** converts prob(period).dat to sequential file pbdata(period).dat for use
in excel *****
IF wfl = 1 THEN
basename$ = "c:\dos\aintemp\pbdata" + LTRIM$(STR$(period))
OPEN basename$ + ".dat" FOR OUTPUT AS #100
voldata = 1: fitdata = 1
WRITE #100, voldata, fitdata, probdead, probdead
END IF
    FOR j = volmin * 10 TO volmax * 10 STEP gap10
    FOR k = xcritical + 1 TO capacity

        IF flag2(1, j / 5, k) = 2 THEN
            GET #1, ((capacity - xcritical) * j) + k - 1, start
            probdat3 = start.st3
        ELSE
            probdat3 = 0
        END IF

        IF flag(1, j / 5, k) = 1 THEN
            GET #1, ((capacity - xcritical) * j) + k - 1, start
            probdata = start.st2
        ELSE
            probdata = 0
        END IF
        voldata = j / 10: fitdata = k
        IF wfl = 1 THEN
            WRITE #100, voldata, fitdata, probdata, probdat3
        END IF

    NEXT k
    NEXT j
IF wfl = 1 THEN CLOSE #100
wfl = 0

REM ***** moves array flag() on one period *****
FOR i = 1 TO rmax
    FOR j = volmin * 10 TO volmax * 10 STEP gap10
        FOR k = xcritical TO capacity
            LET flag(i, j / 5, k) = flag(i + 1, j / 5, k)
            LET flag2(i, j / 5, k) = flag2(i + 1, j / 5, k)
        NEXT k
    NEXT j
NEXT i
    FOR j = volmin * 10 TO volmax * 10 STEP gap10
        FOR k = xcritical TO capacity
            LET flag(rmax + 1, j / 5, k) = 0
            LET flag2(rmax + 1, j / 5, k) = 0
        NEXT k
    NEXT j
NEXT i

```

```

NEXT j

CLOSE #1: REM ***** closes files prob*.dat and lopt*.dat *****
PRINT period;
period = period + 1:          REM*****time now moves to time after
handling*****
LOOP UNTIL period > horizon: REM ***** continue until time ends *****
CLOSE #4
PRINT "END"
END
```

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